Some Aspects of the Breeding Behaviour of the Lesser Florican Sypheotides indica (J.F. Miller) and the Bengal Florican Houbaropsis bengalensis (Gmelin)

Thesis submitted to the University of Bombay
for
the degree of
Doctor of Philosophy
in
Zoology

by
Ravi Sankaran

Department of Field Ornithology
Bombay Natural History Society

1991

CONTENTS

Chapter 1
INTRODUCTION

The family Otididae, commonly known as the bustards, is an ancient one, with the earliest fossil record from the Eocene period, 40-50 million years ago (Osborne et al. 1984). The bustards probably originated in Africa, and the continent is possibly the centre of their divergence, though present day distributions include Europe, Asia and Australia (Bannermann 1931, Priest 1934, Ali and Ripley 1969, Cramp and Simmons 1980, Osborne et al. 1984, Collar et al. 1986).

The relationship between bustards and other avian taxa is unclear, but most taxonomists now place the bustards in the Order Gruiformes (Ripley 1961, Ali and Ripley 1969, Cramp and Simmons 1980, Walters 1980, Osborne et al. 1984, Collar et al. 1986). However, certain anatomical peculiarities distinguish them sharply from other crane like birds. These include hexagonal (rather than transverse) tarsal scales; the absence of an oil gland, the body being covered instead with a dense friable powder-down, and completely different egg-white proteins (Stressmann 1959, Hendrickson 1969, Cramp and Simmons 1980).

Some confusion exists in the taxonomic classification within the family (Osborne et al. 1984). For instance, Howard and Moore (1980) classified the Otididae into 11 genera with 24 species and 44 subspecies. More recently, Osborne et al. (1984) divided them into 8 genera with 22 species and 47 subspecies. Early workers had placed the Lesser Florican and the Bengal Florican in the same genera (Jerdon 1864 - Sypheotides). However, they now occupy monotypic genera Sypheotides and Houbaropsis respectively (Osborne et al. 1984).

Bustards are medium to very large terrestrial birds, with males of the largest species close to the theoretical maximum weight for flying birds (Osborne et al. 1984). Their flight is typically powerful, with sustained wing beats, and they glide only while descending to land. The wings are long and broad, with 10 primaries and 16-24 secondaries. The tails are of short to medium length, broad and either square tipped or slightly rounded.

Certain morphological characters distinguish the bustards from other Avian taxa. Typically, bustards have long necks, with a stout body carried horizontally on long legs. The bills are straight, broader at the base and compressed laterally at the tip. The toes are short with thick soles and broad claws, and the hind toe is absent. All bustards are cursorial and do not perch. The preen gland is absent, but dust bathing and the dense, friable, powder-down which covers their feathers help in maintaining their plumage. There are no bare tracts on the neck, and the contour feathers have an aftershaft. The caeca is long and of distinctive form and the crop is absent. The penis is rudimentary. (Cramp and Simmons 1980).

Bustard ecology is poorly known, with only seven species having been studied in any detail. In fact, even the breeding displays, perhaps the most fascinating aspect of their behaviour, has not been described for many species (Osborne et al. 1984). Those species that have been studied are polygynous (Cramp and Simmons 1980, Osborne et al. 1984, Shulz 1985, Ridley et al. 1985, Collar et al. 1986, Caranza et al. 1989, Rahmani 1989, Narayan 1990). Males of most species perform spectacular courtship displays, that include both aerial and ground displays. The males are conspicuously coloured, and the ornamentation includes crests, moustaches and elongated plumes on the neck and head. The larger species, which have ground displays, have the ability to puff up the subcutaneous tissue of the neck till it resembles an inflated balloon. Females are cryptically coloured, and usually smaller than males. This sexual size dimorphism is most pronounced in the larger species. The Lesser Florican and the Bengal Florican, however, show reversed sexual size dimorphism.

