Social Organisation in the Malaysian Peacock Pheasant

Thesis

How to cite:

McGowan, Philip James Kevin (1992). Social Organisation in the Malaysian Peacock Pheasant. PhD thesis. The Open University.

Social organisation in the Malaysian peacock pheasant

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Thesis submitted for the degree of Doctor of Philosophy

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February, 1992

Date of submission: 20 February 1992
Date of award: 16 June 1992

ABSTRACT

This thesis reports a study of the behaviour and morphology of the Malaysian peacock pheasant *Polyplectron malacense*, an inhabitant of lowland rain-forest in Peninsular Malaysia. A total of 21 months was spent in the field and museum collections were visited.

Micro-habitat analysis, radio-tracking and contextual analysis of calling behaviour and call playback experiments were used to collect data on the species in the wild.

Periods of calling and display scrape maintenance were infrequent and unpredictable. Not all of the available micro-habitats within the primary forest were used by the birds as some areas were consistently avoided. Within calling periods males used particular micro-habitats to call and maintain display scrapes. Three different call types were heard. There were differences between calling periods in the number of birds calling, the types of calls given and the overall amount of calling. The number of display scrapes maintained also differered.. Based on contextual observations, call playback experiments were conducted and stimulus tapes elicited responses and permitted investigation of call function.

There are several morphological features of the male which seem likely to be subject to sexual selection. Males appear to possess several sexually-selected traits which show considerable variability among individuals.. Several male morphological characters have evolved in association with particular epigamic display elements, suggesting that they are potentially under selection through female choice.

These results suggest that a female is presented with variation among males in several different ornamental traits. A qualitative model, based on food availability, is proposed to explain variation in calling and scrape maintenance among males. It is argued that opportunities for males to display to females may be very rare and that this may explain the evolution of the male's plumage and display. Females lay a single-egg clutch and hence only one male can fertilise a clutch, with the result that competition between males for paternity is likely to be very strong.

ACKNOWLEDGEMENTS

This thesis is dedicated to my parents for their unfailing support for my travels and fieldwork abroad and especially throughout my time in Malaysia.

In Malaysia, I have benefitted from the help and interest of many people. The Socio-Economic Research Unit of the Prime Minister's Department granted permission to conduct research in Malaysia. En. Mohd. Khan *bin* Momin Khan, Director-General of the Department of Wildlife and National Parks, Peninsular Malaysia gave me permission to work at Kuala Lompat and was always very interested and happy to discuss my fieldwork. I appreciate his personal interest very much indeed. At Universiti Kebangsaan Malaysia, I am grateful to the Dean, Centre for Graduate Studies and to Prof. Dr. Zakari A. Hamid, Dean of the Faculty of Life Sciences and Prof. Madya Dr. A. Wahab *bin* Datuk Kosai, Head of the Zoology Department for facilities. The Forest Research Institute of Malaysia permitted me to use Pasoh Forest Research Station. Siti Hawa *binte* Yatim, Head of Ornithological Research at the Department of Wildlife and National Parks and Tunku Nazim *bin* Yaacob at Zoo Negara were always prepared to discuss my research and permitted measurement of birds in their captive collections. En. Shamsuddin, Park Superintendant at Taman Negara, and his wife,Emma, were generous hosts during a visit to other peacock pheasant localities.

For help in the field, I am especially grateful to the *orang asli* who worked with such good humour and obvious amusement, especially Ahmad, Yun and Nun. Lorna Brown, Geoffrey Davison and Pete Hopkins also helped boost data collection. In 1990 Louise McGowan helped in many ways and provided excellent company throughout much of the field season. I appreciate the friendship that Abu Bakar and Hashim, Wildlife Rangers at Kuala Lompat during 1990 and 1991, extended during those two field seasons. About Clive Bealey and his unique sense of humour, there is little to say except that he is an ideal field companion.

My supervisors, Tim Halliday and Geoffrey Davison have provided assistance at all stages and read a previous draft of the entire thesis. I especially appreciate Tim Halliday's patience and Geoffrey Davison's very generous provision of accommodation in Malaysia and help with a variety of administrative matters.

I have sought advice from many people and I am extremely thankful to all of them for freely giving me so much of their time and expertise. Early on, Mike Brooke provided thought-provoking comments and John Marchant advised on Common Bird Census analysis. I am particularly grateful to Peter Robertson for advice on radio-tracking, analyses and for permission to quote unpublished data, David Hill and Clive Bealey for help with micro-habitat analysis and Peter McGregor for comments and advice on calling behaviour and its study and for producing the sonograms. Nicholas Aebischer kindly commented on Chapter 4 and Robert Kenward allowed me to use his software package and to quote a manuscript currently in press. Peter Garson has provided much discussion on many aspects of the study and Steve Pruett-Jones and Derek Holmes provided a few words of encouragement on ornithological work in the tropics when it was most needed. Marion Petrie and John Baker have discussed morphological variation with me and Matt Ridley kindly read and commented on my Introduction. David Wells was always happy to read whatever I gave him and to discuss Malaysian birds. He also provided access to specimens in the Universiti Malaya Reference Collection. Norman Grey, Kevin McConway, Bridget Smith and Dave Stanford helped me sort out the practicalities of the DECORANA software package and/or sundry other computing/statistics problems. Many of those above have read and commented on a draft of at least one chapter of the thesis.

During my visit to Hong Kong to video-tape displays of peacock pheasants, Ken Searle kindly provided access to the birds at Hong Kong Zoological and Botanical Gardens and Jo Rushton loaned me her video camera. Lew Young very generously provided accommodation and David Melville was thoroughly entertaining. Dieter Arnold and John Corder made available their footage of the displays of various peacock pheasants and the argus pheasant. Many aviculturalists in the U.K. allowed me to measure their peacock pheasants and I gladly acknowledge their help and interest: Ivan Burgess, John Gorham, Will Harrison, Brian Hildick, Gary Robbins, Andy Swales and Tony Turk at Lilford Park. For access to museum

specimens I thank Peter Colston (BMNH), Ray Symons (Cambridge Museum of Zoology) and Mrs C.M. Yang at the National University of Singapore.

At The Open University, I wish to thank John Baker, Phil Bateman, Helen Budgey, Emma Creighton, Chris Raxworthy and Verina Waights for general discussion throughout the project and criticism of various parts of this thesis and for their friendship. Barbi Pedder has sorted out many hitches extremely efficiently. The friendship of many people in the Biology Department is warmly appreciated and I thank Alistair Barber, Fiona Clarke, Tim Doubell, Fiona Freeman, Adrian French, John Gigg, Maria Gulinello, Mike Lowndes, Terry Patterson, Fiza Rashid-Doubell, Carmen Sandi, Andy Scholey, Tracy Stone, Alison Taylor and Reza Zamani for re-habilitating me after each field season. Norman Gray lifted tea making and rice cooking to an art form (usually). I should like to give my fondest thanks to Lottie Hosie for field assistance, discussion, manuscript criticism and for keeping me going.

I am very grateful to John Brocklehurst, John and Pat Corder, Richard Howard and Gary Robbins for help in a great variety of ways and I thoroughly appreciate their interest and assistance. The research was funded by an Open University/World Pheasant Association matched funds studentship and I am grateful to the Open University, World Pheasant Association, International Trust for Nature Conservation, Lady Y.P. McNeice and World Wide Fund for Nature (Malaysia) for funding. Malaysian Airlines System provided a discount ticket in 1988 and British Airways-Assisting Nature Conservation provided three free return flights (to the World Pheasant Association) between 1989 and 1991. I should like to thank especially Rod Hall (British Airways-Assisting Nature Conservation), En. Said Abubakar (BA in Kuala Lumpur), Frances Hawkins (International Trust for Nature Conservation), Keith Howman (World Pheasant Association) and Ken Scriven (World Wide Fund for Nature [Malaysia]) for their personal interest and encouragement. The Association for the Study of Animal Behaviour, *Cage and Aviary Birds* Avian Research Fund, the Biology Dept. at the Open University and the World Pheasant Association provided me with grants to attend three international conferences where I presented and discussed this research.

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CHAPTER 1: INTRODUCTION

1.1 Darwin, sex and tropical forest birds

In formulating his ideas on selection in relation to sex Darwin (1874) seems to have been greatly influenced by a number of tropical bird species. The bird families that he refers to include the birds of paradise and bowerbirds of New Guinea and the Australian rainforest, the cotingas of Central and South America and the argus and peacock pheasants of South-east Asia. The different species excited Darwin for different reasons. He was struck by the communal displays (known as leks) of many extravagantly plumaged male birds of paradise, the peculiar 'bowers' constructed from twigs and decorated with coloured objects of the bowerbirds, the loud calls and cleared areas of some of the cotingas and, as he saw it, the progression of increasingly eye-like patterns (ocelli) on some feathers of male peacock pheasants, argus pheasants and peafowl.

Because the females of many of these species are much duller in coloration and/or do not call, display or make bowers or dancing grounds like the males, Darwin suggested that these features of the male were important in attracting females for mating. In addition, he suggested that variation between males in these features may result in variation in mating success (numbers of matings obtained) and that the favoured features would be more evident in the next generation.

Whilst this idea that males attract females for mating through, for example, morphological or behavioural ornaments has, in recent years, resulted in a considerable amount of empirical and theoretical work in many bird species, this has largely been centered around species inhabiting temperate habitats. There have been very few detailed studies of any tropical forest bird species that have contributed to this discussion. However, data from the few studies that have been conducted hint at intriguing differences between tropical and temperate forest birds. There are indications that selection pressures on various life-history parameters are different from those acting on birds in temperate forest or woodland. Several of the selection pressures that differ seem likely to influence the mating system. For example, smaller clutch sizes (see Skutch, 1949 and 1985; Murray, 1985) and lower nesting success (*e.g.* Fogden, 1972: but see Oniki, 1979) are reported for tropical passerines compared to temperate passerines and males of many tropical bird species exhibit delayed maturation (Foster, 1987; Snow, 1976). Together with lower annual mortality rates and much longer life spans (see Wells (1990) for longevity records of some Malaysian passerines) these features indicate that selection pressures on life-history parameters are different in tropical species compared with temperate species. Differences in behavioural patterns related directly to reproductive behaviour have also been recorded. Snow (1976) indicates that court-clearing in birds is only known from tropical forest, and Terborgh (1985) reports that territory sizes of some Amazonian understorey passerines are an order of magnitude larger than their North American relatives and Karr (1981) suggests that behavioural differences from north temperate birds are the main reasons why tropical birds are difficult to survey. Among the features of tropical forest birds that Karr mentions are increased secretiveness, decreased levels of singing and extensive overlap of home range.

Many of these differences are associated with the mating system of the species exhibiting them and influence or reflect the form that it takes. The marked differences from well studied temperate species hint at undocumented variety in avian mating systems in tropical forest species.

My aim in this introduction is to discuss recent research on tropical birds and their features that interested Darwin. This is important because Darwin noticed features that do require explanation. After referring to relevant differences between various species in families that are restricted to the tropics, I turn to general trends among these species. I then introduce the pheasants (tribe Phasianinae) and finally the study species. This provides a context for both the bird species which inhabit the same habitat type and exhibit similar behavioural and morphological features and also of close relatives of the Malaysian peacock pheasant: an environmental and evolutionary context. Finally, I discuss the features of the Malaysian peacock pheasant that are of interest and the aims of the study.

Although 90% or so of bird species are believed to be monogamous, there is considerable interest in the evolution of other avian mating systems. There have been several studies conducted recently on a number of the tropical bird species or close relatives of those that Darwin discussed which exhibit such mating systems. These have concentrated on the species inhabiting rainforest in the Neotropics (*e.g.* cock-of-the-rock, bellbirds and manakins) and in Australasia (*e.g.* Lawes' parotia and satin bowerbird). There are two points of considerable interest here. First, the taxonomy of the species mentioned and, second, their geographical distribution; I shall discuss each of these in turn.

1.1.1 Recent tropical passerine studies

These Neotropical and Australasian species (cotingas, birds of paradise or bowerbirds) are passerines (of the order Passeriformes - perching songbirds), whereas the tropical bird species of South-east Asia that captured Darwin's interest are pheasants, a distantly related family of birds (from the order Galliformes) that also have evolved elaborate displays and in at least some of which males construct display courts *i.e.* they exhibit convergent evolution.

Apart from the pioneering studies by Lill (1974; 1976), it is only recently that quantitative studies of tropical forest passerines have addressed specific questions concerning lek evolution and lek behaviour (*e.g.* Trail, 1985; Foster, 1981; Pruett-Jones, 1985). The picture that emerges is one of considerable variation in both male display dispersion and male behaviour patterns exhibited, such as whether or not display arenas are maintained. Areas where leaf litter has been cleared from the forest-floor by a male bird for display pruposes have been called courts, arenas, dancing grounds and display scrapes by the authors that describe them. For each species that I discuss, I use the name that the relevant author adopted, but this is simply semantic - it does not imply that the areas are cleared for different reasons.

Species in which males display in aggregations have proved most amenable to quantitative study. Such Neotropical studies have shown male dominance on the lek in certain species such as the swallow-tailed manakin *Chiroxiphia caudata* (Foster, 1981) and golden-headed manakin *Pipra erythrocephala* (Lill, 1976). Dominance, however, is only predictable on the basis of residency in some species *e.g*. Guyanan cock-of-the-rock *Rupicola rupicola* (Trail, 1985) and is not found at all between residents in others, including the white bearded (= black-and-white) manakin *Manacus manacus* (Lill, 1974). Females visited courts that are clumped in preference to more dispersed courts on the lek and the males that reside on such courts gain significantly more matings in the golden-headed manakin *Pipra erythrocephala* (Lill, 1976) and Guyanan cock-of-the-rock *Rupicola rupicola* (Trail and Adams, 1989). Foster (1981) reports that virtually all copulations are made by a dominant male in the swallow-tailed manakin *Chiroxiphia caudata* but the relationship between the territory itself and male competitive behaviour can be more complex in other species. For example, Trail (1985) indicates that resident males on the lek are larger, more experienced and have higher reproductive success when compared to challengers. Furthermore, although a male's dominance is predictable on the basis of residency, it is so unpredictable off his territory (*i.e.* in other parts of the lek) that Trail (1985) argues that the best cue a female has for assessing male competitive ability is the territory itself.

In northern Australasia, studies have been concerned with the role of diet in the evolution of arena polygamy. Fruit-eating has been suggested as a pre-requisite for the evolution of elaborate courtship displays of the cotingas and manakins in the Neotropics (Snow, 1976) because a frugivorous diet allows males to spend less time feeding and they therefore have more time 'spare'. Supporting this, Beehler and Pruett-Jones (1983) observed that increasing frugivory is correlated with increasingly clumped male display dispersion and ultimately the lek dispersion across nine species of bird of paradise in Australasia. Bradbury (1981) and Beehler (1983), however, suggest that frugivory alone is not sufficient to promote the evolution of arena polygamy and that it is the large home ranges and resultant increase in contact rates between individuals that is important. Indeed, Diamond (1986) points out that the evolution of such extremes of ornamental plumages and displays cannot be a sole consequence of frugivory. This is because there are both other frugivores in the same forests that do not show the same development and some court- and arena-displaying birds of paradise that are insectivores. Beehler (1987) reports on one such case, the Buff sicklebill *Epimachus albertisi* which exhibits non-pair bonded, court-based polygynous breeding behaviour and is a forest insectivore. Conversely, MacGregor's bird of paradise *Amblyornis macgregoriae* is a monogamous frugivorous species with a tight pair bond (Pruett-Jones and Pruett-Jones, 1982).

1.1.2 Differences in fruiting patterns

An even more interesting difference between these two groups of birds is the ecological backgound within which their mating systems have evolved. The passerines mentioned above are largely fruit-eaters and are also species in which communal male displays are typical. In contrast, in South-east Asia the only passerines believed to be restricted to a frugivorous diet are the green broadbill and the fairy bluebird (Wells 1988) although Fogden (1972) suggests that the fairy bluebird does take some insects at his Bornean study site. It should be noted that dietary infromation on all species is scanty.

Snow (1981) has suggested that the present forest avifaunas evolved after many of the fruits which are important for tropical frugivores. Thus, between-continent differences in fruiting patterns may well be expected to result in differences between continental avifaunas in the utilisation of fruit by frugivorous animals. In South-east Asia, for example, there is a periodic general flowering and mast fruiting among many tree species in the climax lowland rain forests of the west Malesian floristic region (Appanah, 1985). This phenomenon occurs at varying intervals, usually of 5 - 10 years and has not been reported from outside this region. In between these gregarious (*sensu* Whitmore, 1984a) flowerings, considerably fewer species and individual trees flower and bear fruit (Medway, 1972; Raemaekers *et al.*, 1980). This cycle of brief periods of abundant fruit followed by several years of relatively sparse fruit production has been suggested as one possible cause of the low biomass in a number of animal groups when compared with the Neotropics (see Appanah, 1985 and references therein).

These differences in fruiting patterns between the Neotropics and Australasia on the one hand and South-east Asia on the other may help to account for differences in the levels of frugivory and the resultant variation in male display dispersions between them. Diamond (1986) suggests that, within an avifauna, fruiting levels alone cannot explain the evolution of striking plumages and elaborate displays by the males. This contention is supported between continental avifaunas by the presence of the Malaysian peacock pheasant *Polyplectron malacense* and the argus pheasant *Argusianus argus* in the 'fruit poor' lowland rain forests of the Malesian region. Both of these species are strikingly plumaged, to a human observer at least, and perform elaborate displays.

1.1.3 General trends among tropical passerine mating systems

Comparisons either within or between these families have been attempted periodically, to search for general patterns and differences among species in male display dispersions, dimorphism and court-clearing. Of particular interest is the evolution of polygamous (especially lek) mating systems (Beehler and Foster, 1988; Bradbury, 1981; Bradbury and Gibson, 1983; Bradbury *et al.*, 1986) and the striking sexual dimorphism in these tropical passerines (Payne, 1984; Hoglund, 1989). Borgia *et al.* (1985) have proposed a hypothesis to explain the evolution of display courts in birds, particularly bowerbirds. In this they suggest that cleared, undecorated courts are an intermediate stage in the the evolution of bower-building. The cleared courts were the original 'markers' which function in place of showy plumage and these were elaborated to form decorated bowers. Males displaying at high quality markers are likely to be dominant in the local population and may, thus, indicate a resident male's aggressive abilities.

Payne (1984) explored the relationship between lek and arena behaviour and sexual size dimorphism in 16 avian families (including tropical passerines) 'as a test of Darwinian sexual selection theory' (*sic*). He concluded that the intensity of sexual selection is higher in lekking species than in monogamous species and in most polygynous species where males provide a resource. Increased sexual size dimorphism was seen in most lekking species when compared with monogamous species except in species in which males perform active aerial displays. This, Payne suggests, is consistent with a hypothesis of intra-sexual aggression and competition as a main form of sexual selection and that intra-sexual competition may explain most instances of evolved sexual selection in lekking birds. In taking this analysis of size and plumage dimorphism in lek-breeding birds a stage further, Hoglund (1989) has controlled for common ancestry. Initially, in his analysis of 11 families which contain lekking species (not just tropical passerines), he found that more lekking species were dimorphic in size and plumage colour than other species in these families. When common ancestry is controlled for using a phylogenetic approach, however, the correlation across all species disappears. Within families, neither size nor plumage dimorphism are correlated with lekking. In some groups, but not all, lekking does seem to have favoured the evolution of plumage dimorphism. Coddington (1992), however, commented that to test the hypothesis that lekking and sexual dimorphism *per se* are associated, the analysis should not be limited just to one clade that supports the hypothesis, but should include random samples from any taxa that lek and are sexually dimorphic (*e.g.* flies, frogs). For some of the other groups in his analysis, Hoglund advances explanations for the lack of correlations with lekking. For example, in species with active male acrobatic displays (*eg*. manakins Pipridae), size monomorphism may be the result of selection for small agile males. Larger males are found especially in species belonging to groups with ground displays. He also suggests that in some groups where the association is lacking, sexual selection may have acted on acoustic displays, as discussed by Loffredo and Borgia (1986a).

To provide a full context for discussion of the Malaysian peacock pheasant in relation to tropical birds, I give a very brief overview of pheasant relationships and distribution. This is because, unlike the tropical passerine families already discussed, most pheasant species are extra-tropical in distribution and many do not inhabit forested habitats.

1.2 The pheasants

1.2.1 Background to relationships and distribution

The Pheasants, family Phasianidae, tribe Phasianini, comprise a group of 49 species of generally non-migratory and terrestrially adapted birds of moderately large size (Johnsgard, 1986). Delacour (1977) suggests that the Phasianinae (in his terminology) "do not differ from other game birds [here referring to the Phasianidae] by very well-defined or important characteristics". Male pheasants do, however, possess "both a highly specialized ornamental plumage and large size", whereas game birds "lacking one or both of these attributes are named 'Partridges' and 'Quails' and they include such diversified groups as the Snowcocks, the Francolins, the Spurfowls and the American Quail" (*i.e.* the Perdicinae). Crowe (in press) reveals the relationships within the Galliformes to be much more complex.

The pheasants are almost exclusively Asian in distribution, the Congo peacock *Afropavo congensis* (which occurs in Central Africa) being the only non-Asian species, although several species have been introduced into Europe and North America. Within Asia they occur from Java in Indonesia at ~8°S (green peafowl *Pavo muticus* and green junglefowl *Gallus varius*) through the equatorial forests of Malaysia to Indochina and China (koklass *Pucrasia macrolopha*, ring-necked pheasant *Phasianus colchicus*, Reeves' pheasant *Syrmaticus reevesi*, and blue eared-pheasant *Crossoptilon auritum*) at ~50°N. The western limit of the tribe, excluding the Congo peacock from Africa, is in the Caucasus (ring-necked pheasant *Phasianus colchicus*) and they occur along the Himalaya and eastwards to the island of Taiwan (mikado pheasant *Syrmaticus mikado* and Swinhoe's pheasant *Lophura swinhoei*) in the East China Sea. They are distributed in habitats as diverse as lowland tropical rainforest (*e.g.* crested fireback *Lophura ignita*), montane tropical forest (*e.g.* mountain peacock pheasant *Polyplectron inopinatum*), temperate coniferous forests and alpine meadows (*e.g.* blue eared-pheasant) and above the Himalayan tree line at 16,000ft. (*e.g.* monal *Lophophorus impeyanus* and the blood pheasant *Ithaginis cruentus*).

1.2.2 The peacock pheasants *Polyplectron*

The genus *Polyplectron* (from the Greek meaning 'many spurred') comprises six (Delacour, 1977) or seven (Johnsgard, 1986) species, which replace each other geographically or are ecologically isolated from one another. All are little known in the wild, although Davison (1983a; 1983b) has made behavioural observations on the Malaysian peacock pheasant, and the Palawan peacock pheasant *P. emphanum* has been the subject of preliminary ecological studies (Caleda, 1986 and unpub. ms.). An assessment of the latter species' conservation situation has been made (McGowan *et al.* 1991). There is limited natural history information on all species, but most information has come from museum skins and studies of captive birds.

The montane peacock pheasants (*P. chalcurum* from the mountains of Sumatra and *P. inopinatum* from the Malaysian mountains) are regarded as the most primitive members of the genus (*e.g.* Delacour, 1977), although a rigorous analysis of relationships is lacking. 'Primitiveness' seems to be determined on characters associated with the mating system (*e.g.* degree of sexual dimorphism, [Johnsgard, 1986]). Davison (1986a) reports on rectrix number in the genus, suggesting that eight pairs of tail feathers is the 'primitive' number, present in both sexes of *chalcurum* as well as in females of some other species. *P. germaini* and *P. bicalcaratum* are considered more 'advanced' and *P. malacense*, *P. (malacense) schleiermacheri* and *P. emphanum* the most 'advanced'. Sexual dimorphism (in plumage) increases along this gradient.

1.3 Pheasant mating systems

Males of many pheasant species possess ornamental plumage and specialised morphological structures used in courtship (*e.g.* wattles, 'horns' and lappets) and perform elaborate sexual displays. For example, male Temminck's tragopans *Tragopan temmincki* expose their colourful lappet only during frontal display and the male Bulwer's pheasant *Lophura bulweri* engorges his facial skin to produce dramatic elongated wattles during lateral display. Consequently, some species, most notably the Indian peafowl *Pavo cristatus*, have often been quoted as evidence for sexual selection by female choice despite a lack of data supporting this idea (Ridley, 1981). Recently, however, there have been attempts to investigate these elaborate morphologies and behaviour patterns critically and these have largely been confined to the three species introduced into Europe and North America. Manning (1987, 1989) has demonstrated that the 'extravagance' of the train of the Indian peacock increases with age and Petrie *et al.*(1990) report that females choose males with more extravagant trains. The mating system of the ring-necked pheasant *Phasianus colchicus* is reasonably well documented (*e.g.* Ridley, 1983; Ridley and Hill, 1987) and it has recently been claimed that female ring-necked pheasants select a viability-based male trait (spur length) (von Schantz *et al.*, 1989; Goransson *et al.*1990), although there are both theoretical uncertainties (Kirkpatrick, 1989; Pomiankowski, 1989) and oversights of ring-necked pheasant biology (Savalli, 1989; Hillgarth, 1990) in this argument.

1.3.1 Overview

An overview of galliform mating systems is provided by Ridley (1983: ch.5) and Avery and Ridley (1988). The latter, however, is more concerned with the managed gamebird species of temperate habitats such as black grouse *Tetrao tetrix*, red grouse *Lagopus lagopus* and grey partridge *Perdix perdix* rather than with pheasants other than the ring-necked pheasant. Ridley (1983) reported that 19 of the 63 galliform genera contain non-monogamous species. He also compared aspects of the ecology (diet, habitat *etc.*) with aspects of the social behaviour, especially sexual behaviour (mating system, size dimorphism, colour dimorphism) of various phasianid genera. In his qualitative model, based on the need for mate guarding by males, forest dwelling species are solitary because females are concealed by vegetation and do not need mate guarding by males after copulation. This leads to greater opportunity for non-monogamous mating in males. This discussion has been expanded in Avery and Ridley (1988) to explore the possible relationship between mate guarding and sperm competition.

Sigurjonsdottir (1981) used multivariate techniques to investigate whether several ecological and behavioural variables were related to sexual dimorphism in gamebirds, waterfowl and raptors. Among the 89 galliform species (including pheasants), for which data were obtained, the extent of paternal investment and reproductive effort was negatively correlated with sexual size dimorphism. Colour dimorphism was positively correlated with sexual size dimorphism and several other variables produced no significant correlations. Sigurjonsdottir concluded that sexual dimorphism among the galliforms, which are omnivorous and herbivorous and have independent young, is largely the result of sexual selection.

Within the indigenous range of the pheasants, research on behaviour patterns associated with sex has been very limited. The centres of pheasant diversity lie in the Himalaya, central

Vietnam and the Malay Peninsula; each area containing eight sympatric species (Johnsgard, 1986). As noted above, however, most quantitative research on pheasant ecology and behaviour has concentrated on the three species that have been successfully introduced to temperate areas; the red junglefowl *Gallus gallus* (*e.g*. Zuk *et al*., 1990a, b; Sullivan, 1991), ring-necked pheasant *Phasianus colchicus* (*e.g*. Hill and Ridley, 1987; Goransson *et al*., 1990) and Indian peafowl *Pavo cristatus* (Manning, 1989; Manning and Hartley, 1992; Petrie *et al*., 1990).

Davison (1981a; 1981b and 1982) has reported on some aspects of the sexual behaviour of the argus *Argusianus argus* and proposes a crude method of female choice (between males with and without dancing grounds) that may explain the evolution of the male's plumage. This is, however, based on a single observation. Kaul (1989) has just completed an in-depth study of aspects of the ecology and behaviour of the Cheer pheasant *Catreus wallichi*, a monogamous species, in the wild (mid-altitude grassy hillsides of the west-central Himalaya) and he documents calling and territoriality by males.

1.3.2 Mating system of the Malaysian peacock pheasant

Reproductive behaviour

Davison (1983a) provides qualitative information on some aspects of the breeding behaviour of the Malaysian peacock pheasant in the wild. For two sites in West (=Peninsular) Malaysia, he gives estimates of male density based on the number of calling centres, each of which he assumed to be the territory of a single male. These calling centres were slightly clustered. During the study, birds were seen 55 times and 51 of these sightings were of single birds, indicating solitariness. As with the argus pheasant, male Malaysian peacock pheasants make display areas (also called dancing grounds or display courts) and Davison describes these and their construction, together with considerable year to year differences in the number of such areas maintained and number of calling males.

Male Malaysian peacock pheasants give three loud call types (discussed more fully in Chapter 8) and Davison (1983a) reports that calling by one male elicits calls from others. He found no evidence of a dominance hierarchy among males that maintained display areas.

Two visits by females to display areas were seen and display was watched during one of these. The ritualised courtship display of the male is described by Davison (1983b).

Morphological variation

Davison (1985a and 1986a) has quantified some morphological variation in the peacock pheasants *Polyplectron*, based on male features that may be important in attracting females (*e.g.* number of tail feathers and hence ocelli) and characters that may be important in male-male combat (*e.g.* body size and spur number). This is interesting because, apparently, features used to attract females *i.e.* the ornament (plumage extravagance) do not also function as a weapon (which are possibly the spurs in this pheasant) in intra-sexual competition. In other study animals, the same structure probably performs both functions (*e.g.* the antlers of the Red Deer). In a discussion on sexual selection in tropical forest birds, Davison (1986b) suggested that the genus shows high levels of genetic polymorphisms which are phenotypically expressed. As these polymorphisms show low levels of correlation with one another and with body size, Davison (1986b) suggests that this is due to weak gene linkage and that consequently *Polyplectron* may be useful in separating out individual variations in reproductive success into their intra- and inter-sexual components. Whilst this is a compelling idea, there is insufficient information available on the variation in the range of individual behavioural and morphological characters that must be associated with the adoption of such strategies. Furthermore and perhaps more importantly, there is no clear idea of relationships between the characters and whether or not there are correlations between behavioural and morphological characters in particular.

1.4 Aims of this study

Before Davison's interesting ideas on male polymorphisms and their influence on mating success can be tested, however, three fundamental steps must be taken. Firstly, techniques must be available for collecting large data sets on a rarely encountered species in dense tropical forest. Therefore, developing or adapting techniques and/or approaches that are widely used in temperate studies has been a crucial but sometimes painstaking step forward. Surprisingly these techniques have been rarely, if ever, used in tropical forest. Indeed, Mabberley (1991 p. 1) states "The diverse and rich flora and fauna of the tropics have bewildered, overwhelmed and humbled those trained in the biologically impoverished temerate regions. Such an experience is essential for those who wish to pursue tropical studies...". Secondly, more general information is needed on aspects of the species' ecology and behaviour that are likely to influence or reflect the mating system. For example, possible ecological reasons for clustering of calling males, gross patterns of calling *etc.* would provide a suitable context within which to discuss differences in behaviour and morphology. Finally, although it has been suggested that males of the species are polymorphic, there is little firm evidence that there are consistent and discrete differences between groups of males. There does seem to be variation amongst males in, for example, numbers of tail feathers or whether males call or remain silent during periods of calling, but whether this variation constitutes polymorphism is not clear. Consequently, a clear picture of the nature and extent of this morphological and behavioural variation is needed. Assessment of individual differences in morphology and behaviour is especially important.

Because these three steps must be taken first, this study was essentially concerned with the development of techniques applicable to tropical rainforest research, investigating gross patterns in male social organisation and with studying the variation within the morphological and behavioural ornaments of male Malaysian peacock pheasants. In addition to studying within-species variation, comparisons across the genus should help in understanding their evolution. This is possible with morphology and sexual displays. Explicitly the study addressed the following topics.

1.4.1 Techniques

i) An assessment of the feasibility of trapping and radio-tagging individuals to monitor movements of both males and females and provide other behavioural data (Chapter 4).

ii) The development of a field procedure for collecting data on the micro-habitat relations of the species. Specifically this will be used to ask whether males call and maintain scrapes in particular areas of the forest (Chapter 5).

iii) Adapting existing approaches to the study of vocalisations to investigate the function of calls in a species in which the sender and receiver are invisible to the observer, including assessment of the utility of call playback in elucidating the functions of vocalisations of this species (Chapter 8).

1.4.2 General features of male social organisation

Conspicuous features of the mating system must be documented and quantified. Of particular interest are assessment of temporal and spatial variation in calling and display scrape maintenance and analysis of vegetation structure in areas where calling occurred. Once the techniques are satisfactory in the forest, a combination of both radio-tracking (despite a likely small sample size) and call playback should give insights into male spatial distribution during and outside calling periods as well as elucidating female ranging patterns.

1.4.3 Analysis of morphological and behavioural variation among males

Against this background, variation among males can be investigated with respect to morphological variation and calling behaviour.

1.5 Structure of the thesis

The data chapters in this thesis fall into three distinct parts. First, Chapters 3, 4 and 5 provide information on male social organisation. Second, Chapter 6 explores the variability of morphological traits and, then, in an attempt to understand the evolution of characters associated with male display to the female, Chapter 7 investigates inter-specific variation in those characters. Finally, Chapter 8 addresses the function of a behavioural ornament - calling - and investigates whether there is variation among males in calling behaviour.

CHAPTER 2: STUDY SITES AND GENERAL METHODS

"The tropical forest ecologist, to some extent is still in limbo or rather in a 'green hell. According to some fantastic tales, hell would be a place where normal dimensions lack their normal constancy, leaving one in a permanent state of confusion. In tropical forest, such a state of the mind of ecologists is at least partly due to the use of temperate forest models. These may be efficient in temperate forests, but in tropial rain forests they too often act as confusing rather than guiding devices." Oldeman (1989)

2.1 Introduction

Peninsular Malaysia is a part of the floristic subregion of West Malesia. This subregion is also known as the Sunda subregion and is bounded in the north by the isthmus of Kra (~10° N) and Wallace's Line in the east. It includes the Malay Peninsular, Sumatra, Java and Borneo. A vegetation map of the Malesian region is provided by Whitmore (1984b). Landforms, climate and soils are described by Tjia (1988) and Whitmore (1984a).

The role that fruiting patterns may have played in the evolution of male display dispersion in tropical forest birds was discussed in the Introduction, where it was mentioned that there was a unique floristic community in South-east Asian lowland rain forest.

The principal forest formation is lowland evergreen rain forest (Whitmore, 1984a), often referred to as Dipterocarp forest (*e.g.* Davison, 1983a; Lambert, 1987) because of the large numbers of huge trees belonging to the family Dipterocarpaceae. This density of top-of-canopy trees is unique to the West Malesian region (Whitmore, 1984a: p. 7) and is more pronounced in Malaya than further east in the subregion (Whitmore, 1984a: p. 219). Accounts of various aspects of this forest formation can be found in Ashton (1988 and references therein), Symington (1943) and Whitmore (1984a). The unique phenomenon of gregarious (= mast) fruiting is discussed by Janzen (1974), Medway (1972), Appanah (1985) and those above, among others.

2.2 Study sites

2.2.1 Kuala Lompat

The study was mostly conducted at the Kuala Lompat Ranger Post (3° 43'N, 102° 17'E) (Fig. 2.1) which lies on the eastern edge of the Krau Wildlife Reserve in Pahang. The study was conducted within the two square kilometres adjacent to the Ranger Post. This area is 50 - 100m above mean sea level and contains an excellent system of trails (Fig. 2.2)

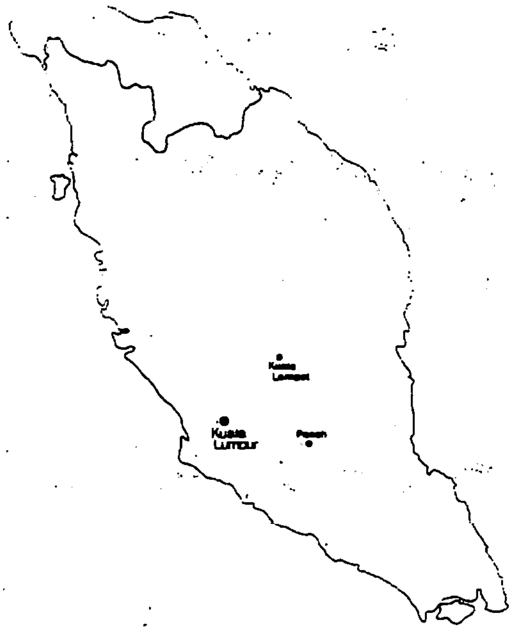


Fig. 2.1: Peninsular Malaysia showing the position of the two study sites. The peninsular is about 350km wide at its widest.

The lowland evergreen dipterocarp forest is mostly undisturbed, although *orang asli* (aborigines) collect minor forest products. Most botanical descriptions have been made from a vertebrate point of view, such as documenting the phenology of canopy trees within the home range of a particular primate group (*e.g.* Chivers, 1980; Bennett, 1983). The most complete botanical description can be found in Raemaekers *et al.* (1980). Bennett (1983), Pannell and Koziol (1987) and Lambert (1987) also provide data on phenology of some canopy tree species, understorey species of the genus *Aglaia* (Meliaceae) and fig (*Ficus*) species respectively.

Essentially, the vegetation can be split into four zones (Raemaekers *et al.*, 1980; Bennett, 1983) based on the water table. These zones are (i) a riverine zone adjacent to the two rivers and (ii) an inland zone where the ground starts to rise to the north-west (Fig. 2.3). In between there is (iii) an intermediate zone and (iv) the seasonal swamps (Fig. 2.2) are also floristically distinct.

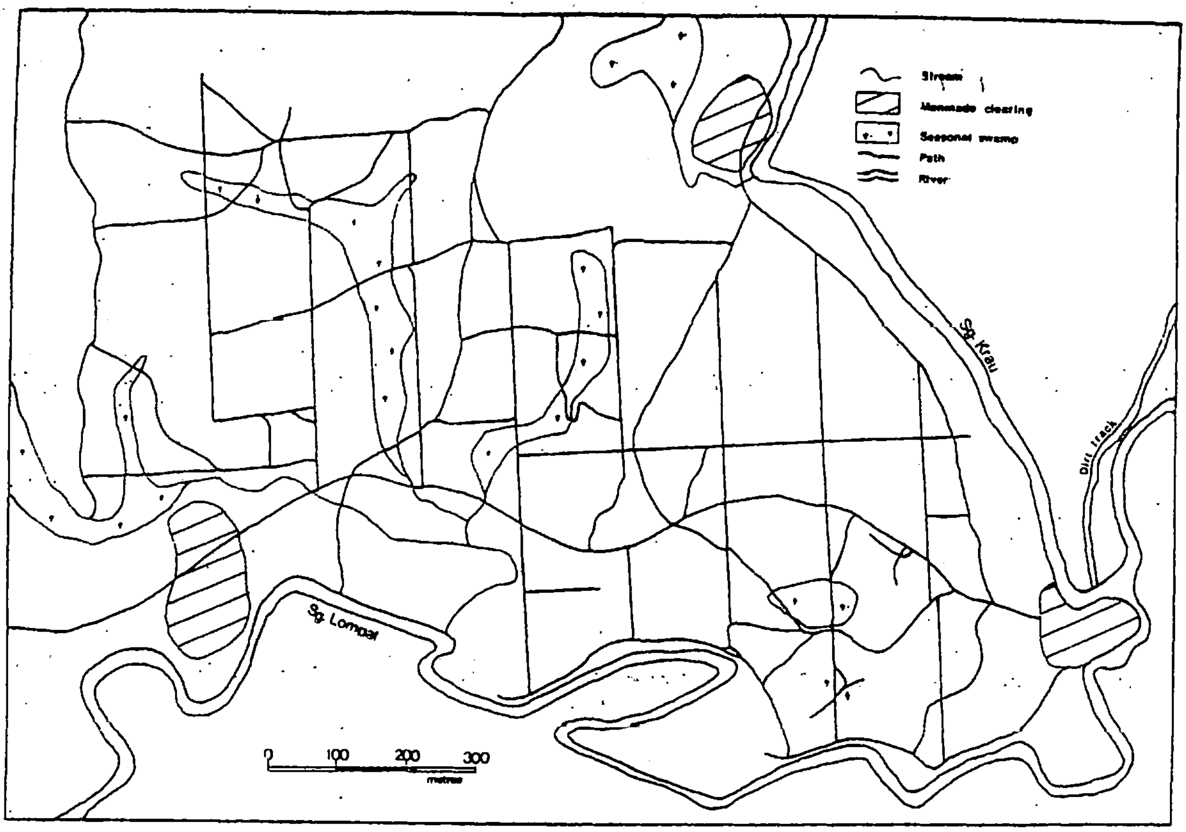


Fig. 2.2: The Kuala Lompat study site in West Malaysia, showing rivers, trails, seasonal swamps, streams and man made clearances. The trail system covers approximately 2 square kilometres.

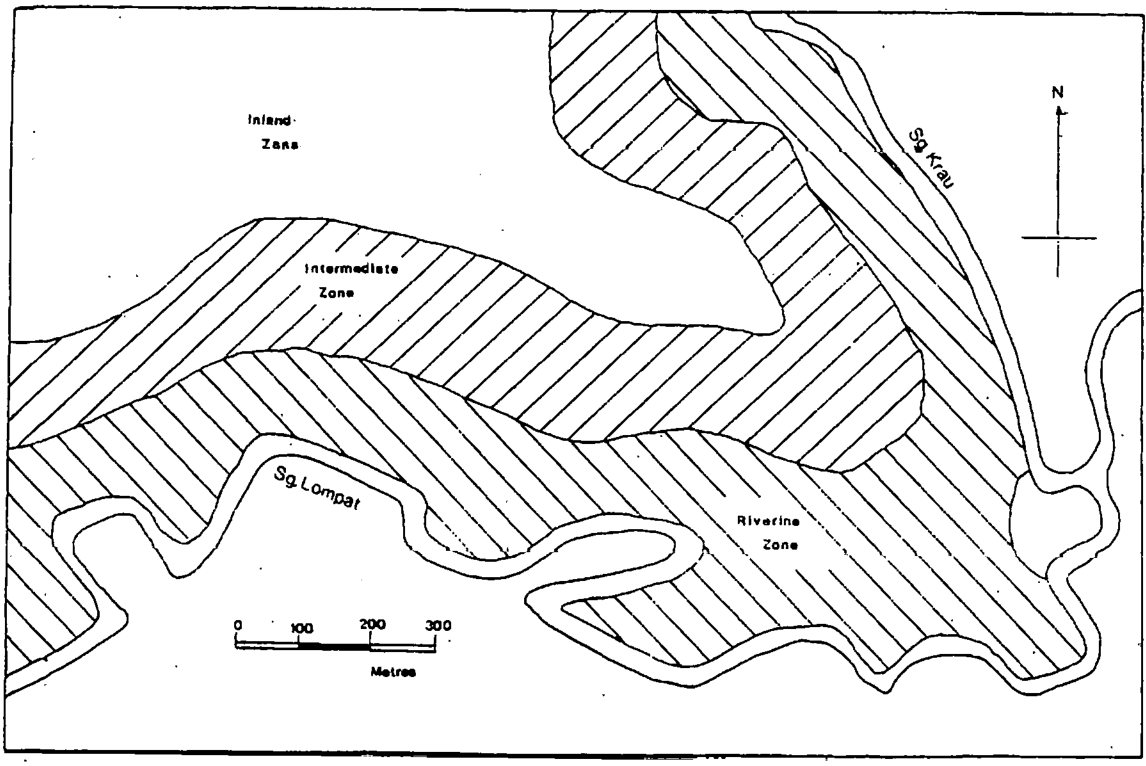


Fig. 2.3: The four vegetation zones within the Kuala Lompat study site as proposed by Raemaekers *et al.* 1980.

The canopy contains many fewer trees of the family Dipterocarpaceae than other forests in the Peninusular and a higher proportion of Leguminosae (Chivers, 1974). Lambert (1987) has found 38 species of figs in the study site, 29 of which have seeds regularly dispersed by birds. These 29 species exhibited a markedly aseasonal fruiting pattern. Kuala Lompat lies in a rainshadow and may receive less than 1800mm of rain a year (Chivers, 1980).

2.2.2 Pasoh

The second study site used is the Pasoh Forest Reserve near Simpang Pertang in Negri Sembilan (2° 58'N, 102° 17'E) (Fig. 2.1). The reserve covers some 16 square kilometres of lowland evergreen dipterocarp forest on level and gently sloping ground at about 100 - 150m. above mean sea level. It receives about 2000mm of rain per year.

I used the trail system within primary forest in the central seven square kilometres of the reserve. This seven square kilometres also contains forest that was lightly logged in 1955 and 1956 (Davison, 1983a). Trails in a 250m grid (see Fig. 2.4) are the only evidence of disturbance.

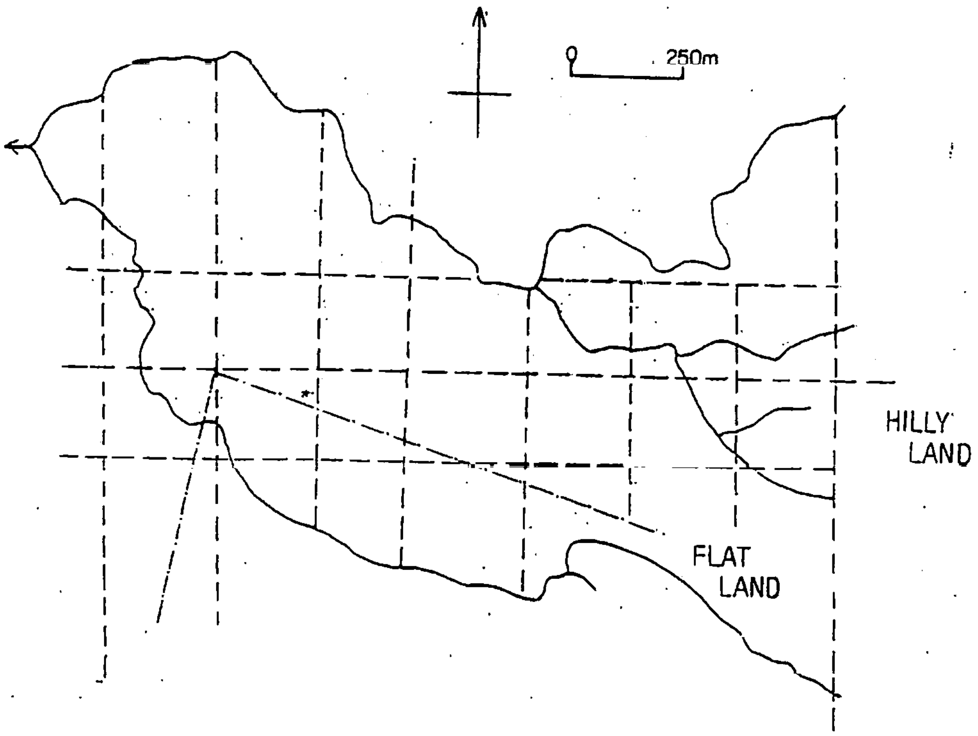


Fig. 2.4: The trail system in the Forest Research Instsiute Research Station at Pasoh in West Malaysia. * indicates the western edge of the 50ha botanical plot (see section 2.2.2) and — • — • — represents the main trail used in survey walks.

Davison (1979) and Wong (1986) studied pheasants and understorey birds respectively at Pasoh and provide a general description of the site. There are considerably more floristic data available about this forest than Kuala Lompat and many ecological data were collected during the International Biosphere Programme. To study the population dynamics of tropical tree species, a 50ha plot has been set up, within which all individual trees with a girth at breast height of 10cm and above have been identified and numbered. The 835 tree species recorded within this plot (Payne, 1990) is over twice the 350-odd species recorded from similar plots in Panama and Costa Rica.

2.3 General methods

Avian behaviour away from fixed display courts and single species ecology has been studied rarely in tropical forest. This is presumably because birds are encountered much less frequently in lowland tropical rainforest than in temperate forests. Consequently, data collection is slower and fewer topics are amenable to study than in other habitats. Many pheasants and partridges are amongst the most rarely encountered species in South-east Asian tropical forest and consequently remain poorly known. Karr (1981) has listed several reasons why observers encounter tropical birds rarely and believes that the biology of the birds themselves is the biggest obstacle to even simple study of avian communities. Among the biological attributes suggested by Karr that make tropical birds difficult to census are secretiveness, decreased levels of singing and extensive overlap of home range. There are, therefore, a number of approaches and techniques that I have had to develop or adapt in this study. The successful development and/or modification of these techniques has, of necessity, been a fundamental part of the work described in this thesis. Consequently, I include detailed discussion of the approaches that I have taken to each technique employed within the relevant chapter. This will, I hope, permit better evaluation of the applicability of the technique concerned.

2.3.1 Field schedule and adapting techniques

Very little indeed is known about the ecology and behaviour of any peacock pheasant in the wild. This made it difficult to establish a satisfactory annual field routine. Whilst most previous fieldworkers in Malaysia have been concerned with collecting data on the ecology of their study species over an annual cycle, this was not appropriate in this case. This is because of the following reasons.

i) There are no long-term data on the seasonality of calling and scrape maintenance. Such an assessment would have permitted me to target periods when increased behavioural activity was likely. This does, of course, assume that there are predictable seasonal patterns and this is by no means certain.

ii) Much of the data on the behaviour of the Malaysian peacock pheasant that was available prior to this study was obtained during a single mast fruiting year (Davison *in litt*, 1990). The increase in data collection at this time was due to increased behavioural activity during the mast-fruiting year compared to other years.

iii) This implied that in non-mast years methods must be found to collect data outside periods of calling that is relevant to social organisation. When birds are not calling they effectively become undetectable and encounters become very limited indeed.

iv) The rate of contact with the species can be increased outside calling periods by the attachment of radio-tags. I felt that the results of the first trapping effort (see section 4.2.1) demonstrated that trapping and radio-tracking could not be used intensively at that stage and much modification was needed to allow me to use it again.

v) There are several techniques that have been used widely in temperate habitats to investigate the problems that I addressed. These have, rather surprisingly perhaps, been little used in tropical forest and, therefore, I needed to seek advice from outside Malaysia on micro-habitat analysis, investigating the functions of calls and designing a radio-tracking programme, once the technique was usable.

As a result, therefore, I split my time between fieldwork in Malaysia and data analysis, seeking specialist advice and consulting literature in the U.K. (Table 2.1). This, I believe, allowed me to maximise data collection during contact with the species. As such, attention was given to collecting as much accurate information as possible for part of the year rather than a smaller amount of less accurate information over the whole year.

						Month						
Year	J	F	M	A	M	J	J	A	S	O	N	D
1988		—	—	—	—	—	—	—				
1989	—	—										—
1990	—	—	—	—	—	—	—					
1991	—	—	—	—	—	—	—					

Table 2.1: Months in the field.-- indicates fieldwork. The 1989 season was cut short by ill-health and was replaced by an extra field season in 1991.

2.3.2 Survey walks

Rationale

The most fundamental field method used was the survey walk conducted at Kuala Lompat each month. During each month in the field all trails were walked at set times for several consecutive days and any calls heard or scrapes seen were recorded. This served to provide an index of calling and scrape maintenence throughout my time in the field and helped to determine which aspect of fieldwork would be pursued for the rest of that month. If birds were calling, fieldwork concerned this aspect, otherwise habitat analysis or trapping and radio-tracking were conducted.

Procedure

To ensure consistent field effort across the study site, the site was divided into three approximately equal areas. The boundaries between each area are, of necessity, determined by the distribution of trails. Each area contains three north-south trails. During 1988, survey walks were conducted on six days between the times of 0800 - 1200hrs and 1500 - 1830hrs. These times were suggested as those most likely to coincide with daily peaks of peacock pheasant calling activity if they were calling (Davison, pers. comm.). This meant that each area was covered twice during the morning and twice during the afternoon. I did not conduct survey walks during rain, because of reduced audibility and so sometimes survey walks took longer than six days to complete.

At the end of the 1988 field season, this was reduced to three days of survey walks, so that each of the three areas of the study site was walked once in the morning and once in the afternoon. The reduced effort made no difference to my being able to determine whether or not there was a period of calling, but allowed me to spend the 'extra' time studying calling during such periods.

During the 1990 season, there was no calling at Kuala Lompat and very little during 1991. Consequently, I visited Pasoh regularly and conducted systematic survey walks at this site. The effort was not comparable to that made at Kuala Lompat as I merely wished to assess whether there was a period of calling and if so, to locate calling birds for playback experiments. Survey walks here were conducted between 1700 - 1930hrs and 0800 - 1100hrs and only along the main trail to the '50ha. plot' (Fig. 2.4). As such, the results are not quantitatively comparable to those obtained from Kuala Lompat, but a qualitative comparison does, I believe, reflect differences in calling levels between the two sites at the same time. The results from the survey walks are given in Chapter 3.

2.4 Other techniques

Because of the difficulty that I experienced in finding techniques suitable for collecting behavioural data that are tried and tested in Malaysian rain forest, I discuss trapping and radio-tracking (Chapter 4), micro-habitat analysis (Chapter 5) and the functional analysis of calling (Chapter 8) in the appropriate chapter.

CHAPTER 3: SOCIAL ORGANISATION I: TEMPORAL AND SPATIAL VARIATION IN CALLING AND SCRAPE MAINTENANCE

3.1 Introduction

My aim in this chapter is to provide baseline quantitative information on two conspicuous aspect of Malaysian peacock pheasant reproductive behaviour. These aspects are calling and the maintenance of display scrapes. As mentioned in the Introduction (section 1.3.2), Davison (1983a) found considerable variation in the number of calling males and the number of scrapes maintained in different years. In addition, he described how display scrapes are made and provided a qualitative discussion of calling behaviour. As mentioned in section 1.1.3, Borgia *et* (1985) proposed that cleared display courts are markers of male quality in the bowerbirds at leas In the very large argus pheasant, Davison (1981a) concluded that the primary function of the display area that the males clear is to provide space for unrestricted active display. He suggested that such diplays were not possible elsewhere in the forest because of undergrowth. The cleared display area itself may also serve as a signal to the female (Davison, 1981a). The same possibilities are recorded for the Malaysian peacock pheasant (Davison, 1983a).

Here I wish to document monthly variation in both the amount of calling and numbers of scrapes maintained to explore how frequently and to what extent these two traits are exhibited within a population (*i.e.* at the Kuala Lompat study site). This will also serve as a background to the rest of the thesis. Because of the considerations raised in 2.3.1, however, this is not a study of the seasonality of calling and scrape maintenance. In particular, the following questions were asked:

i) What is the temporal and spatial dispersion of calling birds?

ii) What is the temporal and spatial dispersion of display scrapes?

iii) Are scrapes maintained during calling periods?

iv) Are scrapes maintained in the same area as calls are given?

v) Is it possible to determine territorial boundaries from calling locations as assumed by Davison (1979, 1983a).

vi) If droppings are found at different scrapes, are there differences in parasite load of droppings between scrapes? Can hides be used to observe males at scrapes?

3.2 Methods

I have outlined how the survey walks were conducted in Section 2.3.2. If a calling cluster was detected during these survey walks, I conducted intensive sampling effort within the cluster to determine the boundary of the cluster accurately. Any scrapes found on trails during survey walks were noted. In both 1989 and 1991, after I found at least one scrape on a trail, I employed *orang asli* (aborigines) to search for scrapes on the forest floor off the trails. This permitted a more accurate assessment of scrape numbers and their spatial distribution than could be gained by restricting searches to trails. Any droppings found at display scrapes were collected and preserved in a weak solution of potassium permanganate to allow any coccidia to sporrulate (N. Hillgarth, pers. comm.).

In 1988, I made a preliminary attempt to determine calling territory boundaries within a calling cluster. To do this, I followed the conventions for recording calling locations that the British Trust for Ornithology use in their Common Bird Census (CBC) (Marchant, 1983). As a test of this technique's utility in this study, my analysis of territory boundaries was compared with a similar assessment of the same data conducted by an experienced CBC analyst, Mr. John Marchant.

3.3 Results

3.3.1 Temporal variation in calling levels

There are four possible measures of the level of calling by which variation can be assessed (McGowan, 1990: see Appendix 1). Rather than present graphs of all four measures for all four years (or part years), I just present the results for the variation in the number of calling locations (Figs. 3.1 a-d).

3.3.2 Determining calling periods

Calling periods were not simply characterised by an increase in the number of calling registrations. For example, in March 1988 there was a relatively large number of

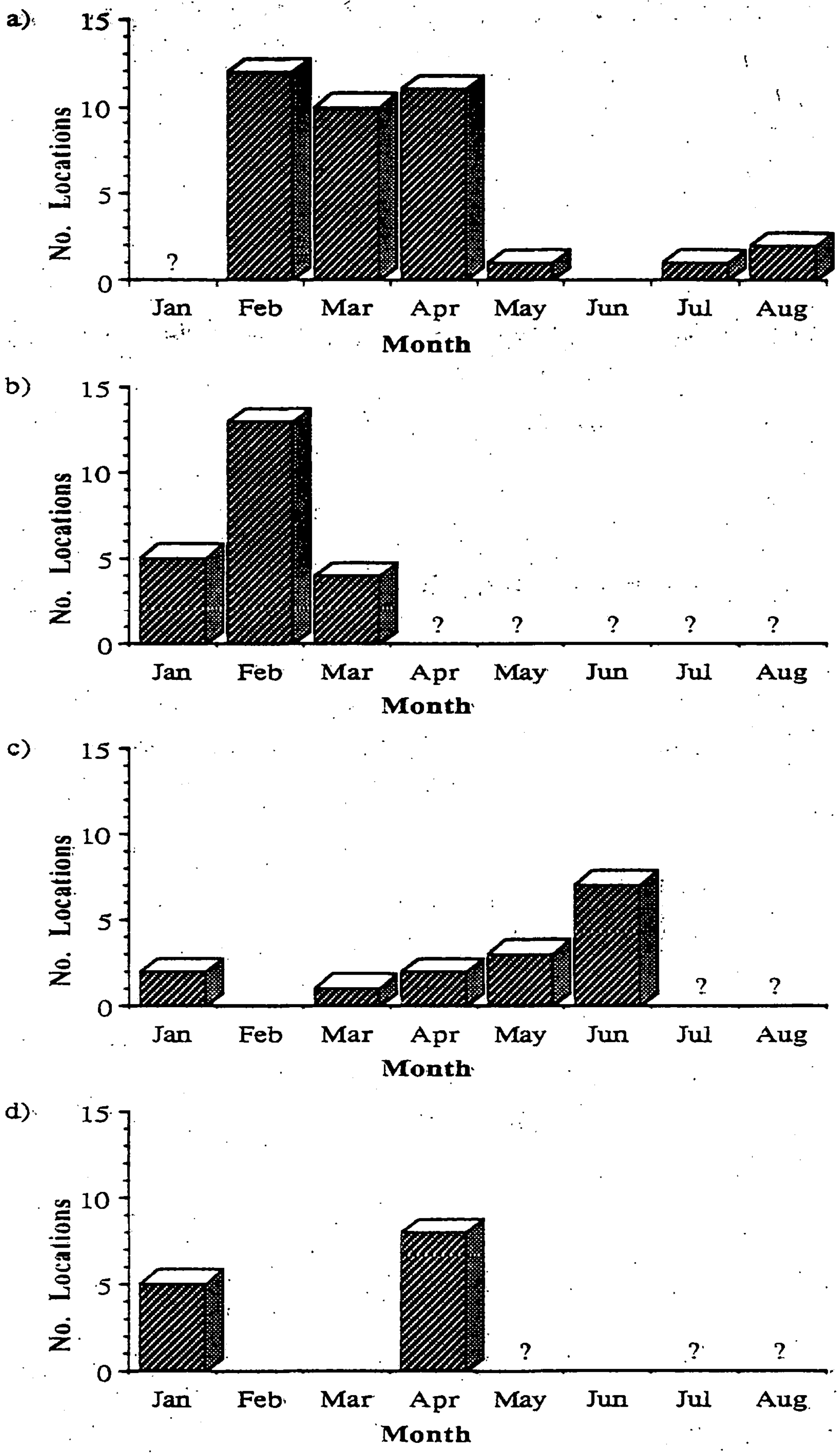


Fig. 3.1 Temporal variation in the number of locations from where calls were heard. ? = no data.

locations from which calls were heard, as shown in McGowan 1990a (see Appendix 1, Fig. 2). However, this reflected a few clucks from each individual and there was none of the calling behaviour usually associated with calling periods that I describe in detail in Chapter 8. Hence, this was not classified as a calling period.

At Kuala Lompat, calling periods occured in January/February 1988, April 1988, January/February 1989 and, to a lesser degree, in April 1991. Interestingly, there were periods of calling at Pasoh Forest Reserve during March and May 1990 when there was no calling at Kuala Lompat.

3.3.3 Temporal variation in maintenance of display scrapes

Display scrapes were maintained in January/February 1988, April 1988,January/February 1989 and in April 1991 (Table 3.1).

		Site of display scrape		
Year	**Month**	**Trail**	**Forest**	**Total**
1988	Feb	4	?	4+
"	Apr	1	?	1+
1989	Feb	2	3	5
1990	Jan-Jun	0	-	0
1991	April	2	9	11

Table 3.1: Temporal distribution of display scrape maintenance from standard survey walks.

The most striking result is that there were few periods of scrape maintenance and that few scrapes were found during these times. Comparison of Fig. 3.1 and Table 3.1 indicates that scrapes were maintained during calling periods. Although scrapes sited on the forest floor off trails were missed in 1988, I believe that the *orang asli* found a large proportion of all scrapes in February 1989 and April 1991 when areas off trails were searched. These results for 1989 and 1991 indicate that more scrapes are made off trails than on them.

3.3.4 Spatial variation in calling levels and scrape maintenance

If all scrapes and calls detected during all survey walks are plotted on a single map, there is clearly part of the study site that is not used for these two activities (Fig. 3.2a). Within the

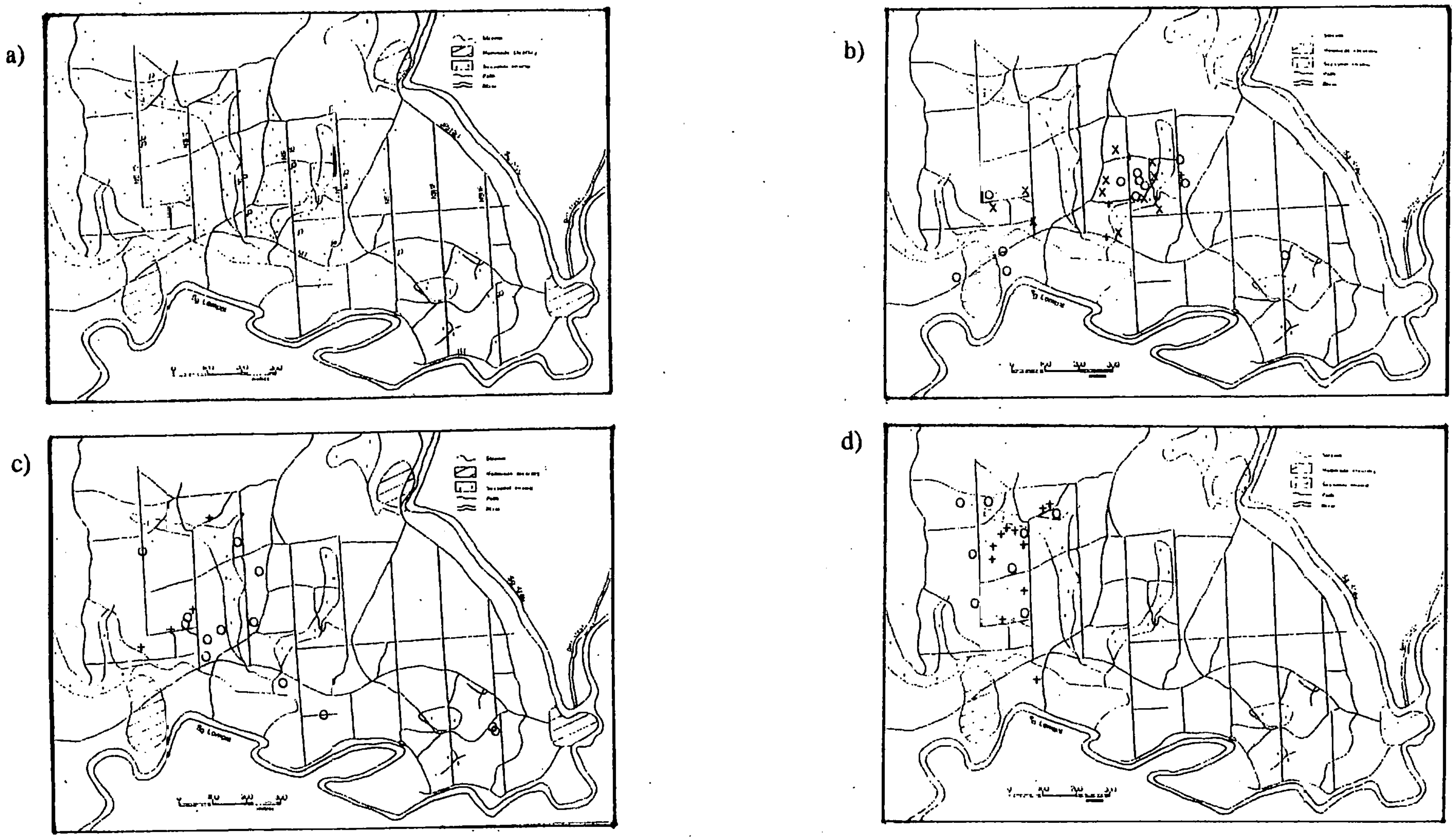


Fig. 3.2: Locations of calling records during standard monthly survey walks: a) all months in which I was in the field - ⦶ = calling location; b) calling periods in February and April 1988 - o = calling locations in February and x = calling locations in April. Maintained display scrapes are also shown (+); c) calling period in February 1989 - o = calling location and + = display scrape; and d) calling period in April 1991 - o = calling location and + = display scrape.

area that is used for these activities, Figs. 3.2b-d show that within a single calling period both calling and scrape maintenance are not evenly distributed. Both of these behaviour patterns do, in fact, occur in a single cluster within the study site at any one time. Within the study site there are two definite areas in which clusters occured - one used in 1988 (February and April) (Fig. 3.2b) and one used in both February 1989 (Fig. 3.2c) and April 1991 (Fig. 3.2d). McGowan (1990a, Fig. 6: Appendix 1) showed that there was a significant shift in the position of these clusters between 1988 and 1989. It is apparent from Figs. 3.2c-d that the calling locations recorded during survey walks did accurately reflect the position of the calling cluster, as revealed by subsequent intensive sampling.

3.3.5 Preliminary assessment of territoriality

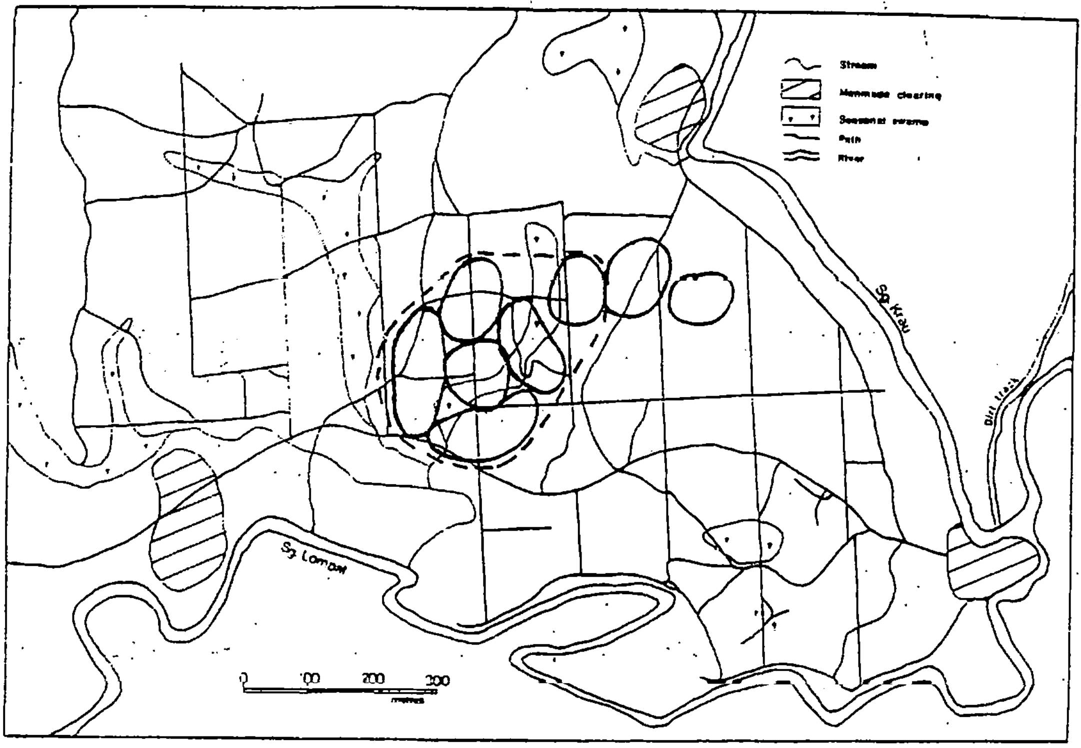
Calling registrations were too infrequent and confined to such a small area that territory boundaries were not obvious to me from visual inspection of maps of calling records.

CBC analysis of the February 1988 data revealed some similarity between my interpretation of calling registrations and the interpretation provided by Mr. John Marchant (Figs. 3.3a&b). The differences that exist between our two maps of territory boundaries, however, are too great to allow many calling bouts to be assigned confidently to a particular individual. Hence, individual calling rates and inter-individual interactions could not be investigated by this method alone.

My assessment of the number of calling territories, however, does not differ markedly from Mr. Marchant's. I estimated that there were six males calling within the cluster and two without, whereas Mr. Marchant estimated eight within and one without (3.3a&b).

3.3.6 Scrapes, droppings and parasites

Six droppings were found on three scrapes in 1989. Only one of these contained any parasites and these large polycystic oocysts were probably either a *Barrouxia* sp. or an *Adelea* sp., both of which are parasites of centipedes (C. Norton *in litt* to N. Hillgarth,



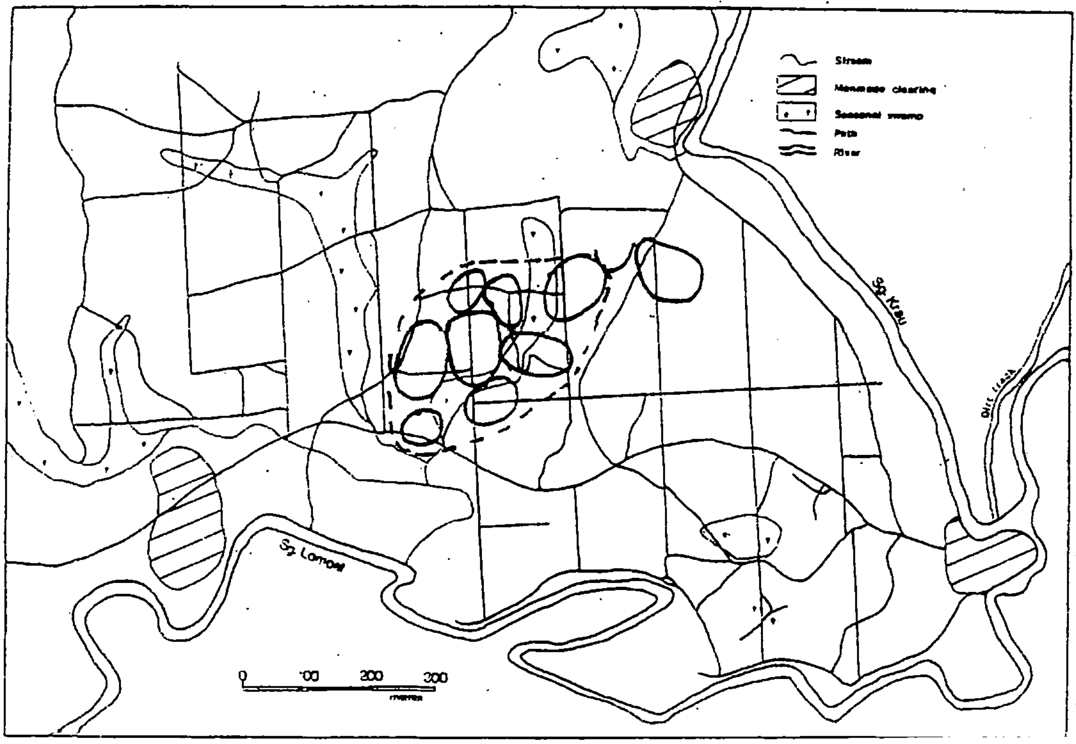


Fig. 3.3: Common Bird Census analysis of all calling registrations made in February and April 1988. Upper is my interpretation and lower is Mr. John Marchant's.

Attempts to watch males at a very clean display scrape were not successful. Two observers each spent six hours a day in a hide for three consecutive days (36hrs). A single male peacock pheasant was seen walking along a trail towards the scrape and the hide. The bird peacock pheasant was seen walking along a trail towards the scrape and the hide. The bird glanced at the scrape and walked out of sight. The whole observation lasted less than three minutes (out of the 36hrs) and no scrape maintenance activity was seen.

3.4 Discussion

In 21 months in the field at Kuala Lompat, there were four calling periods, each lasting less than one month. Scrapes were maintained during each of these periods and were not found outside such calling periods. During calling periods, calling locations were clustered and scrapes were maintained within these clusters only. CBC analysis is not specific enough in this instance to allow detailed study of calling behaviour during calling periods and I discuss how I investigated calling in Chapter 8. That birds call and maintain scrapes so infrequently means one of two things in terms of reproduction; either reproduction occurs just as infrequently, or these behaviour patterns are not necessary for reproduction to occur. Finding out what the birds are doing when they are not calling is very difficult, but I describe how I tried to do this in the next chapter.

The clustering of calling males is of particular interest in studies of sexual selection and mating systems and presumably results from the distribution of both ecological resources and conspecifics (Brown and Orians, 1970). I address the possibility that ecological factors influence male display dispersion in the Malaysian peacock pheasant in Chapter 5. Possible behavioural reasons for clumped male dispersions have been the subject of some empirical work and much theoretical study. A particular focus of this work has been the evolution of the dispersion pattern characteristics of leks (*e.g.* Beehler and Foster, 1988, Bradbury, 1981; Bradbury and Gibson, 1983; Bradbury *et al.*, 1986 and Queller, 1986). Although not a lek system (the calling males are not in visual contact), I begin to explore the possibility that there may be a behavioural influence on clumping in the Malaysian peacock pheasant by making a preliminary test of the 'hotshot' model of clumped male display dispersion (Chapter 8).

CHAPTER 4: SOCIAL ORGANISATION II: RANGING BEHAVIOUR OUTSIDE CALLING PERIODS

"*While by no means the rarest, yet this proved to be one of the most difficult of the Malay pheasants to locate. Day after day we gave up to its search, finding now and then a feather to keep up our hope, but taking many weary tramps to places where the natives said it was common, only to find not the slightest trace.*" Beebe (1922: p. 77)

4.1 Introduction

The preceding chapter demonstrates strikingly that Malaysian peacock pheasants are, for much of the time, silent and do not maintain scrapes. As a result they were undetectable for much of the time that I was in the field. This prompts the question of what do they do, reproductively, for the rest of the time? If birds are silent in some years in months in which they call in other years, is it possible to determine if males might adopt some other reproductive strategy? If birds are undetectable, some means must be found to collect data on movements of individuals during these periods when there is no calling. I saw trapping and radio-tracking as methods by which the species could be encountered more frequently, individuals recognised and the species' ranging behaviour studied in some detail. Territory or home range area *per se* is not very informative, although Hixon (1988) provides a model in which territory area is a determinant of the mating system. There are two aspects of home range use in the Malaysian peacock pheasant that I investigated. These are whether or not there is differential use of micro-habitats within the home range (see Chapter 5) and ranging behaviour, which I discuss below. Particular questions addressed with reference to ranging were:

1) do Malaysian peacock pheasants occur in areas of the forest where no calls were heard?;

2) what is the ranging behaviour of males and females? Specifically;

i) do individuals occupy home ranges with core areas?;

ii) if there are defined areas of use, is there any evidence of sexual difference in the size of this area?;

iii) do individuals show any fidelity to areas over a number of months?;

iv) is there any evidence that males and females associate outside calling periods?

Because radio-tracking has not been used very extensively in Malaysian rain forest and not at all on the Malaysian peacock pheasant, the first priority was to establish how feasible the technique is for collecting large data sets on pheasants in tropical forest.

4.1.1 Previous use in Malaysian rainforest

The earliest study to use radio-transmitters in Malaysian rainforest was the Sandersons' (1964) study of rats (Table 4.1). Since then radio-transmitters have been attached to elephants (Olivier 1978), tapir (Williams 1979) and seladang (Conry 1980). Table 4.1 shows that radio-tracking has not yielded large data sets in any previous study in Malaysian rain forest. From this background, I wished to develop the technique to ask the basic questions above and an inevitable by-product of this is the assessment of its suitability as a study tool in tropical rain forest.

Species	N	Sampling protocol	Duration	Reference
RATS				Sanderson & Sanderson 1964
R. mulleri	7	various	1 - 16 days	
R. sabanus	1	various	8 days	
LARGE MAMMALS				
Tapir *Tapirus indicus*	3	2; 5; 16 fixes	1; 51; 143 days	Williams 1979
Seladang *Bos gaurus*	3	3; 27; 70 fixes	1; 10; 14 months	Conry, 1980
Asian elephant *Elephas maximus*	4	10/18; 16/24; 16/23; 17/23 *a*	114; 176; 303; 188 days	Olivier, 1978
BIRDS				
Argus pheasant *Argusianus argus*	2	every 15 mins/5 spaced days/month	4 months	Davison, 1981
Yellow-crowned barbet *Megalaima henricii*	1	1, 380 t-m *b*	4 days	Lambert 1989
Black and white bulbul *Pycnonotus melanoleucos*	1	2, 200 t-m *b*	7 days	Lambert, 1989
Green broadbill *Calyptomena viridis*	6	0; 0; 360; 410; 2, 046; 2, 189 t-m *b*	0; 0; 2; 1; 6; 7; days	Lambert, 1989
Brown barbet *Calorhamphus fuliginosus*	1	0 t-m *b*	0 days	Lambert 1989

Table 4.1: Species which have been radio-tracked previously in Malaysian rain forest, with sample sizes, sampling procedures and duration of tracking effort. *a* = no. successful searches over no unsuccessful searches; t-m *b* = transmitter-minutes.

Only two studies have managed to track the movements of birds in Malaysia's tropical forests and a quick perusal of these studies indicates potential problems. Davison (1981) tagged two male argus pheasants that maintained dancing grounds on hills and produced daily ranges for them. In addition, time at the dancing ground, time spent roosting and perching and time spent walking were estimated. Lambert (1989) tracked six fruit-eating birds of three canopy dwelling species for up to seven days, also producing daily ranges and roost locations. All these studies have tracked small numbers of individuals for each species and consequently the generality of the data is unclear. The small numbers of individuals tagged is itself due to the difficulty and/or effort involved in catching tropical forest mammals and birds.

4.2 Methods

4.2.1 Trapping and radio-tagging

In May 1988 birds were trapped using a traditional trap design and the routine employed by Davison (1979: p. 133), the Department of Wildlife and National Parks (Siti Hawa *bt.* Yatim, pers. comm.) and Zoo Negara (Tunku Nazim *b.* Yaacob, pers. comm.). A total of 471 traps were set about 20 m apart along trail edges between trails JPJT(E) and NS14 (Fig. 4.1). Two people could manage the two to four checks per day made by Davison and various morphological measurements were taken. The result (Table 4.2) was alarming. Five Malaysian peacock pheasants were caught, but four died within 72 hours of capture (three within 24hrs). Subsequently, traps were restricted to about 1 - 1.5 kilometres of trail and all of these could be checked within 30 minutes by one person. Traps were checked every 1.5 - 2 hours and no morphological measurements were taken. This seemed to eliminate the worst effects of stress due to capture (Table 4.2).

4.2.2 The equipment

Birds were equipped with single stage transmitters (with magnetic switch) that emitted pulsed signals on channels between 154.200 and 154.475 MHz. They were attached with necklace harnesses (Kenward 1987, Marcstrom *et al.* 1988) and the whole package weighed 10g which is 3% (Kenward 1987; p. 5) of the estimated minimum weight of Malaysian peacock pheasants (Davison, pers. comm.). The signals were detected during radio-tracking with a Mariner 57 portable receiver and a 3 element Yagi antenna.

Trail No.	Date	No. traps	No. days	No. trap-days	No. birds trapped
12/13	3 Feb.'89	120	3	360	1 (F*a*)
	6 Feb.'89	180	3	540	-
	14 Feb.'89	120	2.5	300	2 (AF1, AM1)
	16 Apr.'91	118	3	354	-
14/15/16(N)	15 May '88	60	8	480	)
	16 May '88	96	7	672	) 3(M*b*, F*b*, JM1)
	17 May '88	106	6	636	)
15/16(N)	18 Dec.'89	106	1.5	159	1 (AM2)
	15 Jan.'90	100	1	100	1 (AF2)
	16 Mar '91	85	1	85	1 (J?*c*)
17/18/19	14 May '88	131	9	1179	)2 (M*b*, F*b*)
	15 May '88	78	8	624	)
Part 17	15 Jan.'90	17	1	17	-
16(S)/RT/17	13 Feb.'90	113	3	339	-

Table 4.2: Protocol and success rate of trapping attempts. In the right hand column, A = adult, J = juvenile; F = female, M = Male, ? = sex unknown; 1, 2 = individual codes used in the text. *a* = no signals heard from the radio attached to this bird, although the radio was working before attachment; *b* = bird died within 72 hrs; *c* = bird predated after 72 hrs.

Single stage transmitters (Biotrack, Wareham, U.K.) were used because paths in the study site are up to 150m apart and because it was planned to monitor ranging over a number of months. These transmitters had an expected life-span of 10 months and an anticipated range of about 150m. Field testing, however, showed the range to be up to 230m and the life was up to about 10 months.

4.2.3 Radio-tracking

The field procedure has been described earlier, together with a preliminary assessment of the feasibility of using radio-transmitters to reveal movements of the Malaysian peacock pheasants (McGowan 1990; see Appendix 2). Briefly, each radio-location was obtained by triangulation from at least three mapped positions (Kenward 1987, Mech 1983). Analysis of 72 error polygons/triangles of radio-locations made between April and August 1988 revealed the longest diagonal of a polygon or side of a triangle to be up to 52m (n = 72) with an average of about 21m. Therefore by taking the centre of the triangle as the best estimate, the average maximum error is half of this - ie. 10.5m (0 - 26m).

30 radio-locations were taken at least two hours apart over a five to seven day period each month in which birds were radio-tagged.

4.2.4 Analyses

Because of variation in the number of radio-locations made during each calendar month, data have been lumped to give two-month sampling periods. These are December/January, February/March *etc.*

All analyses were carried out using the software package RANGES IV (Kenward, 1990). Initially, incremental analysis (Kenward 1990) was used to investigate ranging behaviour. This describes the rate at which new areas are used and indicates whether an animal's movements can be neatly packaged into home ranges which are the standard units for discussing an individual's movements. The area used during each two-month period has been estimated using three measures. The total area used is given by Minimum Convex Polygons (MCP) and core areas are given by two estimates of the core 90% of the area used made by the contouring techniques of Polynuclear Clusters (PNC) and Harmonic Means (HM). Details of the merits of, and problems with, these and other home range estimators are given by Harris *et al.* (1990) and Kenward (1987; in press). Briefly, MCP gives the total area defined by the outermost fixes and is directly comparable with most other studies. HM is a contour method and detects if more than one core area is present in the home range, as do cluster analysis methods such as PNC. PNC conforms much better to all recorded fixes than HM and was used for this reason.

Considerable attention has been focussed on the need for non-autocorrelated fixes when using parametric estimators of home range. This is because parametric estimators assume that data are statistically independent. Initially, I attempted to collect statistically independent fixes (McGowan, 1990b; see Appendix 2) but subsequently abandoned this for two reasons. First, there are problems associated with using parametric home range estimators that require statistical independence (Harris *et al.*, 1990; Kenward, 1987; in press), but also because autocorrelated data do not necessarily bias estimates of home range size (Andersen and Rongstad, 1989; Harris *et al.*, 1990). The statistical analysis of home range data is still the subject of much debate (see references above) and this is because there is no standard idea of exactly what a home range is. Without a clear definition of what is being studied, analytical techniques will remain controversial. The main problem seems to stem from considering the home range as two dimensional when it is more rigorously defined as the trajectory of an individual through time (Robertson, pers. comm). That is, the animal uses a single and continuous path rather than the area defined within particular (outermost) parts of that path.

4.3 Results

4.3.1 Trapping success

Eleven individuals were trapped in a total of 5845 trap-days giving a success rate of one bird caught every 531.4 trap-days (Table 4.2). The initial (May 1988) trap rate of one bird per 718.2 trap-days was improved to one bird per 375.6 trap-days in all subsequent trapping sessions.

Individuals were not caught in all areas where traps were set and the distribution of trapped individuals coincided with the distribution of calling records from standard survey walks (Fig. 4.1).

Because of the problem of high mortality due to trapping encountered in 1988, once a bird was radio-tagged every effort was made not to stress the bird through re-trapping. Consequently, traps were struck as soon as an individual was caught and subsequently were not set in areas frequented by radio-tagged birds. Unfortunately this reduced the chance that several birds would be tagged in the same area simultaneously. This is shown by Table 4.3 which indicates that only one or two birds were being tracked for most of the time. I have no ranging data from calling periods.

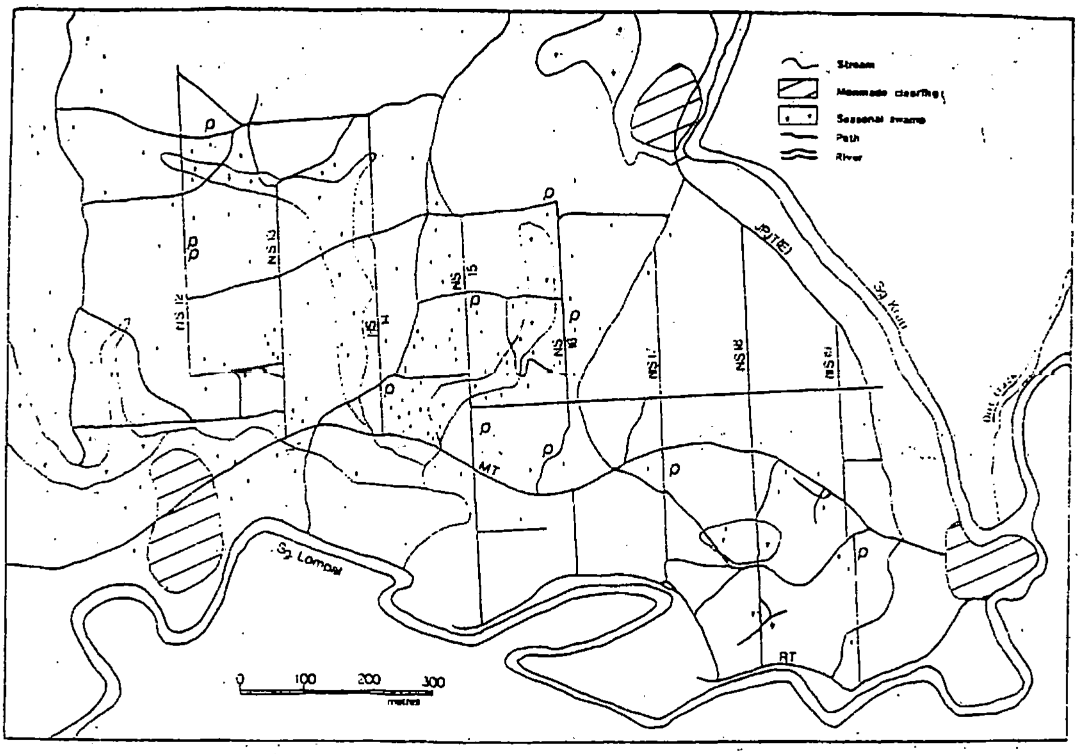


Fig. 4.1: The distribution of successful traps where Malaysian peacock pheasants were caught (*p*). Calling records from standard survey walks are also shown (0).

Year	J	F	M	A	M	J	J	A	S	O	N	D
1988	-	-	-	-	JM1	JM1	JM1	JM1	JM1	JM1	-	JM1
1989	JM1	JM1	-		-	-	-	-	-	-	-	AM2
	-	AF1	AF1	-	-	-	-	-	-	-	-	-
	-	AM1	AM1	-	-	-	-	-	-	-	-	-
1990	AM2	AM2	AM2	AM2	AM2	AM2	AM2	-	-	-	-	-
	AF2	AF2	AF2	AF2	AF2	AF2	AF2	-	-	-	-	-

Table 4.3: Months in which individuals were radio-tracked. Individual codes as in Table 4.2 and text. Most of 1989 was lost due to illness.

4.3.2 Ranging patterns

There is considerable variation within and between animals in their ranging behaviour during different sampling periods which is independent of the number of radio-locations mapped each period (Fig. 4.2). The total areas used by each individual (*i.e.* over all sampling periods) is to a large degree, however, a function of the number of radio-locations taken. That is, the length of time for which individuals were tracked (Table 4.4). This implies that individuals are continually using new areas of the forest in each sampling period.