Six species of bustards have been recorded form the Indian subcontinent. The Great Indian Bustard, the Lesser Florican and the Bengal Florican are resident, while the Great Bustard, the Little Bustard and the Houbara Bustard are winter migrants. Both the Lesser Florican and the Great Indian Bustard are endemic to the subcontinent, while a subspecies of the Bengal Florican is found in Kampuchea and Vietnam as well (Ali and Ripley 1969, Osborne et al. 1984, Narayan and Rosalind 1990).

Amongst the earliest references to the floricans was by the Moghul emperor Jehangir (Alvi and Rahman 1968). He wrote "The Charz (probably applicable to either species) is of two kinds; one is mottled black and the other buff. I now discovered that they are not two kinds, but that which is mottled black is the male, and that which is buff is the female". The late nineteenth and early twentieth century, the era of the gentleman sportsman, added considerably to our knowledge about the floricans through annals of several sporting and natural history journals.

Of the two species, the biology of the Lesser Florican has been documented in greater detail due to its abundance and wide distribution. Jerdon (1964) held that the Lesser Florican was found throughout India from near the foot of the Himalaya to the southern most districts. Hume and Marshall (1878), however, argued that this was somewhat erroneous, as this species is found in the plains and open country and are not found in the hills or thick forests. Baker (1921) found that the florican is widely scattered in the country in all suitable grassland habitat. Ali & Ripley (1969) have summarized its distribution as "resident, irregular local migrant and nomadic in the rainy season". More recently Lachungpa & Rahmani (1990) have presented a comprehensive account of its former distribution based on an extensive literature survey.

The breeding range of the Lesser Florican is far more restricted and has been increasingly reduced in recent years (Fig 1.1). The main breeding range is in western India, where the birds immigrate during the south west monsoon and settle to breed in suitable grassland habitat (Jerdon 1964, Baker 1921, Dharmakumarsinhji 1950). After breeding, the birds move into Peninsular India (Jerdon 1964, Dharmakumarsinhji 1950), though the details of the winter range or migration are still poorly known (Ali and Ripley 1969, Sankaran et al. 1990). A few birds breed in southern India (Jerdon 1864, Sankaran and Manakadan 1990).

Morphological and general behavioural descriptions of the Lesser Florican's display, nesting and habitat ..Fig. preferences have been presented in most major nineteenth century ornithological publications (e.g. Jerdon 1864, Hume and Marshall 1879, Blanford 1898, Baker 1921). Dharmakumarsinhji (1950) comprehensively described the displays and movement patterns and Ridley et al. (1985) studied in some detail the display leap. However, while the Lesser Florican behaviour has been generally described, this dissertation is the first quantitative study of its breeding biology.

The Bengal Florican was comparatively much more poorly known, primarily due to its habitat being thinly populated and inaccessible. It was once fairly common in a narrow belt at the foot of the Himalaya, in the terai and duar grasslands of Uttar Pradesh, Bihar, Bengal and the Brahmaputra valley of north eastern India (Jerdon 1864, Hume and Marshall 1878, Baker 1921, Ali and Ripley 1981). However, due to extensive fragmentation of its habitat, this species is now restricted to disjunct pockets in Nepal, Uttar Pradesh, Bengal, Assam and Arunachal Pradesh (Narayan and Rosalind 1990).

Early accounts of the behaviour of the Bengal Florican were both scanty and inaccurate (Jerdon 1864, Baker 1921, Ali and Ripley 1969). It was not until 1988 that accurate and exhaustive descriptions of its breeding biology was published (Narayan & Rosalind 1988, Narayan et al. 1989, Narayan 1990). These accounts were from Assam, at the western extremity, and the wettest part of its breeding range in the Indian subcontinent. While the general biology of this species during the breeding season is now fairly well understood, the non-breeding habits of the Bengal Florican continues to be very poorly known (Rahmani et al. 1988). The breeding behaviour from the dry part (Uttar Pradesh terai) of its breeding range has, not been documented until now.