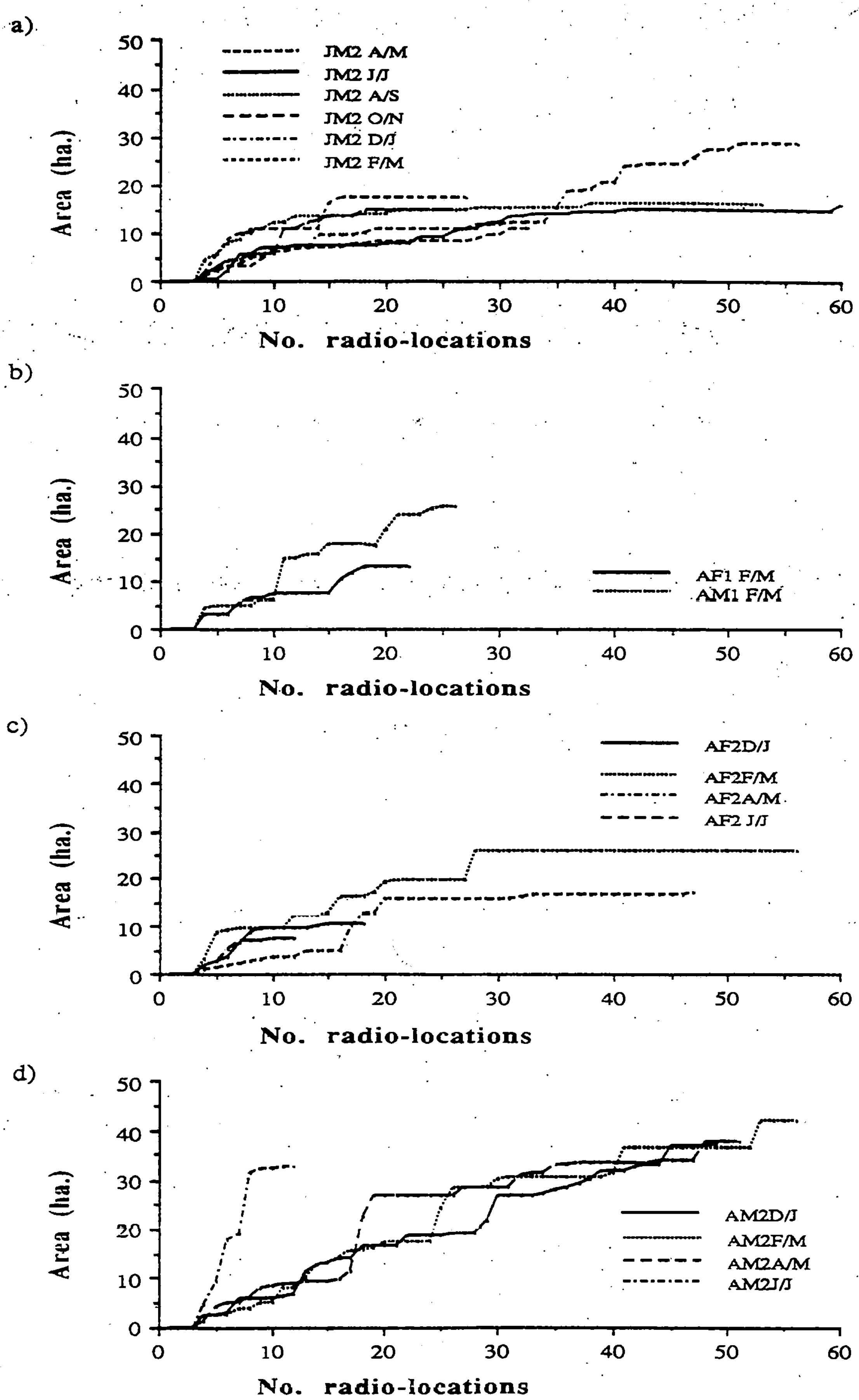


Fig. 4.2: The rate at which all five individuals used new areas in each sampling period a) JM1, b) AF1 and for AM1, c) AF2 and d) for AM2. A/M = April/May sampling period *etc.*

Individ.	Months	N	MCP	90%PNC	90%HM
JM1	A/M	33	10.81	5.58	3.89
JM1	J/J	61	15.88	8.63	10.05
JM1	A/S	59	15.94	5.20	10.37
JM1	O/N	29	14.85	5.35	4.35
JM1	D/J	58	28.71	13.09	13.64
JM1	F/M	28	17.65	5.91	3.04
JM1	All	268	49.84	21.40	30.10
AF1	F/M	25	12.94	4.48	3.39
AM1	F/M	28	25.39	11.07	8.02
AF2	D/J	18	10.66	3.80	2.23
AF2	F/M	60	25.76	9.82	11.53
AF2	A/M	51	16.98	9.13	10.39
AF2	J/J	12	7.33	6.51	1.12
AF2	All	141	30.7	19.00	17.02
AM2	D/J	52	37.31	10.63	10.82
AM2	F/M	60	42.26	22.60	16.86
AM2	A/M	51	37.65	16.46	11.98
AM2	J/J	12	32.91	5.90	2.36
AM2	All	175	58.32	30.10	35.41

Table 4.4: Estimates of area (in hectares) used by each individual in each two-month sampling period. N = number of radio-locations made in each sampling period. MCP = Minimum Convex Polygon, 90%PNC = 90% Polynuclear Clusters and 90%HM = 90% Harmonic Mean estimators of core area used.

The smallest MCP area described within a two-month period was 7.33ha. and the largest was 42.26ha (Table 4.4). The two 90% core estimators differed considerably and the 90% PNC estimate was larger than the 90%HM estimate in 11 out of 19 instances (Table 4.4). Within males, the smallest two-monthly range recorded was 10.81ha and the largest 42.26ha. The smallest female range was 7.33ha and the largest 25.76ha. The mean two-monthly MCP and 90% core ranges for the two females are smaller than all the estimates for the three males apart from a single male range estimated by 90%PNC (Table 4.5).

Estimator	Female	Male
MCP	12.94; 15.18	17.31; 25.39; 37.53
90%PNC	4.48; 7.32	7.29; 11.07; 13.90
90%HM	3.39; 6.32	7.56; 8.02; 10.51

Table 4.5: Mean two-monthly range areas (in hectares) for all five individuals, estimated using three estimators as described in the text.

As there do appear to be general differences between males and females in ranging behaviour, I shall now treat individuals separately to explore these differences further.

Male JM1

This bird was trapped as a juvenile but was in fully adult male plumage when re-trapped and fitted with a new radio-transmitter in mid-February 1989. The total area used was determined in only 4 (out of 6) sampling periods for JM1 (Fig. 4.2a) and varied from 10.81 to 28.71 ha. In each period at least 10.5% of the range used in the previous period was overlapped and as much as 88.8% (Table 4.6). There was no overlap with either AM1 or AF1 when tracked simultaneously (February/March 1989).

Female AF1

It appears that the total area used during the sampling period was described (Fig. 4.2b). The total area used was 12.94ha. and the core area was 26.19% (HM) or 34.62% (PNC) of this (Table 4.4). There was some overlap with areas used by AM1. The total area used by AF1 was overlapped by AM1 by 58.2% although the core area overlap was only 7.5% (PNC) and 3.7% (HM).

Male AM1

The minimum area used by male AM1 during the single sampling period was still increasing when tracking stopped (Fig. 4.2b). As this male also ranged out of radio contact (*ie*. over 230m from a trail, despite new trails being cut) on a number of occasions, 25.39ha. is an underestimate of the total area used by this male. Even so, this range is twice that of the female tracked simultaneously (AF1). 30.3% of the total range of AM4 was overlapped by the total area used by AF1 but only 1.6% (HM) or 3.9% (PNC) of the core area overlapped.

Female AF2

The maximum area was described for female AF2 in all four sampling periods and varied between 7.33ha. and 25.76ha. Whilst the sample sizes do vary across periods, stable estimates of total range were obtained quickly in all four sampling periods (Fig. 4.2c). The proportion of a previous period's range that was overlapped in each sampling period varied considerably, whether considering the total area used or either of the 90% estimates (Table 4.6). The area used was overlapped extensively by AM2, particularly in the February/March and April/May periods when all three range estimators indicate considerable overlap between birds (Table 4.7).

Individual	Months	MCP	90%PNC	90%HM
JM1	A/M by J/J	10.5	14.2	5.8
	J/J by A/S	73.1	44.5	63.9
	A/S by O/N	25.6	27.8	10.6
	O/N by D/J	88.8	54.1	61.4
	D/J by F/M	58.8	14.1	15.5
AF2	D/J by F/M	100.0	63.9	80.3
	F/M by A/M	52.7	27.4	30.3
	A/M by J/J	29.1	20.0	4.6
AM2	D/J by F/M	91.4	59.1	31.4
	F/M by A/M	72.9	35.6	16.0
	A/M by J/J	65.6	17.3	0.4

Table 4.6: Percentage overlap of area used by three individuals in successive sampling periods. Percentages are calculated by three range estimators, Minimum Convex Polygons (MCP), 90% contour Polynuclear Clusters (90%PNC) and 90% Harmonic Means (90%HM).

Overlapping ranges.	Months	MCP	90%PNC	90%HM
AF2 by AM2	D/J	100.0	26.9	19.2
	F/M	98.9	95.1	88.9
	A/M	100.0	94.1	55.7
	J/J	28.3	0.0	0.0
AM2 by AF2	D/J	29.2	9.9	5.9
	F/M	61.0	41.3	60.0
	A/M	45.0	52.1	61.0
	J/J	6.4	0.0	0.0

Table 4.7: Percentage overlap of areas used by AF2 and AM2 in each sampling period. Range estimators used are Minimum Convex Polygons (MCP), 90% contour Polynuclear Clusters (90%PNC) and 90% contour Harmonic Means (90%HM).

Male AM2

The maximum area used by this male was described in only two of the four sampling periods and this is not an artefact of the number of radio-locations made (Fig. 4.2d). This male used a much larger area than the female that was tracked at the same time (AF2), using between 32.96ha. and 42.26ha. in each sampling period (Table 4.4). The core areas were also larger, except in June/July as estimated by Polynuclear Clusters. The overlap between total areas used in successive sampling periods was more consistent than for AF2, but the core area overlap was also very variable (Table 4.6). The area used by this male was overlapped to a lesser extent by AF2 than vice versa (Table 4.7).

4.4 Discussion

4.4.1 Use of space

The distribution of successful traps coincides with the distribution of calling locations (despite trapping mostly being carried out outside calling periods) and indicates that Malaysian peacock pheasants only inhabit certain areas of the forest. Such differential use of available habitat within tropical forest has been recorded before. Schemske and Brokaw (1981) found that the assemblages of mist-netted birds inhabiting treefall gaps were quite distinct from those inhabiting mature forest in Panama. This implies that the species are not evenly spread throughout the forest. Whilst Malaysian peacock pheasant calls were heard wherever individuals were trapped, there were both calls and captures outside centres of calling activity. Although there are centres of calling activity, some males will give at least a few calls throughout the whole area inhabited by the pheasant during the calling periods. This suggests that there is differential use of micro-habitats within the forest stand, which may be ecologically and/or behaviourally determined.

4.4.2 Ranging behaviour

The two females used smaller total and 90% core areas than the males sampled simultaneously (except for the 90HM estimate for JM2 and AF5 in February/March 1989 and the 90PNC estimate for AM2 and AF2 in June/July 1990). The females also defined their maximum area used in each sampling period more quickly than the males. The data for the males do not always reach an asymptote, thus not constituting a total range used. These two results suggest that the two females are more loyal to particular areas in each month than the wider-ranging males. There are data on range shifts between sampling periods for only two individuals which were tracked simultaneously, the male AM2 and the female AF2. The position of the 90% core area seemed to shift in a similar manner for both of these birds, but the MCP area of the male shifts much less than that of the female. These data indicate that the females' ranging behaviour is centred on a core area within a home range, whereas males range more widely and do not necessarily use a core area when there is no calling. The high proportion of overlap between AM2 and AF2 indicate that males and females do associate at least outside the calling periods and suggests that individuals are not necessarily solitary.

The only other pheasants for which there are estimates of home range size are the ring-necked pheasant *Phasianus colchicus*, Cabot's tragopan *Tragopan caboti* and the argus pheasant *Argusianus argus* (Table 4.8). The first two species inhabit temperate forest and were tracked in winter and spring (ring-necked pheasant) or just winter (Cabot's tragopan). Sampling protocols were different in all four studies, but as noted above in section 4.2.4, this probably does not bias estimates of home range size.

Species	MCP	90%PNC	90%HM	Reference
Ring-necked pheasant	5.5[a] - 16.3[b]	1.3[a] - 2.5[b]	-	Robertson *et al.* (in prep.)
Cabot's tragopan	3.7 - 23.3	-	2.9 - 20.0	Young *et al.* (1991)
Argus pheasant	1.1 - 6.2	-	-	Davison (1981a)
Malaysian peacock pheasant	12.9 - 37.5	4.5 - 13.9	3.4 - 10.5	This study

Table 4.8: The largest and smallest monthly home range sizes (in hectares) recorded for four pheasant species using three different home range estimators - MCP = Minimum Convex Polygon, 90%PNC = 90% Polynuclear Clusters and 90%HM = 90% Harmonic Mean. All figures are for individual birds apart from [a] = mean of 17 birds and [b] = mean of 26 birds.

4.4.3 Future use of radio-tracking in Malaysian rainforest

After using the modified trapping regime several times, I am now satisfied that birds can be caught and fitted with radio-transmitters safely. Using this trapping regime the intensity of trapping could be increased by trapping more frequently and in areas already frequented by radio-tagged birds. This would increase the likelihood of several birds being radio-tagged simultaneously. In this study, collection of morphological data during processing was abandoned, as it is likely to have contributed significantly to the stress suffered by the birds in May 1988. There are three ways in which the amount of data collected could be increased in future studies.

The use of anaesthetics

The application of an anaesthetic immediately after capture would permit morphological measurements to be made without causing more stress to the bird. Although Pruett-Jones (1985) has used the inhalent Methoxyflurane (Metofane TM) to anaesthetise Lawes' parotia (a bird of paradise) during processing, I am not aware of an anaesthetic that has been used on a large (400 - 600gm.) tropical bird that is susceptible to stress. There are possibilities, however, as turkeys are routinely drugged for capture in the U.S. (*e.g.* Williams and Austin, 1988 and references therein) and clinical trials on chickens of a new anaesthetic have yielded encouraging results (John Cooper, pers. comm.)

Increasing tracking efficiency

Consistently tracking birds to a point close enough to take a reading when the radio-transmitter has a range of only 230m is very tiring in a hot and humid forest and especially in the mornings when wet vegetation along trail edges soaks the radio-tracker within minutes. This could be eased in two ways. Firstly, when radio-tracking rats throughout the night over a number of nights, Sanderson and Sanderson (1964) used two field crews of three people each who radio-tracked the rats for about six hours each. Some allowance of this sort must be made when designing radio-tracking programmes in this climate. Secondly, the use of sufficiently small radio-transmitters that have both long life and long range. At present, short signal range is a necessary consequence of long battery life. Long life is needed because it is important to try and 'accumulate' radio-tagged birds over a period of two to three years. In addition, the timing of calling periods is not predictable and so to investigate the relationships between calling and other behaviour patterns, birds must already be tagged when calling starts. Small transmitters with a life of two to three years and a range of one to two kilometres are a prerequisite to documenting ranging behaviour in a variety of South-east Asian tropical forest birds. Alternatively, radio-transmitters with a time switch could be used. This would allow the transmitters to be switched off for the 12 hours or so of darkness and hence double the number of months for which the battery lasts. The relationships between ranging and behaviour patterns that are exhibited infrequently and at unpredictable times could then be investigated.

Small sample sizes are currently inevitable in many aspects of the study of tropical birds. Numbers of radio-tagged Malaysian rain forest birds are almost certain to remain small in the short term, but this alone does not preclude radio-telemetry from being used on such species. Provided that the questions are well defined and the sampling procedure designed accordingly, the technique can provide more than anecdotal information on some tropical bird species. The simple description of movements discussed above elucidates some features of the social organisation of the Malaysian peacock pheasant and answers several interesting questions about ranging behaviour outside periods of calling. What is now of interest are the relationships between ranging, morphology and other behaviour patterns such as calling and scrape maintenance. For example, during periods of calling do home ranges of males overlap and are their sizes and arrangement influenced by calling? How do males without scrapes behave? Radio-telemetry is the only method by which individuals of many species can be identified in dense rainforest and questions such as these answered.

CHAPTER 5: SOCIAL ORGANISATION III: MICRO-HABITAT CORRELATES OF SOCIAL ORGANISATION

"To right and left of the path the forest appears to be almost impenetrable. The trees grow so thickly together that you are closed in by a small but unbroken circle of tree trunks. Between the trees there are tangled masses of bushes, briars and saplings. Rattans and creepers of every kind creep along the ground and among the trees, sometimes hanging in heavy festoons and sometimes tense with the pressure they exert. .... After an hour's walk along the forest path a casual observer might say that, so far as he could see, the forest contained no flowers, no butterflies, no birds, no life of any kind." Maxwell (1907: p. 6)

5.1 Introduction

The importance of an animal's ecology in shaping its mating system has long been accepted (see Vehrencamp and Bradbury (1984) for a review and Emlen and Oring (1977) for an ecological classification of mating systems). Despite this, the ecological context in which mating behaviour is exhibited is often overlooked by biologists interested in functional questions concerning mating systems. The resultant search for functional answers to behavioural problems is conducted in complete isolation of any possible ecological influences on the behaviour pattern being investigated and this fails to give a complete and accurate discussion of the selective forces shaping a behavioural pattern. For example, leks are commonly cited as ideal systems within which to study sexual selection, but in species where displaying males are clumped, it must be demonstrated that males are more clumped than females and that males are not clumped around some resource for the mating system to be considered a 'lek' from an ecological standpoint (see Bradbury, 1981 for further criteria for a lek). Although such classifications can provide a useful background to discussion of sexual selection, it can be clumsily used to confuse reasons for the variation that is seen in mating strategies. An example from the pheasants is, do male Indian peafowl lek? As noted above 'lek' now implies compliance with some very strict criteria (see Bradbury, 1981). Perhaps the distribution of sites which are suitable for male display influences the dispersion of displaying male Indian peafowl and hence the reproductive strategy that they use. Understanding the factors which determine male dispersion will help to understand the selective forces that lead to differential male mating success, the females' pattern of movement and hence discussion of the evolution of the male's train. The reason(s) for male clumping is central to understanding the evolution of such 'alternative' mating strategies and it is readily apparent that this lack of consideration for the ecological context of a number of mating systems seems to be a major weakness in understanding the selective forces that lead to differential male mating success. Therefore, I felt that ecologial reasons for the observed male calling dispersion should be investigated.

The locations from which Malaysian peacock pheasants call are clustered within a field season (see 3.3.4) and although the males are not in visual contact during the display period, the 'system' is functionally similar to a lek if some part of female mate choice is made on the basis of male calling. Initially, however, it is important to investigate whether there are ecological reasons for such male clumping. In tropical forest, there are two possible avenues that can be investigated. Firstly, an assessment of the structure of the vegetation may reveal differences in the habitat between areas where males call and areas where little or no calling was heard. Although the features measured need not be those that directly influence calling, they should be chosen to reflect the habitat in a particular place and this assumes that the features measured are correlated with those that do directly influence calling. Secondly, some index of temporal and spatial variation in food abundance may be correlated with male calling rates. Although the diet of the Malaysian peacock pheasant is poorly known, Davison (1983a) found some between-year relationship between levels of calling, fruiting levels and invertebrate abundance. Because the diet is poorly known and the species is probably opportunistically frugivorous, insectivorous or both, depending on local (and patchy) food availability, monitoring invertebrate levels would not add much to Davison's (1983a) interpretation in the time available in this study.

An assessment of the micro-habitat relations of the Malaysian peacock pheasant may indicate potential reasons for spatial variation in calling levels. Given the practical problems of collecting accurate data in dense tropical forest, the following questions are those most readily addressed.

i) quantification of the variation and/or patchiness in forest structure

ii) are core areas within home ranges of radio-tagged individuals comprised of particular micro-habitats that differ from those in the rest of the range?

iii) do calling clusters occur in particular micro-habitats in the forest?

iv) is the habitat at sites where display scrapes are constructed any different from other sites within calling clusters?

5.2 Methods

No standard method of analysing micro-habitats of tropical ground-dwelling animals has been adopted by tropical ecologists. Consequently, in order to devise satisfactory field and statistical procedures, the extensive literature on avian habitat relationships has been reviewed.

In such a structurally variable habitat, using a suitable and sensitive field methodology to detect any systematic variability is absolutely critical. Therefore, I present a critique of existing methods of evaluation and outline the development of the procedure that I used.

5.2.1 A review of studies of bird-habitat relationships

There has been considerable interest in the study of the structure of avian habitats since MacArthur and MacArthur (1961) reported that bird species diversity could be predicted from the height profile of foliage density. Furthermore, they suggested that plant species diversity has nothing to do with bird species diversity, except by influencing habitat structure.

Temperate bird community studies.

Subsequently, studies of avian habitats in temperate regions have investigated overall vegetation structure as it affects total avian diversity (*e.g.* Rotenberry and Wiens, 1980; Sabo, 1980; Bibby *et al.*, 1985). Some of these studies use habitat structure to analyse relationships between species occuring in the same areas and have permitted quantitative investigation of the ecology of bird communities with emphasis on aspects such as resource partitioning, niche breadth, competition and diversity (*e.g.* Whitmore, 1977; Wiens and Rotenberry, 1981; see Dueser and Shugart (1978) and M'Closkey and Fieldwick (1975) for a similar discussion of sympatric rodents). Other studies, following MacArthur and MacArthur (1961), relate bird species diversity to habitat structure (*e.g.* Wiens and

Rotenberry, 1981) on the assumption that predictable relationships exist between the occurence of a bird species and its characteristic habitat requirements (James, 1971; Whitmore, 1975). Several of these studies have also used habitat structure measurements to try and separate the effects of habitat selection and interspecific competition on currently observed patterns of habitat use.

Tropical bird community studies.

In the tropics "the richness and complexity of lowland tropical rain forest make it difficult to investigate faunal and floral patterning and possible interactions" (Kemper and Bell, 1985). Nonetheless, bird-habitat relationships have been investigated in a number of ways. These have included assessing theories for the current structure of bird communities (*e.g*. Pearson, 1975; 1977a), investigation of habitat structure correlates of rainforest birds (*e.g*. Kikkawa, 1982), how such correlates should be accounted for when studying interspecific competition in communities (*e.g*. Mountainspring and Scott, 1985; Pearson, 1977b) and comparison of bird assemblages in mature rainforest with those present at treefall gaps (Schemske and Brokaw, 1981).

Temperate single species studies.

Some studies in temperate habitats have investagated habitat use in a single, predominantly ground dwelling species. These have been restricted to a simple investigation of whether vegetation cover types ('macro-habitats') have been used in proportion to their availability. Such studies include Robertson (1985) and Hill and Ridley (1987) on the ring-necked pheasant *Phasianus colchicus* and Zwank *et al*. (1988) on female turkeys *Meleagris gallopavo*. Other studies have investigated some aspect of micro-habitat use and also seem inappropriate. This is primarily because temperate habitat variables, such as those measured in a number of north American quail studies (*e.g*. Wilson and Crawford, 1987; Brennan *et al*., 1987), are inapplicable in tropical forest. Several variables measured by Jones (1988) for investigating selection of incubation mound sites by another Galliform, the Australian brush-turkey *Alectura lathami*, are subjective estimates (see below).

Studies of tropical forest floor-dwelling birds and small mammals.

Compared with this interest in understorey and midstorey avifaunas and ground dwelling temperate bird species, little attention has been paid to quantifying the habitat relations of animals inhabiting the forest-floor of lowland tropical rainforest and none provide field procedures that are satisfactorily objective and detailed enough for the current study. For example, in a study of the habitat of small, forest-floor mammals in peninsular Malaysia, Kemper and Bell (1985) ranked habitat features according to importance/abundance. They suggest that this subjective approach eliminated "the all but impossible task of direct measurements in this complex system." Davison (1981c) restricted his study of the habitat requirements of the crested fireback pheasant *Lophura ignita*, also in peninsular Malaysia, to a comparison of the number of sightings of the species in each of six forest categories. The categories were mapped and classified according to tree species present and subjective assessment of ground water conditions and topography. Although Kemper and Bell (1985) suggest that small mammal captures were correlated with several habitat variables, they do admit that interpretation of their 'average' scores should be done with caution and also that this appears to conceal some of the real variability present within each site. Davison (1981c) reported that the majority of crested fireback sightings were in forest that represented the riparian fringes and flood limit forest. Habitat studies of the closely related Palawan peacock pheasant *Polyplectron emphanum* have highlighted the need for a robust, objective field methodology. Caleda (unpub. ms.) sampled 100 tree specimens in known peacock pheasant habitat and identified 95% of them as comprising 50 species belonging to 27 families. The result reflects the species richness of tropical forest, but provides little information on habitat determinants. Cursory investigation of Palawan peacock pheasant microhabitats (McGowan *et al.*, 1991) has clearly demonstrated the need for a more satisfactory field procedure for investigating habitat relations of tropical forest ground dwelling birds and mammals.

Problems with these studies.

For the present purposes the approach and, consequently, the methodologies employed in these studies seem inadequate for the following reasons;-

i) Many methodologies have been 'study specific' (see Farina, 1985) and thus preclude comparison between studies in both space and time in instances where this might prove informative. This 'study specificity' takes two forms;-

a) some, if not all, parameters are often subjective estimates. For example, % abundance of, say, ground cover or canopy cover are often 'determined' by visual inspection. Such subjective estimates probably vary between any two observers (*e.g.* at different sites in extensive studies) and also over time in intensive studies, even if all 'measurements' are taken by a single observer. The problems with this approach have been documented (Block *et al.*, 1987)

b) virtually without exception, no two studies have measured the same parameters and in the same way (see Farina, 1985)

ii) By investigating overall variation in vegetation structure, these studies often pay particular attention to measuring vertical profiles of the vegetation structure (*e.g.* vertical foliage profiles). For ground dwelling animals it seems desirable to consider the vegetation close to the ground in more detail, but noting that ground flora may be correlated with canopy and other structural cover.

iii) Typically, the 'focus' of the habitat data collection is the point at which the observer is sited for a point census, location of a singing male etc. (the "organism centered point'). These are precisely located points and can be accurately sampled and compared with bird species recorded. In forested habitats, galliforms are sighted relatively rarely and in tropical conditions, in contast to Himalayan forests, other signs (tracks, droppings *etc.*) are virtually, if not completely, undetectable. Consequently, the detectability between species is very variable. The most readily detectable species are those with conspicuous aspects of their breeding biology. For species that are vocal for part of the year, although calls are easy to detect, locating the calling individual precisely is virtually impossible in dense forest. This results in the likelihood that the organism-centred point will not correspond to the exact location of the organism. Consequently, a simple comparison of organism-centred points with randomly chosen points will not provide any meaningful, accurate information, because points classified as 'organism-centred points' will really be 'random points'.

5.2.2 Devising a new field procedure

Given these problems with existing techniques, it seems appropriate to construct a methodology that will both provide useful and accurate information and prove practical in the field. Such a methodology should be subject to the following considerations;-

i) Data to be collected must be as objective as possible, preferably precisely measured or counted. This will ensure that data collected throughout the study are comparable, whereas subjective estimates may be influenced by the observer's differing perception of the forest over time. This should allow habitat monitoring, if required, in other circumstances and such objectivity will also permit comparison between observers and studies, should the method be more widely used.

ii) Parameters chosen should represent 'biologially meaningful' variation. For example, previous division of individual trees into understorey or overstorey trees is rather arbitrary in tropical forests where tree size (both height and girth) shows continuous variation and is better represented by a gradient of tree girths.

The approach taken by Dueser and Shugart (1978) for selection of habitat variables chosen to investigate the micro-habitats of small, forest-floor mammals seem reasonable and, where applicable, is adopted here. Therefore, each variable;-

i) should be quickly and precisely measurable with non-destructive sampling procedures;

ii) should have intra-season variation that is small relative to inter-season variation;

iii) should describe the environment in sufficient detail to detect subtle variation in a habitat that may appear to be uniform. Such subtle variation has been qualitatively reported for tropical forest (Kemper and Bell, 1985). This may be important because of the patchiness of the understorey and because the Malaysian peacock pheasant inhabits extreme lowland forest but appears to be restricted even within this forest type. Davison (1986c) suggests that pheasants of Sundaic origin (see section 2.1 for the geographical limits of the Sunda subregion) have a narrow range of habitat preference. This may be because of some subtle difference(s) within this forest type.

Dueser and Shugart's (1978) included variables that measured the environment in a way which was either known or reasonably suspected to influence the distribution and local abundance of forest-floor small mammals. This seemed inapplicable in this study because of the absence of any information on how particular microhabitat structures may affect pheasant distributions. Habitat parameters, therefore, were chosen to reflect the most evident vegetation structures and, as a result, were regarded as 'general' habitat measurements. This is an important distinction, as any positive associations do not necessarily indicate that pheasants are selecting particular habitat features.

5.2.3 Statistical procedure

Ordination was used to understand the inter-relations of the data matrix of 23 variables x 197 samples. Ordination techniques were initially developed to examine vegetation as a continuum (Austin, 1985) and therefore "Ecological ordination refers to the arrangement of samples in relation to environmental gradients, or axes that may correspond to environmental gradients" (Gauch *et al.* 1977). Assessment of the application of quantitative methods to rainforest vegetation surveys indicates that ordination is more satisfactory at lower levels of variation (within forest types) than classification, which is more informative at higher levels of variation in vegetation composition (Greig-Smith *et al.*, 1967). In ecological investigations of aspects of avian or small mammal relations the most commonly used technique is Discriminant Function Analysis (DFA) (*e.g.* Dueser and Shugart, 1979; Rosenzweig and Winakur, 1969; M'Closkey and Fieldwick, 1975; Jones, 1988; see also Green, 1971). Williams (1983), however, suggested that this method has often been inappropriately used in such investigations because various assumptions have been violated. Whilst this need not necessarily negate the statistic's effectiveness, some violations are serious and under these conditions, it is not known how robust the statistic is. A second technique that has been used is Principal Components Analysis (PCA) (*e.g.* Rotenberry and Wiens, 1980; Wiens and Rotenberry, 1981; Bibby *et al.*, 1985). This technique was used in a preliminary analysis of part of the micro-habitat data presented here (McGowan, 1990c; see appendix 3). Unlike DFA, this does not maximise the distance between plots in multi-dimensional space but describes their relative positions without emphasising species differences (James, 1971; Rotenberry and Wiens, 1980). James (1971) used both techniques in a study of habitat relations among breeding birds and concluded that using both methods was more informative than using either alone.

Hill and Gauch (1980) suggested that detrended correpondence analysis (DCA) was better than other techniques of ordination that they were aware of. Despite this and the problems with using other ordination techniques to describe ecological data, DCA seems to have been little used in avian community studies (but see Hill *et al.* 1990 and Sabo, 1980). When producing the environmental gradients, or axes that may correspond to environmental gradients, mentioned above, ordination techniques, such as DCA, normally indicate how much of the variation in the original data matrix is explained by each of these gradients. This is relevant when attaching importance to the interpretion of the final stage of the ordination which is a graph of the first two axes (*ie.* those that explain a greater proportion of the variation in the original data matrix than the other axes).

Because the variables had different ranges (Table 5.1), they were all standardised to a range of 0 - 100 before ordination so that each variable had equal weight in the analysis. DCA was carried out using the programme DECORANA (Hill, 1979).

Mann-Whitney U tests were used, initially, to test for differences in the variables between samples (*e.g.* micro-habitat plots within vs those without calling clusters). Because variables may be correlated, however, DECORANA ordination was used to provide Axis I and Axis II scores for each micro-habitat plot. These single values were then compared between samples.

5.3 Results

5.3.1 Overall habitat description

Table 5.1 shows that there was considerable variation between points in most of the features measured. Trees over 160cm gbh., herbs over 0.5m tall and pandans were recorded from few plots. Smaller trees were more numerous at each plot than larger trees and there were also many woody stems (mostly treelets) that were less than 0.5m tall. Herbaceous plants were much less common than woody plants. Pandans (*Pandanus* spp., at Kuala Lompat typically found in swampy areas) were confined to areas that were marshy and periodically contained standing water. Gingers comprised most of the tall herbs recorded and were typical of disturbed areas, such as the early stages of regeneration after tree falls, at the edges of some wider trails and around the *padang* (clearing).

Abbrev.	Definition	med.	range
TREETEN^{1}	Number of woody stems over 2m tall and with girth at breast height <10cm. within 5m of focal point.	30	1-100
TREETWT^{2}	Number of woody stems >2m tall and with girth at breast height 10<20cm. within 5m of focal point.	8	0-30
TREEFOR^{3}	Number of woody stems >2m tall and with girth at breast height 20cm<40cm. within 5m of focal point	5	0-20
TREEEIG^{4}	Number of woody stems over 2m tall and with girth at breast height 40<80cm. within 5m of focal point	1	0-9
TREEONE^{5}	Number of woody stems >2m tall, with girth at breast height 80<160cm. within 5m of focal point.	1	0-4
TREEBIG^{6}	Number of woody stems >2m tall, with girth at breast height of >160cm. within 5m of focal point.	0	0-3
WSTEMSM^{7}	Number of woody stems at ground level of plants less than 2m tall within 1m of the focal point.	40	0-200
WSTEMMD^{8}	Number of woody stems at 0.5m above ground level of plants <2m tall within 1m of the focal point.	7	0-40
WSTEMLG^{9}	Number of woody stems at 1.0m above ground level of plants <2m tall within 1m of the focal point.	4	0-30
HSTEMSM^{10}	Total number of non-woody stems at ground level of plants less than 2m tall within 1m of focal point.	2	0-200
HSTEMMD^{11}	Number of non-woody stems at 0.5m above ground level of plants <2m tall within 1m of focal point.	0	0-20
HSTEMLG^{12}	Number of non-woody stems at 1.0m above ground level of plants <2m tall within 1m of focal point.	0	0-10
TLLHERB^{13}	Number of herb stems over 2m tall recorded within 5m of the focal point.	0	0-40
PANDANS^{14}	Number of pandan (*Pandanus* spp.) stems over 2m tall recorded within 5m of the focal point.	0	0-50
PALMNOS^{15}	Total number of palm stems over 2m tall within 5m of the focal point.	5	0-30
PALMSPP^{16}	Number of palm species within 5m of focal point.	3	0-6
FALLDST^{17}	Distance to nearest treefall (up to a maximum of 50m)	8	0-50
FALLSTG^{18}	Stage that treefall is in (little regrowth, much regrowth, canopy closed over rotting log).	2	0-3
TERMNOS^{19}	Number of quarters that contain termite mounds.	2	0-4
TERMDST^{20}	Distance from the focal point to the nearest termite mound (within 10m) in each quarter.	5	0-10
TERMCRC^{21}	The basal circumference of each termite mound above.	8	0-30
TERMHGT^{22}	The height of each termite mound recorded above.	0.6	0-3
OVHDOBJ^{23}	Height of the lowest object over the focal point.	0.9	0-50

Table 5.1: Definition, median and range of the habitat variables measured at each habitat point. Abbrev. = abbreviation; med. = median. Superscript indicates number on Fig.5.1.

5.3.2 What is the variation and/or patchiness in forest structure?

The first four axes of the DECORANA ordination have eigenvalues of 0.191, 0.126, 0.056 and 0.049 respectively and so the first two axes do appear to describe much of the variation

(Hill 1979: p. 22). Unlike Principal Components Analysis, DECORANA does not indicate the proportion of the variation that is explained by each axis. Ordination of the habitat variables (Fig. 5.1a) indicates that Axis I represents a gradient from areas with many small plants (herbaceous and woody) and more large termite mounds through to open areas (Pandans *Pandanus* spp. in swampy patches and few low leaves or branches) with more large trees and larger distances to tree falls. This riverine to inland axis is based on the water table as described for the study site by Raemaekers *et al.* (1980: p. 39). Axis II represents a gradient from more stable areas of the forest (few tree falls, larger trees *etc.*) to areas that are more susceptible to disturbance with more ground flora and smaller trees.

The ordination of the habitat plots shows that they are continuously distributed with respect to Axes I and II and concentrated towards the lower end (Fig. 5.1b). There are no discrete types of micro-habitat but they are widely distributed.

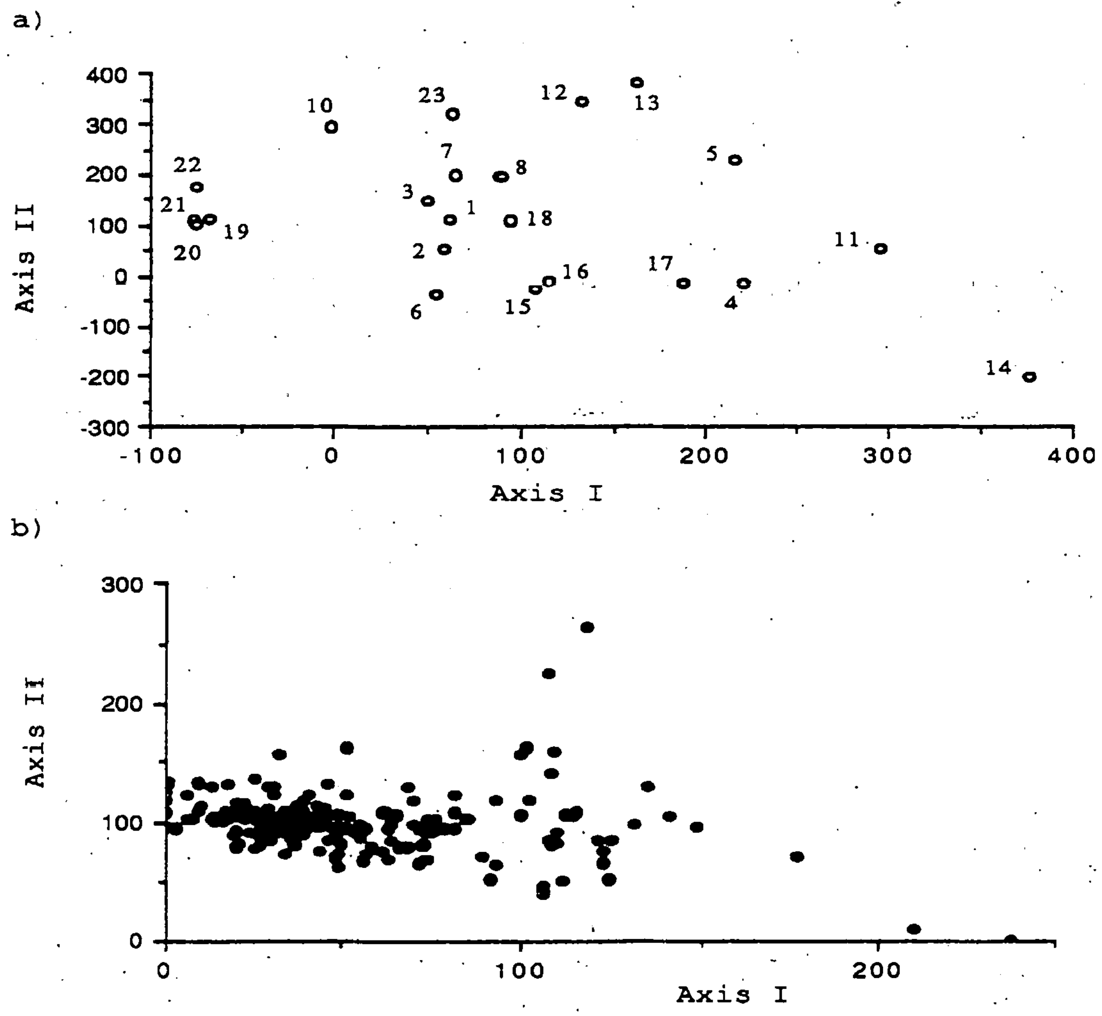


Fig. 5.1: Ordination of a) habitat variables and b) all micro-habitat plots. Superscript numbers on a) refer to variables listed in Table 5.1. Axis scores refer to the standard deviation x 100. Axis I represents a gradient from riverine → inland (dry/swamp) and Axis II represents a gradient from stable → unstable.

5.3.3 Are particular micro-habitats within a home range used?

To investigate this, axis I and axis II scores for plots within 90%PNC core areas (see 4.2.4) were compared with those for plots outside the core area but within the MCP total range used. This was done for each individual peacock pheasant that was radio-tagged (Table 5.2).

Individ	N (core)	N (ex-core)	Axis I	Axis II
JM1	35	41	*(X)	N.S.
AM1	13	23	*(X)	N.S.
AF1	17	14	N.S.	N.S.
AM2	54	54	N.S.	***(C)
AF2	42	28	N.S.	N.S.

Table 5.2: Comparison of ordination axis scores between micro-habitat plots within core areas and outside core areas for five radio-tagged individuals (Mann-Whitney U test * = $p < 0.05$; *** = $p < 0.001$; N.S. = non-significant. (X) = plots outside the core have the higher mean rank; (C) plots within the core have the higher mean rank).

As Table 5.2 shows, there are no significant differences between the plots in the core area and those outside that were consistent across all five individuals. The males did seem to use micro-habitat plots differentially, but whereas two males used only axis I differentially, the third used only axis II differentially. Table 5.2 shows that the first two males were using more areas towards the lower end of Axis I and were therefore using more inland, swampy areas in the core areas than in the rest of the range. Male AM2 was using areas that were susceptible to more natural disturbance in the core than outside the core.

5.3.4 Do calling clusters occur in particular micro-habitats in the forest?

The delimitation of the calling cluster areas was described in 3.2 and 3.3.4. There were 84 micro-habitat plots within the two calling clusters and 113 outside.

There were significantly fewer trees of <10cm (*i.e.* less than 10cm at gbh) and 20 - 40cm gbh (*i.e.* between 20 and 40 cm at gbh), woody stems at ground level and 0.5m above ground level, herbaceous stems at 0.5m above ground level, pandans, termite mounds and termite mounds of smaller basal circumference at plots within the calling clusters when compared to plots in other parts of the forest (Table 5.3). There were more trees of 40 - 80 cm gbh and more palms of more species at plots within calling clusters.

Variable	p	Higher mean rank
Treeten	**	non-cluster
Treetwt	N.S.	------
Treefor	***	non-cluster
Treeeig	*	cluster
Treeone	N.S.	------
Treebig	N.S.	------
Wstemsm	**	non-cluster
Wstemmd	*	non-cluster
Wstemlg	N.S.	------
Hstemsm	N.S.	------
Hstemmd	*	non-cluster
Hstemlg	N.S.	------
Tllherb	N.S.	------
Pandans	**	non-cluster
Palmnos	***	cluster
Palmspp	***	cluster
Falldst	N.S.	------
Fallstg	N.S.	------
Termnos	*	non-cluster
Termdst	N.S.	------
Termcrc	*	non-cluster
Termhgt	N.S.	------
Ovhdobj	N.S.	------

Table 5.3: Comparison of habitat variables between micro-habitat plots within calling clusters (n = 84) and those plots outside calling clusters (n = 113):(Mann-Whitney U test; * = $p< 0.05$, ** = $p< 0.01$, *** = $p< 0.001$ and N.S. = non-significant).

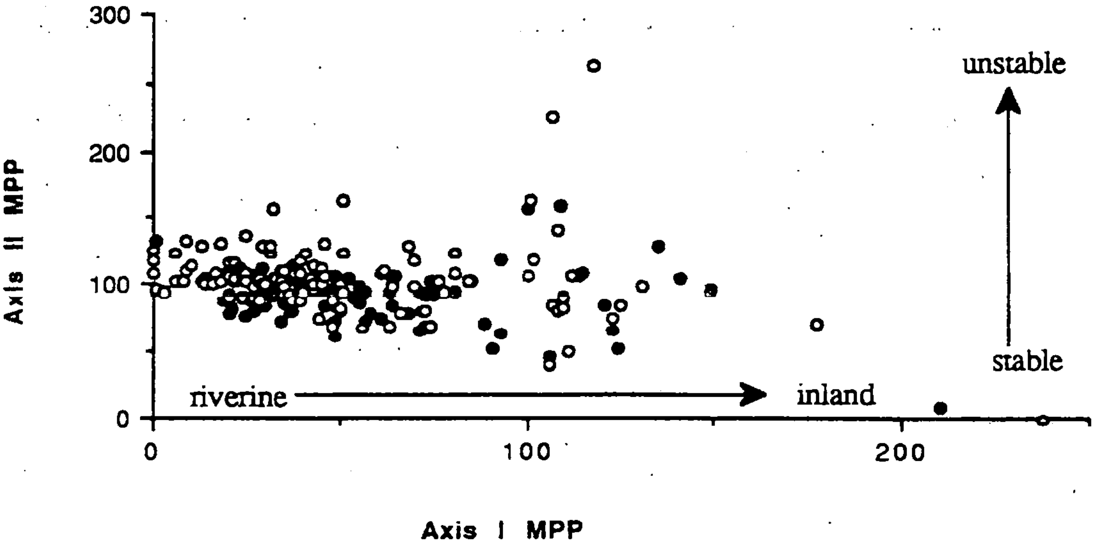


Fig. 5.2: Ordination of the micro-habitat plots within (•) (n = 84) and without (o) (n = 113) calling clusters.

Fig. 5.2 shows the distribution of micro-habitat plots on the ordination according to whether they were inside or outside calling clusters. Most interestingly, the plots within the calling cluster had significantly higher scores on axis I and significantly lower scores on axis II (Table 5.4).

Axis	p	Higher mean rank
Axis I	**	cluster
Axis II	***	non-cluster

Table 5.4: Comparison of DECORANA axis scores between micro-habitat plots within calling clusters (n = 84) and those plots outside calling clusters (n = 113). (Mann-Whitney U test; ** = $p< 0.01$, *** = $p< 0.001$).

This suggests that calling clusters were sited in areas where micro-habitats were drier and more stable. The siting of calling clusters was more determined by habitat variables reflected in Axis II than Axis I.

5.3.5 Within calling clusters, are display scrapes sited in particular microhabitats?

Of the 84 micro-habitat plots within calling clusters, 15 were on display scrapes and 69 elsewhere in the forest. There were significantly fewer trees over 160cm and woody and herbaceous stems (all measures) at sites where scrapes are maintained compared to random sites within the calling clusters (Table 5.5). In addition, there were more palms and more taller termite mounds, tree falls were further away and the lowest object over the centre of the plot was much higher than in other plots (Table 5.5).

Both of the DECORANA axes provide gradients that are meaningful in terms of display scrape siting (Fig. 5.3).

Variable	P	Higher mean rank
Treeten	N.S.	------
Treetwt	N.S.	------
Treefor	N.S.	------
Treeeig	N.S.	------
Treeone	N.S.	------
Treebig	**	random
Wstemsm	***	random
Wstemmd	***	random
Wstemlg	***	random
Hstemsm	*	random
Hstemmd	**	random
Hstemlg	**	random
Tllherb	N.S.	------
Pandans	N.S.	------
Palmnos	*	scrapes
Palmspp	N.S.	------
Falldst	*	scrapes
Fallstg	N.S.	------
Termnos	*	scrapes
Termdst	N.S.	------
Termcrc	N.S.	------
Termhgt	***	scrapes
Ovhdobj	**	scrapes

Table 5.5: Comparison of habitat variables at display scrapes (n = 15) and at random (n = 69) micro-habitat plots within calling clusters. (Mann-Whitney U test; * = p< 0.05, ** = p< 0.01, *** = p< 0.001 and N.S. = non-significant).

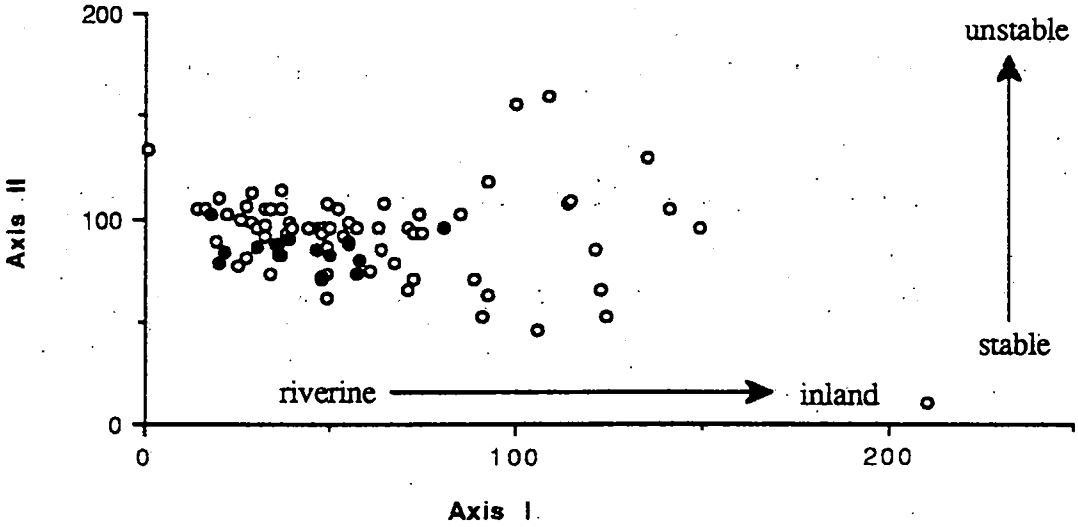


Fig. 5.3: Ordination of micro-habitat plots at scrapes (•) (n = 15) and elsewhere (o) (n = 69) within calling clusters.

The micro-habitat plots where scrapes were sited are distributed significantly lower on both axes (Table 5.6), indicating use of the more stable areas that were wetter within the calling clusters.

Axis	**P**	**Higher mean rank**
Axis I	*	random
Axis II	**	random

Table 5.6: Comparison of DECORANA axis scores between micro-habitat plots at display scrapes (n = 15) and random plots (n = 69) within calling clusters. (Mann-Whitney U test; * = $p < 0.05$, ** = $p < 0.01$)

As with the micro-habitats within calling clusters, it is axis II that appears to be a better predictor of the siting of scrapes than axis I.

5.4 Discussion

This chapter has three main findings: i) two gradients explained much of the variation observed in forest structure. these were riverine → inland and stable → unstable;

ii) outside periods of calling, two radio-tagged females did not define their range cores on the basis of micro-habitat structure, whereas the core areas of the three males did contain particular micro-habitats. Two males preferentially used plots that were wetter (*i.e.* around swamps) and the third using more disturbed areas rather than the stable areas within its home range;

iii) within calling periods, particular micro-habitats were used for two male reproductive activities, namely, calling and the maintenance of display scrapes. Calling clusters were sited in the inland and more stable areas of the study site, but within these calling clusters, display scrapes were sited in the wetter, stable areas.

These results do suggest that male display dispersion is at least partly determined by ecological factors. There are two possible reasons why males use particular micro-habitats. These are:

i) these micro-habitats contain better resources (*e.g.* food, nesting cover), which may be absent from the other micro-habitats. Smith and Shugart (1987) found a strong relationship between habitat structure, prey abundance and territory size in the ovenbird in temperate woodland. This monogamous passerine (a bunting) feeds by stalking invertebrates on the forest-floor but does not pick over the leaf litter, which the Malaysian peacock pheasant is known to do. Habitat structure accounted for 73% of the variation in prey abundance between ovenbird territories. The dynamics of invertebrate populations in tropical forests, however, are probably very much more complicated (section 9.4.2);

ii) the calls of the males require particular acoustic conditions, which are satisfied within these micro-habitats, but not in others. Two other studies are of relevance here - both from New Guinea rain forest. Pruett-Jones (1985) believed that sites where male Lawes' parotia (a lek-breeding bird of paradise) cleared display courts were closer to ridge lines in his hilly study site. He suggested that close to these ridges vocal ranges of the males were larger than if they were lower down because of the elevation and reduced noise interference from streams in the valleys. In addition, although such courts were in sites structurally different from other sites in the available habitat, they were not limiting. Pruett-Jones and Pruett-Jones (1982) also found that display sites were not evenly distributed within available habitat for Macgregor's bowerbird. Although males were evenly distributed throughout available habitat, the bowers were in areas with greater canopy closure and sapling density along wider and more level ridges.

My study site is flat and therefore use of display sites according to the transmission characteristics of the habitat is less obvious to a human observer. Pruett-Jones and Pruett-Jones (1982) suggest that dispersion in many promiscuous (*i.e.* non-monogamous in this case) species may be explained by males responding to female movements according to habitat availability.

CHAPTER 6: MORPHOLOGICAL VARIATION I: INTRA-SPECIFIC VARIATION

6.1 Introduction

In this chapter and the next, I explore two aspects of morphological variation. Firstly, in this chapter, I shall investigate variation in morphometric features (spur number, tarsus length, wing length *etc.*) within *Polyplectron malacense* and then, in the next chapter, I shall describe the variation in morphology (including plumage patterns) across the genus. In both of these aspects, I will use the distinction used by Cracraft (*e.g.* 1982; 1983) for his speciation analyses, between pattern and process; thus I use *pattern* to mean the distribution of phenotypic similarities and differences among individuals or taxa which may have been brought about by various *processes*. My objective in both intra- and interspecific exercises is to explore the patterns of variation and to propose hypotheses of process.

6.1.1 Intraspecific variation

The proposal that *Polyplectron* species in Malaysian forest show high levels of genetic polymorphisms that are phenotypically expressed (Davison, 1986b) is based on two studies of museum skins (Davison, 1985a; 1986a). Few polymorphisms have been reported from avian populations and in only a few studies have the ecological, behavioural, biochemical or genetic basis of a polymorphism been worked out (Parkin, 1980).

In the first of his papers, Davison (1985a) reports that spur number is highly variable and is related to size (measured as wing and tail length) in *Polyplectron*. In the second paper he suggests that the frequency of variations in rectrix (tail feather) number is most plausibly explained as being the result of genetic polymorphism (Davison, 1986a). Indeed, these results lead Davison (1986b) to suggest that there is a network of poorly related variations in wing length, tail length and spur number that are likely to be the result of weak gene linkage. Within a single peacock pheasant species, however, there is no clear picture of variation in the morphological traits measured.

Because Davison (1986b) suggests that "field studies of *Polyplectron* thus hold prospects of separating out the individual variations in reproductive success into their intra-sexual and inter-sexual components", I wish to investigate these morphological traits within the Malaysian peacock pheasant. In particular it is important to assess the amount of variation within particular traits and to test for correlations between them.

As Alatalo *et al.* (1988) report, very little attention has been paid to male ornaments themselves in tests of sexual selection. Studies of museum specimens provide valuable quantification of the variation in these ornaments, despite some limitations (Barnard, 1991) and provide a more complete background to understanding their evolution. That is, a clear picture of the *pattern* will permit proposal of hypotheses about the *process(es)* (*sensu* Cracraft, 1982).

6.1.2 Morphological description of *P. malacense*

Delacour (1977) and Johnsgard (1986) provide detailed plumage descriptions of the adult male and female. The species is markedly dimorphic, with males possessing a crest, spurs (3 - 6, but usually 4 per individual) and ocelli on the mantle, wing coverts and tertiaries. Both sexes have ocelli on the tail feathers. Delacour (1977) and Johnsgard (1986) reported that males have 11 pairs of rectrices, but Davison (1986a) reported that males have 9 or 10 pairs of rectrices and that females have 8 pairs. The male has a light buffy-coloured band down the middle of the breast.

In describing morphological variation within the Malaysian peacock pheasant, I address the following questions;

a) how variable are morphometric traits that may be subject to sexual selection compared with other traits? Traits that males possess and females lack, or traits that differ between the two sexes, are presumably the result of differences in selection pressures between the sexes. Such traits are often assumed, perhaps wrongly (Selander, 1972; pp. 181-182) to be subject to sexual selection, resulting either from male-male competition or female choice or a combination of these two processes. Hence, from the above plumage description of *P. malacense*, it might be proposed that the crest, spurs and upper-part plumage are (or have been) under sexual selection, as might the number of tail feathers. Examination of the display posture of the male supports this proposal for plumage features (see Davison, 1983b for drawings of various postures). In this posture, the crest is drawn forward so that its tip extends beyond the tip of the bill and the body feathers are ruffled and do not lie close to the body so that the male appears larger and the pale breast band becomes much more distinct. In the culminating display posture, the male adopts a lateral pose, lowers the wing nearest to the female and raises the distal wing such that the wings appear spread. The tail feathers are also spread laterally. When spread, the ocelli on the mantle, wing coverts, tertiaries and tail become much more apparent and form an arc of ocelli. When considering male-male combat, it is easy to perceive that differences in spur number and length and body size may influence competitive ability (see below) and hence that selection is likely to act upon these traits.

b) are measured traits positively allometric? Petrie (1992) reports that secondary sexual characters in a range of species are positively allometric *i.e.* larger individuals have relatively larger morphological characters. She also suggests that, theoretically, the function of the trait should influence the allometric slope. Hence, the relationship between body size and competitive ability may explain positive allometry in intra-sexually selected traits, but the relationship between body size and traits involved in mate attraction is less well known. Green (1992) argues that positive allometry may occur in traits used in mate choice and therefore, that its presence alone is not evidence that a trait displays competitive ability.

c) is there any evidence of correlations among these traits? Davison (1985a) provides Spearman rank correlations for several pairs of morphological traits in several *Polyplectron* taxa. Within *P. malacense* there is little in his data to suggest a network of poorly correlated traits. I re-examine this idea using a larger sample of individuals and more morphological traits, detailed below.

6.1.3 Fluctuating asymmetry

Møller (1990) found a positive correlation between ornament size (tail length) and symmetry in male swallows *Hirundo rustica*: *i.e.* long tails are more symmetrical than short tails. This led him to propose that symmetry of bilaterally symmetrical ornaments may be a reliable indicator of male quailty because symmetry in large ornaments indicates that males can pay the cost of producing a costly ornament. Although calculated slightly differently to Møller, Manning and Hartley (1991) have also shown that there is a similar relationship between the number of ocelli on the train of a peacock and their symmetry.

The epigamic display repertoire of the male Malaysian peacock pheasant is not known to include a bilaterally symmetrical posture. Therefore, it is not easy to envisage that fluctuating asymmetry has been an important mechanism by which selection through female choice has operated on any male ornaments. There is some controversy over the function of the spurs in pheasants (see Section 1.3) and it might be possible for females to assess spur length (see Frontispiece photograph). As noted in Section 6.3.3, if a male has one long spur he is likely to have all long spurs. Therefore, if spurs are subject to selection by female choice and Møller's hypothesis is correct, spur length should exhibit fluctuating asymmetry.

6.2 Materials and methods

6.2.1 Specimens

Alatalo *et al.* (1988) used museum specimens to assess the amount of variation in ornament size in seven species of long-tailed passerine. Barnard (1991) shows that the coefficients of variation derived from measurements of live birds in the field were larger then those obtained from museum specimens in *Vidua macroura*, a brood-parasitic whydah. Although this suggests that studies of museum specimens may provide an incomplete picture of the pattern of variation in sexually-selected characters, I felt that the use of museum specimens was justified for three reasons. First, there are few data on the variation in sexually selected traits in pheasants and none for the Malaysian peacock pheasant. Second, there is no possibility of collecting a large set of morphological data from one population of wild Malaysian peacock pheasants at one time (*c.f.* Barnard, 1991). Third, museums are a superb resource for studies of variation and provide an ideal opportunity for initial investigations of pattern.

Specimens from a variety of sources were measured: British Museum (Natural History), Sub-dept. of Ornithology (23 males; 7 females); Zoological Reference Collection, National University of Singapore (10 males; 4 females); Cambridge University Museum of Zoology (5 males; 1 female); Reference Collection, Universiti Malaya (3 males) and Reference Collection, Department of Wildlife and National Parks of Peninsular Malaysia (4 males). Live birds in the breeding collection of the Department of Wildlife and National Parks of Peninsular Malaysia (5 males), Zoo Negara, Kuala Lumpur (5 males) and 2 males trapped at Kuala Lompat in 1988 were also measured.

Variables measured largely follow Davison (1985a and 1986a) with two differences. First, I made no attempt to measure the area of ocelli on the tail and wings because I felt that the edges of ocelli are often too indistinct to allow reliable measurement of diameter. Secondly, I did, however, measure bill length and crest length. Thus, I measured traits that are either related to body size or that have been suggested as sexual ornaments or intrasexual weapons. The full list, plus measurement details is given in Table 6.1.

Trait	Measurement details
Upper left spur	Length of upper spur on the left leg (in mm.)
Upper left spur 2	Length of middle spur (if present) on the left leg (in mm.)
Lower left spur	Length of lower spur on the left leg (in mm.)
Upper right spur	Length of upper spur on the right leg (in mm.)
Upper right spur 2	Length of middle spur (if present) on the right leg (in mm.)
Lower left spur	Length of lower spur on the left leg (in mm.)
Number of spurs	Total number of spurs (both legs) (in mm.)
Tarsus length	
Bill length	Length from tip of bill to culmen (in mm.)
Crest length	Length from base to tip of longest feather in the crest (in mm.)
Wing length	Length of chord from carpal joint to tip of longest primary (in mm.)
Tail length	Length of central tail feather from point of insertion to tip (in mm.)
Number of tail feathers	Number of tail feathers, taking care to include positions of missing feathers (moult *etc.*)

Table 6.1 Morphometric traits measured with measurement details.

6.2 Analyses

To analyse the pattern of morphological variation within the species, I used coefficient of variation, correlation matrices and principal components analysis. Coefficient of variation (mean/standard deviation, expressed as a percentage) provides a standard measure of the variability of each trait. The influence of body size on each of the measured traits was then investigated to see how much of the observed variation is explained by variation in body size. For traits that may be subject to sexual selection, it is also important to assess whether body size is related to ornament and/or weapon size. Freeman and Jackson (1990) suggest that univariate metrics are often not a particularly good measure of body size, but if such a measure is required, tarsus length or mass are the best estimates. I chose tarsus length as an estimate of body size for two reasons. Firstly, weight data were not available for the museum specimens and, secondly, tarsus length shows a higher correlation with weight than wing, tail or spur length in male ring-necked pheasants (Wittzell, 1991), the most closely related species for which there are data. Tarsus length also shows less variation with season than wing or tail length (Petrie, pers. comm.). To explore the relationship between tarsus length and each of the measured traits, there does not appear to be an ideal regression technique. I used simple regression because it is the most widely used regression technique, although it consistently undervalues the true value of the slope (Harvey and Pagel, 1991). All measurements were logarithmically transformed before conducting the regressions so that the rate of change in x could be related to the rate of change in y. The slope of the line of this equation is a measure of the differential changes in y given x.

To test Davison's polymorphism hypothesis, a correlation matrix of measured traits was constructed for each sample. To assess the possibility of traits forming a weakly correlated network among males in adult plumage, principal components analysis was then used to describe the relationships between the morphological traits in the adult-plumaged male sample only. As mentioned in Chapter 5, ordination methods, such as principal components analysis, arrange the samples in relation to axes that may correspond to biological gradients. Here, the 11 traits measured form an 11-dimensional space. Principal components can be drawn through this 11-dimensional space, such that each new axis explains most of the remaining variance. This permits a direct visual examination of the relative positions of the 11 morphological traits.

Fluctuating asymmetry

Møller (1990) and Manning and Hartley (1991) use different formulae to calculate the symmetry of the character. Møller (1990) defines symmetry as the numerical difference of [Left - Right/(Left + Right/2)], whereas Manning and Hartley (1991) simply use the formula [Largest number- Smallest number] to indicate symmetry. I adopted Møller's original method.

6.3 Results

6.3.1 Variation in individual traits

Table 6.2 gives the mean, range and coefficient of variation for all measured traits, except for the length of any fifth or six spurs. These have been omitted because most individuals posessed two spurs per leg and a third (on either the left or right leg) was found on only 10 out of 57 birds and only one of these had a sixth spur. Therefore, these spurs were omitted from Table 6.2 because the sample sizes were too small.

Variable	N	mean	range	c.v.(%)
Upper left	56	8.4	0-18	56.9
Lower left	56	8.6	0-16	58.3
Upper right	55	9.4	0-16	48.3
Lower right	56	9.9	0-15.5	44.4
No. spurs	57	3.9	0-6	24.3
Tarsus	52	78.6	60-87	6.63
Bill	40	22.7	19-26	8.5
Crest	51	34.8	0-54	38.0
Wing	56	203.7	171-233	5.5
Tail	53	219.4	121-263	14.2
No. tail feathers	53	19.3	14-24	13.0

Table 6.2: Mean, range and coefficient of variation of morphological variables for all males measured.

Considering all males measured, the highest coefficients of variation are found in the lengths of each of the four spurs and the crest length (Table 6.2). The number of spurs and tail feathers and the length of the tail have moderately high coefficients of variation and the lowest values are obtained for tarsus, bill and wing lengths. Because a high proportion of the specimens measured were not in fully adult plumage, the total sample of measured males was subdivided to see whether these patterns of variation are found in juvenile and adult-plumaged birds separately (Tables 6.3 and 6.4). I discarded two birds in juvenile plumage at this point as they had no spurs and I considered that the other measurements indicated that they were too young to possess spurs. Thus the juvenile sample presented in Table 6.3 contains only individuals that are old enough for spurs to have erupted.

Variable	N	mean	range	c.v.(%)
Upper left	20	6.2	0.5-13	64.2
Lower left	20	6.2	0.5-16	77.5
Upper right	19	6.6	0-15	72.2
Lower right	20	7.5	0-15	62.2
No. spurs	21	4.0	2-5	13.7
Tarsus	18	76.6	60-86	9.0
Bill	16	21.9	19-25	8.1
Crest	20	27.5	0-40	39.6
Wing	21	199.4	172-219	5.7
Tail	20	202.2	153-238	11.64
No. tail feathers	21	19.2	14-24	13.14

Table 6.3: Mean, range and coefficient of variation of morphological variables for measured males which were in juvenile plumage and had spurs at least erupting.

In the juvenile sample (Table 6.3), all skeletal measurements (spur, tarsus and bill lengths) have smaller means and, except for bill length, are more variable than in the total sample. In addition, the mean wing, crest and tail lengths are all smaller, but coefficients of variation are similar to the total sample. Numbers of spurs and tail feathers have similar means and coefficients of variation between the two samples.

Males in adult plumage have larger skeletal traits that are less variable than both the total and juvenile sample (Table 6.4). Mean crest, wing and tail lengths are also larger and less variable than both the total and juvenile sample. As with the juvenile sample, the mean numbers of spurs and tail feathers are similar to the total sample and have reasonably similar coefficients of variation.

Variable	N	mean	range	c.v.(%)
Upper left	34	10.2	0-18	42.0
Lower left	34	10.6	0-16	38.9
Upper right	34	11.5	3.5-16	22.7
Lower right	34	11.8	3-15.5	20.9
No. spurs	34	4.1	3-6	15.2
Tarsus	32	80.1	75-87	4.2
Bill	24	23.3	20-26	8.0
Crest	29	42.2	18-54	16.7
Wing	33	207.8	194-233	3.8
Tail	31	236.6	191-263	6.3
No. tail feathers	30	19.6	14-24	13.8

Table 6.4: Mean, range and coefficient of variation of morphological variables for measured adult-plumaged males only.

Some of these differences between samples are not surprising and probably simply reflect the fact the fact that juvenile birds are still growing relatively quickly, and are, therefore, much more variable than adult-plumaged birds. However, it may also suggest that there are many birds that are as large as adult-plumaged and that, therefore, there is delayed plumage maturation in males. This would support a previous conclusion by Davison (1985a) who found a very high (40%) percentage of juvenile-plumaged birds in the museum collections that he inspected.

Fewer adult females were measured than adult males and these individuals did not possess all of the traits that the males exhibited. One female had a single spur on the left leg, but in general females do not possess spurs and never have crests. Apart from the number of tail feathers, the adult females had larger coefficients of variation than adult males for all traits; tarsus, bill, wing and tail.

Variable	N	mean	range	c.v.(%)
Tarsus	12	66.8	62-73	5.1
Bill	10	21.1	19-25	10.1
Wing	14	184.2	172-199	4.3
Tail	12	162.9	139-184	8.7
No.Tail feathers	12	19.5	16-22	8.9

Table 6.5: Mean, range and coefficient of variation of morphological variables for measured females only.

6.3.2 Relationship between traits and body size (tarsus length)

Simple regression of each trait on tarsus length indicates that the relationship with body size accounts for only a small variation in any of the traits (Table 6.10 and Fig. 6.1 a-j).

Trait	Slope	R^2
Upper left	-0.31525	0.001
Lower left	0.25036	0.002
Upper right	-0.18611	0.001
Lower right	0.38352	0.003
No. Spurs	0.24821	0.005
Bill	-0.31249	0.029
Crest	1.1666	0.055
Wing	0.19363	0.050
Tail	0.19917	0.017
No. Tail feathers	0.82373	0.068

Table 6.6: Regression slope and R^2 (proportion of variation explained) for the relationship between tarsus length and each of the morphological traits measured. All measurements were log-transformed.

If the slope of a regression has a gradient of one, the dependant variable is increasing at the same rate as tarsus length. As Table 6.6 shows, none of the traits measured here give a regression slope of one and therefore the rate of increase of each of the traits differs from the rate of increase of tarsus length. The only trait that increases in size at a greater rate than tarsus length is crest length. The spurs in the two lower positions (lower left and lower right), number of spurs, wing length, tail length and number of tail feathers increase at a slower rate than tarsus length. The two upper spurs and bill length actually get smaller with increasing tarsus length.

6.3.3 Correlated traits

Correlation matrices

The sample of all measured males suggests that many traits are correlated with each other (Table 6.7). The lengths of all spurs appear highly correlated with each other, suggesting that, if a male has one long spur all his spurs are long and if one short spur, all are short. Crest length is correlated with every other trait except for number of tail feathers; wing and tail length are each correlated with all traits except bill length and number of tail feathers. Many of these correlations may simply be the result of traits becoming longer as birds grow.

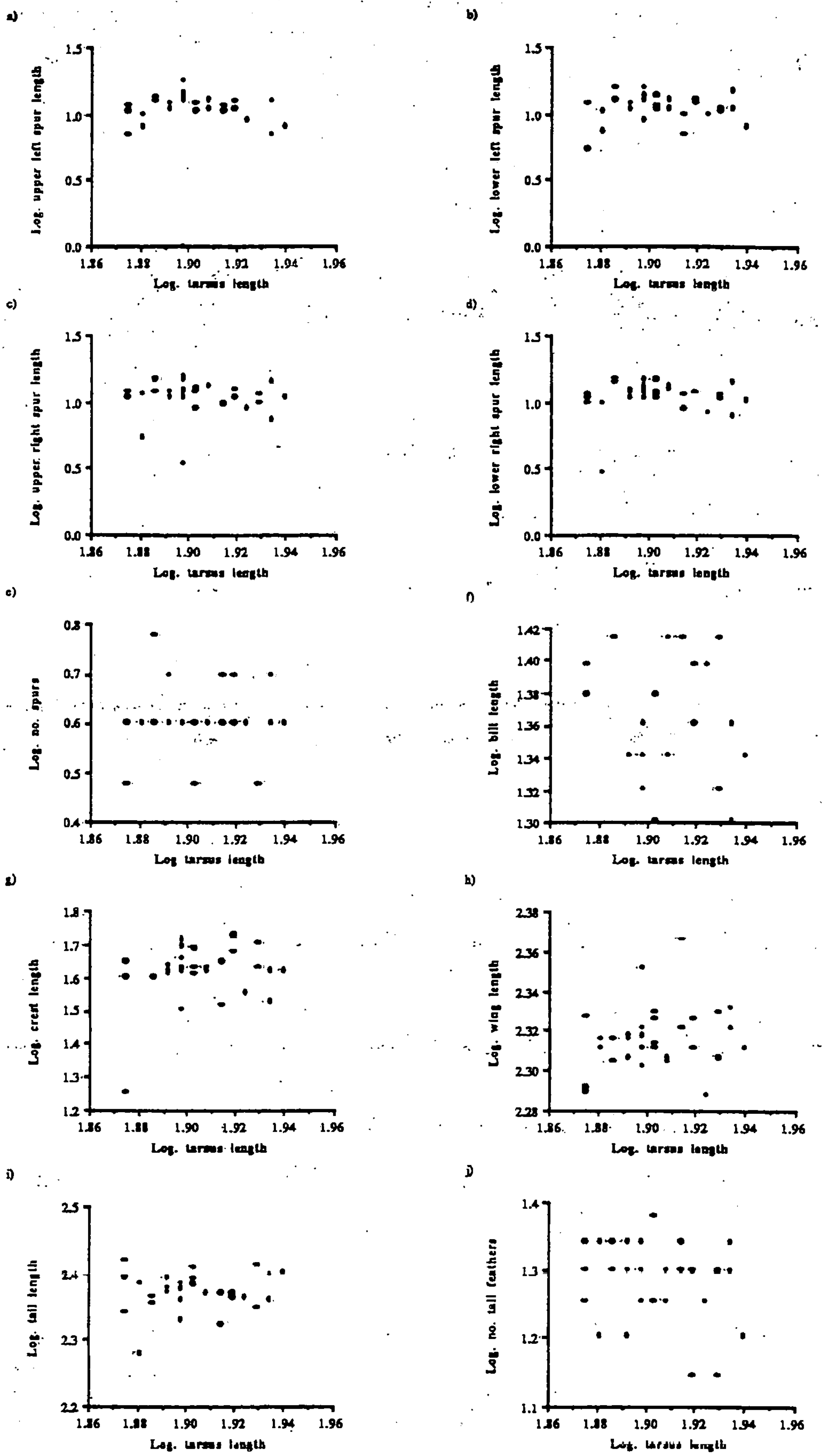


Fig. 6.1: Log. - log. regression of each morphological character on tarsus length (an indicator of body size - see text). The slope and R^2 of each regression is given in Table 6.2.

Therefore, correlations between the traits were also examined within each of the two subsamples, juvenile- and adult-plumaged birds (Tables 6.8 and 6.9).

Many significant correlations among the traits disappeared when the juvenile-plumaged birds only were considered (Table 6.8). The correlations among spur lengths were, however, still very high and tail length was correlated with all traits except bill length. The length of the tarsus, crest, wing and tail are all correlated with each other except for crest *vs.* wing.

In the adult-plumaged males there are also many fewer significant correlations than in the total sample (Table 6.9). The lengths of the spurs are still very highly correlated with each other, but there is no other clear pattern of correlated variables. The number of tail feathers is significantly correlated with the length of both the upper left and lower right spurs, but not with the length of the other two spurs.

The female sample shows few correlations between traits (Fig. 6.10). Tarsus and wing lengths are significantly correlated with each other as are tail length *vs.* number of tail feathers.

Principal components analysis

As there are several significant correlations in the adult-plumaged male sample, principal components analysis was used to compare the positions of the traits in two dimensional space (*i.e.* on a graph). Table 6.11 gives the eigen values for each of the first three components and indicates how much of the variation in the adult male data matrix is explained by each of these components. In addition the component loadings are given, which describe the loading of each trait on each component.

The first principal component explains only 23.7% of the total variance and four components are required to explain 68.0% of the total variance. These values are low and suggest that there is no strong relationship between the morphological traits in this sample.

	Upper left	Lower left	Upper right	Lower right	No. Spurs	Tarsus	Bill	Crest	Wing	Tail
Lower left _56_	0.631***									
Upper right _55_	0.770***	0.712**								
Lower right _56_	0.795***	0.763***	0.847*** _55_							
No. Spurs _56_	0.348**	0.270	0.154 _55_	0.223*						
Tarsus _52_	0.131	0.369	0.225	0.289*	0.079					
Bill _39_	0.158	0.161	0.125 _38_	0.181	-0.144 _49_	0.087 _36_				
Crest _50_	0.424**	0.574***	0.533*** _49_	0.632***	0.250* _51_	0.429** _47_	0.319* _40_			
Wing _55_	0.3279**	0.416**	0.397** _54_	0.395**	0.253*	0.545*** _52_	-0.052 _40_	0.338**		
Tail _52_	0.438**	0.482**	0.613*** _51_	0.554**	0.166* _53_	0.398** _49_	0.311 _39_	0.697*** _49_	0.530*** _53_	
No. T. fthrs. _52_	0.230	0.100	0.266* _51_	0.164	0.116 _53_	0.053 _49_	0.194 _39_	0.205 _49_	0.190 _53_	0.360*

Table 6.7: Spearman rank correlation matrix for all male birds measured. Sample sizes in italics in left hand column are for all correlations in that row unless otherwise noted in the matrix.* = p<0.05, ** = p<0.01, *** = p<0.001.

	Upper left	Lower left	Upper right	Lower right	No. Spurs	Tarsus	Bill	Crest	Wing	Tail
Lower left _20_	0.859***									
Upper right _20_	0.860***	0.701** _19_								
Lower right _20_	0.899***	0.822***	0.844*** _19_							
No. Spurs _20_	0.127	0.150	0.213 _19_	0.196						
Tarsus _18_	0.401	0.363	0.381	0.401	-0.012					
Bill _19_	-0.151	0.437	-0.125	0.015	0.230 _20_	0.148 _17_				
Crest _20_	0.155	0.331	0.294 _19_	0.298	0.384 _21_	0.449* _18_	0.620**			
Wing _20_	0.322	0.277	0.364 _19_	0.298	0.054 _21_	0.806*** _18_	-0.205	0.008 _21_		
Tail _19_	0.477*	0.549*	0.587** _18_	0.538*	0.381* 20	0.634** _17_	0.258	0.605**	0.618** _20_	
No. T. fthrs. _20_	-0.209	-0.120	0.104 _19_	-0.273	0.035 _21_	0.252 _18_	0.19	0.423*	0.253	0.520*

Table 6.8: Spearman rank correlation matrix for male birds in juvenile plumage and with spurs at least erupting. Sample sizes in italics in left hand column are for all correlations in that row unless otherwise noted in the matrix.* = p<0.05, ** = p<0.01, *** = p<0.001.

	Upper left	Lower left	Upper right	Lower right	No. Spurs	Tarsus	Bill	Crest	Wing	Tail
Lower left *34*	0.565***									
Upper right *34*	0.670***	0.680***								
Lower right *34*	0.754***	0.670***	0.767***							
No. Spurs *34*	0.236	0.216	-0.008	0.141						
Tarsus *32*	-0.216	0.085	-0.133	-0.072	-0.050					
Bill *24*	-0.031	-0.081	-0.063	-0.082	-0.310	-0.133 *23*				
Crest *29*	-0.049	0.362*	0.069	0.289	0.052	0.130	0.030 *24*			
Wing *33*	0.010	0.113	-0.043	0.018	0.227	0.229	-0.091	-0.061		
Tail *31*	-0.169	-0.010	0.164	-0.023	-0.177	0.016	0.051	0.105 *28*	0.196	
No. T. fthrs. *30*	0.342*	0.125	0.268	0.326*	-0.003	-0.216	0.156 *23*	-0.020 *27*	-0.018	0.185

Table 6.9: Spearman rank correlation matrix for male birds in adult plumage. Sample sizes in italics in left hand column are for all correlations in that row unless otherwise noted in the matrix.* = p<0.05, ** = p<0.01, *** = p<0.001.

	Tarsus	Bill	Wing	Tail
Bill	0.145*8*			
Wing	0.761***12*	0.149*10*		
Tail	0.162*10*	-0.019*8*	0.304*12*	
No. T. fthrs.	0.221*10*	0.134*8*	0.236*12*	0.669**12*

Table 6.10: Spearman rank correlation matrix for female birds measured. Sample sizes in italics.* = p<0.05, ** = p<0.01.

Trait	Component			
	I	II	III	IV
Upper left	-0.838	-0.100	-0.361	0.123
Lower left	-0.247	0.740	0.029	0.016
Upper right	-0.784	0.177	0.017	-0.262
Lower right	-0.827	0.222	0.131	-0.205
No. Spurs	-0.135	0.311	-0.628	0.527
Bill	-0.075	-0.309	0.666	0.125
Tarsus	0.472	0.624	-0.039	-0.077
Crest	-0.081	0.578	0.217	-0.458
Wing	0.109	0.509	0.172	0.626
Tail	-0.073	0.328	0.633	0.299
No. Tail Feathers	-0.528	-0.306	0.274	0.447
EIGENVALUES	2.609	2.014	1.541	1.316
% OF TOTAL VARIANCE	23.7	18.3	14.0	12.0
CUMULATIVE % VARIANCE EXPLAINED	23.7	42.0	56.0	68.0

Table 6.11: Component loadings and explained variance of morphological traits of adult males on the first four components.

The lengths of three of the spurs and the number of tail feathers have high negative loadings on the first component, whereas the lower left spur, tarsus, crest and wing all have high positive loadings on the second component. Visual inspection of these two components suggests that there may be two clusters of related traits.

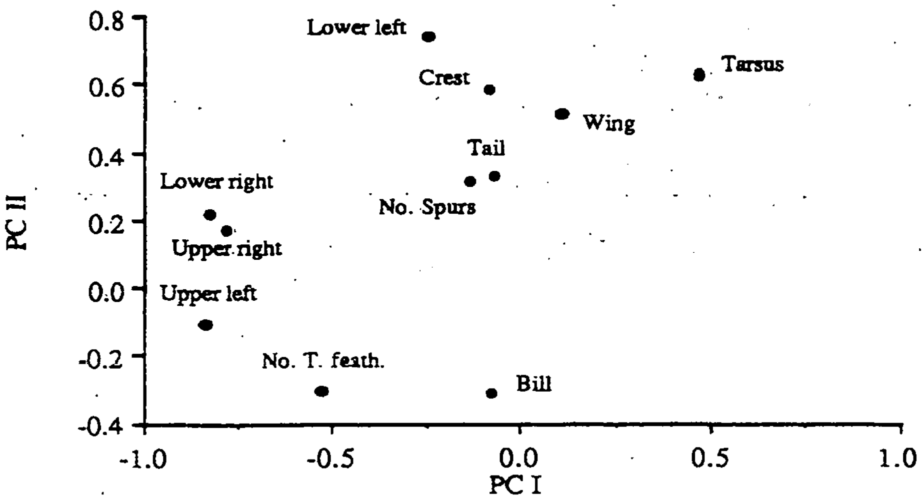


Fig. 6.2: Component loadings of adult male morphological traits on the first two principal components.

At the lower end of both axes one cluster includes the length of three of the spurs and the number of tail feathers (Fig. 6.1). Higher on both axes there is a second cluster containing the lower left spur, crest, tail, wing, number of spurs and tarsus. These two clusters do not describe relationships among the measured traits that can be interpreted easily in terms of biological patterns.

6.3.4 Fluctuating asymmetry

The correlation between total spur length (*i.e.* the lengths of all spurs added together) and symmetry between left and right legs in shown in Fig. 6.3). Symmetry in spur length is correlated with total spur length ($r_S = 0.397$, $N = 34$, $p = 0.05$). Spurs one one side were not consistently longer than spurs on the other side: spurs on the left leg were longer than spurs on the right in 9 males, shorter in 23 and the same in 2.

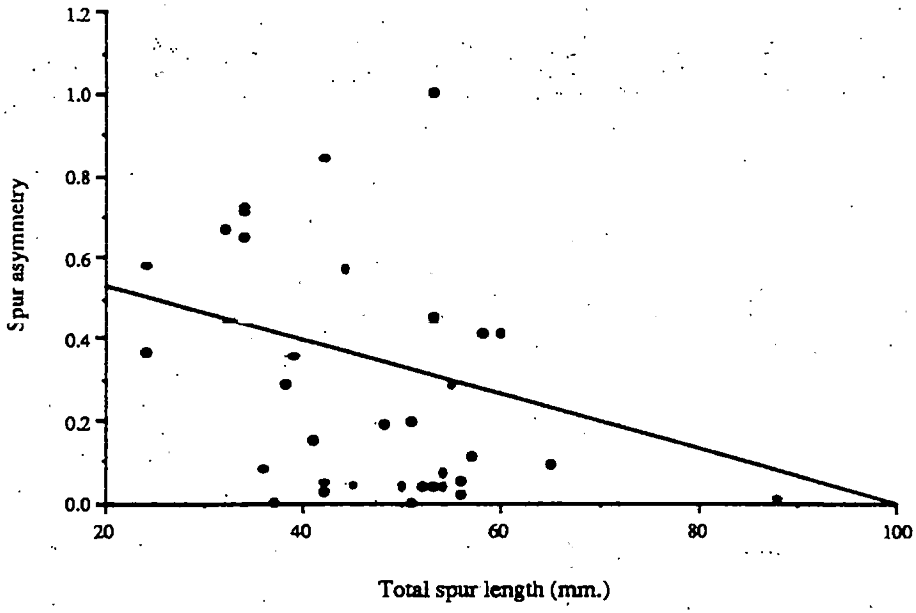


Fig. 6.3: The relationship between fluctuating asymmetry and spur length (numerical difference in length of spurs on left leg and the length of spurs on the right leg (mm) in male Malaysian peacock pheasants and the total length of all spurs (mm)). The linear regression equation is spur asymmetry (mm) = 0.707 - 0.009spur length (mm) ($F = 6.004$, d.f = 1, 32, $p = 0.02$).

6.4 Discussion

6.4.1 Variation in traits

The very large amount of variation within traits among males in juvenile plumage may be due to two factors. First, it may simply be the result of including juveniles of a wide range of ages, and birds with spurs just erupting being much smaller than those in partly adult plumage. Second, and much more interesting, is the possibility that juveniles are naturally very variable and that this variation provides the basis for variation in adults, as suggested for amphibians (Halliday and Verrell, 1988). Unfortunately, comparison of the coefficients of variation found in juveniles (Table 6.3) with those found in adults (Table 6.4) are not very revealing, as some traits seem to become more variable in adulthood and others less so. It is interesting to note that the coefficients of variation of bill length and number of tail feathers are almost identical in both samples. Perhaps this suggests that these two traits grow most rapidly and that all the variation across the males is evident very early in life.

Several traits show considerable variation among males which are in fully adult plumage. Alatalo *et al.* (1988) suggest that sexually-selected elongated tail feathers in whydahs and flycatchers are extraordinarily variable, having coefficients of variation of 11%. This is three times more variable than other morphological measurements, which Alatalo *et al.* (1988) indicate are not ornamental and thus not under sexual selection. The variation detected in *P. malacense* is considerably higher, both in traits possibly under sexual selection and in those which are not. The most variable traits are the lengths of the four spurs that are commonly present and the number of spurs is also highly variable. Two traits that are exhibited during display also show much variation: the length of the crest, which is erected, and the number of tail feathers, which are spread laterally. All of these traits are absent in the female, except for the number of tail feathers, which is less variable in the latter. Interestingly, the other measured traits (tarsus, bill, wing and tail) are 13 - 40% more variable among females than males (Tables 6.5 and 6.6).

6.4.2 Comparison with other pheasants

Comparison with other pheasant species for which the coefficients of variation of morphological traits are known does not suggest that Malaysian peacock pheasants are systematically more variable in traits that are probably not sexually selected, such as wing, tarsus, tail and bill. The other traits included possibly do have some sexual function, but experimental evidence is not easy to obtain. As noted in the introduction, von Schantz *et al.* (1989) report that spur length in the ring-necked pheasant is subject to female choice. Zuk *et* *al.* (1990a&b) suggest that it is features around the eye of male red junglefowl upon which females base their choice, a finding not corroborated by Sullivan (1991). These studies have used different measures of female response, namely proximity to male by von Schantz *et al.* (1989), solicitation crouch or copulation by Zuk *et al.* (1990b) and rate of response to males' tidbits by Sullivan (1991). Consequently, these studies could be measuring different degrees of sexual preference and, as noted by Sullivan (1991), some idea of the paternity of chicks is essential before the success of males with particular traits can be assessed.

Morphological trait	**ring-necked pheasant**	**red junglefowl**		**Malaysian peacock pheasant**	
	male	female	male	female	male
Weight		28.1	10.6		
Wing	1.88	4.1	2.1	4.3	3.8
Tail		8.0	13.7	8.7	6.3
Tarsus		4.8	5.0	5.1	4.2
Bill		16.7	11.1	10.1	8.0
Upper left spur					42.0
Lower left spur	14.29		16.0		38.9
Upper right spur					22.7
Lower right spur			15.8		20.9
No. spurs					15.2
Comb length			6.8		
Comb height			20.4		
Wattle depth			18.2		
Crest					16.7
No. tail feathers				8.9	13.8

Table 6.12: Coefficients of variation for morphological traits of males in adult plumage in three pheasant species. Ring-necked pheasant data are from von Schantz *et al.* (1989) Table 3, red junglefowl data are from Sullivan (1991). Male ring-necked pheasants have one spur per leg and von Schantz *et al.* (1989) give a coefficient of variation for the mean spur length, and red junglefowl also have one spur per leg and coefficients of variation are given for each spur.

6.4.3 Comparison with other bird species

Coefficients of variation of ornament size in some long-tailed passerines are summarised by Barnard (1991). Although Barnard (1991) indicates that there are several methodological problems in making comparisons between coefficients of variation from different studies, two points are very striking. First, is the number of ornaments. The passerines mentioned are believed to have a single ornament, a long-tail. In contrast, it seems likely that Malaysian peacock pheasants possess several ornamental traits and certainly several measured here that are under one or other (or both) forms of sexual selection. Second, although the coefficients of variation of the ornamental tail length are considerably larger than other measured traits in the passerines, they are often considerably smaller than those recorded for sexually selected traits in this study.

6.4.4 What does variation mean?

Having established that there is considerable variation in some traits, the problem then arises of how to interpret such variation. If a trait is very variable is this because there is weak or no selection acting upon it and, therefore, the size of a trait is of little consequence or, conversely, because there is considerable pressure leading to such traits consistently becoming more extreme (*e.g.* longer spurs, more tail feathers)? In this study, the most variable traits are those that males possess but females do not (spurs and the crest). Therefore, if such traits are adaptive, it seems reasonable to assume that males possess them for a particular reason or that females lack them for a particular reason. Since a majority of species within the Phasianidae lack crests and multiple spurs, it is likely that it is the possession of these traits by the males that is important, rather than their absence in the females. The full length of the crest and the number of tail feathers, the other very variable trait, are usually only revealed during display to females (Davison, 1983a). Whilst few agonistic displays have been observed, Davison (1983a) observed two agonistic encounters in the wild and reports that male-male displays seem more concerned with exposing the buffy breast band and ruffling the body feathers, presumably to make the male appear large. Consequently, the length of the crest and the number of tail feathers seem likely to be subject to selection by female choice.