There are significant differences between the breeding environments, and the breeding behaviour of the Lesser

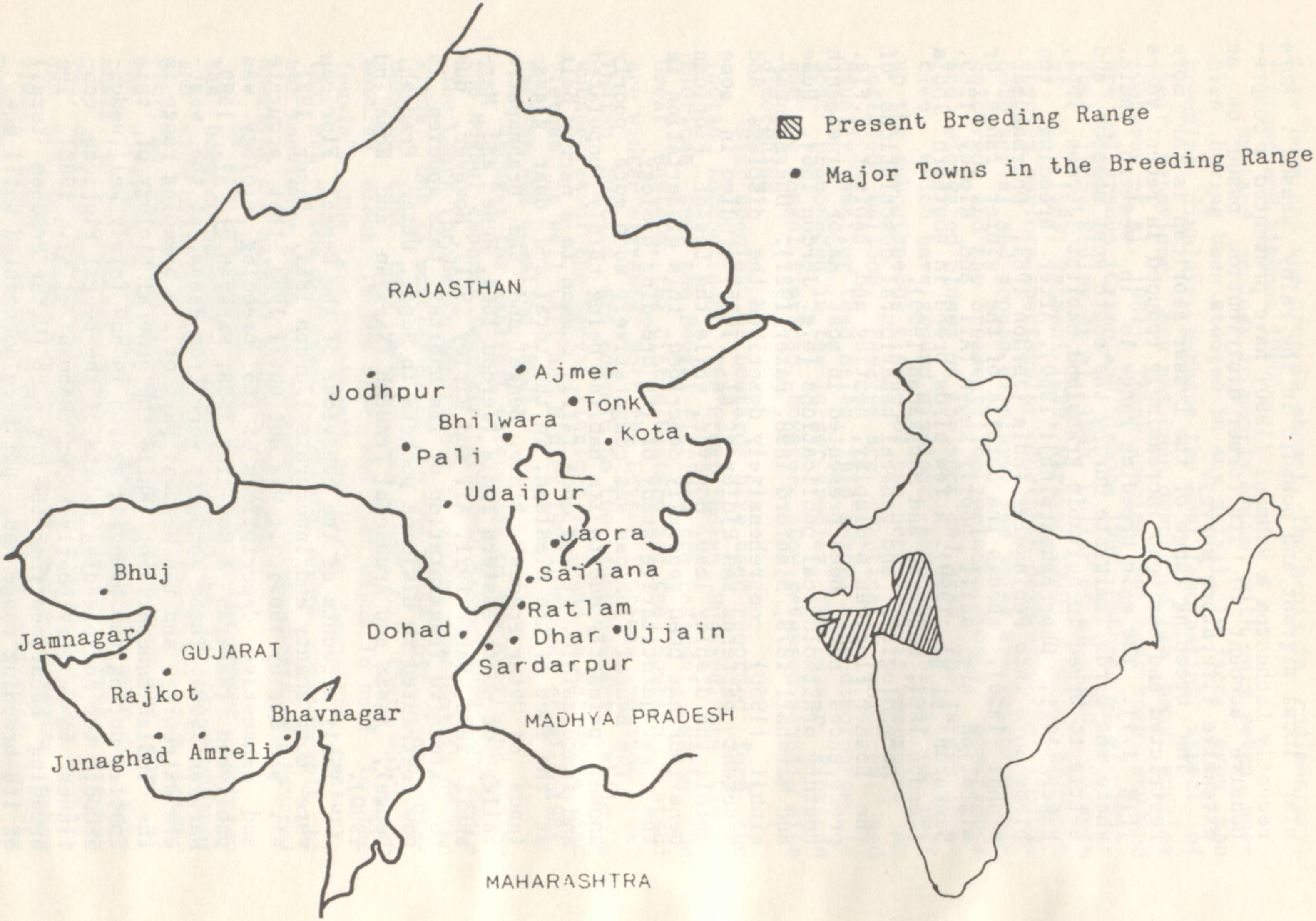


FIG. 1.1. PRESENT BREEDING RANGE OF THE LESSER FLORICAN

Florican and the Bengal Florican. Those that have broad biological significance include nomadism in the Lesser Florican and most probably site tenacity in the Bengal Florican. These two breeding strategies are examined in detail, and the explanations are based primarily on the stability or instability in their respective breeding environments. As a result of a strong inter-annual variability in its breeding environment, the Lesser Florican follows a nomadic strategy whereby individuals attempt placing themselves in areas with an abundance of resources. Thus site tenacity is almost entirely absent in this species. On the other hand, the breeding environment of the Bengal Florican is far more stable, with insignificant fluctuations between years. As a result of which individuals should attempt returning to locations of prior territory possession as the probability of suitable breeding environment being present there in successive years should be higher than the probability of it not being there. As an extension of this argument towards broader biological application it is suggested that the primary criteria for the evolution of site tenacity should be a stable breeding environment. The description, presentation of data and the build up of the arguments occupy the second and third chapters.

The breeding behaviour of these two species is described in detail. Based on these descriptions, the relation between the Lesser Florican and the Bengal Florican is speculated upon. The most significant difference of these two species from the other members of this family, namely the presence of reversed sexual size dimorphism is explained. The arguments regarding this aspect are based primarily on sexual selection through female choice. It is argued that male fitness is, broadly speaking, displayed through two kinds of signals. Those that are based primarily on inter-male dominance will result in courtship displays having components of aggressive displays and in those species males will be larger than females. In species where females choose males based on 'quality' rather than strength, male courtship display will not possess components of aggressive displays. It is argued that this is the basic requirement before other forces select for smaller sizes in males.

ENDANGERED SPECIES PROJECT AND ITS OBJECTIVES