The number and lengths of the spurs are the most variable of all traits and are also absent in females. Davison (1985a&b and von Schantz *et al.* [1989]) suggest that spurs are under sexual selection in pheasants, but whether they are subject to selection through male-male competition or by female choice is controversial. The classic assumption has been that spurs are used by males during combat and this idea has been summarised most clearly by Davison (1985b). He suggested that visual inspection of spurs by females in Galliformes is unlikely because spurs are situated in an inconspicuous position, are inconspicuously coloured and no spur-revealing display is known. He thus assumed that spur number (he did not consider spur length) was an intra-sexually selected trait that is important in male-male fighting. von Schantz *et al*. (1989), however, contend that female ring-necked pheasants choose males on the basis of spur length. Females that mate with males with longer-spurs produce offspring with higher survival than do females who mate with shorter-spurred males. As mentioned in the Introduction (Section 1.3), however, this result remains controversial.

Møller (1990) argued that the degree of ornamentation should be positively correlated with symmetry in males of sexually dimorphic species. That the total spur length is positively correlated with symmetry in male Malaysian peacock pheasants suggests that spur length has an ornamental function. Although Davison (1985b) suggests that no spur-revealing displays are known among the Galliformes, it is possible that females are shown spurs during the erect movement (Table 7.4; Davison (1983b); see also frontispiece photograph). Hence females may be able to assess how symmetrical spur lengths are.

6.4.5 Allometric relationships

Only one male Malaysian peacock pheasant trait that I measured is positively allometric and that is crest length. Indeed, the regression slope of three traits actually have negative gradients indicating that larger individuals have relatively smaller traits. That there is no consistent pattern is surprising considering that these traits are all skeletal and two are spur lengths. Variation in any one of the traits measured explains no more than 6.8% of the variation in body length (here represented by tarsus length).

As indicated by Petrie (1992), the commonly found relationship between body size and competitive ability would be expected to result in traits used in combat showing positive allometry. Hence, if this relationship is universal and Davison's proposal of spur function is correct, spur length and number should show positive allometry. They do not and the two upper spurs are relatively smaller in males with larger tarsi. Other traits which may be thought to reflect body size and hence competitive ability (bill, wing and tail lengths) lack positive allometry. Petrie (1992) suggests that no such clear allometric relationship is predictable for traits that have evolved through female choice, unless there are size dependent costs. If these two proposals about the nature of the allometric relationship for intra- and inter-sexually selected traits are correct, the only trait measured here that may be under intra-sexual selection is crest length. Even this cannot be claimed with confidence, because it cannot be predicted that inter-sexual selection will *not* result in positive allometry. Indeed Green (1992) suggests that positive allometry may occur with competitive ability, mate choice and a variety of other reasons. Therefore, positive allometry *per se* is not a predictor of function. What is of interest, however, is that features of the spurs and wing length are not positively allometric and the absence of positive allometry may indicate absence of function. These traits, therefore, are not predicted to display competitive ability. Of course, should a particular trait have a role in both intra- and inter-sexual signalling, the relationship between character and body size would be, presumably, even less predictable. Indeed, Halliday (1990) has argued that the accepted distinction between intra-sexual and inter-sexual selection is theoretically illogical and practically unhelpful. A way forward is to consider all possible selection pressures, whether they are classically regarded as one of the forms of sexual selection or of natural selection, that may be acting, either singly, in concert or antagonistically, on a particular feature. Thus, in any given situation, there are costs and benefits associated with possession of morphological (and behavioural) features and it is the overall sum of these which will influence the form that the feature takes.

The lengths of the four spurs are highly correlated with one another and thus a male is likely to possess spurs of roughly equal length. Spur lengths are not correlated with tarsus length (representing body size) or, indeed, systematically with any other trait. Principal components analysis does not reveal any clear separation of traits into those suspected of having intra- and inter-sexual functions, a logical prediction of Davison's polymorphism hypothesis. Thus these data do not support Davison's hypothesis that there is a network of weakly related variations in wing length, tail length and spur number that are likely to be the result of weak gene linkage.

To summarise, this Chapter has presented the pattern of variation in some morphological traits in the Malaysian peacock pheasant. Traits predicted to be subject to sexual selection are much more variable than other traits. Of those traits that are predicted to be under sexual selection, allometric theory, such as it is, suggests that none are under purely intra-sexual selection, except possibly crest length. It has recently been proposed that morphological traits may have a dual sexual function *i.e.* they may fulfil both intra-and inter-sexual roles. This is likely to confound the problem of interpreting allometric relations in terms of sexual function considerably. This proposition implies that only a very few traits will have a single sexual role and thus have predictable allometry. There are few correlations among traits in adult males and principal components analysis reveals no clear separation of traits according to a single sexual function. These results suggest that the size of all the traits are unrelated (except for the lengths of the spurs that are present) and that selection pressure varies from trait to trait.

In the next chapter, I explore whether or not the evolution of some morphological traits mirrors the evolution of some epigamic display movements and hence whether these traits may be subject to sexual selection by female choice.

CHAPTER 7: MORPHOLOGICAL VARIATION II: INTER-SPECIFIC VARIATION

".... but it is to the birds that we must turn for gorgeous display, weird dances and extraordinary vocal efforts. The higher animals, curiously enough, are often brutal in their love-making." Ealand (1921: 154-155)

7.1 Introduction

The classification of the peacock pheasants is based largely on male morphology (see Beebe, 1922; Delacour, 1977; Johnsgard, 1986). Several of the characters used to classify species are likely to be under sexual selection (see Chapter 6). These include presence or absence of a crest, tail length, number of tail feathers and the distribution of ocelli on the upperparts. Johnsgard has used these characters, and the degree of sexual dimorphism to infer the mating system of some species and which species are 'primitive' members of the genus. All of these authors regard the Malaysian peacock pheasant as 'advanced' within the genus as it possesses a greater number of specialised male morphology and display characters.

Using secondary sexual characters to propose phylogenies has several theoretical problems (Halliday and Arano, 1991). Therefore, my first objective in this chapter is to describe the pattern of inter-specific variation in a wide variety of male morphological characters (secondary sexual and non-secondary sexual characters) and to propose a phylogenetic hypothesis based on external male morphology. I shall then determine whether these data support the hypothesis that the Malaysian peacock pheasant is advanced within the genus (*i.e.* possesses a greater number of derived [apomorphic in cladistic terms] characters).

Because this phylogenetic hypothesis is based on character-state changes, it will also be possible to construct a hypothesis of changes in characters involved in sexual selection. This can then be compared to a phylogenetic hypothesis constructed from male display data to determine the degree of congruence. Only some aspects of the male's morphology are likely to be important in displays to the female and in no other context. Similarly, only some elements of the display are likely to involve exhibiting particular morphological characters to the female.

My second objective in this chapter is to make an assessment of the correlation between these two sets of data. As stated by Halliday and Arano (1991), conspicuous secondary sexual characters are often associated with specific displays. Whilst in some studies this is a problem, here it is this association that I wish to explore and the comparative approach has proved invaluable in investigating adaptation (Clutton-Brock and Harvey, 1984). Comparison of phylogenetic trees generated from these reduced data sets of characters and display elements should indicate whether they are associated. Thus I shall:

i) construct a phylogeny based on all morphological characters;

ii) construct a phylogeny based on all display elements. I shall then assess the congruence of these two phylogenies;

iii) construct a phylogeny based on morphological characters which are exhibited during display;

iv) construct a phylogeny based on display elements which show off particular morphological characters. Thus I should be able to test the prediction that particular display movements have evolved in association with particular morphological characters and hence are subject to sexual selection through female choice. Thus, a clear picture of the *pattern* will permit proposal of hypotheses about the *process(es)* (*sensu* Eldredge and Cracraft, 1981; Cracraft, 1982).

In addition, a clear description of the variation in morphological characters across the genus should permit clarification of the confusion over the taxonomic status of the Bornean peacock pheasant. Delacour (1977) regarded this taxon as a subspecies of the Malaysian peacock pheasant - *Polyplectron malacense schleiermacheri* - unlike previous authors (Beebe, 1922; Ogilvie-Grant, 1897; Peters, 1934). Both he and Johnsgard (1986), who reverted to accepting the taxon as a species - *Polyplectron schleiermacheri* - give few reasons for their decision. Sibley and Monroe (1991) have recently accepted the specific status of the Bornean peacock pheasant and regard it and the Malaysian peacock pheasant as comprising a super-species: *i.e.* distinct allospecies that are more closely related than other members of the genus. Thus an assessment of the pattern of morphological variation across the genus should provide a clearer basis for the classification of these taxa.

7.2 Materials and Methods

7.2.1 Choice of morphological characters and assignment of character-states

Specimens from a variety of sources were examined (Table 7.1). Characters examined were chosen to give a general description of the male's plumage. They included the background colour of feathers of various body parts, as well as characters which may be sexually selected (*e.g.* presence of ocelli on various feathers). Because the coloration of the soft parts changes when the specimen is killed, the facial colour was taken from Johnsgard (1986). All characters were assigned a character-state (Table 7.2) before input into the numerical cladistic programme, Phylogenetic Analysis Using Parsimony (PAUP) (Swofford, 1991).

	Collection							
Taxon	**BM(NH)**	**CMZ**	**ZRC**	**UM**	**DWNP**	**Captive**	**KL**	**Total**
Argus	6							6
Bronze-tail	6		3			6		15
Mountain	3		6	1	2			12
Germain's	7					3		10
Grey	64					20		84
Malaysian	23	5	10	3	4	10	2	57
Bornean	2							2
Palawan	12		1			10		12

Table 7.1: Sources of specimens which were examined. BM(NH) = British Museum (Natural History), Sub-dept. of Ornithology ; CMZ = Cambridge University Museum of Zoology; ZRC = Zoological Reference Collection, National University of Singapore; UM = Reference Collection, Universiti Malaya; DWNP = Reference Collection, Department of Wildlife and National Parks of Peninsular Malaysia (4 males); Captives = birds in the several collections (see acknowledgements for a full list; KL = trapped at Kuala Lompat in 1988 (see Chapter 4).

7.2.2 Choice of display characters and the assignment of character-states

Data on the display of males of each species were collected from several sources. I watched and video-taped the displays of five peacock pheasant taxa (Mountain, Germain's, Grey, Malaysian and Palawan) during a visit to the Hong Kong Zoological and Botanical Gardens in May 1991. John Corder and Dieter Arnold provided video-tape of the displays of male Grey, Malaysian and Palawan peacock and Argus pheasants. Davison (1982, 1983, 1985c and in press) gives detailed descriptions of Argus, Malaysian peacock, Bronze-tailed and Mountain peacock pheasant displays respectively. Johnsgard (1986) also provides descriptions of part of the display of the males of all species. The single exception is the

Bornean peacock pheasant, which has rarely been kept in captivity and for which there are no behavioural data from the wild.

Most information used in this analysis is from my own observations, the video-tape and Davison's descriptions. My observations in Hong Kong allowed me to standardise my data and terminology with that of Davison.

Prior to this study, descriptions of the complete displays of males of all peacock pheasant species were not available. As noted above, Davison has provided complete descriptions of all stages of the display for three species as well as for the Argus pheasant. Other descriptions (*e.g.* Bruning, 1977; Jeggo, 1975: Pocock, 1911; Spedan-Lewis, 1939; Stapel, 1976) have largely concentrated on the culminating posture of one or two taxa (*e.g.* the striking lateral display of male Palawan peacock pheasants). Therefore, my aim was to provide a list of all display elements used by males of each species to which I had access. All of the display elements that I observed and include in my analysis are fully described by Davison (1982, 1983, 1985c and in press) and, therefore, I shall not repeat the description of all 18 display elements here. Provision of a list of display elements does pose several problems. Firstly, I only saw a few displays by each male and the display that a particular male gives may vary from time to time. Secondly, I only had access to small numbers of males that readily displayed and displays may well vary between males of a species. However, as a first attempt at comparing the displays systematically, I merely wished to record the presence (and hence assume absence) of a display element in a species' display repertoire. Consequently, I feel the aim is sufficiently robust to allow for such limitations. Obviously, to thoroughly explore the displays of males of any given species, it would be necessary to watch, say, twenty displays by each of twenty different males under natural circumstances and record how often various elements were incorporated. Even this may not be sufficient in some taxa, such as in the European amphibian genus *Triturus*, perhaps the most phylogenetically studied genus in the world (see Halliday and Arano, 1991).

7.2.3 Phylogenetic analysis

PAUP was used to construct trees that maximise parsimony. These trees minimise the number of character-state transformations that are necessary to explain the data set being analysed. I used the ordered option for most characters, which represents a linear transformation series. Thus an ordered character-state list of 012 indicates that a character assigned 0 must pass through 1 before becoming 2. It cannot move straight from 0 to 2. No polarity is implied (*i.e.* which character-state is the ancestral [plesiomorph] state of a given character and which are derived [apomorph]), however, and so 2 → 1 ← 0 or 2 ← 1 → 0 are also possible as there is no requirement that 0 be the ancestral character-state (Swofford, 1991). Several characters were left unordered as it seemed that they may move from character-state 0 → 2 without passing through character-state 1 (*e.g.* forehead colour, colour of back feathers). I did not assume polarity for any character.

I included the Argus pheasant (*Argus argusianus*) in the analysis. The same trees were computed regardless of whether or not this was designated as an outgroup. Trees were found using the branch-and-bound setting in PAUP, which guarantees finding the most parsimonious tree(s) (see Swofford, 1991, p. 27 for exact details).

7.3 Results

7.3.1 Pattern of variation in morphological characters

The variation among taxa in the morphological characters examined is given in Table 7.2. The characters which vary most (*i.e.* possess most character-states) between taxa are those which describe the ground colour of the body feathers. These are the feathers of the forehead, back and underparts. The colour of the feathers of chin, lower back and wing is also very variable. Characters exhibited during displays to the female vary less, but not all characters recorded are present in all taxa. Thus variation is not necessarily in the character-state but also in the presence or absence of a character.

7.3.2 Phylogentic hypothesis based on all morphological characters

Two most parsimonious trees were generated from the data given in Table 7.2: *i.e.* two trees possess the fewest number of character-state transformations compared with all possible

	Character																			
Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Argus	0	0	0	0	0	0	1	0	4	2	1	2	0	0	4	1	0	4	0	0
Bronze-tailed	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0
Mountain	0	0	0	2	1	2	1	1	1	1	1	1	0	2	0	1	0	0	0	1
Germain's	0	0	3	3	2	3	2	2	2	1	2	2	2	3	0	0	0	2	0	1
Grey	1	2	1	3	1	2	3	2	2	2	2	2	0	3	0	0	0	2	0	1
Malaysian	2	2	2	3	2	2	4	2	3	3	3	2	2	4	3	0	0	3	1	1
Bornean	2	1	3	3	2	4	4	2	3	0	3	2	2	4	2	0	1	4	2	1
Palawan	3	2	3	4	3	5	5	3	3	0	4	3	2	4	1	0	1	5	0	1

Table 7.2: Morphological character-state data. Character (character-state) key: *1)* crest colour: (0) absent, (1) light brown and white, (2) black and white, (3) black; *2)* crest length: (0) absent, (1) <30mm, (2) >30 mm; *3)* facial colour: 0) no bare skin, (1) yellowish flesh, (2) orange, (3) red; *4)* chin colour: (0) sparsely feathered, (1) light brown, (2) light brown & white, (3) white (4) black; *5)* facial pattern: (0) none, (1) whiter cheek patches (2) light eye stripe & dark cheeks, (3) white eye stripe and cheeks; *6)* forehead colour: (0) bare, (1) plain brown, (2) dark brown & white, (3) charcoal & white, (4) black & white, (5) black; *7)* colour of back feathers: (0) black & dark brown bands, (1) dark brown & light brown, (2) dark brown spotted white, (3) light brown spotted white, (4) golden brown and dark brown, (5) iridescent blue; *8)* upper back ocelli: (0) absent, (1) black spots with some iridescence, (2) present, (3) whole of visible portion; *9)* lower back pattern: (0) black & dark brown bands, (1) black spots with some iridescence, (2) brown spotted white, (3) golden brown and dark brown, (4) light brown spotted with dark brown; *10)* mean wing length: (0) <200mm, (1) 200<220mm, (2) >220mm; *11)* wing colour: (0) black & dark brown bands, (1) dark brown & light brown, (2) dark brown spotted white, (3) golden brown and dark brown, (4) dark brown; *12)* wing ocelli: 0) absent, (1) black spots with some iridescence, (2) present, (3) whole of visible portion; *13)* tail length: (0) >300mm, (1) 300>250mm, (2) <250mm; *14)* tail ocelli shape: (0) absent, (1) long, iridescent patches, (2) long defined ocelli, (3) ellipse, (4) elipse circular; *15)* webs of outer tail feathers: (0) ocelli on both webs, (1) outer webs only & iridescence on black patches on inner webs, (2) outer webs only and black patches on inner webs, (3) outer web only, (4) no ocelli; *16)* webs of central tail feathers: (0) both webs, (1) no ocelli; *17)* terminal band to tail feathers: (0) absent, (1) present; *18)* underpart feather colour: (0) charcoal & off white bands, (1) chocolate brown, (2) brown & off white bands, (3) brown mottled white, (4) light brown mottled dark brown, (5) dark brown & black; *19)* breast pattern: (0) none, (1) light breast band, (2) dense white band, *20)* upper tail coverts: (0) no ocelli, (1) ocelli on both webs.

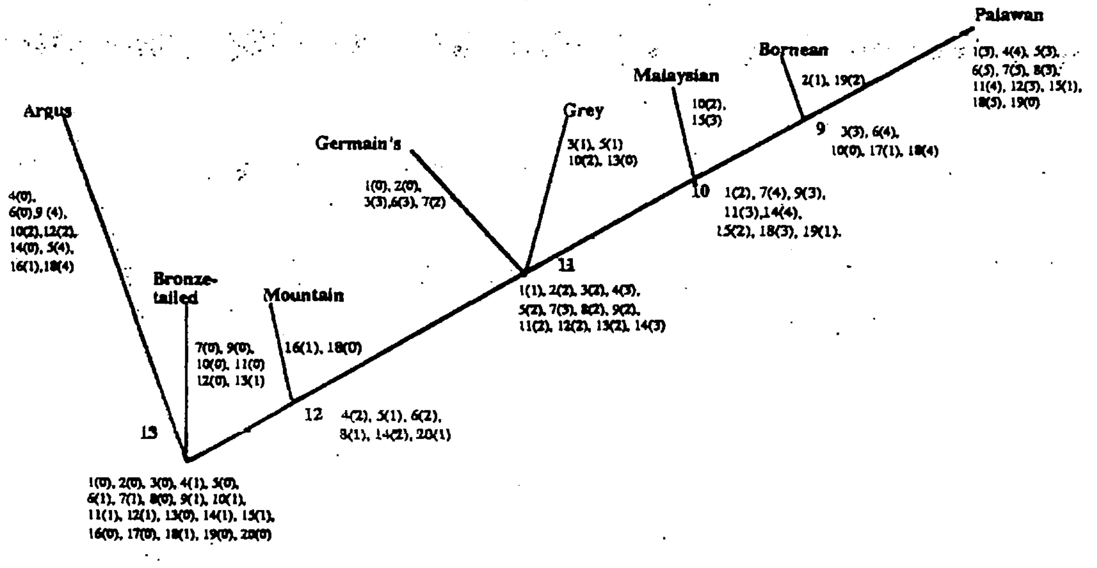


Fig. 7.1: Phylogenetic hypothesis for the genus *Polyplectron*. The strict consensus tree was based on 20 ordered characters (see Table 7.2) and involved 89 steps (=89 character-state changes). The closely related genus *Argusianus* was used to root the tree. Distances between the nodes and terminal taxa are proportional to the number of character-state changes involved. At the root node, the hypothesised ancestral character-states are given (character number and character-state [in parentheses] as in Table 7.2). Changes in characters are given at each point where they change, using the same code. Numbers between 9 and 13 in bold are the numbers of each node and refer to numbers in Table 7.3.

solutions. A strict consensus tree was constructed from these two trees (Fig. 7.1). This tree provides a hierarchical summary of information common to both of the most parsimonious trees.

The changes in all characters in this hypothesis can be followed in Fig. 7.1. It is, however, worth summarising the character-state changes in characters which are exhibited during displays to the female (Table 7.3).

Branch	**Changes**
13 - Argus	i) increase in wing length; ii) black spots with some iridescence on wing become ocelli: iii) tail ocelli disappear.
13 - Bronze-tail	i) decrease in wing length; ii) black spots with some iridescence on wing disappear; reduction in tail length.
13 - 12	i) upper back ocelli appear as black spots with some iridescence; ii) tail ocelli change from long iridescent patches to defined ocelli iii) ocelli appear on both webs of upper tail coverts.
12 - Mountain	i) central webs of tail feathers lose ocelli.
12 - 11	i) crest appears and has feathers of light brown and white; ii) black patches with some iridescence on the upper back and wing become ocelli; iii) large reduction in tail length; iv) long defined ocelli on tail become more elliptical in shape.
11 - Germain's	i) long crest lost.
11 - Grey	i) further reduction in wing length; ii) increase in tail length.
11 - 10	i) crest feathers become black and white; ii) elliptical ocelli on tail become more circular; iii) ocelli on the inner web of outer tail feathers become black patches.
10 - Malaysian	i) increase in wing length; ii) black patches lost from inner webs of outer tail feathers.
10 - 9	i) decrease in wing length; ii) appearence of terminal band on tail feathers.
9 - Bornean	i) decrease in crest length.
9 - Palawan	i) crest becomes all black; ii) ocelli on upper back and wing expands into iridescence on the whole of the visible portion of the feather.

Table 7.3: Changes in characters which are exhibited to the female during display. Changes are shown along each branch of the phylogenetic tree hypothesised in Fig. 7.1 from data on all morphological characters (numbers refer to the nodes marked in Fig.7.1) The characters (from Table 7.2) are 1) crest colour, 2) crest length, 8) upper back ocelli, 10) wing length, 11) wing colour, 12) wing ocelli, 13) tail length, 14) tail ocelli shape, 15) webs of outer tail feathers, 16) webs of central tail feathers, 17) terminal band on tail feathers, 20) upper tail coverts. Summarised from the phylogenetic hypothesis (Fig. 7.1).

These charcters are the crest, wing, tail and ocelli on the upper back, wing, tail and upper tail coverts. The two trichotomies (nodes 13 and 11) require some explanation as they indicate two possibilities (Maddison, 1989; Swofford, 1991). First, they may be an artefact due to areas of uncertain resolution which arise from insufficient data to permit a binary tree (*i.e.* one in which all branches are dichotomous). Second, they may accurately represent events of multiple speciation. Because polytomies are "messy things" (Maddison, 1989), PAUP only yields polytomies if there is not even potential support for a dichotomous solution. This suggests that trichotomies proposed by PAUP may well be real events of multiple speciation, rather than an area of unceratainty.

7.3.3 Pattern of variation in display elements

The variation in the display elements exhibited by each species is shown in Table 7.4. As stated in the methods, I only assigned character-state values on the basis of presence or absence. This table, therefore, merely indicates which species exhibit each of the display elements and not how variable each element is between the species. It is worth noting that I did not add any elements to the display repertoire of the Malaysian peacock pheasant that Davison (1983b) recorded.

	Character																	
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Argus	0	0	1	1	1	0	1	1	0	1	0	0	0	1	0	0	1	1
Bronze-tailed	0	1	1	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0
Mountain	1	1	0	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0
Germain's	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0
Grey	0	0	0	1	1	1	0	0	1	1	0	0	1	0	1	1	0	0
Malaysian	0	1	1	1	1	1	0	0	0	1	1	1	0	0	1	1	0	0
Palawan	0	1	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0

Table 7.4: Display character-state data. Character (character-state) key: *1)* wing adjusting while walking: (0) absent, (1) present; *2)* wing flap: (0) absent, (1) present; *3)* head feather ruffling: 0) absent, (1) present; *4)* body shake: (0) absent, (1) present; *5)* erect posture: (0) absent, (1) present; *6)* lateral movement with tail spread: (0) absent, (1) present; *7)* lateral movement with no tail spread: (0) absent, (1) present; *8)* crouching run: (0) absent, (1) present; *9)* head bobbing: (0) absent, (1) present; *10)* tid-bitting: (0) absent, (1) present; *11)* shuffle: (0) absent, (1) present; *12)* ritual preening: 0) absent, (1) present; *13)* high stepping: (0) absent, (1) present; *14)* frontal movement with wings spread: (0) absent, (1) present; *15)* frontal movement with tail spread: (0) absent, (1) present; *16)* crest erection: (0) absent, (1) present; *17)* stamping: (0) absent, (1) present; *18)* tail high walk: (0) absent, (1) present.

7.3.4 Phylogenetic hypothesis based on male display

The data given in Table 7.4 were used to generate a phylogenetic hypothesis based on male display characters (Fig 7.2). According to this phylogenetic hypothesis, the Bronze-tailed and Mountain peacock pheasants are as dissimilar from the Germain's, Grey, Malaysian and Palawan peacock pheasants as is the Argus pheasant.

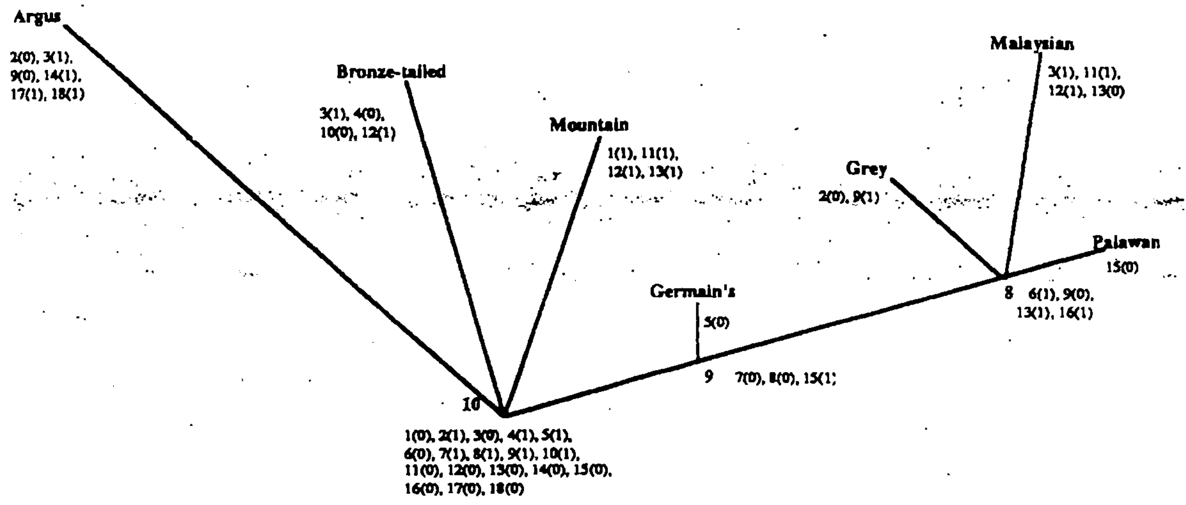


Fig. 7.2: Phylogenetic hypothesis for the genus *Polyplectron* based on male display. The strict consensus tree was based on 18 binary characters (see Table 7.4) and involved 29 steps (= 29 character-state changes). The closely related genus *Argus* was used to root the tree. Distances between the nodes and terminal taxa are proportional to the number of character-state changes involved. At the root node, the hypothesised ancestral character-states are given (character number and character-state [in parentheses] as in Table 7.4). Changes in characters are given at each point where they change, using the same code. The nodes are numbered in bold.

7.3.5 Comparison of phylogenetic trees based on male morphology and display

The hypotheses shown in Figs. 7.1 and 7.2 do show some degree of congruence, most notably in the position that each taxa occupy on the phyogenetic trees. However, there are some differences which should be explored and which may allow clarification of the pattern of morphology and display across the genus. There are two initial considerations. First, the presence of data on the Bornean peacock pheasant in one data set (Table 7.2 and Fig. 7.1) and not the other (Table 7.3 and Fig. 7.2), may influence the hypotheses generated and thus to compare hypotheses, these data should be removed. Second, and more interesting, is the relationship between morphology and display. It is likely that not all morphological characters are shown-off by the male during display and, conversely, not all display movements involve showing off parts of the male's plumage to the female.

To investigate the possible co-evolution of display and morphology, I repeated the earlier tree generation after removing the Bornean peacock pheasant. I also used only morphological characters that I suspected to be important in display (characters numbered 1, 2, 8, 10, 12, 13, 14, 15, 16, 17 and 20 in Table 7.2) and only those display elements that presented particular morphological characters to the female (characters numbered 3, 4, 5, 6, 7, 9, 14, 15, 16 and 18 in Table 7.3). There is considerably more congruence between these two phylogenetic trees (Figs. 7.3 and 7.4) than those generated by data on all morphological and display characters (Figs. 7.1 and 7.2).

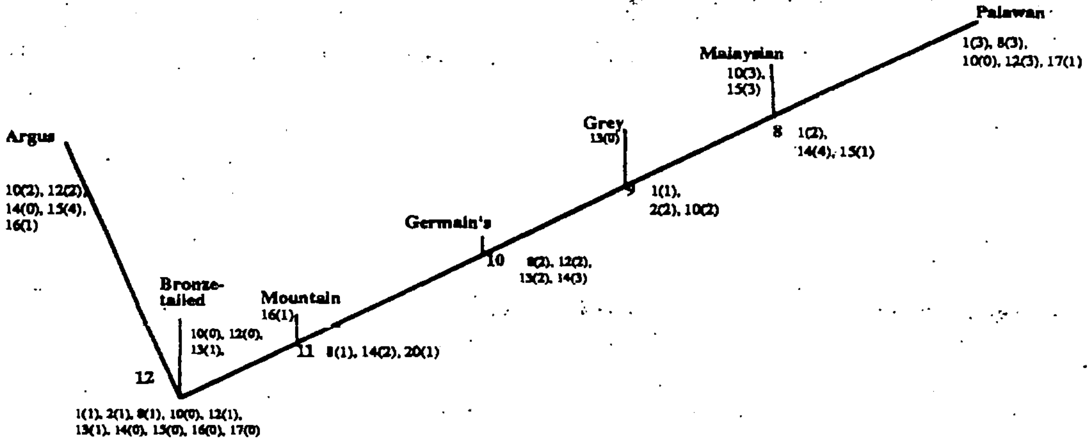


Fig. 7.3: Phylogenetic hypothesis for the genus *Polyplectron* based *only* on morphological characters which the male exhibits to the female during display. The tree was based on 11 ordered characters (character numbers at node 13 correspond to character numbers in Table 7.2) and involved 38 steps (= 38 character-state changes). The closely related genus *Argusianus* was used to root the tree. Distances between the nodes and terminal taxa are proportional to the number of character-state changes involved. At the root node, the hypothesised ancestral character-states are given (character number and character-state [in parentheses] as in Table 7.2). Changes in characters are given at each point where they change, using the same code.

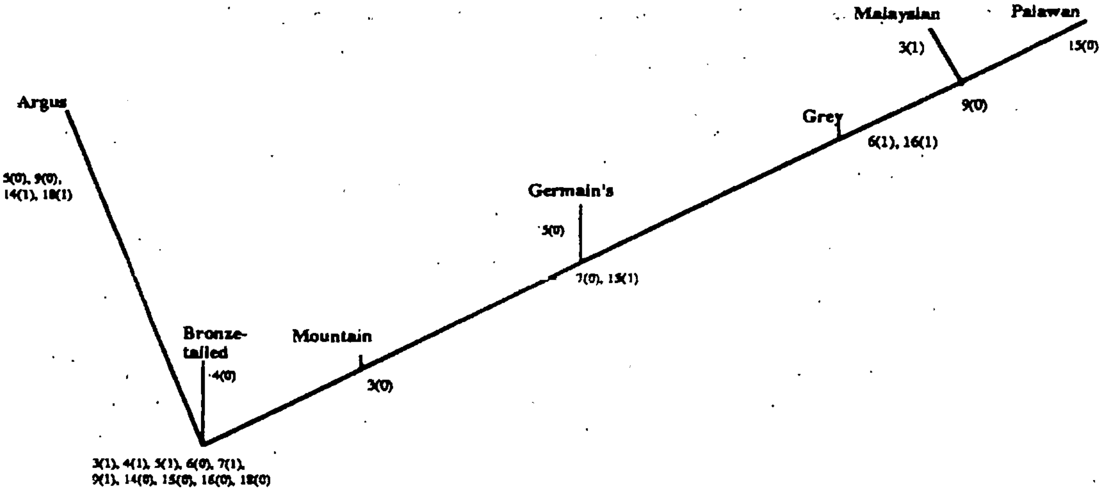


Fig. 7.4: Phylogenetic hypothesis for the genus *Polyplectron* based *only* on display elements that exhibit particular morphological characters to the female. The tree was based on 10 binary characters (character numbers at node 13 correspond to character numbers in Table 7.4) and involved 14 steps (= 14 character-state changes). The closely related genus *Argusianus* was used to root the tree. Distances between the nodes and terminal taxa are proportional to the number of character-state changes involved. At the root node, the hypothesised ancestral character-states are given (character number and character-state [in parentheses] as in Table 7.4). Changes in characters are given at each point where they change, using the same code.

The congruence between these two phylogenies may simply be a consequence of the relationships of the taxa rather than indicating that the two data sets are associated: *i.e.* coincidence rather than co-evolution (Brooks and McLennan, 1991; p. 152). Therefore, as a specific test of the co-evolution of the morphological characters and display elements, I predict that they will change at the same postion on both phylogenetic trees. Consequently, the changes in the characters in the two data sets can be compared to test this prediction.

The changes at each stage in both phylogenetic trees generated from the character sub-sets are compared in Table 7.5.

Branch	**Morphological changes**	**Display changes**
12 - Argus	i) increased wing length; ii) wing ocelli appear; iii) tail ocelli lost.	i) erect posture and head-bobbing lost; ii) frontal display with wings appears; iii) tail-high walk appears.
12 - Bronze-tailed	i) reduced wing length; ii) loss of wing ocelli; iii) reduced tail length.	i) loss of body shake.
12 - 11	i) upper back ocelli start to appear; ii) long, defined tail ocelli; iii) upper tail covert ocelli appear.	i) loss of head-feather ruffling.
11 - Mountain	i) ocelli on central tail feathers lost.	
11 - 10	i) upper back and wing ocelli present; ii) reduced tail length; iii) ocelli less elongated.	i) lateral movement with no tail spread lost; ii) frontal movement with tail spread appears.
10 - Germain's		i) erect movement lost
10 - 9	i) crest appears; ii) reduced wing length	i) crest erection; ii) lateral display with tail spread appears.
9 - Grey	i) increased tail length.	
9 - 8	i) crest colour changes; ii) ocelli more circular; iii) ocelli disappearing on inner webs of outer tail feathers.	i) head-bobbing lost
8 - Malaysian	i) increase in wing length; ii) ocelli lost on inner webs of outer tail feathers.	i) head-feather ruffling re-appears.
8 - Palawan	i) crest colour changes; ii) upper back and wing ocelli replaced iridescent patches; iii) reduced wing length; terminal band to tail feathers appears.	i) frontal movement with tail spread lost.

Table 7.5: Changes in morphological characters and display elements that are predicted to be associated. The changes are based on phylogenetic trees generated from morphological characters that are exhibited during display and display elements which show these morphological characters off.

The most notable changes occur along the tree branches node 12 → Argus, node 11 → node 10 and node 10 → node 9. From node 12 to the Argus, increased wing length and the evolution of wing ocelli are matched by a frontal display in which the wings only are spread. Hence any trace of tail ocelli disappears. Between nodes 12 and 11, there do not appear to be any striking changes in the display that are related to morphology. From node 11 → 10, there is a major change in the display as the lateral movement with no tail spread disappears and a frontal movement with the tail spread is incorporated. At the same time, ocelli appear on the upper back and wings and the reduction in tail length is accompanied by the tail ocelli becoming less elongated. Between nodes 10 and 9, there appears the crest which is erected during display and wing length is reduced and a lateral movement with tail feathers spread is incorporated into the display.

The other major change occurs between node 8 and Palawan, where the frontal movement with tail feathers spread disappears. The only tail spreading display is the lateral movement; there is a corresponding reduction in wing length, plus the appearance of a terminal band to the tail feathers. The whole of the visible portion of each feather of the upper back and wing coverts is iridescent rather than bearing an ocellus.

7.4 Discussion

7.4.1 The phylogenetic hypothesis

The phylogenetic hypothesis generated from a wide spectrum of morphological characters, those suspected of being both sexually selected and non-sexually selected functions broadly agree with previous qualitative assessments of relationships within the genus. Of particular importance in this study is the position of the Malaysian peacock pheasant on this phylogenetic tree. The position of this species (far from the root) implies that description of the pattern of variation in particular morphological characters and display elements across the genus will permit the proposal of a hypothesis about the evolution of epigamic display in the Malaysian peacock pheasant.

7.4.2 Patterns of variation in characters

There was only moderate agreement between phylogenetic trees based on the two large data sets - all morphological characters and all display elements. This is not particularly surprising because not all morphological characters are concerned exclusively with display to females and not all display elements are concerned with showing morphological characters to the female. Hence some morphological characters are likely to be under other forms of selection and some display elements are likely to demonstrate other types of character to the female (*e.g.* perhaps tid-bitting is a ritualised indication of food finding ability).

7.4.3 Evolution of characters involved in display

I predicted that certain morphological characters and display elements have evolved together for display to the female. Phylogenies were generated based on the two subsets of morphological and display characters to test this and there was considerable agreement between the two trees. This agreement could simply be due to the phylogenetic relationships between the species hypothesised above, rather than associations between particular morphological characters and display elements. To test for particular associations between the morphological characters and the display elements of interest, I investigated the postions on the two phylogenetic hypotheses where each character changed. Changes in the morphological characters were often associated with changes in display elements that revealed such morphological characters most fully.

The display elements that are most closely related to particular morphological characters are those which show the ocelli (or iridescent feathers) and crest to the female. These display elements are the frontal and lateral movements that involve the spreading of the tail feathers (or wing feathers in the Argus). These characters are not evident in the Bronze-tailed and Mountain peacock pheasants, the displays of which do not involve such extreme display movements. There are as many distinct elements in the display repertoire of these two species, however, as in the more morphologically specialised species - the Malaysian and Palawan. It seems likely to me that the display of these latter species is much more concerned with showing off morphological characters than in the more generalised species - the Bronze-tailed and Mountain.

It seems logical to assume that morphological characters which are exhibited to females during display are, potentially, subject to female choice. Thus, from the foregoing discussion, it would be predicted that crest length and features of the ocelli will be under sexual selection through female choice in those species which possess them. What it is about these features that may be subject to such choice is not certain. It could simply be, for example, the length of the crest or it could be the length of the crest relative to bill length. When erected, the crest lies foward along the bill. Similarly, the number of ocelli may be important. There is an increase in the number of tail feathers from the Bronze-tailed to the Palawan (Davison, 1986a), but it has not been possible to assess the number of the ocelli-bearing upper-tail coverts, as these seem to be easily lost in museum specimens. Alternatively, or additionaly, it could be some feature of the ocellus that is subject to female choice, such as its size or shape.

Of the morphological characters that are not so closely related to particular display elements, several may still be important. Wing and tail length could be revealed in a number of display elements, including lateral movements with or without tail spreading. A number of other display elements may also serve to indicate or exaggerate the size of the male or of various parts - such as head feather ruffling.

7.4.4 Classification of the Malaysian and Bornean peacock pheasants

The fullest description of the males' morphology is given in Table 7.2. The phylogenetic hypothesis generated from this data set is shown in Fig. 7.1. Comparison of the number of the number of character-state changes involved between the branches node 10 → Malaysian and node 10 → Bornean suggest that there are more character-state differences between the Malaysian and Bornean taxa than between the Germain's and Grey taxa. Consequently, I suggest that the classification adopted by Sibley and Monroe (1991) be followed, whereby the Malaysian and Bornean peacock pheasants are regarded as two distinct species forming a super-species.

In the introduction to Chapter 6, I stated that I would explore the patterns of morphological variation in both the Malaysian peacock pheasant and across the genus as a whole, in order to propose hypotheses of process. This I have done and the main conclusions are as follows.

1) There are several morphometric traits (number of spurs and their lengths, crest length and number of tail feathers) that are likely to be under sexual selection in the Malaysian peacock pheasant. Whether this sexual selection is the result of female choice or male-male conflict, which have been traditionally regarded as distinct selection forces, is not clear from intra-specific analysis. This may be because these forces do not in fact act separately on these characters. The positive correlation between spur length and symmetry suggests that spur length may be subject to female choice according to Møller's (1990) hypothesis.

2) There is no support for the proposal that male Malaysian peacock pheasants are polymorphic, and traits that have been suggested as having specific roles in female choice or intra-sexual roles are not correlated among themselves. The only exception is spur length; thus, if a male has one long spur, it has all long spurs and if one short, all are short.

3) From interspecific analysis of patterns of variation, I propose that the Malaysian peacock pheasant is morphologically specialised compared to other members of the genus. Thus comparison of associated morphological characters and display elements should indicate whether they have co-evolved.

4) It is of note that the display repertoires of those species in which males do not possess specialised morphological characters (*i.e.* Bronze-tailed and Mountain) do not seem to contain substantially fewer display elements. Instead, they contain more 'mobile' elements, such as crouching run, wing-adjusting or ritual preening, on average, than the other species (see Table 7.4).

5) Comparison of phylogenetic trees based on morphological characters that are exhibited during display to the female and of display elements that reveal particular morphological characters to the female shows almost complete congruence. These traits, including crest length and the presence of ocelli on the upper parts of the male are, therefore, probably subject to female choice.

CHAPTER 8: CALLING BEHAVIOUR

"It was a land of dreadful silences. ...... the (Malay peacock) pheasants were silent, listening somewhere deep among the leech-infested undergrowth." Beebe (1922: p. 77-79)

8.1 Introduction

There are a number of tropical bird species that Darwin discussed in relation to sexual selection that have now been studied in some detail (see Chapter 1). The behavioural aspect of these studies has been concerned primarily with the social organisation (most notably male dominance) and display of the male at the lek or fixed display-court. Whilst the plumage and display of the males of such species are often particularly striking, the distance at which these features can be perceived by conspecifics is limited in this very complex habitat. As such, it seems intuitive that visual display, for example, has little or no scope as a means of distance communication, although it can be used when individuals are in visual contact.

Most of the authors mentioned in Chapter 1 who have studied these species have commented in passing that their study species give very conspicuous vocalisations, often audible for quite some distance from the source (*e.g.* about 1 km. for the argus). The sometimes quite considerable variation in vocal behaviour has also attracted comment. Very surprisingly, however, there has been no quantitative study of the nature of this variation. This is despite sound being the most conspicuous form of communication over any distance greater than a few metres in tropical forest.

The only exception seems to be a study of the possible role of breeding vocalizations as cues by which females may assess male age. In the satin bowerbird *Ptilinorhynchus violaceus* Loffredo and Borgia (1986b) suggest that the complexity of male courtship vocalizations (which include mimetic singing and are apparently commenced only after a female has approached the bower) are correlated with male age, and that they may influence female choice. In the Malaysian peacock pheasant *Polyplectron malacense* vocalizations seem to be a very important aspect of sexual behaviour. In dense tropical forest such vocalizations are the most apparent method by which males both 'advertise' their presence and can be detected, by both other males and females.

8.1.1 Calls of the Malaysian peacock pheasant

This species gives conspicuous vocalisations which are audible to a human observer up to 200 - 300 metres and are, therefore, more amenable to study than other aspects of the species' behaviour. This also provides the chance to gain some insight into how long distance communication works in a species in which the male is extravagantly plumaged, maintains a display scrape and has an elaborate display.

Davison (1983a) mentions three types of call given by male Malaysian peacock pheasants, namely "short calls", "long calls" and "clucks". The short call is a two note whistle which apparently varies little and is usually given about a minute after the previous short call for up to 30 minutes. This is the "melancholy double whistle" of Medway and Wells (1976). Long calls are a series of loud, grating single notes (the "*tchorr*" of Medway and Wells, 1976) with brief intervals (1.5 - 5 seconds) between calls. Davison heard up to 117 notes in a series lasting 2 - 3 minutes. Clucks are harsh, grating sounds ("explosive cackles" of Medway and Wells, 1976), which trail off in amplitude as a long series of clucks. The maximum number of clucks heard by Davison in a series was 230, with bursts of clucks occuring at intervals of around 20 -60 seconds. Davison (1983a) reports a transition from bursts of clucks to long calls and finally to short calls. To standardise these two sets of call nomenclature and provide succinct and descriptive names, I shall use *whistle*, *tchorr* and *cluck* respectively. In addition, I use *wark* to refer to call types included in the gradation from clucks to tchorrs.

8.1.2 Studying the vocal behaviour of a tropical forest bird species

The majority of studies concerned with evolution and function of calls and/or songs have been conducted in temperate habitats on the song of passerine birds. Such geographical and taxonomic bias has two important procedural considerations which are concerned with behaviour patterns associated with song production and influence their study.

Firstly, one of the most studied aspects of avian vocal behaviour is the precise role that male song plays during breeding. This is made quite straightforward in many species by two patterns of behaviour which are strongly correlated with the production of song by males, namely chorussing at dawn and the use of song perches. These result in the production of song over a very short period of time by very conspicuous individuals. As such, it is often possible to determine the function of song because visible behaviour patterns also provide contextual clues and provide additional information that may help in the interpretation of experimental studies.

Secondly, because these associated behaviour patterns have made singing males so conspicuous, there have been many studies that have addressed very specific questions of function without an adequately quantified background. For example, investigating the ability of an individual to discriminate between strangers' songs and neighbour's songs will only make sense if song repertoires of individuals in the population have been quantified and shown to vary consistently between individuals, and it has then been demonstrated that individuals do respond differently to different song types, singing rates *etc*. Once this is documented, its functional significance can be addressed.

In temperate areas these considerations seem less pressing because the context and function of song is often apparent, at least subjectively. In addition, visual information can be very helpful in investigating function (*e.g.* of song in spring) as well as the functional significance of any variation (*e.g.* difference in mating success). This also helps in partitioning vocal behaviour patterns, contexts *etc*. into very discrete categories, such that very objective quantitative methods are rarely needed to assess, for example, the grading of calls between call types and to determine what is a call given as a response to a particluar stimulus, rather than a spontaneous call (*i.e.* in this instance, a call given not as a response to the stimulus).

Studies of vocalizations in tropical rainforest

Because of these limitations, I needed to clarify the approach that I adopted to this study. Adapting techniques and approaches that have been used to study vocalizations in temperate passerines to tropical rainforest situations presents a number of problems. Firstly, the lack of visual clues that an observer has to the context of a given vocalization limits the amount of information available for suggesting functional hypotheses from the context. On the other hand individuals of the species being studied may be similarly restricted to auditory communication for much of the time. If this is so, it does provide the rare opportunity to investigate the nature and function of particular vocalizations in the absence of a visual context. In other words, the context and the calls themselves must carry all the information in the absence of associated visual behaviours.

A common, very subjective, observation made upon entering rainforest is that animals are recorded far more often by call and/or song than by sight when compared with other habitats. Although this relationship has not been investigated quantitatively, it may mean that vocalisations are used in combination with visual communication to different degrees in different habitats. This may result in selection pressures on vocalizations varying, perhaps a great deal, between habitats.

Studies of the ecological constraints on vocalizations are few, but it has been demonstrated that the frequencies used by bird species in habitats of varying openness vary with attenuation characteristics of different frequencies in each habitat (*e.g*. Marten *et al*., 1977; Morton 1975; Richards and Wiley, 1980; Wiley and Richards, 1978; 1982).

Analysing the vocal behaviour of the Malaysian peacock pheasant

Because of the lack of a systematic approach to the study of the vocalizations of a species from first principles a field procedure must be devised. This must sytematically address all possible factors which may have influenced the evolution of vocal behaviour. Catchpole (1982) suggested a general approach for investigating the evolution of male sexual vocalizations. In order to identify the selection pressures acting on male vocalizations in different bird species, he adopted three different techniques. These involved contextual correlations (observations), correlations with different mating and spacing systems (comparative studies) and direct effects on males and females (lab. or field experiments).

In order to investigate the constraints on and function(s) of the calls of the Malaysian peacock pheasant, this approach has been expanded to provide one which encompasses documentation of the vocal repertoire and any contextual correlations or patterns and then appropriate experiments (Fig 8.1). By context, I mean a situation within which the calls are given. Hence, calling context refers to the pattern of calling within which a call bout is given:

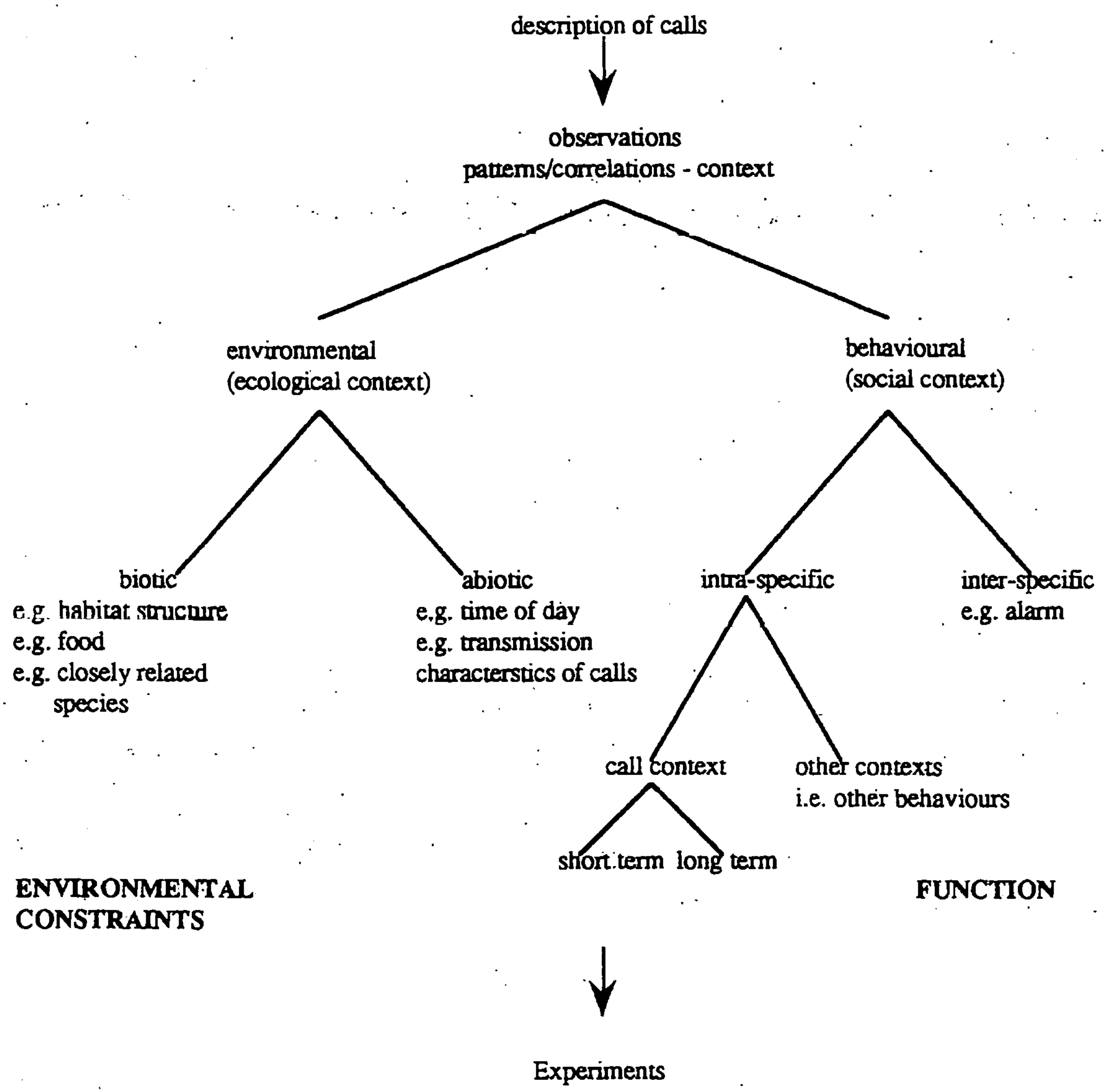


Fig. 8.1: Schematic representation of possible influences on the evolution of calls.

This approach simply outlines a number of factors that may be important in producing the currently observed pattern of calling in this species. The list is by no means exhaustive, but provides a logical framework within which to analyse calling. In this study it is not possible to explore all of these possible influences. For example, to investigate the role of food fully would require long term monitoring of food supply and calling behaviour to allow these two variables to be correlated as well as more detailed assessment of food availability to particular males compared with their calling rate *etc.* and experimental food supplementation.

8.1.3 A test of the 'hotshot' hypothesis

The 'hotshot' hypothesis of lek dispersion proposes that a clumped male display dispersion has evolved because of the presence of a 'hotshot' male (Beehler and Foster, 1988). The hotshot male is supposedly of very good quality and other males are attracted to him in an attempt to parasitise his superior displaying ability by intercepting females which are attracted to the 'hotshot' male. A clumped dispersion in which males are in vocal but not visual contact offers a system which can be most easily manipulated to test this hypothesis (see Chapter 3), without removal of males. This is because vocal displays can be played back as imitations of 'hotshot' males, whereas visual displays cannot. Therefore, if the presence of a 'hotshot' male is important in stimulating males to display in a clump I predict that call playback should stimulate other males to call (*i.e.* display vocally), both in immediate response to the playback and at other times. Such a test must be regarded as a preliminary test because the status of the playback male was unknown (*i.e.* 'hotshot' or satellite male).

Thus, my aims were to document the context in which calls were given and then to conduct experiments to investigate vocal behaviour further.These experiments were conducted to; i) investigate the function of the call types by testing whether an example of a wark call bout is responded to differently than an example of a whistle call bout and; ii) to permit delimitation of calling territory boundaries (see CBC analysis in section 3.3.5). Also call playback can be used during non-calling periods to try and start-up calling - a preliminary test of the 'hotshot' model of the evolution of clumped male display dispersion (Beehler and Foster, 1988; see Chapter 3 discussion).

8.2 Methods

8.2.1 Observation

During calling periods in 1988 and 1989 (see Chapter 3), all-day listens were conducted to provide descriptions of the calls and to document variation in calling rate by call type and by hour of the day. Instances of simultaneous calling, when individuals may be responding to each other, were also recorded.

All calls given between dawn and dusk were noted for a total of eight full days during two periods of peak calling at Kuala Lompat in 1988. This was done from first light to 1315hrs on one day and from 1315hrs to dusk on the following day for a total of 16 half days. In addition, three full days were added in 1989, including the periods from 0630 - 0700hrs and 1930 - 2000hrs, which were not included in 1988.

When a bird called, the following data were noted;- time of day, type of call, number of calls per bout, duration (in minutes) of the call bout and the approximate position of the calling bird.

8.2.2 Call playback experiments

The most obvious manipulation of context is to alter the call context in which the birds find themselves. This is easily done by call playback and is, potentially, useful for investigating how important the calls of conspecifics are in determining the observed pattern of calling. Although the technique is widely used in temperate studies, it seems to have been used rarely in tropical forest. It is used by birders to 'call up' some species (*e.g.* pittas) and has been used in some primate studies to elucidate call function (*e.g.* Waser and Waser, 1977; Chivers and MacKinnon, 1977).

Kroodsma (1989a; 1989b; 1990) has reported that many playback experiments do not actually test the stated hypothesis. This is usually because the hypothesis that the experimenter wishes to test usually involves a considerable amount of work. I readily accept Kroodsma's critique and have stated the experimental hypothesis accordingly when investigating the function of the calls. Because the level of calling was quite low and the calling period is of unknown duration, it was not possible to investigate the function of the huge variety of call bout compositions (number of calls and call types used). Thus I chose representative exemplars that were of a similar duration. Unfortunately, I was not able to apply Kroodsma's criteria to my preliminary test of the 'hotshot' model and I shall indicate how this experimental design should be improved.

Equipment

Calls were recorded using a Sony Professional Walkman WM-D6C Stereo Cassette Recorder (reviewed by Margoschis, 1988) and an Audio Technica Directional Microphone. The amplifier used for playback was built by the Physics Lab. at UKM from a design used to playback calls of the cheer pheasant in north-west India (P.J. Garson and V. Sharma, pers. comm.). An old wireless speaker was used to broadcast the calls.

Procedure

The playback experiments were conducted at Pasoh in 1990, using calls recorded at Kuala Lompat in 1989. They were conducted over relatively few days as I did not know for how many days birds had been calling or how many more days they were likely to call for. The two tapes used were 'clucks' (tape also included three widely spaced whistles) and 'whistles' and each bout lasted six minutes.

To control for any possible time of day effects (*i.e.* the same stimulus call eliciting a different response according to time of day) both stimulus calls were played at all times of the day. Therefore, both tapes were played, in random order, on every hour between 0700 and 2000hrs. Both tapes were also played, in random order, every hour between 0730 and 1930hrs.

Sonograms

Calls for presentation were chosen using a real time spectrum analyser, the Appleton Ultrasound Floscan Plus. Recordings were filtered to remove sounds below 500Hz and a

Loughborough Sound Images speech workstation software produced the frequency/duration printouts on a laser printer. The sample rate was set to 8kHz, which effectively determines the frequency range as 4kHz, and the band width was 100Hz for clucks and tchorrs and 40Hz for whistles.

8.2.3 Individual differences in calling behaviour

At Pasoh in 1990, it was possible to attempt a more accurate assessment of calling territoriality than was possible at Kuala Lompat in 1988 (see Chapter 3). This was due to a combination of the increased level of calling (probably due to playback) resulting in many instances of counter-calling and particular responses to playback in particular areas. Consequently, I drew calling territory boundaries based on responses both to playback and to other calling individuals.

8.2.4 A preliminary test of the 'hotshot' hypothesis

As a preliminary test of the hypothesis that a clumped male display dispersion results from a number of males clustering around a single male 'hotshot', I conducted a number of playbacks when there was no naturally occuring calling. This was done in a month (March 1991 at Kuala Lompat) when there had been calling in previous years: *i.e.* presumably within the calling season (if one exists) although I had heard no calling at Kuala Lompat or Pasoh that year (see Chapter 3).

Playbacks were conducted in the morning and evening over five days. As I merely wished to simulate a peacock pheasant starting to call, I did not consider there to be any reason to adopt a particular pattern to the timing and choice of the stimulus tape. I did, however, usually play whistles early in the morning and late in the evening and clucks later in the morning and earlier in the evening. Playbacks were 1.5 - 2hrs apart as this may be a better simulation of the calling pattern of an individual peacock pheasant rather than the very frequent playback used in the rigid procedure adopted in section 8.2.3. I conducted playback from three different places in the forest that were close together. The status of the male(s) used in the playback experiment was unknown (*i.e.* 'hotshot' or satellite male).

8.3 Results

8.3.1 Observation

Description of the calls

The calls of the Malaysian peacock pheasant fall readily into two subjective categories, which I have called 'warks' and 'whistles'. I have combined both clucks and tchorrs into one category, warks, because of the gradation between the two (the structure of the two call types at the extremes is shown in Fig. 8.1: see also the call type definitions that I have adopted at the end of Section 8.1.1). 'Whistles' (Fig. 8.1), on the other hand seem very discrete and show considerably less variation in structure. Table 8.1 gives some parameters of the calls. Marler (1955; 1959) and Collias (1987) have suggested that the sonagraphic strucure of a call determines how locatable it is. From their studies, I imply the locatability of the vocalisations of the Malaysian peacock pheasant (Table 8.1) and this is different for calls and bouts, because repetition enhances locatability. My subjective impression of locatability is the same as these authors.

Call type	**Warks**			**Whistle**	
	Clucks		***Tchorrs***		
Notes/call	2-50 (112 Davison)		1	2	
	1st note	2nd note		1st note	2nd note
Frequency (Hz)	500-6800	2600-4800	1840-3968	780-1028	840-1184
Duration (ms)	400	600	468-960	450-1552	858
Configuration	vertical		horizontal	horizontal	
Locatability	easy → difficult		difficult	difficult	

Table 8.1: Frequency and duration characteristics of Malaysian peacock pheasant calls and their locatability (implied from Marler [1955; 1959]). I only give characteristics for two notes of a cluck call, even though there can be up to 112 in a call.

Description of call bouts

Calls did not fall readily into discrete bouts and survivorship analysis was used to determine the bout criterion interval (BCI) (Martin and Bateson, 1986). This is the maximum time between calls in a bout and for all calls heard at Kuala Lompat in 1988, the BCI was determined to be one minute (Fig. 8.3). Thus, all calls given by an individual within one

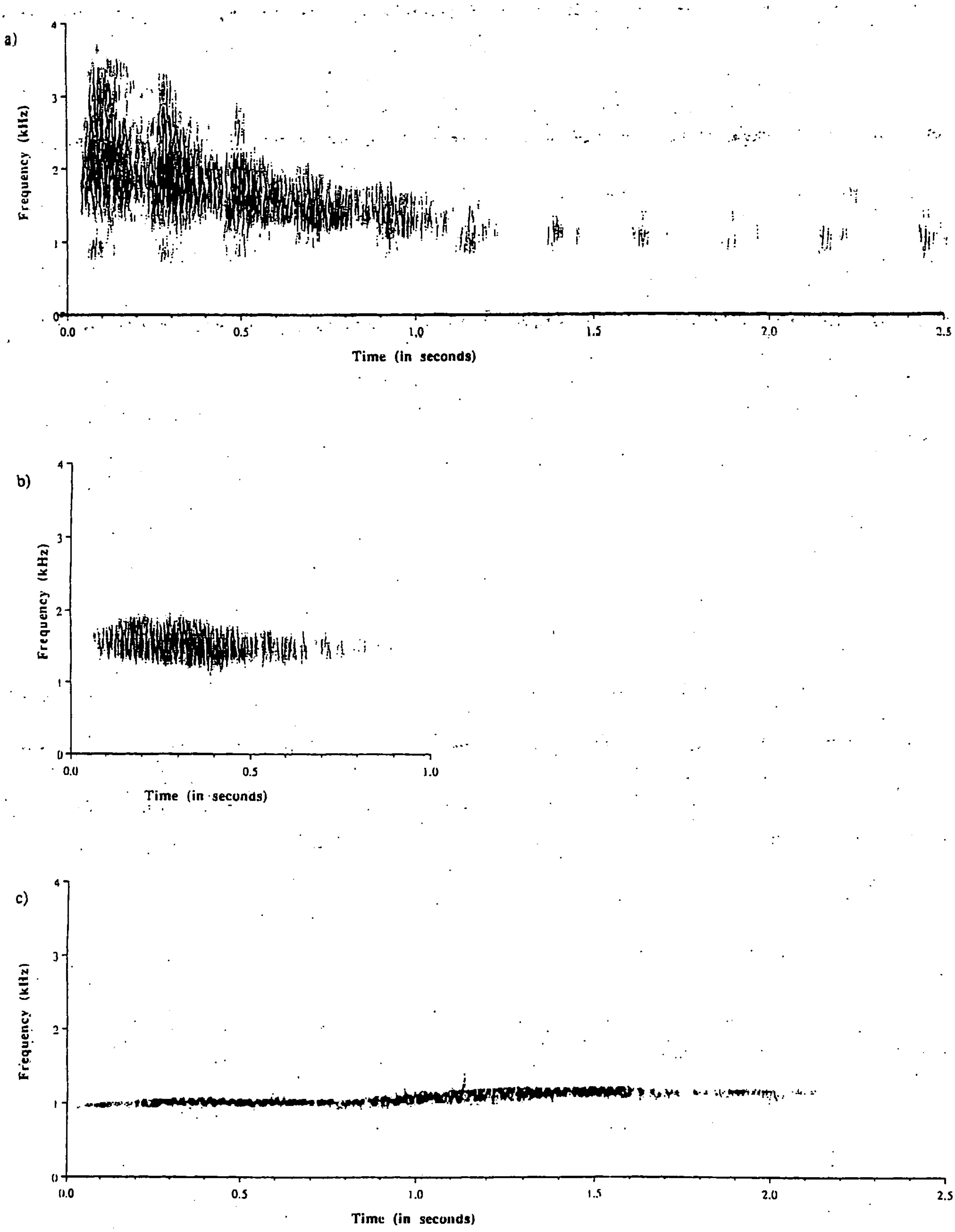


Fig. 8.2: Sonograms of all three Malaysian peacock pheasant call types. a) cluck, b) tchorr and c) whistle.

minute of its previous call, was ascribed to the same call bout. Any call given more than one minute later than the previous call was determined to belong to a new bout.

At Kuala Lompat in 1988 and 1989, bouts containing clucks only were the commonest bouts heard (Table 8.2). Towards the end of a number a cluck bouts, the calls became increasingly like tchorrs. In these cases, the call consists of few cluck notes, as few as two or three, and the first note was emphasised and very 'tchorr-like'. Whistle bouts were given almost as often over the same time period and 36 bouts contained both warks (clucks or tchorrs) and whistles. Tchorrs were heard only in two bouts.

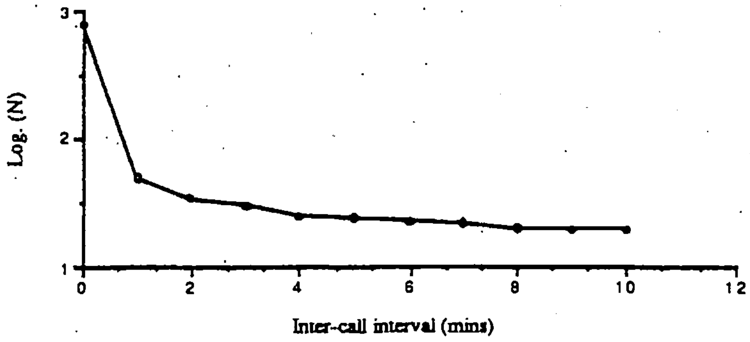


Fig. 8.3: Log survivorship plot to determine the bout criterion interval for both major call types.

Bouts	N		Calls per bout	
		range	mean	s.d.
clucks	151	1-96	8.08	12.40
whistle	126	1-63	8.64	12.20
cluck/whistle	35	3-114	36.8	26.1
cluck/tchorr	1		79	----
tchorr	1		30	----

Table 8.2: Summary of call bouts heard during 1988 at Kuala Lompat

The number of clucks heard in a bout varied from one to 96 and the number of whistles heard in a bout varied from one to 63 (see Fig. 8.4). The distribution of number of calls per bout was not significantly different between these two types of calls ($p > 0.36$, Mann Whitney U test). This suggests that selection on number of calls per bout is similar for both call types. Therefore, the important differences between the call types must be in some other parameter, such as frequency or context.

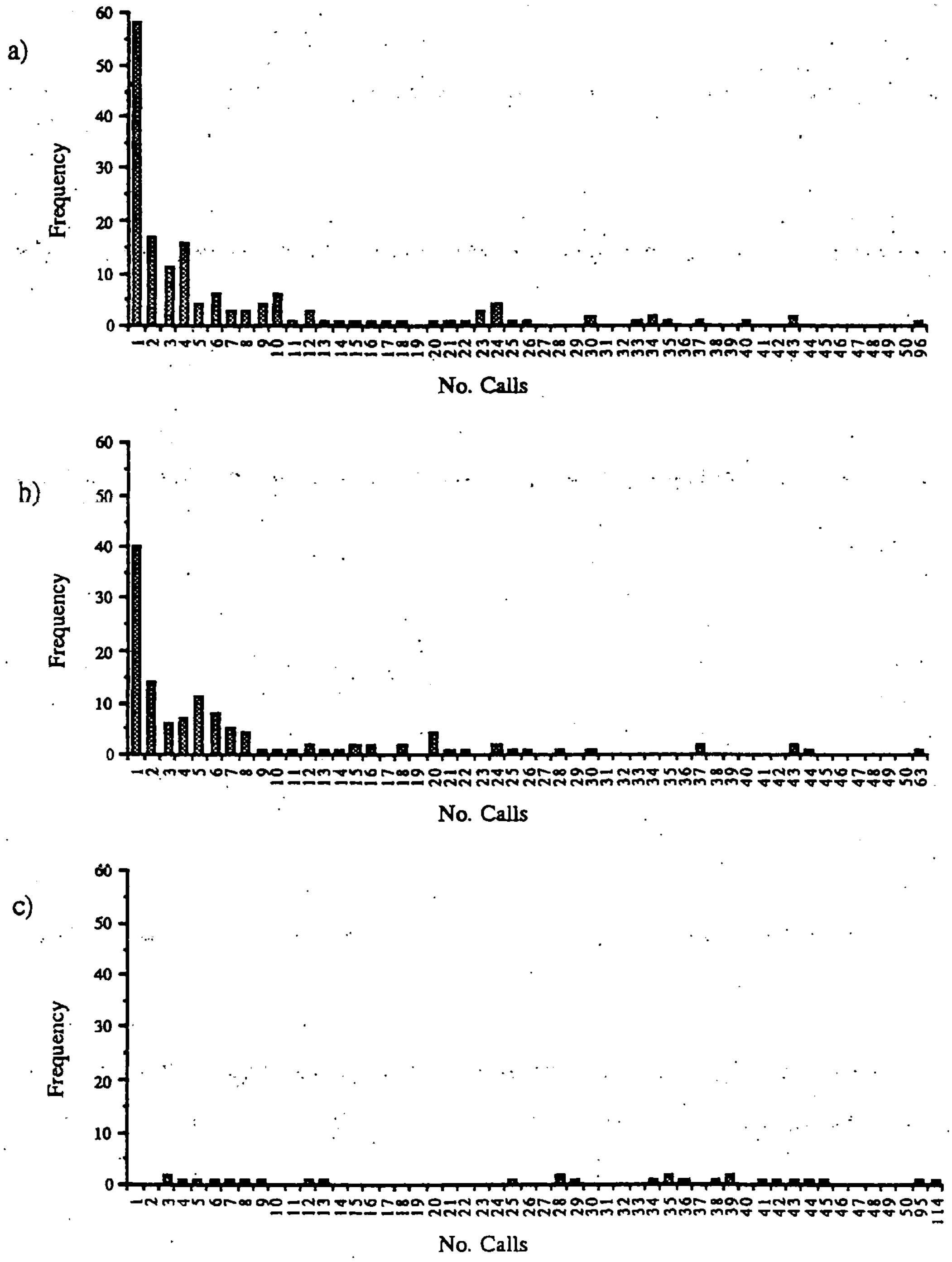


Fig. 8.4: Number of calls per bout for a) clucks; b) whistles and c) mixed bouts. Data from Kuala Lompat, 1988 and 1989.

8.3.2 Contextual observations

Diurnal pattern in calls

Calling at Kuala Lompat during the two calling periods in 1988 and the one calling period in 1989 showed few obvious patterns. There was no half-hour period throughout the day when one call type could be predicted to be heard or not heard (Table 8.3a&b). There were a few trends, however.

Clucks were heard during all half-hour periods between 0730 and 1900 (Table 8.3a and Fig. 8.4). No clucks were heard during the periods 0630 - 0700hrs (n = 3 days) and 0900 - 0930hrs (n = 11 days) in the morning or 1900 - 1930hrs (n = 11 days) and 1930 - 2000hrs (n = 3 days) in the evening. Clucks were heard on more days than not during the periods 0730 - 0900hrs and 1830 - 1900hrs ($\chi^2 = 5.81$, d.f. = 1, $p < 0.05$; see Table 8.3a). Between 0900 and 1000hrs and 1730 and 1830hrs, clucks were heard on more days than not, but this is only just over half of the days and does not represent any predictable pattern. The variation in average cluck calling level between half hour periods is shown in Fig. 8.5 (averages of 11 days, except where noted). Clucks were often given as a response to the observer and loud noises, such as hornbill calls and crashes from tree falls.

Tchorrs were heard rarely (n = 7 bouts) and as such little can be deduced about their calling pattern (Fig. 8.5).

Whistles were heard on at least one day during every half-hour period between 0700 and 1930hrs except 1500 - 1530hrs. Call bouts could be heard most consistently, however, between 0700 and 0830hrs in the morning and 1830 and 1930hrs in the evening, but even this is not predictable ($\chi^2 = 1.32$, d.f. = 1, N.S.; see Table 8.3b). Even during these periods, whistles were heard only on just over half the days, except during 0800 to 0830hrs (Fig.8.3b). Mean number of whistles per half-hour period is highest between 0700 and 0800hrs in the morning and 1830 and 1930hrs in the evening. The range, however, is considerable (Table 8.3b and Fig. 8.5).

Diurnal pattern in call bouts

The most striking feature of the diurnal call bout pattern is the extremely low mean number of bouts of any call type heard during any one half-hour period (Fig. 8.6). When averaged a)

	Time of day																									
	0630	0700	0730	0800	0830	0900	0930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530	1600	1630	1700	1730	1800	1830	1900	1930
No. days calls	0	0	7	8	7	6	6	5	5	3	4	4	4	4	5	5	5	5	5	4	5	4	6	6	8	0	0
No. days no calls	3	11	4	3	4	5	5	6	6	8	7	7	7	7	6	6	6	6	6	7	6	7	5	5	3	11	3
Min. no. calls	0	0	1	2	1	1	6	7	2	8	9	12	1	1	2	1	2	1	12	1	1	6	1	2	1	0	0
Max. no. calls	0	0	41	93	52	11	54	25	101	65	30	96	48	31	111	72	45	7	37	75	34	18	43	54	33	0	0
Mean no calls	0	0	10	14	10	3	21	6	15	12	6	16	8	6	15	8	7	3	10	11	6	4	8	10	6	0	0
Total	0	0	101	150	106	33	236	68	160	127	71	178	89	66	170	96	80	23	109	119	70	41	95	113	67	0	0

b)

	0630	0700	0730	0800	0830	0900	0930	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1530	1600	1630	1700	1730	1800	1830	1900	1930
No. days calls	0	6	6	8	5	2	4	4	3	2	1	1	1	2	3	3	3	0	1	2	2	2	3	2	6	6	0
No. days no calls	3	5	5	3	6	9	7	7	8	9	10	10	10	9	8	8	8	11	10	9	9	9	8	9	5	5	3
Min. no. calls	0	5	11	1	1	13	3	3	5	9	2	1	26	13	3	2	2	0	11	3	6	5	7	2	22	20	0
Max. no. calls	0	43	55	22	16	16	14	5	55	35	2	1	26	16	24	37	4	0	11	5	21	16	31	44	113	50	0
Mean no calls	0	16	10	6	3	3	3	1	6	4	0.2	0.1	2	3	3	4	1	0	1	1	2	2	4	4	34	21	0
Total	0	173	110	67	34	29	36	15	68	44	2	1	26	29	32	42	8	0	11	8	27	21	46	46	371	234	0

Table 8.3: Duirnal pattern of number of calls heard throughlight daylight hours. a) number of clucks b) umber of whistles. $N = 11$ days except for 0630 - 0700hrs and 1930 - 2000hrs when $N = 3$. The maximum and minimum number of calls give the maximum and minimum number for the days when there were calls. As indicated by the values for the number of days with no calls, across al 11 days, every half-hour had a minimum of zero.

over the 11 days on which observations were made, the highest frequency of bouts heard during any half-hour period in a day was less than three bouts.

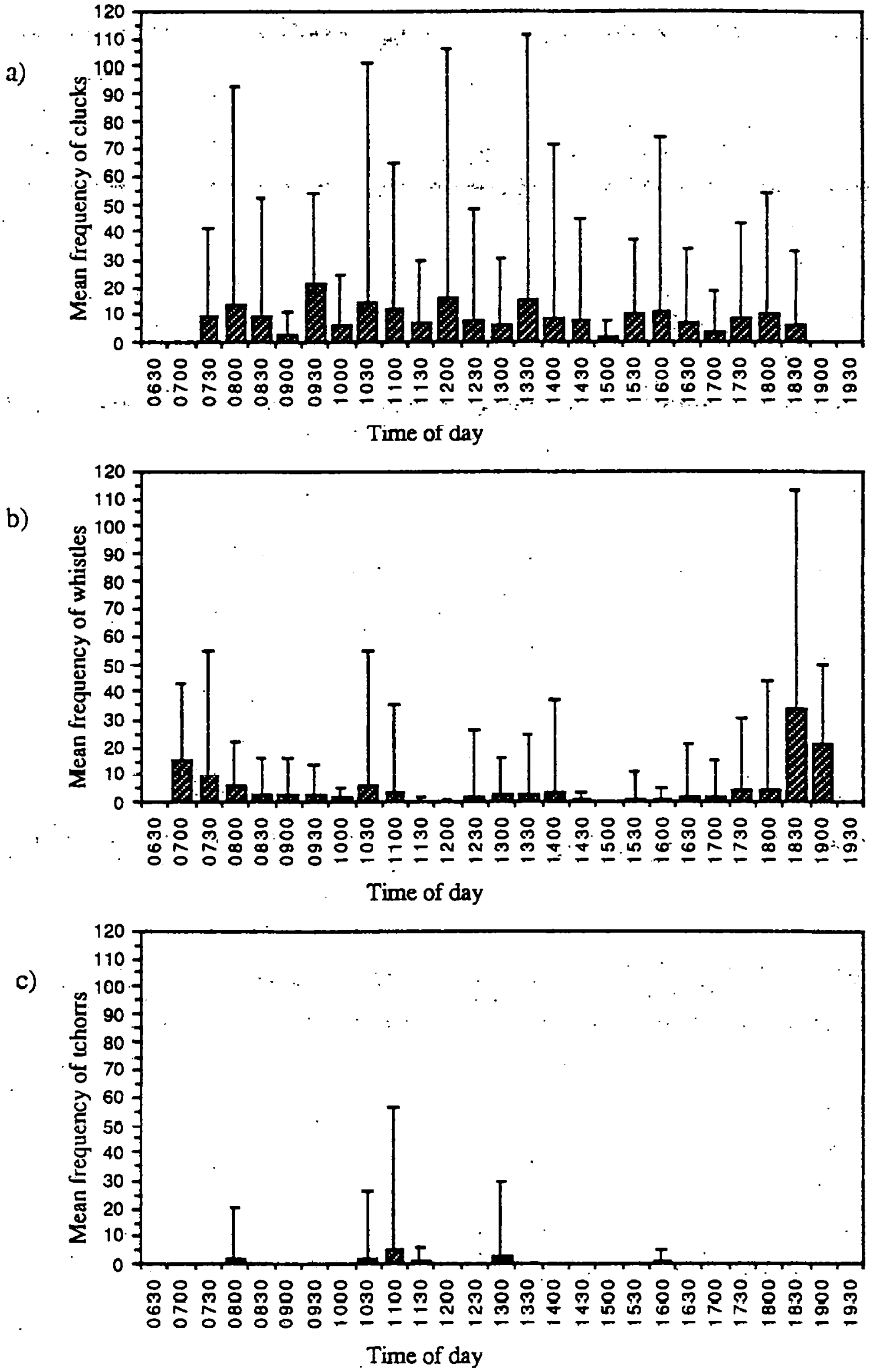


Fig. 8.5: Mean rate of calling in each half-hour period for a) clucks; b) whistles and c) tchorrs. Data are from Kuala Lompat in 1988 and 1989 and values are means for 11 days, except for 0630-0700hrs and 1930-2000hrs, which are means for 3 days. The range bars indicate maximum values; minima were all zero.

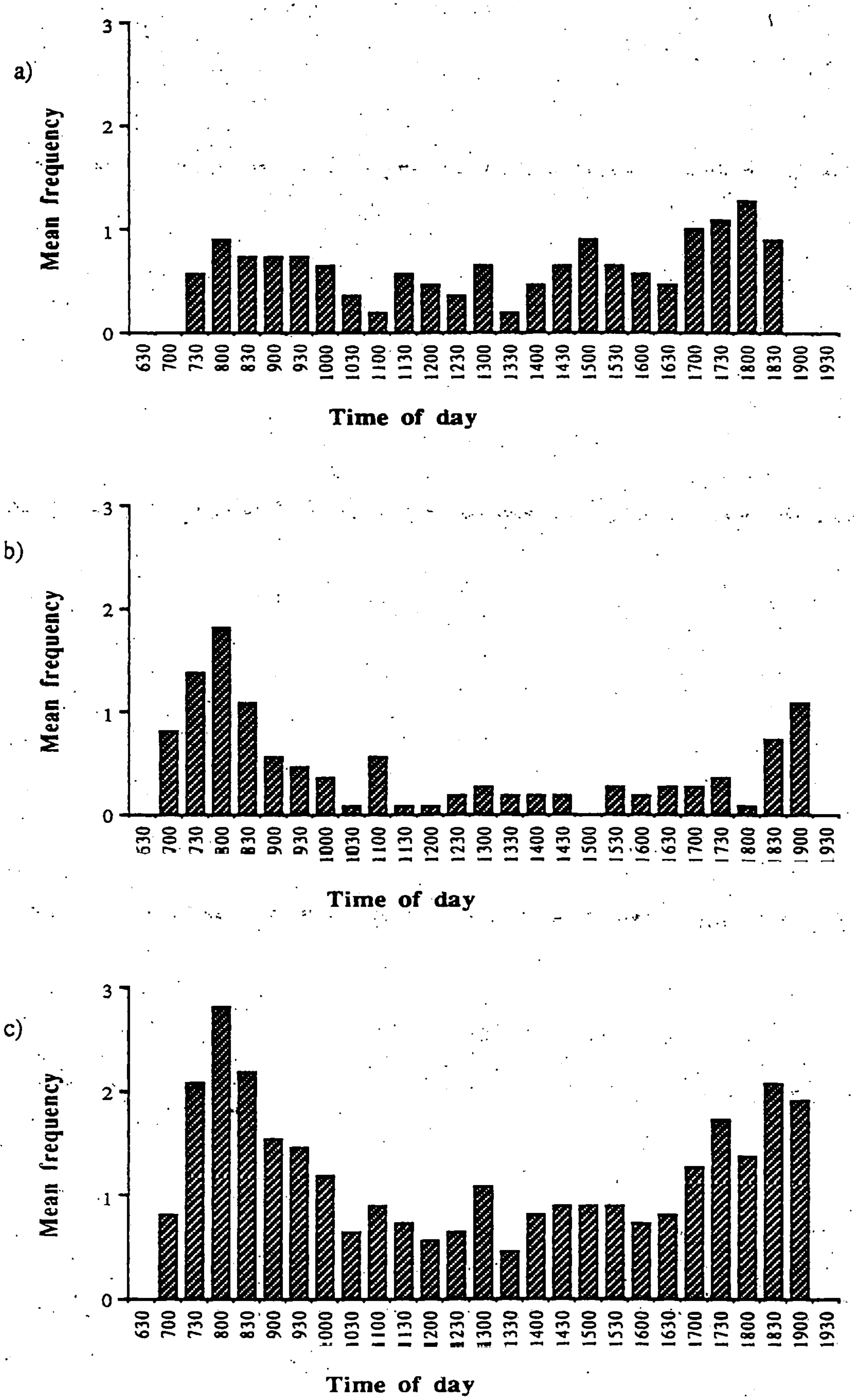


Fig. 8.6: Mean number of call bouts of (a) clucks, (b) whistles, (c) all call types heard during each half hour period from 0630 - 2000hrs at Kuala Lompat in 1988 and 1989. Frequencies are means for 11 days (0700 - 1930hrs) or 3 days (0630 - 0700hrs and 1930 - 2000hrs).

Within a call type, the only pattern readily apparent is the tendency for whistle bouts to be heard more often in the morning and evening than during the rest of the day (Fig. 8.6).

Although when summed over enough days, a pattern does emerge, this does not seem to constitute a predictable daily chorus, especially when considering that calls are not heard every day during these periods (Table 8.3). Fig. 8.6 indicates that more whistle bouts were heard during the morning peak (0700 - 0900hrs) than the evening peak (1830 - 1930hrs), but Fig. 8.5 shows that there are more calls during the evening peak than the morning peak. Together, these imply that bouts given in the evening are longer than those given in the morning.

Influence of a call on calling immediately afterwards

From simple observation, it is impossible to objectively determine whether any particular call is a 'response' to another call or not (*i.e.* it is 'spontaneous'). Nonetheless, inspection of calls used during instances of simultaneous calling may provide some useful information. Birds were regarded as calling simultaneously if an individual was heard calling within one minute of another bird. Although this definition is arbitrary, the log. survivorship plot of inter-calls (Fig. 8.3) suggests that this time is a reasonable estimate. The duration of periods of simultaneous calling varied from one bird calling once within a minute of another individual to birds calling simultaneously for 44 calls (Fig. 8.7).

29 instances of simultaneous calling were recorded; 24 involved two birds, four involved three birds and one involved four birds. Although both call types were heard at least once during most instances of simultaneous calling (86% of bouts contained whistles and 72% contained warks), most responses were whistles (79%). 23 of the 29 instances of simultaneous calling (79%) have whistles as the last call and only six interactions (21%) have warks as the final call ($\chi^2 = 9.96$, d.f. = 1, $p < 0.01$).

Half of all 'responses' (51%) occur after 1830hrs, but only 21% of instances of simultaneous calling, reflecting longer periods of simultaneous calling in the last hour of daylight. As noted above, this is also the peak time for whistles, the commoner call heard as a 'response' during simultaneous calling.

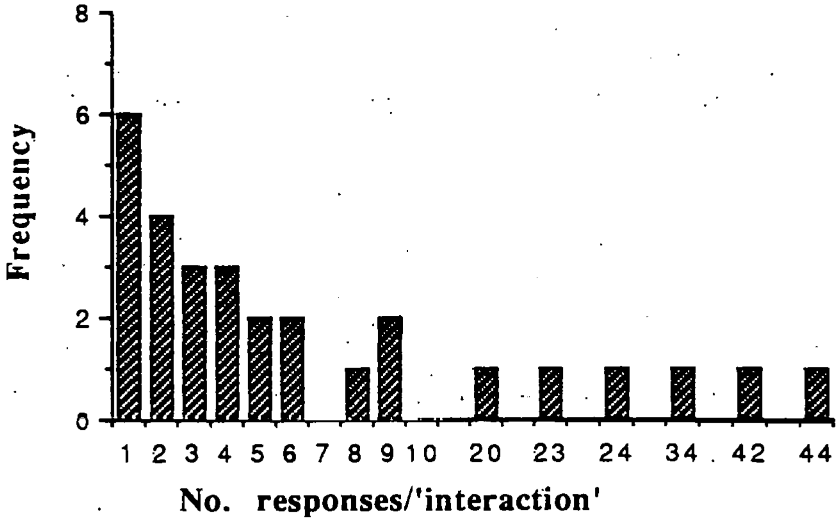


Fig. 8.7: Instances of simultaneous calling (see text) at Kuala Lompat in 1988. No. responses/'interaction' refers to the number of times that a male called within a minute of a conspecific in each instance of simultaneous calling. The frequency of such instances is shown. Note that the x axis has been condensed at the right hand end.

Influence of the overall calling pattern on calls given

Comparison of the overall calling patterns during the two periods of calling at Kuala Lompat during 1988 reveals that the distribution of call bouts between call types was similar in both periods (Table 8.4). In addition, the length of wark bouts was similar between February and April ($p > 0.4$, Mann Whitney U test), as was the length of whistle bouts ($p > 0.07$, Mann Whitney U test). This suggests that if the calling levels are similar (number of bouts), call types are given in bouts in similar proportions. However, this gives no information on how, if at all, different calling levels influence calling patterns.

Month	cluck	cluck/ tchorr	tchorr	cluck/ whistle	whistle	Total
February	66	0	1	19	51	137
April	65	1	0	7	51	124
Total	131	1	1	26	102	261

Table 8.4: Number of call bout-types heard at Kuala Lompat in two periods of calling in 1988 only. The distribution of bouts between the possible combinations is not significantly different between the two months ($\chi^2 = 6.98$, d.f. = 4, $0.20>p>0.10$).

8.3.3 Call playback experiments

Variation in overall calling levels between calling periods

As a background to the results obtained from call playback, Table 8.5 gives the overall pattern of calling for the days sampled during the two calling periods in March and May. Although not directly comparable with Kuala Lompat (different site, different year and non-playback vs. playback), it is obvious that there is a considerable difference from 1988 and 1989 Kuala Lompat data in the number of tchorr bouts heard.

Month	cluck	cluck/ whistle	cluck/ tchorr	cluck/ tchorr/ whistle	tchorr	tchorr/ whistle	whistle	Total
March	30	0	12	3	5	0	2	52
May	35	2	7	7	19	5	26	101
Total	65	2	19	10	24	5	28	153

Table 8.5: Overall level of calling in the two calling periods at Pasoh in 1990. The distribution of bouts between the possible combinations is significantly different between the two months ($\chi^2 = 26.02$, d.f. = 6, p = 0.001).

There is a significant difference ($\chi^2 = 26.02$, d.f. = 6, p = 0.001) in the total number of call bouts heard between the two months - virtually twice as many bouts were heard in May as in March. By inspection, it is apparent that the difference is due to an increase in the number of tchorr, tchorr/whistle and whistle bouts.

Call playback experiments

Initially, the utility of the technique for investigating the function of the calls was assessed: *i.e.* does playback alter calling in a measureable way? Fig. 8.8 shows the pattern of calls following playback. Fig. 8.8 gives the distribution latencies to all bouts following playback and the distribution of first bouts following all playbacks. What is most apparent from both graphs is the peak of bouts within ten minutes of the start of a stimulus call.

Comparison with a similar analysis from the two calling periods at Kuala Lompat in 1988 (distribution of latency to first bouts and all bouts from the start of an hour) suggests that this peak is due to the playback of stimulus calls. Therefore, playback does seem to alter the pattern of calling by eliciting response calls and all calls heard within 10 minutes of the start of a playback tape were considered the best estimate of such response calls.

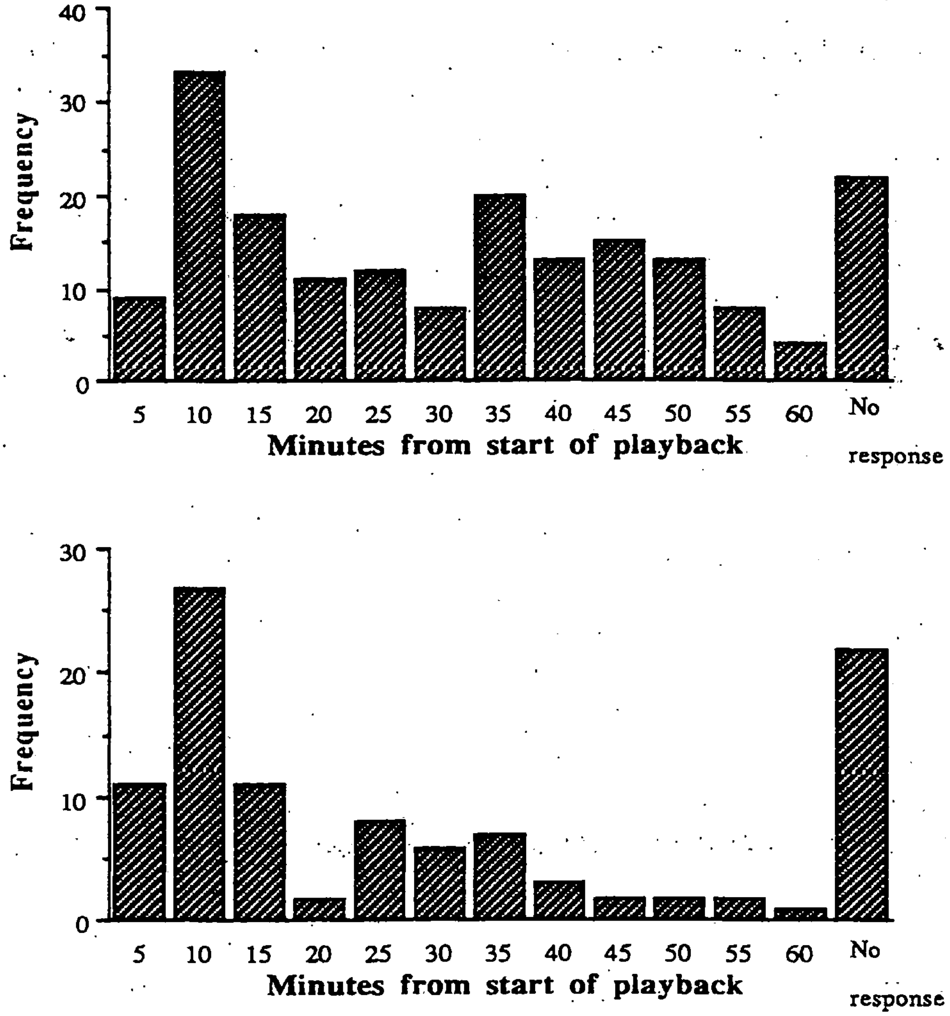
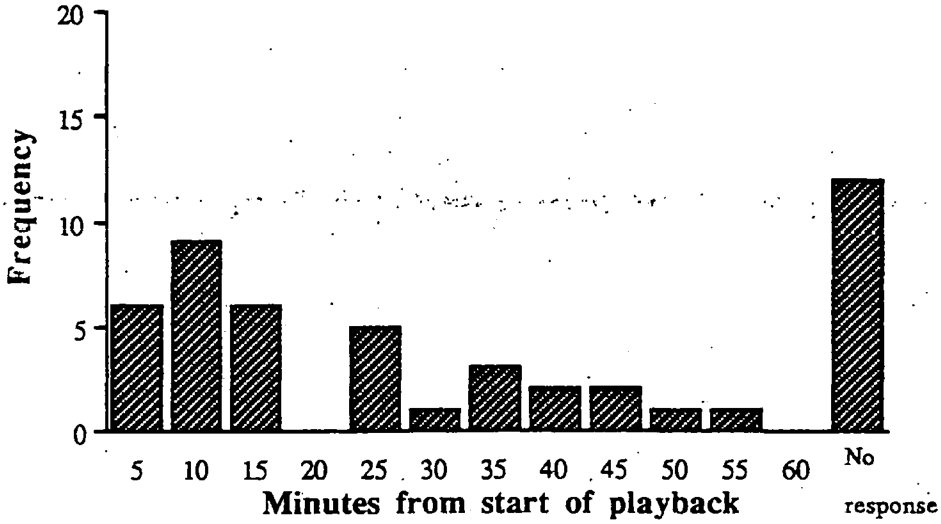


Fig. 8.8: Pattern of calls in each 5-minute interval following a playback: the upper graph gives the frequency of calling bouts (99 playbacks, 164 call bouts) and the lower graph gives the time to the first call after the start of a playback (101 playbacks).

A response call bout has two obvious properties - latency from the start of the stimulus call bout and call type(s) given in the response bout. These may vary independently.

Latency to first call

A comparison of the distribution of latencies to first call between the two different stimulus calls will test the null hypothesis that each stimulus influences the distribution of latencies to first call in a similar way. Considering both March and May calling periods, there was no overall difference in latency to first call between the two stimulus call types (p = 0.29, Mann Whitney U test, $n_1 = 40$ and $n_2 = 44$ and see Fig. 8.9). However, this may mask underlying differences. Therefore, latencies were compared, firstly, within calling periods (March or May) and between stimulus call types (wark or whistle) and, secondly, within stimulus call types and between calling periods. Results are given in Table 8.6.



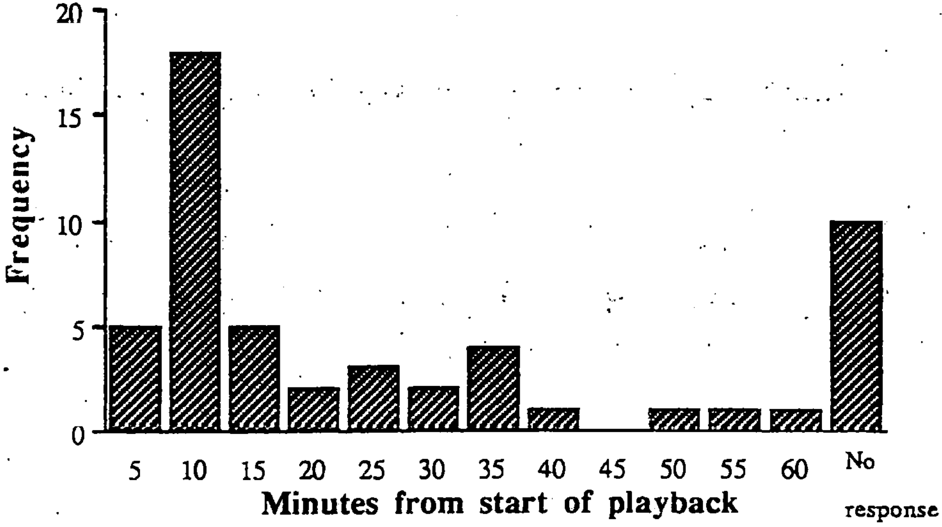


Fig. 8.9: Time to first call from the start of playback tape: upper graph gives the results for the cluck stimulus tape and the lower graph gives the results for the whistle stimulus tape.

The first call after a whistle stimulus is given significantly faster than that following a wark playback in March ($p < 0.01$, Mann Whitney U test $n_1 = 18$ and $n_2 = 19$). In, May, however there is no significant difference (p = 0.20, Mann Whitney U test $n_1 = 19$ and $n_2 = 24$).

When compared within stimulus call type, it is apparent that this is because wark playbacks are responded to significantly faster in May than in March ($p < 0.05$, Mann Whitney U test $n_1 = 18$ and $n_2 = 19$), whereas there is no significant difference in latency following a whistle playback ($p > 0.05$, Mann Whitney U test $n_1 = 18$ and $n_2 = 24$). In other words, the lack of difference in latencies between the playbacks in May is due to first calls after warks being given more quickly than in March.

Comparison	**Month/ call type**	**Samples compared**	**P**
Between stimulus call types	Overall	Wark vs Whistle	0.29
	March	Wark vs Whistle†	<0.01**
	May	Wark vs Whistle	0.20
Between months	Wark	March vs May†	<0.05*
	Whistle	March vs May	>0.05

Table 8.6: Latency to first call from the start of a playback tape. Latencies were compared using the Mann Whitney U test (see text for sample sizes).* = $p < 0.05$, ** = $p < 0.01$, † = faster response.

Call type given as a response

If a call bout given within 10 minutes of the start of a stimulus call is deemed a response, the type of call given as a response can be compared with the overall proportion of call types given. This will indicate if particular call types are more likely to be given as a response than spontaneously. In addition comparisons between stimulus call types and calling periods will indicate whether these variables influence response calling.

Month	**Stimulus call bout**	**N**	**No. responses**
March	wark	26	5 (19.2)
	whistle	26	12 (46.2)
May	wark	26	12 (46.2)
	whistle	28	14 (50.0)

Table 8.7: Number of responses to each stimulus tape in each month. N = number of playbacks and numbers in parentheses are percentages.

The number of responses that each stimulus call elicited in each month is given in Table 8.7, There were more bouts given as a response in May than March. As with the latency to first call, the whistle stimulus elicited the stronger response in March - more tchorrs and whistles.

The increased level of calling in May is associated with tchorrs being given in more bouts overall and as responses to both stimulus tapes.

Table 8.8 indicates which combinations of call types were included in bouts given as responses to each stimulus call type in each month, together with the number of each call-bout type given overall (the latter from Table 8. 5). In March, there are markedly more bouts given in response to whistles than to warks, which is to be expected considering the significant difference between latencies to first call following each stimulus call type noted above. Unfortunately, sample sizes are too small to test for significance.

Stimulus tape	cluck	cluck/ whistle	cluck/ tchorr	cluck/ tchorr/ whistle	tchorr	tchorr/ whistle	whistle	Total
a)								
Warks	4 (80)	1 (20)						5 (100)
Whistles	5 (42)	1 (8)			5 (42)	1 (8)		12 (100)
Control	30 (58)		12(23)	3 (6)	5 (9)		2 (4)	52 (100)
b)								
Warks	3 (25)		3 (25)	2 (17)	2 (17)	1 (8)	1 (8)	12 (100)
Whistles	1 (7)	2 (14)		1 (7)	3 (21)	3 (21)	4 (29)	14 (100)
Control	35 (35)	2(2)	7 (7)	7 (7)	19 (19)	5 (5)	26 (26)	101 (100)

Table 8.8: Combinations of calls given in bouts as responses to each stimulus tape in (a) March and (b) May. (Numbers in parenthese are percentages). 'Control' refers to the total number of each call bout type given, whether as a response or not.

Despite small numbers of responses, it seems that the proportion of call bout types is different between the responses to whistle playback and the overall pattern. Particularly striking is the very high proportion of tchorr bouts given as a response to whistles (42% of responses) compared to the proportion of this bout type given naturally. In fact all these tchorr bouts were given as responses to whistle playback - none were given at any other time in March.

In May the number of each call type given as a response is also small and there are no siginificant differences between the type of call given as a response to whistle playback and those given as a response to wark playback ($\chi^2 = 3.11$, d.f. = 2, N.S.). Several trends are, however, evident. Bouts given as responses to whistles tended to contain whistles (10/14) and tchorrs (7/14) rather than clucks (4/14), whereas more bouts given as responses to warks contained clucks (8/12) and fewer contained whistles (4/12). A similar proportion contained tchorrs (8/12).

Influence of call playback on overall calling level

As well as influencing response calling, playback may well influence the overall pattern of calling in the hour following the start of a playback (Table 8.9). Comparisons between stimulus call type within calling period reveals no significant difference in the number of times each call type was incorporated in a call bout between stimulus call types in March ($\chi^2 = 0.51$, d.f. = 2, $p > 0.05$) or May ($\chi^2 = 2.24$, d.f. = 2, $p > 0.05$). Between months, however, there are significant differences in the overall pattern of calling following both wark ($\chi^2 = 6.11$, d.f. = 2, $p < 0.05$) and whistle playback ($\chi^2 = 11.26$, d.f. = 2, $p < 0.01$). Both differences seem to be due to an increase in the number of times that tchorrs and whistles were used in bouts.

			Call type	
Month	**Stimulus**	**Clucks**	**Tchorrs**	**Whistles**
March	Wark	22	8	2
	Whistle	23	12	3
May	Wark	27	16	15
	Whistle	24	21	25

Table 8.9: The number of bouts containing each call type in the hour following each of the two stimulus tapes in each month. There are no significant differences between the number ot times each call was given as a response to the two tapes within a month (*i.e.* in March or in May).

8.3.4 Individual differences in calling behaviour

The call bouts given by each calling individual are summarised in Table 8.10. There were twice as many individuals calling in May as in March and each individual called more often. The number of bouts containing tchorrs and whistles was also higher in May than March.

Table 8.10 indicates that, within a calling period, there is a lot of variation among individuals in the type of call given in bouts. An increase in the number of bouts given appears to result in more tchorrs and whistles. Simple regression indicates that much of the variation between individuals in the total number of bouts given is accounted for by increase in the number of bouts containing whistles (Table 8.11).

Individual	No. bouts	No. bouts containing each call type clucks	tchorrs	whistles
a)				
A	11	9	3	1
B	15	12	8	2
C	11	9	4	4
D	14	12	5	0
b)				
A	18	4	7	8
B	25	8	14	14
C	10	3	2	6
D	9	8	3	1
E	24	19	6	10
F	19	9	3	9
G	10	2	6	4
H	4	2	4	1

Table 8.10: Number of bouts and the call types that they contained for all individuals in a) March and b) May 1990. *N.B.* Individual A in March is not necessarily A in May *etc.*

Call type	Slope	R^2
cluck	0.46	0.34
tchorr	0.33	0.42
whistle	0.59	0.68

Table 8.11: Slope and R^2 for the regression of each call types on the total number of bouts heard. R^2 gives the proportion of variance in the total number of bouts explained by variance in each of the call types. N = 12 for both March and May.

8.3.5 A preliminary test of the 'hotshot' hypothesis

Playback in March 1991 at Kuala Lompat elicited responses and did start other birds calling (Fig. 8.10). Four birds were calling by the end of the experiment. Only one of three locations (location A) from which I tried playbacks elicited many calls, hence the plateaux at positions B and C. Several of the response calls were distorted, varying considerably from calls given during calling periods in frequency and duration. The commonest distortion was an inability to raise the frequency of the whistle in the second half of the call (*c.f.* Fig. 8.1). Instead, the second half of the call was of wider frequency and considerably less tone-like.

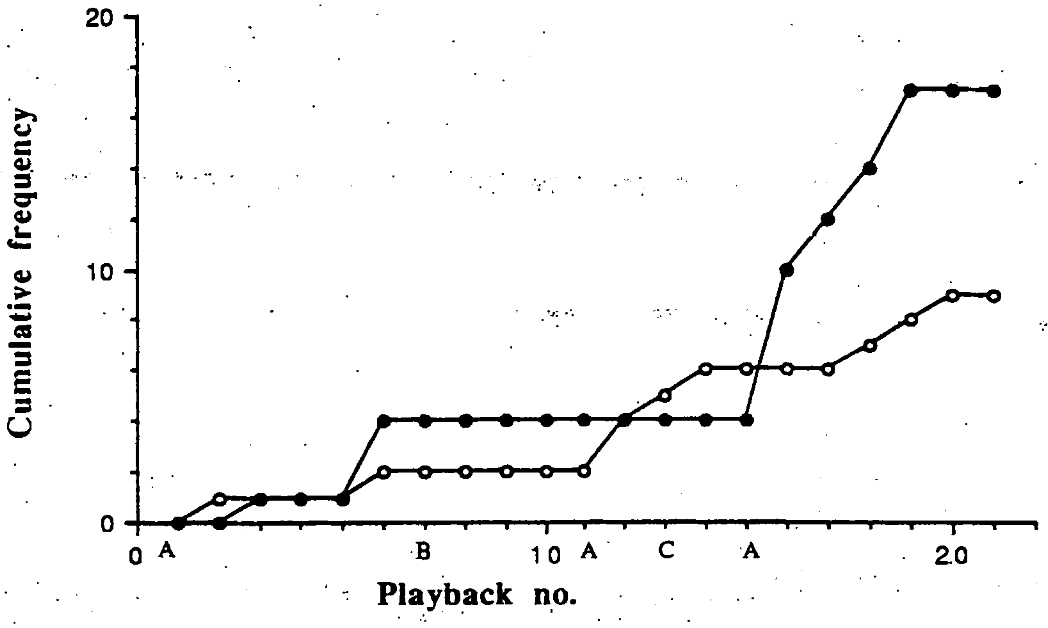


Fig. 8.10: Cumulative frequency of call bouts given during the test of the hotshot hypothesis. The calls are split into two categories, those given as a response - o - (*i.e.* within 10 minutes - see Section 8.3.3) and those given not as response (*i.e.* not within 10 minutes) - • - to the 21 call playbacks. Letters along the bottom axis indicate each time that I moved position (A, B or C) to conduct playbacks.

8.4 Discussion

Vocalizations of the Malaysian peacock pheasant may be regarded structurally as calls *i.e.* they are short and simple (Catchpole, 1979). Functionally, however, there are similarities with song as the vocalizations are probably primarily associated with breeding (discussed in Chapter 9) and are almost exclusively given by males.

8.4.1 Function(s) of the calls

Several results indicate function and these are;

(a) clucks are heard occasionally outside calling periods (Chapter 3);

(b) clucks are heard when the observer is very close and immediately after loud noises (hornbill calls, treefall crashes *etc.*);

(c) call bouts which contain more than one call type follow the sequence cluck → tchorr → whistle;

(d) during simultaneous calling, whistles were the last call in 80% of instances;

(e) when there was relatively little calling at Pasoh in March 1990, whistles playbacks elicited many more responses than warks;

(f) in May 1990, more individuals called, each called more and responses to both stimulus tapes were rapid. Unfortunately, sample sizes are small, but more response bouts contained tchorrs and whistles than in control bouts.

From these results I suggest that, rather than performing separate functions the call types described form a call type hierachy representing escalating levels of sexual motivation. I suggest that condition determines an individual's postion in this hierarchy. Clucks are the most 'general purpose' call, given occasionally outside the calling period and perhaps respresenting a basic 'species recognition' call. Individuals that are in better condition are more sexually motivated and give more tchorrs and whistles. I shall further explore this in the Chapter 9 in a qualitative model of behavioural thresholds.

The variation within the wark category from clucks to tchorrs is not easily interpreted by Morton's (1977; 1982) motivation-structural rule, whereby low, harsh sounds are given in hostile encounters and high, pure tone-like sounds are given in appeasing contexts. The clucks do conform to the hostile structure and are given in alarm situations (8.3.3) as well as at other times. Tchorrs are higher pitched and also harsh sounds, but the 'motivational' context is less easy to determine. As noted above, the calls seem likely to form a hierarchy which can be used to indicate the condition and sexual motivation of the caller and therefore this could be communicating an aggressive message to other males or an attractive message to females. According to Morton's motivation-structural rules, calls carrying these two messages should have very different structures. Whistles represent a further shift towards high, tone-like sounds which are implicated in appeasement. These calls may, however, have more significance for receivers of one sex than of the other. Thus, if Morton's rule is universal, an individual is hostile when clucking (repelling other males), but is appeasing and "friendly" when whistling, with tchorrs somewhere in between (attracting females more than clucks but less than whistles).

8.4.2 Individual differences

Considering the theme of individual differences in morphological and behavioural ornaments, I shall briefly mention individual differences in calling behaviour. Although, I could not see the calling individuals, I felt that I could attempt to determine calling territory boundaries (see Section 8.2.3). There are very marked differences between individuals in both the amount of calling and the duration and composition of call bouts. Such variation could provide the basis for females and other males to discriminate between calling individuals simply on, say, the frequency of bouts containing tchorrs and/or whistles. These are very crude differences (to a human observer at least) and may preclude any need for 'finely-tuned' differentiation based on the properties of the calls themselves. Differences between individuals in frequency and duration characteristics of calls have been demonstrated in the bobwhite quail *Colinus virginianus*, a member of the same family. In this species, it has been suggested that although frequency characteristics might serve individual identification, duration characteristics potentially show much greater inter-individual variation (Baker and Bailey, 1987). I shall place this variation in the context of individual differences in scrape maintenance in the qualitative model of behavioural threshholds introduced in the next chapter.

8.4.3 Environmental constraints

The Malaysian peacock pheasant has two categories of long-distance call, wark and whistle, one of which (warks) grades between extremes which are often given as distinct call types (clucks and tchorrs).

There are considerable structural differences between warks and whistles and within the 'warks' category (*e.g.* duration and frequency characteristics). This probably has several consequences such as:

(i) influencing the propagation of the calls. Long-range communication in any habitat should use the lowest frequencies possible (Wiley and Richards, 1982) because they attenuate less than higher frequencies. Close to the ground, there is also boundary interference which affects frequencies in the range 0.5 - 1 kHz within 1 - 2m of the ground.

Wiley and Richards cite Galliformes - some grouse and cracids - as examples of birds giving extremely low frequencies near to the ground. The Malaysian peacock pheasant call type that has the lowest frequency range (780 - 1184 Hz) is the whistle. This call is often given from the roost at dawn or dusk and hence above the 2m or so which affects these low frequencies. Within Neotropical forest, it has been suggested that there is a frequency 'window' at ground level within which a call carries much further than calls of higher and lower frequency (this is between 1585 - 2500 Hz [Morton, 1975] and 500 - 2000 Hz [Marten *et al.*, 1977] in Panama). Waser and Waser (1977) report a sound window at around 125Hz in the canopy at Kibale Forest, Uganda. Waser and Brown (1984) report flaws in the methodologies of these three studies, but do record sound windows at about 200 Hz in the canopy of a Kenyan rain forest and suggest that they are a potent factor in the evolution of primate communication. The whistles are within such windows which are close to the ground, but clucks and tchorrs are partially outside any recorded sound window. The consequent rapid attenuation of the clucks, however, is probably unimportant in an alarm context. Although there are uncertainties about the methods by which sound windows have been measured, it does appear that the acoustic transmission conditions within a tropical forest can vary a great deal within a few minutes. Thus it is possible that the sonographic variety of the call types has evolved to ensure that there is at least one call type which is not degraded too severely, whatever the transmission conditions. Hence, an individual could transmit its message under any weather conditions;

(ii) brief calls of wide frequency range are easily located (Marler, 1959). Such calls are used for alarm and also in aggressive encounters between breeding males in the gregarious Californian quail *Lophortyx californicus* (Williams, 1969) and are implied, at least in part, for the similarly gregarious red junglefowl (Collias and Collias, 1987). On inspection, a similar relationship seems likely to exist with the Malaysian peacock pheasant. 'Warks' include alarm calls (the clucks), as well as calls given in different contexts (the tchorrs), but with considerable gradation (even within a call bout) between these two extremes. Gatehouse and Shelton (1979) report that bobwhite quail have a greater tendency to orientate to high frequency stimulation. Although this result has been interpreted as localization being easier at high frequencies, it merely suggests that the quail are more likely to respond to the higher frequencies in the 'separation' call. It does also raise the possibility that different frequencies may be more easily located at different distances from the source [see (i) above].

(iii) Locatability is also enhanced by call repetition and some frequencies are more easily located than others. For example, the two calls that Californian quail give to bring individuals together from long distances have restricted frequency range and extended duration and are suggested as intermediate between the easy to locate vertical configuration and the difficult to locate horizontal configuration (Williams, 1969). This may well be a trade off between attracting conspecifics and not alerting potential predators.

In conclusion, clucks, tchorrs and whistles seem to have very different transmission qualities. The frequencies of whistles fall within the previously recorded range of the sound windows close to the ground found by Morton (1975), although it is possible that South-east Asian rain forest may have a different sound window than Afro- or Neo-tropical rainforests. The problems associated with the frequencies of the whistle at ground level are removed when the bird is above about 2m and this is often the case as the call is given from the roost on many occassions. The clucks have characteristics which make them easy to locate, whereas the tchorrs and whistles are more difficult to locate. The long call bouts often heard increase locatability and, consequently, it seems probable that long bouts are used when the sender is 'advertising' its location.

8.4.4 The 'hotshot' hypothesis

It was not possible to rigorously test the 'hotshot' hypothesis by playing back the calls of a number of a 'hotshot' and a satellite male and comparing the responses. Nonetheless, I have demonstrated that males can be stimulated to call at times when they would not otherwise be calling by call playback (representing the presence of a calling male). If food is important in determining the level of calling (see Chapter 9), then it is possible that a male is demonstrating that he is a 'hotshot', simply by calling. The results of this single experiment may suggest that the observed dispersion of calling individuals is at least partly due to the presence of a particular calling male (a 'hotshot') which stimulates those around him to call.

This is, however, a weak test of the 'hotshot' hypothesis; the results of the experiment could simply be due to vocal facilitation.

CHAPTER 9: GENERAL DISCUSSION

"Because ornithology was born in the north temperate zone where broods tend to be large, we ask why the broods of tropical birds are so small. If more ornithologists had grown up in the tropics, we would be asking why birds at high latitudes lay so many eggs - a question easier to answer." Skutch (1985)

This study gathered detailed quantitative data relating to sexual selection in a non-lekking tropical forest bird species. It demonstrates that information can be gathered to describe features of the mating system without observing copulations. By being forced to reduce the emphasis on what can be seen, novel types of data were collected on the mating system of a tropical forest bird. This should benefit studies of sexual selection as it provides a different perspective than has previously been obtained by watching a small repertoire of behavioural patterns at fixed leks. The data collected provide a necessary framework within which to study selection pressures on reproduction in this species. The thesis describes the variation between males in a variety of ornamental traits and indicates that females are presented with variation among males in behavioural and morphological characters. In this discussion I shall first summarise the main results and then propose a qualitative model of the evolution of these features and finally indicate how this model can be tested.

9.1 Summary of behavioural results

The most striking result from the field study was the apparent infrequency of periods of calling and display scrape maintenance. These two activities occurred early in the year at Kuala Lompat in the first two field seasons, but not in the two subsequent field seasons. In any year of the study, it is conceivable that there may have been calling outside my field season. In one such silent field season at Kuala Lompat, however, these two activities were evident at Pasoh, less than 150km away.

Not all of the available micro-habitats within the primary forest were used by the birds, some areas were being consistently avoided. Outside calling periods, the males did appear to use micro-habitats within the home range differentially, but no general pattern emerged. The females did not use particular micro-habitats within their home ranges more than others. Within calling periods, however, males showed very strong micro-habitat preferences for exhibiting two activities, namely calling and maintenance of display scrapes.

There were differences between calling periods in the number of birds that called, the types of calls given and the overall amount of calling. The number of display scrapes maintained also varied.

9.2 Summary of morphological results

There are several morphological features of the male which seem likely to be under sexual selection. These are traits which the males possess and females do not or which the male exhibits during display to the female. Among males the size of these traits varies much more than other (probably non-sexually selected) traits. It is difficult to state for certain whether these latter traits will be under different selection pressures in males than females (and hence under sexual selection in the classical sense [Selander, 1972]) because they possibly reflect some aspect of body size and thus may be under selection through male-male competition. Nonetheless, there does seem to be a clear separation of traits into two groups - sexually selected and non-sexually selected.

The two most notable results from the intra-specific morphological analysis were the number of sexually selected traits and their considerable variability among individuals. Identifying intra- or inter-sexual selection as the major route of selection is very difficult from a purely morphometric study. Whilst these two selective forces may act independently on some features, it is questionable whether they act separately on all features that differ between males and females.

Several male morphological characters appear to have evolved in concert with particular epigamic display elements, suggesting that they are potentially under selection through female choice.

9.3 Evolution of ornaments - a hypothesis

The above summaries paint a picture of considerable variation in behaviour and morphology and of temporal unpredictability in the expression of the behaviour patterns. What is the cause of this unpredictability and variability and how does it influence reproduction?

I suggest that the major cause of the variation in the expression of the behavioural ornaments is food availability. Halliday (1987) suggested that it is important to understand the energetics of sexual behaviour. For example, he proposed that males may vary in their abiliy to meet the energetic demands of some sexual or competitive behaviour patterns and this may strongly influence variation in male reproductive success. Calling is likely to be energetically expensive (see Ryan, 1988) and whilst an individual is cleaning a scrape it cannot be feeding. Whilst Halliday (1987) stressed that there is an acute lack of data on the energetic demands of sexual behaviour, there are some data on the energetics of avian vocal behaviour. Gottlander (1987), for example, found that experimentally manipulated food supply influenced song output in the pied flycatcher *Ficedula hypoleuca*. Consequently, a male Malaysian peacock pheasant that has access to a relatively large food supply should be able to call and maintain a display scrape. Thus, I propose that it is the abundance of food that determines whether males are able to call and maintain scrapes and, therefore, expression of these two behaviour patterns would indicate that a male is in good condition. It should be noted, however, that in a model of daily organisation of singing and foraging, the situation was found to be less clear (McNamara *et al.*, 1987). In this model of singing and foraging in a temperate monogamous passerine, they show that if the energetic gain from foraging and the advantages of attracting a mate are held constant throughout the day, there may still be considerable fluctuation in the amount of song produced during the day.

The availability of food may also influence the type of call given, the number of scrapes maintained and the duration of both activities. As proposed in section 8.4.1, it is likely that the different types of call do not perform separate functions, but are part of a hierarchy that is dependent on condition. Thus, a male that does not have access to much food would not be in very good reproductive condition and as a consequence would not call or make a display scrape. As more food is consumed, the male's condition would improve and calling and scrape maintenance become energetically feasible. Clucks seem to be the most basic type of call whereas tchorrs and whistles are given in more specific (usually interactive) contexts. As concluded in Section 8.4.1, whistles appear to be at the top of the hierarchy. I propose that this is probably because this is the most energetically expensive type of call and thus a male will whistle for as long as it can to demonstrate its condition. Maintaining one or more scrapes (as described by Davison [1983a] in mast fruiting years) at this time may be a large drain on an individual's resources. Therefore, possession of a display scrape may indicate the condition of a male, rather than its aggressive status, as proposed by Borgia *et al.* (1985). It is, however, likely that a male's condition will influence its status. I propose that there is a series of behavioural thresholds which males may attain during calling periods. These are; silent and no scrape, clucking and no scrape, different call types plus scrape, and ultimately many tchorrs, whistles and several scrapes. These thresholds may represent particular levels on a scale of male condition, the further along an individual is the more energetically expensive expression of these behavioural patterns is. Thus, although males may compete vocally, the condition that males are in may limit how many thresholds that they can cross. This should provide females with reliable information about male condition. If condition derives from occupying a territory that is rich in food, the behavioural threshold that a male obtains indicates male quality. Therefore, only males in good territories can exhibit the full range of behavioural ornaments (many tchorrs and whistles and several scrapes). That calling may be condition-dependent was suggested during the preliminary test of the 'hotshot' model. There was no calling 'naturally' and the responses to playbacks were distorted, particularly in the second part of the whistle (section 8.3.5). That ornaments are condition-dependent has been discussed by several authors (*e. g.* Halliday, 1978) and is a crucial assumption of Andersson's (1986) condition-dependent model. In this model, he proposes that, for a monogamous mating system, mating preferences and secondary sexual traits can be based solely on viability differences.

9.4 Variation in food supply

Is there any evidence that food limits the energy available for reproductive efforts? The only direct evidence that food abundance may influence the calling and scrape maintenance behaviour of the Malaysian peacock pheasant was alluded to in section 5.1. In one mast fruiting year Davison (1983a) found that invertebrate levels were much higher than in other years. Calling levels and the number of scrapes maintained were also much higher in the mast fruiting year.

Whilst considering that food may constrain reproduction, it is also worth noting that the Malaysian peacock pheasant is the only one of the 49 species of pheasant to lay a single egg clutch. Although only four nests have been found in the wild, each with a clutch of one egg (Davison, 1983a and Lambert, in Wells, 1990), this is supported by information from birds in captivity in Malaysia (Siti Hawa pers. comm. and Tunku Nazim pers. comm.).

Although the exact diet of the Malaysian peacock pheasant is unknown and probably variable (see Section 5.1), consideration of food restrictions on birds in the Sunda sub-region may prove informative. Because the amount of fruit on the forest-floor seems, typically, to be low and not a major food source for understorey birds and because the pheasants feed by scratching the leaf litter, it seems reasonable to assume that invertebrates form a substantial part of the diet for much of the year. Fallen fruit may, however, provide an occasional super-abundant source of both fruit and invertebrates feeding off the fruit. (Lambert [1987] has seen crested fireback pheasants *Lophura ignita* feeding on fallen fruit at Kuala Lompat).

Invertebrates occur at very low population densities and are from very diverse taxa in tropical forests (Whitmore 1984a). There seems to be very little information on spatial patterning of invertebrate communities in general or of particular taxa, but Wolda (1983) indicates that such data that exist suggest spectacular spatial dynamics when compared with temperate woodlands. Therefore, invertebrate populations might fluctuate unpredictably and this fluctuation may determine food availability to the Malaysian peacock pheasant. Hence, food availability may influence male Malaysian peacock pheasant reproductive behaviour. Fogden (1972) suggested that food ultimately controls the timing of breeding in birds in Sarawak in East Malaysia. He reported that insects are evenly distributed in space and time but that there is a relative 'lean season' in the two months immediately prior to the north-west monsoon. The lack of the vast seasonal variation in invertebrate abundance that is typical in temperate woodland results, Fogden argues, in prolonged parental care of smaller broods. Indeed, Fogden believes that during the 'lean season', insectivorous birds reduced all of their activities to simple maintenance level so as to limit energy expenditure. Because the fluctuations in invertebrate levels are much less pronounced in tropical forest than temperate woodland, this implies that tropical birds are sensitive to smaller differences in prey abundance compared to their temperate forest counterparts.

Inger (1980) found that densities of non-riparian frogs and lizards in three lowland primary rain forest sites on Borneo and in Peninsular Malaysia were approximately an order of magnitude lower than those reported from Central America. Karr (1972) found that the number of birds mist-netted close to the ground at Pasoh in Peninsular Malaysia was much lower than in Afro- or Neo-tropical rain forests and Janzen (1974) suggested that there is a lower animal biomass in forests with periodic mast fruiting. Janzen (1974) believed that the mast fruiting is an adaptation to satiate seed predators in areas with a climate favourable to animals but where poor soils hinder productivity and thus result in low animal biomass. Inger (1980) on the other hand, suggested that reduced animal biomass is a consequence of mast fruiting, rather than a cause. He suggested that mast fruiting results in reduced numbers of seed-eating insects in the intervening non-mast years. This, in turn, limits the numbers of arthropod predators and thus also floor-dwelling frogs and lizards. It is simple to envisage that the same mechanism may limit energy expenditure by male Malaysian peacock pheasants, which are also likely to be insectivorous secondary consumers.

This circumstantial evidence suggests that food may limit the energy available for reproduction for much of the time, *i.e.* non-mast years. These years are far more common than the infrequent mast years when there is probably much more food and, therefore, the situation is probably very different.

At times when food is abundant (*e.g.* during mast fruiting years) it is conceivable that the amount of food available presents Malaysian peacock pheasants with 'spare time' as discussed for frugivores in section 1.1.1. Therefore, if there is a local explosion in food abundance (see Appanah, 1985; Mabberley, 1991: p. 126), the situation becomes functionally similar to the clumped male display dispersions of fruit-eating passerines noted in section 1.1.1. Thus, as Diamond (1986) pointed out, the evolution of extremes of ornamental plumages and displays is not dependent upon a frugivorous diet. The mast fruiting of Sundaic rain forests, whilst not providing a regular fruit source for vertebrates, does provide periodic abundance in a variety of food sources.

Perhaps it is this occasional 'lek-like' system, when calling males are clumped, that has provided the driving force for the evolution of the ornamental plumage and display. Incidentally, I suspect that the full significance of the display will only become apparent when the female's perception of the displaying male is known. Birds can detect ultra-violet light (Burkhardt, 1990) and the sudden spreading of feathers bearing irridescent ocelli may suddenly 'switch on' the male in the eyes of a visiting female. Potential mammalian predators are not cued into this 'extra' communication channel (mammals are trichromatic - 3 primary colours, whereas birds are tetrachromatic - 4 primary colours). When not exhibited in display, the ocelli serve to break up the the outline of the male and hence make it more cryptic (to a human observer at least).

Calling and scrape maintenance appear to occur rarely. Thus, males may rely on attempting to display to females during chance encounters in the forest at other times. Females, may, however, be as energetically constrained in their reproductive behaviour as males seem to be (hence the one egg clutch mentioned above). Therefore, it is more likely that females will be in breeding condition at the same time as males because an increase in food abundance will benefit individuals of both sexes. Consequently, if females are not in breeding condition for much of the time, it is probable that there will be intense selection on any trait that increases a male's chance of mating when females are in condition. As females only lay one egg, each clutch can only have one father. Therefore, selection pressure will be very strong, both for the female to 'choose' a male of high quality and also for a male to attract a female. This would explain the very marked sexual dimorphism in morphological characters that are revealed in display which may well be a very rare event. That there is considerable competition at such times is indicated by the positive responses to playback during the test of the 'hotshot' hypothesis. Males that were probably not in very good condition did call as a response after few playbacks and four individuals began calling spontaneously by the end of the experiment.

9.5 Testing the hypothesis

Two long term monitoring programmes would provide necessary support for the model. These are synchronous monitoring of both the level of calling and invertebrate numbers. This would yield data on the variation between months within particular sampling locations and between sampling locations within a single month. Combined with more data on Malaysian peacock pheasant diet, it would be possible to test whether food abundance coincides with the area occupied by a 'calling clump' at Kuala Lompat during a calling period. The influence of habitat structure on food availability could also be investigated. Given that mast fruiting has, so far, been recorded on about a 5-10 year cycle, there is obviously only a remote chance that this can be achieved. Therefore, experiments are more feasible.

Recently, a large number of Malaysian peacock pheasants have been bred in Peninsular Malaysia. Consequently, there is the possibility that experiments could be conducted in the species' natural climate and in naturally planted aviaries. The possibilities are endless, but the more important experiments to test findings from this thesis are as follows.

1) Food manipulation. Two sets of males could be given different diets - one set given a maintenance diet and one set given the same diet with a supplement. Natural calling and

interactions could be monitored. In addition, playback experiments could be conducted on males of differing nutritional status so as to elicit responses. The responses could be compared to a standard(s) (from recordings made during natural calling periods in the wild) to inspect for vocal inconsistencies. The 'quality' of the call could subsequently be related to diet and hence nutritional status. Female responsiveness in relation to diet could also be explored.

2) The effect of particular vocalisations on males and females. The responses of males and females to the various call types can be thoroughly investigated using either males or pre-recorded calls as the stimulus. It is especially important to know if the proposed hierarchy of call types does in fact relay the same information to other males and to females. Thus, if whistles indicate that males are in very good condition, it would be predicted that other males would be repelled and females would be attracted.

3) The effect of diet on maintenance of display scrape and the display itself could be examined under a similar experimental set up as proposed for 1) above.

4) The effect on the female of particular male morphological ornaments exhibited in display could be investigated. Just how important are ocelli for obtaining copulations? Experiments in captivity involving removal of tail feathers or painting over the ocelli could answer this question.

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Appendices

Appendix 1

McGowan, P.J.K. (1990a) The use of calls to determine status in the Malaysian peacock pheasants. Pp. 110 - 115 in *Pheasants in Asia 1989*. Hill, D.A., Garson, P.J. and Jenkins, D. (eds.). World Pheasant Assoc: Reading, U.K.

Appendix 2

McGowan, P.J.K. (1990b) Radio-tracking to reveal movements in the Malaysian peacock pheasant: is it feasible? Pp. 145 - 150 in *Pheasants in Asia 1989*. Hill, D.A., Garson, P.J. and Jenkins, D. (eds.). World Pheasant Assoc., Reading, U.K.

Appendix 3

McGowan, P.J.K. (1990c) Microhabitat analysis of the Malaysian peacock pheasant: a field procedure. Pp. 209 - 214 in *Pheasants in Asia 1989*. Hill, D.A., Garson, P.J. and Jenkins, D. (eds.). World Pheasant Assoc: Reading, U.K.

CALLING AS A MEANS TO SURVEY THE MALAYSIAN PEACOCK PHEASANT: A PRELIMINARY ASSESSMENT

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INTRODUCTION

In south-east Asia, tropical rainforest is disappearing rapidly. This makes it important to locate and monitor populations of pheasant species that are dependent upon this habitat. Both of these steps have recently been identified as "Priority Areas of Research" in conservation biology (Soulé and Kohn 1989).

In order to locate populations, the species in question must be detected and monitoring populations requires that detection rates bear some relationship to population size. This allows variation in detection rates (between sites or over time at the same site) to be interpreted as differences in population size. A number of pheasant species can be most easily detected by their calls and this has led to populations of some species being 'censused' by calls such as the ring-necked pheasant (e.g. Gates 1966) and Himalayan pheasants (e.g. Gaston 1980).

The problems of 'censusing' tropical pheasants have been highlighted (Davison 1979) and are due to difficulty of detection (many species are difficult to see, lack conspicuous vocalizations and are virtually impossible to detect by droppings, feathers etc.). In species that are detectable by calls, calling is likely to be temporally and spatially much more predictable than is apparently the case in temperate pheasant species. This is probably because calls are often associated with breeding and a number of pheasant species in the tropics are believed to have breeding records from different months in different years (Davison pers. comm.). As many pheasant 'censuses' rely on short periods of fieldwork to obtain some index of population size, it is the amount of this variation in calling behaviour that limits the usefulness of calling as a 'census' technique in vocal tropical species.

The Malaysian peacock pheasant does have conspicuous calls and the calling behaviour is currently under investigation to determine its utility as a 'census' technique.

STUDY AREA METHODS

The study is part of an ongoing investigation into the ecology and behaviour of the Malaysian peacock pheasant, conducted at Kuala Lompat in the Krau Game Reserve in peninsular Malaysia (Fig. 1). Results presented here, therefore, are preliminary.

Variation in calling level

Temporal variations in calling levels are being investigated on two time-scales - seasonal and diurnal. The data on monthly variation are being used to assess spatial variation.

Monthly calling levels are assessed by walking around the study site for three days each month. These walks are conducted between the 4th and 14th of each month and between 0800 and 1200 hrs and from 1500 and 1830hrs. These times were adopted in the hope of maximising the encounter rate with calling birds (Davison pers. comm.). For each call heard, data collected include time, location, call type and duration (number of calls and minutes). Walks are not done during rain, due to reduced hearing range. The study site is divided into three areas of approximately equal size, but influenced by the distribution of paths.

Diurnal variation in calling level was investigated in 1988 when calling levels were high (i.e. February and April). All birds heard calling from one point were recorded from first light until 1315hrs on one day and from 1315hrs to dusk on the following day for 18 half days to give a total of nine full days.

Spatial variation in peak calling levels between years has been assessed, initially, by comparing the position of calling locations in the two months for which there are data in both years (i.e. February and March).

RESULTS

All calls heard were divided into two call type categories - 'warks' and 'whistles'. There are, therefore, four possible measures by which 'calling level' can be determined in each month and these are shown for 1988 (Fig. 2).

Although these criteria largely correspond as measures of the amount of calling across months, there is an important difference in the figures for March. This is because each bird located in March gave very few calls compared with the long bouts often given in February and April. This suggests, therefore, that number of calls is not necessarily a reliable predictor of the number of birds calling and is not likely to be an accurate or precise measure of relative density if used on extensive surveys.

Comparison of the number of calling locations noted in each month of field effort indicates that the number of birds calling is high in each February and April (Fig. 3). The significance of quiet months in 1988 (May-August), in terms of defining a breeding season in this tropical situation, is not yet possible to assess.

Diurnal variation in calling can be similarly investigated by call type, in terms of number of both calls and bouts. Inspection reveals a difference in the patterns of calling throughout the day for each call type (Fig. 4) and suggests that most calls are given outside survey-walk times, but that here is a morning peak of bouts within the survey-walk time.

Spatial variation

The majority of calls have been heard in areas 1 and 2 (● = 1988 and ✦ = 1989 Fig. 5). The spatial distribution of calling was, however, different in each of the two years (Fig. 6).

CONCLUSION

At present it is not possible to propose any sampling regime that will allow Malaysian peacock pheasants to be surveyed accurately or precisely. Although calling obviously indicates the presence of the species, a short survey (e.g. 2-3 days) may well conclude that an area does not contain Malaysian peacock pheasants because calling birds will have been missed. This is because:

1. Calling levels are generally low and intensive effort over several days is needed to record several birds, even during peak calling periods.
2. Although there has been a high level of calling during February in both 1988 and 1989, it has been in different areas. Why is this? Are birds moving from one area to another (distances are small) or are birds in one area silent one year and vocal in another? Further studies including some of ranging behaviour, should make this clearer.

In conclusion, calling is a ready method for locating birds, but some individuals or even populations may well be missed during short survey visits. Monitoring through time is not yet feasible because numbers of calls heard are low, there is considerable variation in time and space and it is not yet known what proportion of the population is likely to be vocal.

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FIGURE 1: Map of peninsular Malaysia, showing Kula Lompat.

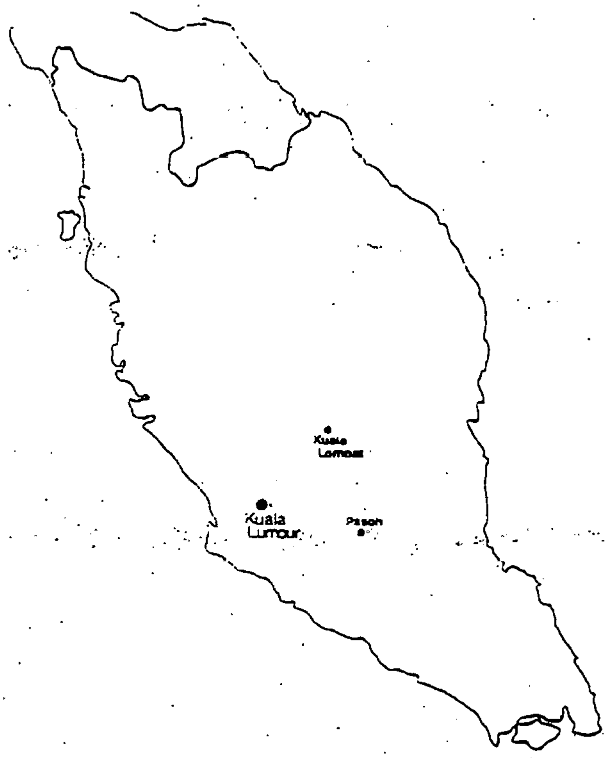


FIGURE 2: Measures of calling level used in 1988. Frequencies are total numbers, summed over the three days of survey walks.

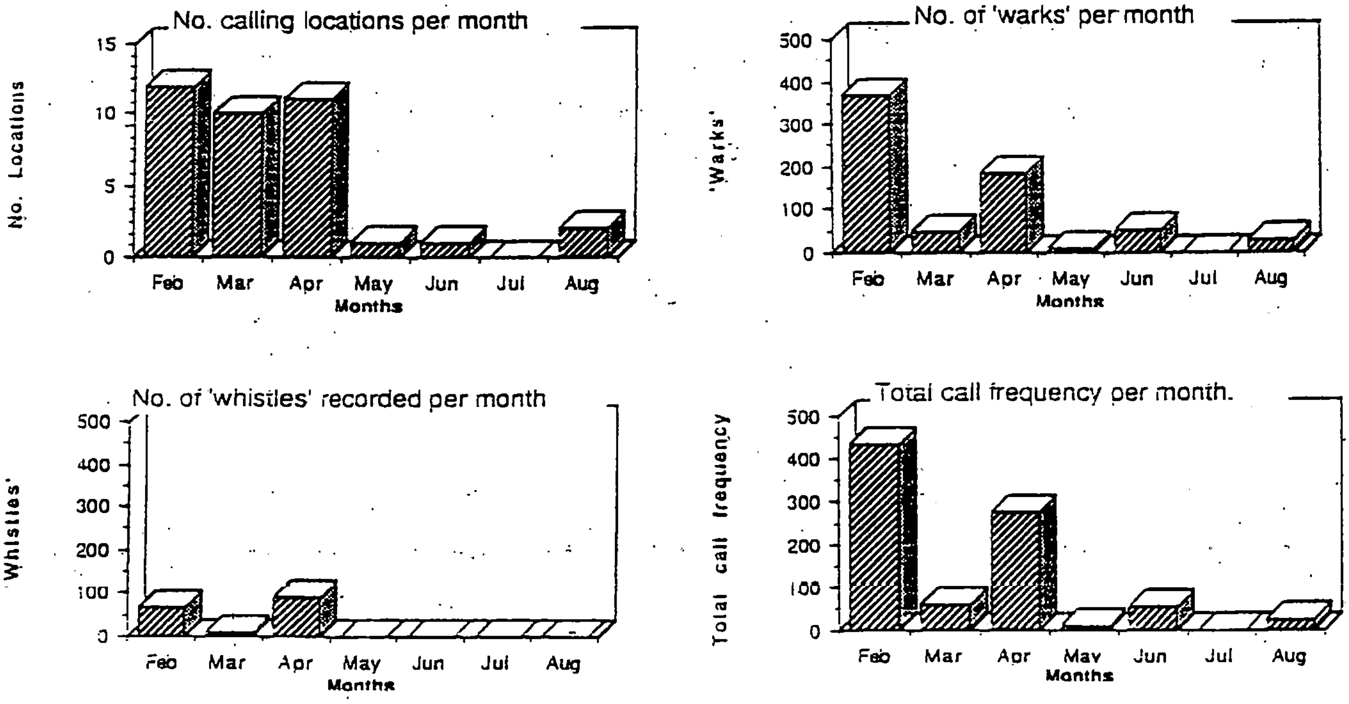
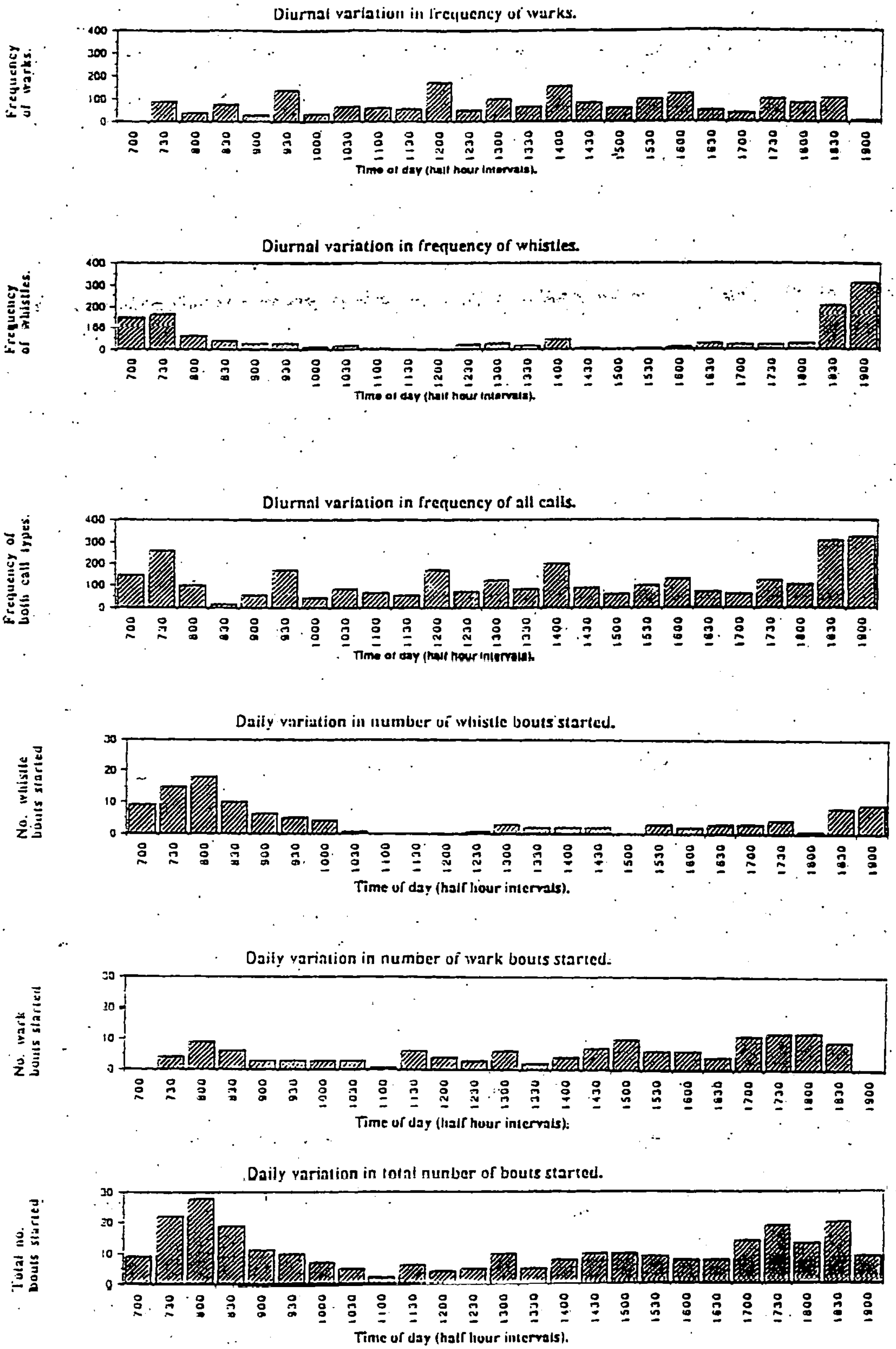


FIGURE 4: Diurnal variation in calling level for various measures of the two call types recorded ('warks' and 'whistles'). For comparison with monthly calling levels note that survey-walk times are 0800-1200hrs and 1500-1830hrs.



Diurnal variation in frequency of warks.

Diurnal variation in frequency of whistles.

Diurnal variation in frequency of all calls.

Daily variation in number of whistle bouts started.

Daily variation in number of wark bouts started.

Daily variation in total nunber of bouts started.

FIGURE 3: Total number of calling locations recorded in three days of survey walks in the months shows. One location is a single encounter with a calling bird on one day. ? indicates months when no samples were taken.

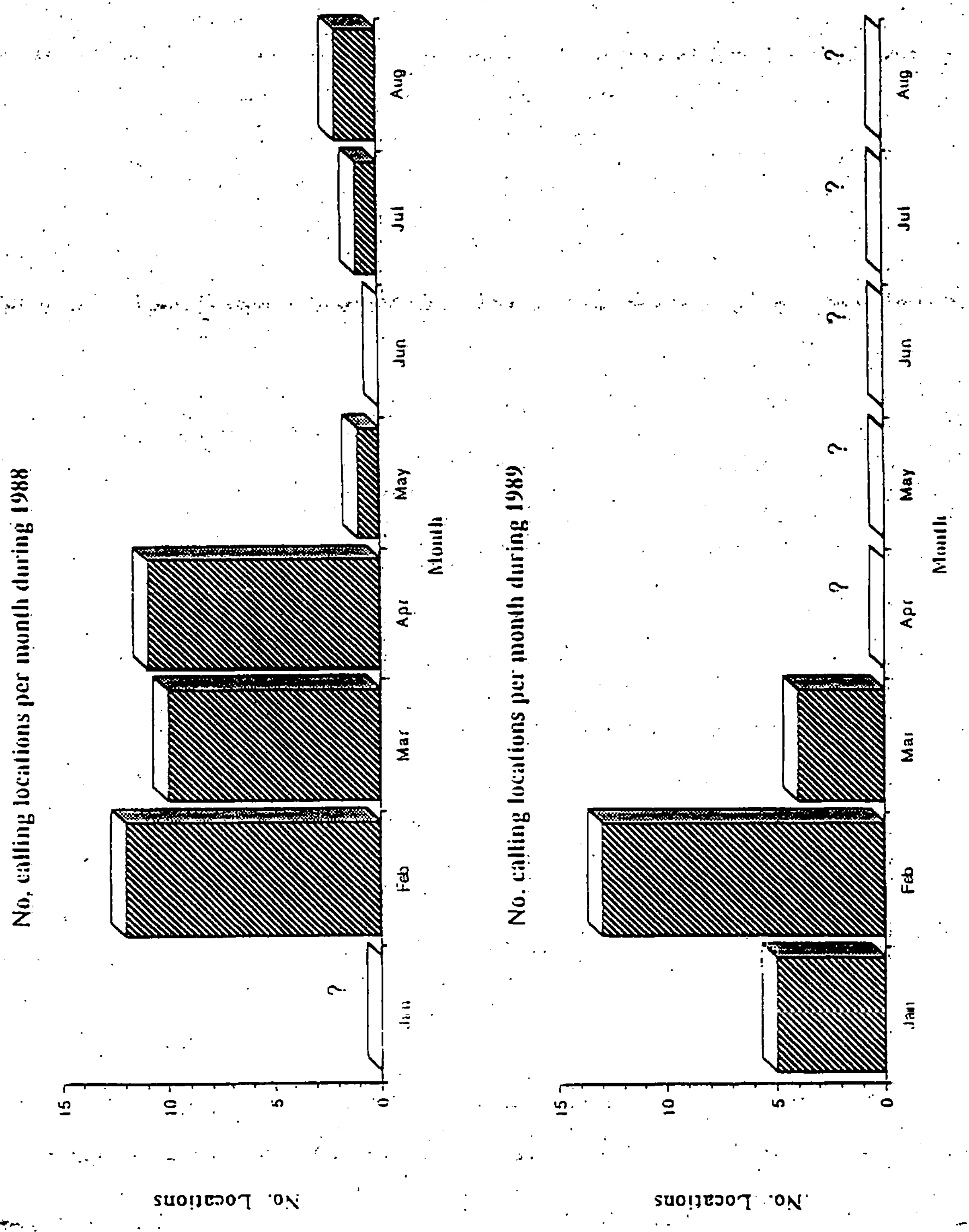


FIGURE 5: Location of calls heard during survey-walks in February and March in both years. Each spot is one bird at one location on one occasion.

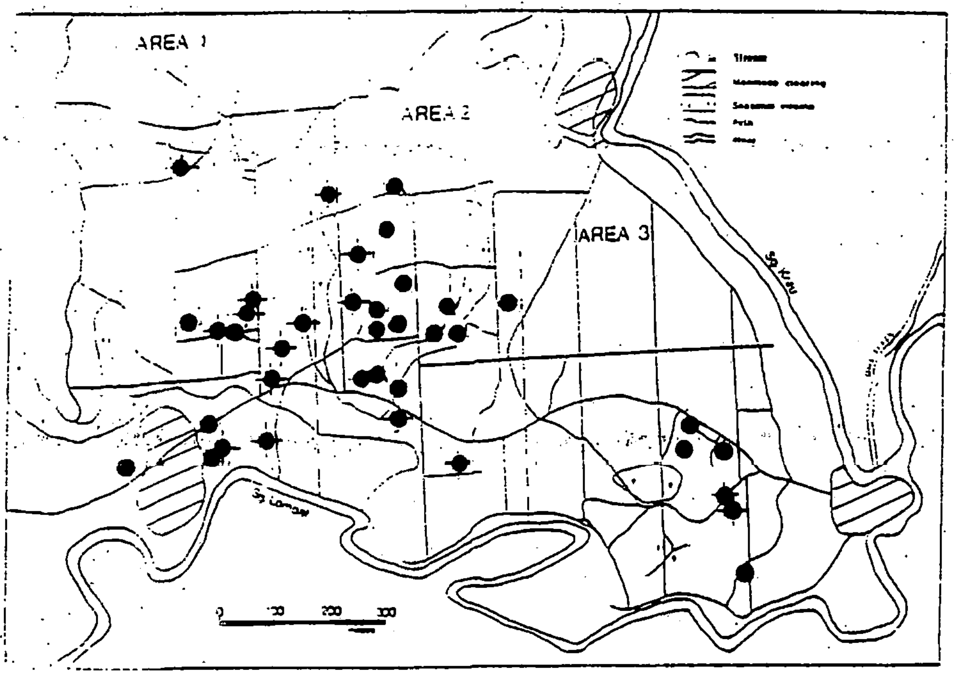


FIGURE 6: Number of birds heard calling during survey-walks in February and March in areas 1 and 2 in both years. The spatial distribution of birds heard is significantly different between the two years (Chi -squared = 4.265, 1 d.f.; $p < 0.05$).

	Year	
Area	1988	1989
1	5	9
2	13	5

RADIO-TRACKING TO REVEAL MOVEMENT IN THE MALAYSIAN PEACOCK PHEASANT: IS IT FEASIBLE?

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INTRODUCTION

Why consider using radio-transmitters?

Birds are encountered much less frequently in lowland tropical rainforest than in temperate forests. Consequently, data collection is slower and fewer topics are amenable to study than in other habitats. Many pheasants and partridges are amongst the most rarely encountered species in tropical forest and consequently remain little known. Two of the better known Malaysian species are the argus and Malaysian peacock pheasants, both of which are reasonably vocal during at least part of the year. During this period, and the rest of the year, when individuals are extremely difficult to detect, it would be valuable to be able to increase the rate of contact with the species and to identify particular individuals.

In addition, the Malaysian peacock pheasant has interestingly conspicuous aspects of its breeding biology. At least some individuals are particularly vocal and/or maintain display scrapes, whilst others may be quieter. Although these features do increase the rate at which the species can be encountered, these traits also pose several interesting questions that cannot be answered without employing a method that guarantees individual recognition of a number of birds and allows systematic study of their ranging behaviour. Do home ranges overlap and are their sizes and arrangement influenced by calling? How much time is spent at, or close to, display scrapes by either sex? How do males without scrapes behave?

Radio-tracking was seen as a method by which the species could be encountered more frequently, individuals recognised and the species' ranging behaviour studied in some detail. This can then be related to calling behaviour and the construction of scrapes in order to allow some aspects of the social system to be described. Investigations of the social organisation of the species are likely to have important implications for future management of the species in a decreasing and progressively more fragmented habitat.

Have radio-transmitters been used on birds in Malaysia?

Only two studies have managed to track the movements of birds in Malaysia's tropical forests and a quick perusal of these studies indicates potential problems. Davison (1981) tagged two male argus that maintained dancing grounds on hills, and produced daily ranges for them. In addition, time at the dancing ground, time spent roosting and perching, and time spent walking were estimated. Lambert (1989) tracked six fruit eating birds of three canopy dwelling species for up to seven days, also producing daily ranges and roost locations. Both these studies have tracked small numbers of individuals for each species and consequently the generality of the data is unknown. The small numbers of individuals tagged is itself due to the difficulty and/or effort involved in catching tropical forest birds.

These constraints on any radio-tracking programme make it vital that the sampling regime to be employed is very carefully thought out in advance, so as to maximise the rate at which information is gained.

How useful is the technique likely to prove?

Although radio-tracking can provide extremely valuable information that cannot be collected in any other way, the technique may not prove to be feasible. Consequently, its utility was assessed during 1988.

The radio-transmitters

Transmitters should weigh 3% (or less) of the bird's body weight (B. Cresswell pers. comm.). Davison (pers. comm.) reported that the lightest Malaysian peacock pheasant would be 300g and, therefore, transmitter packages (including means of attachment) should be no heavier than 10g. Necklace attachments were chosen for the transmitters because they have been used successfully on ring-necked pheasants in the U.K. (P.Robertson pers. comm.).

Given the weight of the transmitter, there is a trade-off between the length of the transmitter's life and the range of the signal. Because paths in the study area were a maximum of 150m apart and because it was planned to monitor ranging over a number of months, transmitters were designed to have long life (up to 10 months) and short range (about 150m). Field testing, however, showed the range to be up to 230m.

STUDY AREA AND METHODS

The study is part of an ongoing investigation into the ecology and behaviour of the Malaysian peacock pheasant, conducted at Kuala Lompat in the Krau Game reserve in peninsular Malaysia. Results presented here are therefore preliminary.

Trapping and tagging

Trapping was attempted during May 1988 using a traditional trap design. Traps were constructed about 20m apart along the edge of trails covering a considerable portion of the study site. The traps were set over four days and remained in operation for up to ten days. Only one Malaysian peacock pheasant (a male in juvenile plumage) was caught and equipped with a radio-tag, although a considerable range of other ground-dwelling birds were caught (Table 1).

Radio-tracking

In dense forest, the most practical method of obtaining radio-locations is by triangulation from fixed positions on paths. Other methods, such as approaching the birds as closely as possible and plotting locations with reference to mapped landmarks, are not feasible in a dense, largely featureless forest. In order to plot radio-locations accurately, the position of the radio-tracker must be known exactly.

A detailed map of the paths in the bird's home range was made and all places from which bearings could be taken (features such as logs across the path, path junctions etc.) were marked.

To obtain a radio-location at least three bearings were taken from known points as quickly as possible (usually within five minutes and always within ten minutes). Bearings taken were always at least 20 degrees apart, because the size of the 'error polygon' becomes smaller as the angle between the bearings increases (Kenward 1987).

A crucial problem with all analyses that are dependent upon the repeated location of animals (e.g. determining ranges, measuring habitat preferences) is the accuracy of the positional information. When plotted on a scale map of a study area, a series of compass bearings from known positions to the estimated location of a radiotransmitter form an 'error polygon'. Assuming that the radiotransmitter is within this polygon, the furthest that any triangulation estimate of its position could be from its real position is given by the polygon's longest diagonal. This distance is therefore an estimate of the accuracy of the system (i.e. the transmitter, receiver, observer and map).

Table 2 gives a summary of some error polygon analyses for radio-fixes on Malaysian peacock pheasants. They suggest that there is little monthly variation in the accuracy of fixes. Assuming that the lengths of error polygons' longest diagonals are normally distributed, it can be said that estimated positions of birds will be within 30-40m of real positions on about two-thirds of occasions (mean + 1SD). This procedure gives the maximum possible error. By using the centre of the polygon (rather than one of its apices) as the best estimate of the real position of the animal, the size of these measurement errors will be much reduced.

For home range analysis, 30 radio-locations were taken at least two hours apart over a five to seven day period each month from May to September inclusive.

30 radio-locations have provided a good estimate of home range size for at least five temperate bird and mammal species (Hill & Robertson 1988, Kenward 1987). To determine a home range, all locations must be independent and the minimum time interval of two hours was chosen as a 'first estimate' of the time taken for successive observations to become statistically independent. A minimum of 90 minutes used for ring-necked pheasants in southern England (Robertson pers. comm.).

The independence of successive observations can be tested objectively (Swihart & Slade 1985) and is, apparently, an approximation of the time taken to cross the home range (Kenward 1987: p.145). Using Swihart and Slade's equations indicates that two hours is not sufficient to obtain independent locations for the data collected in 1988 (see Appendix).

Conclusions from 1988

At the end of the 1988 season, the 'system' was set up, but the major concern was the difficulty in trapping and tagging birds. By intensifying trapping (more traps in a smaller area) it was felt that the trapping rate could be improved considerably.

Procedure in 1989 and evaluation of the technique's utility

During early 1989, a modified trapping regime resulted in three more birds being equipped with radio-transmitters. In addition, the bird tracked in 1988 was caught at the roost and fitted with a new transmitter. Although one female was not subsequently located (radio failure?), three birds were tracked simultaneously for five weeks. One male inhabited the north-west corner of the study site and frequently disappeared out of range. This highlights another crucial consideration - individuals must be located every time they are searched for if the home range is to be accurately described. If the bird is not located it may well be outside the area that is being reported as its home range. New trails were cut to counteract this.

The sampling interval has been altered to four hours which means that the minimum number of days needed to estimate the home range (i.e. collect 30 locations) is ten.

Radio-locations and other data

1. Home ranges can be drawn around plots where habitat measurements are taken and vegetation structure compared between ranges.
2. Although trapping will probably not be done in areas where birds are never heard, the ranging of tagged birds may add support to data on presence/absence in particular areas of the forest. Currently, recording presence is restricted to calling locations. Birds may be present in areas where no calls are heard.
3. The ranging behaviour of females can be analysed with respect to male calling. For example, the female that was tracked during February and March ranged within hearing distance of several males.
4. The juvenile male tagged in 1988 (and re-tagged in 1989) started calling in February 1989. Subsequently, the bird was followed and some calling locations were plotted and calls recorded. Unfortunately, this male was predated five weeks after the new radio-transmitter was fitted.

CONCLUSIONS

Is the technique worth the Effort?

Although much new and interesting information can be collected using radio-transmitters, do the advantages outweigh and disadvantages?

Disadvantages

1. Transmitters are costly and not 100% reliable.
2. A lot of time and effort is needed to catch and equip birds with radio-transmitters.
3. Subsequent monitoring may be difficult due to short periods of tracking (radio-failure, dropped transmitters etc.) or because tagged birds live outside the study area.
4. Sample sizes will be small. This is a widespread problem for such studies and for range analysis five is regarded as an acceptable minimum for any class (e.g. species/sex) (Robertson pers. comm.), provided that range sizes vary by less than a factor of 2 (Pruett-Jones pers. comm.).

Advantages

1. Several birds are individually marked, which permits them to be studied in detail.
2. Ranging information collected here is new, not only for the species, but also for tropical galliforms in general (but see Davison 1981). This is very important for conservation in determining the area that a 'minimum viable population' would require and providing data relevant to the consequent decisions on species management.
3. Comparison with calling data and scrape maintenance will throw light on the very interesting social structure of the species.

In conclusion, I think that it is worthwhile to continue using this technique on the Malaysian peacock pheasant. The range of data that can be collected once an individual is tagged is considerable and otherwise unobtainable. Although the numbers of birds tagged at any one time seems likely to be small, the final sample sizes will be reasonable (compared with similar studies).

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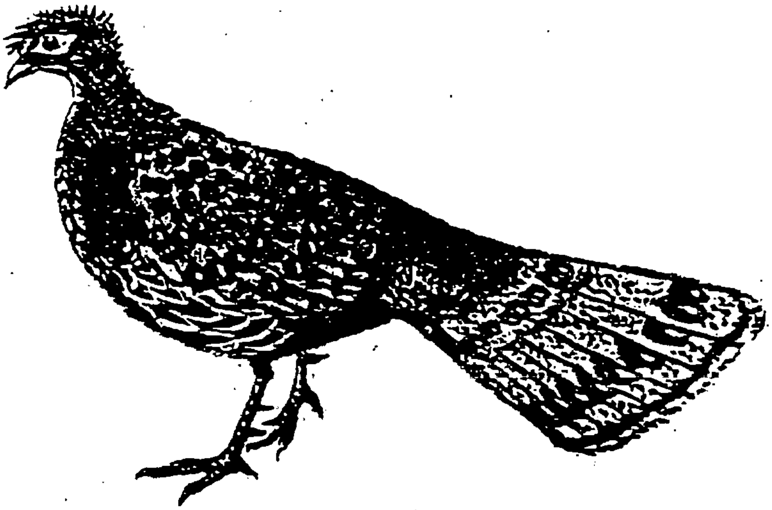

Table 1: Other bird species caught during trapping efforts.

Species caught	Number
Roulroul *Rollullus roulroul*	12
Black wood partridge *Melanoperdix nigra*	1
Crested fireback *Lophura ignita*	5
Argus *Argusianus argus*	3
Emerald dove *Chalcophaps indica*	3
Giant pitta *Pitta caerulea*	1
Garnett pitta *Pitta granatina*	2
Malaysian rail babbler *Eupetes macrocercus*	1

Table 2:'Error polygon' analysis (see text) for radio-fixes on wild Malaysian peacock pheasants (May-August 1988). Monthly estimates of mean and standard deviation for the longest diagonal are given, together with the range (all in metres) and the sample size.

Month	No. of fixes	Longest diagonal (m): mean	s.d.	range
May	20	17.45	14.30	0-52
June	17	23.16	17.42	0-40
July	18	22.56	11.73	6-42
August	17	20.00	12.20	0-38

Appendix: Testing sequential fixes for statistical independence (after Swinhart & Slade 1985).

Calculation of the time to independence.

1) Calculate the co-ordinates of the centre of activity

X co- ordinate $$\frac{\text{Sum of x co-ordinates}}{n}$$

Y co-ordinate $$\frac{\text{Sum of y co-ordinates}}{n}$$

2) Calculate t^2 and r^2 (t^2 = mean squared distance between successive observations and r^2 = mean squared distance of observations from the centre of activity) using the formulae:-

$$t^2 = \frac{1}{m}\sum_{i=1}^{m}(X_{i+1} - X_i)^2 + \frac{1}{m}\sum_{i=1}^{m}(Y_{i+1} - Y_i)^2$$

where m is the number of paired observations and i denotes the order in which the observations were collected.

$$r^2 = \frac{1}{n-1}\sum_{i=1}^{n}(X_i - X)^2 + \frac{1}{n-1}\sum_{i=1}^{n}(Y_i - Y)^2$$

Therefore, calculating t^2 and r^2 using data collected in May 1988;-

		t^2		r^2	
Time between readings (minutes)	Location numbers (from map)	$X_{i+1} - X_i$	$Y_{i+1} - Y_i$	$X_i - X$	$Y_i - Y$
120	1-2	6	5	18	9
255	2-3	40	17	24	14
200	3-4	0	0	16	3
810	4-5	30	1	16	3
		etc. for all locations			
Totals		5328	2675	5304	2876

Therefore: $t^2 = \frac{1}{32} 5328 + \frac{1}{32} 2675$ and $r^2 = \frac{1}{33 - 1} 5304 + \frac{1}{33 - 1} 2876$

Therefore:-

$t^2 = 166.5 + 83.6$ and $r^2 = 160.7 + 87.2$

$= 250.1$ $= 247.9$

3) Put t^2 and r^2 into Swihart and Slade's equation

$$\frac{t^2}{r^2} = \frac{250.1}{247.9} = \underline{1.009}$$

Swihart and Slade suggest that observations are independent if t^2/r^2 is > 2 and, therefore, a minimum of 120 minutes between observations is not sufficient for independent observations in this case.

ANALYSIS OF MICROHABITAT USE IN THE MALAYSIAN PEACOCK PHEASANT: A FIELD PROCEDURE

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INTRODUCTION

The Malaysian peacock pheasant *Polyplectron malacense* inhabits extreme lowland rain forest, but appears restricted even within this habitat type. This is possibly because pheasants of Sundaic origin may be described as stenotopic, having a narrow range of habitat preference (Davison 1986). For example, the species may avoid the gelam forest over the alluvial terraces adjacent to rivers (Davison & Scriven 1987) whilst preferentially inhabiting the areas further from the river. The present study set out to investigate further the microhabitat relationships of the Malaysian peacock pheasant. Initially, however, a satisfactory method had to be devised and its utility determined. Here I propose a field procedure and present initial analyses.

STUDY AREA AND METHOD

The study is part of an ongoing investigation into the ecology and behaviour of the Malaysian peacock pheasant, conducted at Kuala Lompat in the Krau Game Reserve in peninsular Malaysia.

Many studies have investigated the influence of habitat structure on bird distributions. These have mostly been concerned with describing relationships between vegetation structure and avian species diversity (e.g. MacArthur & MacArthur 1961) or have concentrated on how a single species uses different vegetation cover types in relation to its availability in a given area (e.g. Hill & Ridley 1987). Such studies have, almost without exception, used different methodologies and this has prevented comparison between studies where this may prove informative (see Farina 1985).

In addition, assessment of microhabitats in tropical forest have been based on subjective assessments and not on objective counts or measurements of habitat parameters. The problems of this type of approach have been documented (Block *et al.* 1987).

Consequently, any methodology employed in tropical forest should provide accurate data which can be compared over time and space between different studies. Such a baseline methodology is presented here.

Selection Of Parameters

The selection of variables to be measured followed Dueser and Shugart (1978). Each variable to be measured, therefore:

i) should be quickly and precisely measured using non-destructive sampling procedures;

ii) should have intra-seasonal variation that is small relative to inter-seasonal variation;

iii) should describe the environment in sufficient detail to detect subtle variation in the habitat that may otherwise appear grossly similar.

Field Procedure

Twenty four locations were chosen to give an even spread across the study site (Fig. 1). From each of these points, habitat plots were selected 'randomly'. To do this, one of the four main compass bearings (north, south, east, west) was chosen randomly. Random numbers were generated between one and a hundred to give a distance (in paces) to the centre of the first habitat plot. This was repeated to give five plots from each starting point and a total of 120 plots in all. Although not truly random, this seemed to be the best procedure for avoiding bias towards areas with more open undergrowth (i.e. areas that are easier to move about in). Some additional plots were added when birds were exactly located (e.g. display scrape sites).

At each plot, the 23 habitat variables were measured or counted (Table 1 and Fig. 2).

Statistical Procedure

Ordination techniques are the most appropriate method of analysing such multivariate data. These organise habitat plots in a low-dimensional space such that similar plots are close by and dissimilar plots far away. In the first instance, principal components analysis (PCA) has been used to describe quantitatively the variation in habitat structure in the forest.

RESULTS

Initially, PCA determines multivariate 'factors' that explain as much of the variation observed in the data as possible. These factors often represent complex environmental gradients (e.g. dry - wet, shaded - open). If dominant influences of this kind largely determine how the structure of the vegetation varies from place to place, a few PCA factors will explain most of the variance in the data. However, Table 2 indicates that in this case the first factor explains only 16.5% of the variance, and the addition of a second factor contributes just 10.1% more. Note that it requires the inclusion of several more factors to explain most of the observed variation (e.g. 10 factors explain 75%).

These results suggest that there are no dominant environmental gradients that explain spatial variations in forest structure in this study area. In temperate coniferous forests, by contrast, a single PCA factor explains much of this variation, and represents the continuum from young to mature forest (Bibby *et al.* 1985). Figure 3 shows how all the habitat plots are dispersed with respect to the first two PCA factors in my analysis. Habitat plots that are close together in this 'ordination' are not necessarily close together in the study area, suggesting that the forest is very patchy. Plots in areas close to peacock pheasant calling sites are also widely distributed on an ordination graph.

CONCLUSIONS

The field procedure employed satisfies the original demands of practicality and robustness. An initial analysis of the data suggests that there are no dominant environmental gradients that can be used to predict forest structure. The use of different forest microhabitats by peacock pheasants (for calling at least) is also not apparently predictable on this scale.

Further Analyses

1) Comparison of the amount of 'patchiness' in areas where birds were calling with the amount of 'patchiness' in areas where no birds were heard calling may indicate whether it is the variation in habitat structure (or some correlate of habitat structure) that is important in determining the calling distribution of the pheasants.
2) Comparison of habitat structure between sites where display scrapes are constructed and other sites should indicate if scrapes are only cleared in particular areas and, possibly, if such sites are limiting.

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Figure 1: Locations of habitat plots. Dots represent the starting point for each series of five plots.

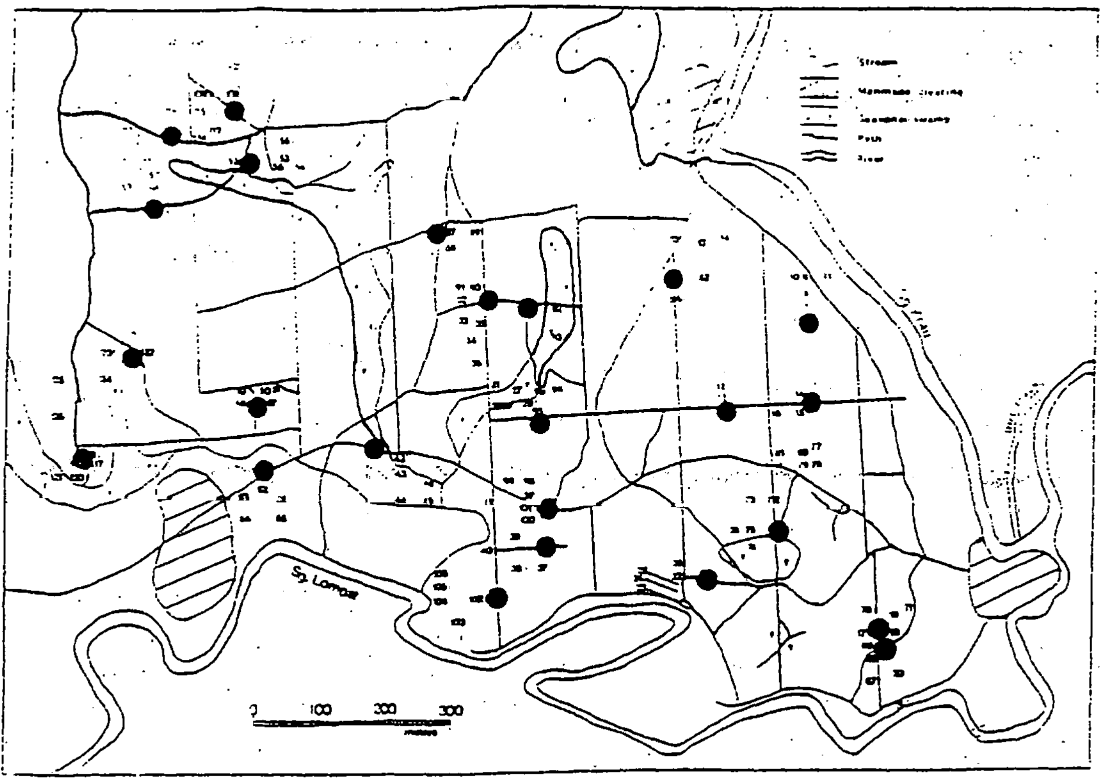

Figure 2: The sampling configuration employed in each habitat plot.

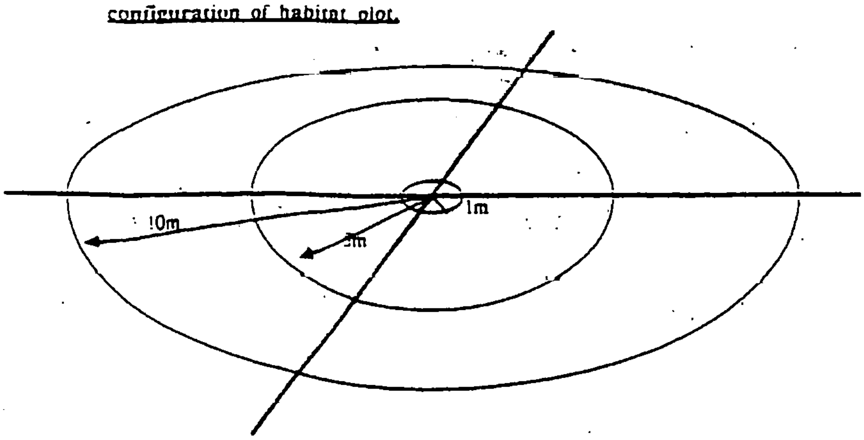

Figure 3: Principal Component Analysis plot, arranging all habitat plots (N = 120) according to structural similarity on the first two Principal Components (see Table 2).

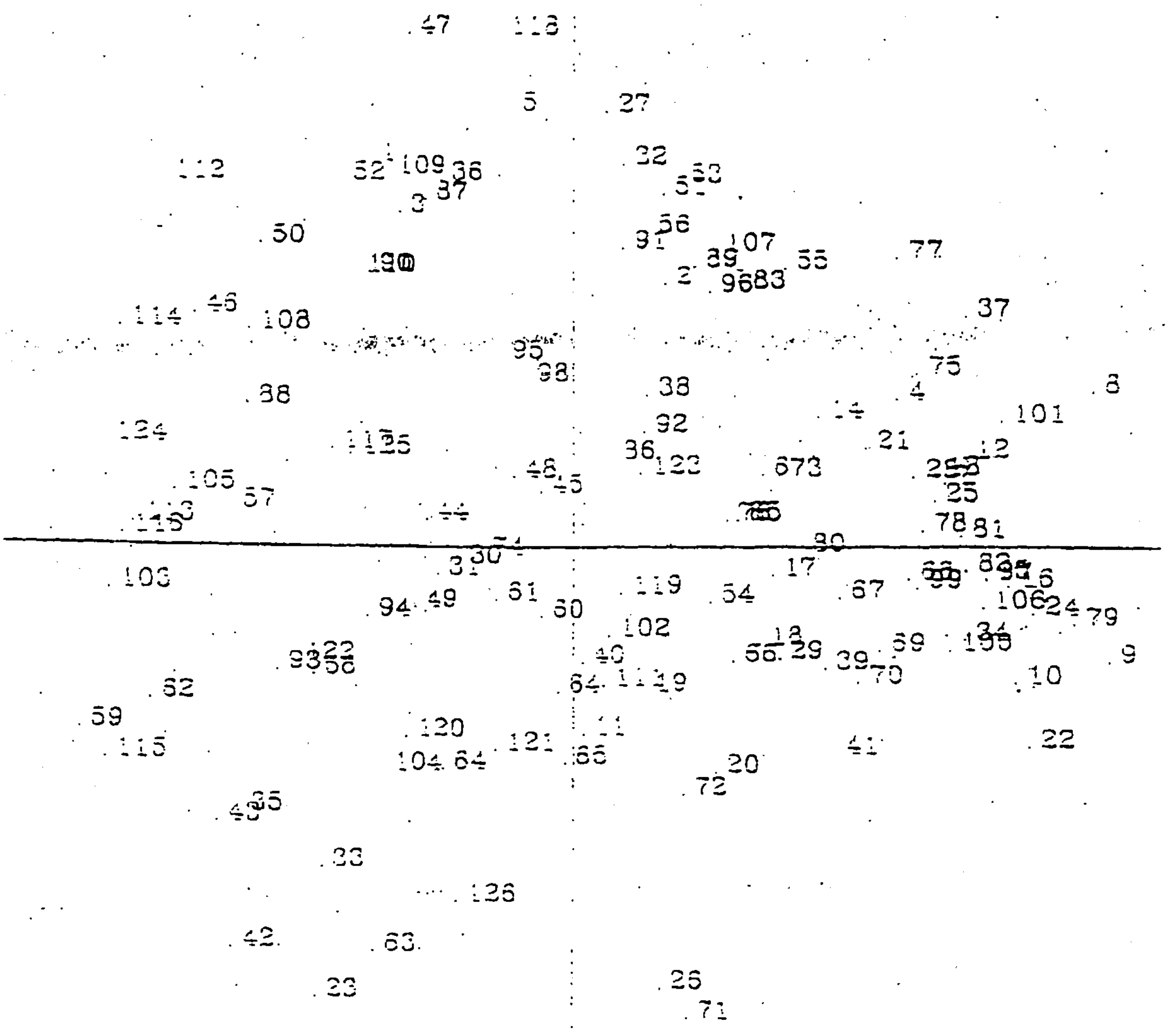

Table 1: Vegetation parameters and their method of measurement.

No.of woody stems (g.b.h. <10cm)	Total number of woody stems (trees, climbers etc.) over 2m tall and with g. b. h. of less than 10cm within 5m of the focal point.
No.of woody stems (g.b.h. <20cm)	Total number of woody stems (trees, climbers etc.) over 2m tall and with g. b. h. of between 10cm and 20cm within 5m of the focal point.
No.of woody stems (g.b.h. <40cm)	Total number of woody stems (trees, climbers etc.) over 2m tall and with g. b. h. of between 20cm and 40cm within 5m of the focal point.
No.of woody stems (g.b.h. <80cm)	Total number of woody stems (trees, climbers etc.) over 2m tall and with g. b. h. of between 40cm and 80cm within 5m of the focal point.
No.of woody stems (g.b.h. <160cm)	Total number of woody stems (trees, climbers etc.) over 2m tall and with g. b. h. of between 80cm and 160cm within 5m of the focal point.
No.of woody stems (g.b.h. >160cm)	Total number of woody stems (trees, climbers etc.) over 2m tall and with g. b. h. of greater than 160cm within 5m of the focal point.
No. palms	Total number of palm stems over 2m tall within 5m of the focal point.
No. palm species	Number of palm species recorded within 5m of the focal point.
No. tall herbs	Number of herb stems over 2m tall recorded within 5m of the focal point.
No. pandans	Number of pandan (*Pandanus* spp.) stems over 2m tall recorded within 5m of the focal point.
No. short woody stems (0m)	Total number of woody stems (saplings, treelets etc.) at ground level of plants less than 2m tall within 1m of the focal point.
No. short woody stems (0.5m)	Total number of woody stems (saplings, treelets etc.) at 0.5m above ground level of plants less than 2m tall within 1m of the focal point.
No. short woody stems (1.0m)	Total number of woody stems (saplings treelets etc.) at 1.0m above ground level of plants less than 2m tall within 1m of the focal point.
No. short herbaceous stems (0m)	Total number of non-woody stems at ground level of plants less than 2m tall within 1m of the focal point.
No. short herbaceous stems (0.5m)	Total number of non-woody stems at 0.5m above ground level of plants less than 2m tall within 1m of the focal point.
No. short herbaceous stems (1.0m)	Total number of non-woody stems at 1.0m above stems ground level of plants less than 2m tall within 1m of the focal point.
Distance to treefall	Distance to nearest treefall (up to a maximum of 30m)
Stage of treefall	Stage that the treefall is in (little regrowth, substantial regrowth or canopy closed over rotting log).
No. termite mounds	Number of quarters that contain termite mounds.
Distance to termite mounds	Distance from the focal point to the nearest termite mound (within 10m) in each of the four quarters created by the four main compass bearings.
Basal circumference of recorded termite mounds	The basal circumference of each termite mound above.
Height of termite mounds	The height of each termite mound recorded above.
Overhead object	Height of the lowest object over the focal point.

Table 2: Factor analysis showing the variation explained by successive factors.

Factor	% of variation explained	Cumulative %
1	16.5	16.5
2	10.1	26.6
3	9.7	36.3
4	8.8	45.2
5	6.5	51.6
6	6.0	57.6
7	5.7	63.3
8	4.8	68.1
9	4.3	72.4
10	4.0	76.4
11	3.7	80.1
12	3.4	83.5
13	3.2	86.7
14	2.5	89.2
15	2.2	91.4
16	1.8	93.2
17	1.6	94.8
18	1.5	96.3
19	1.3	97.6
20	1.1	98.8
21	.7	99.5
22	.5	100.0