The three resident species of bustards in the Indian Subcontinent are currently endangered. This has primarily been due to large scale habitat changes and other human related pressures. At a seminar in Jaipur in 1980 on the status and conservation of the Great Indian Bustard it became obvious that all three species faced an immediate threat of extinction (Goriup and Vardhan 1980). Alarmed at the plight of the bustards and other endangered wildlife the Bombay Natural History Society started a long term project in 1981 titled 'Study of Ecology of Certain Endangered Species of Wildlife and their Habitats'. This project had two target species, namely the Great Indian Bustard and the Asian Elephant. In 1984, an addendum to the endangered species project named 'Ecology of Lesser Florican and Bengal Florican and Status Survey of Rare Bird Species of the Indian Subcontinent' was instituted. This project was funded by the Fish and Wildlife Service of the United States Department of Interiors (Grant No. 14-16-0009-84), and was received through the Ministry of Environment, Forests and Wildlife, Government of India. The Florican Project spanned five years between August 1984 and September 1989. The primary aim was the conservation of the target species and its objectives were :

1. To obtain precise data on the present distribution of the floricans and other endangered birds by field surveys and questionnaires.
2. To examine habitats presently holding these endangered birds.
3. To determine the exact breeding areas of these birds.
4. To study the ecology and behaviour of the floricans and other endangered birds.
5. To prepare, on the basis of the data obtained, a conservation management plan for the endangered birds.

This dissertation is the result of the fourth objective of the Project. The purpose of this dissertation is to describe and explain certain behavioural and ecological components of the breeding biology of the Lesser Florican and the Bengal Florican. Based on the descriptions and explanations, the study attempts to address certain questions of general biological application such as nomadism and site fidelity, role of triggers and stimuli in courtship displays and female choice.

The results of the other aspects of the study undertaken by the Florican Project has been published in a series of technical and annual reports with co-workers of the project. Information on the conservation and status of these species is therefore not included in this dissertation.

EQUIPMENT AND METHODS

Equipment

Optical equipment used for behavioural observations during this study included a Nikon binocular (7 x 35) and an Opticron telescope (15x). Photographs were taken using two SLR cameras : Olympus OM 1 with Zuiko 50 mm and 135 mm lenses and a 2x teleconverter; and a Canon T-90 with Canon 28 mm, 50 mm, Vivitar 70-210 zoom, and Tamron 500 mm mirror lenses.

Rainfall and maximum and minimum temperature were measured every morning at both field stations using standard meteorological equipment. In 1986, a thermo-hygrograph (Lawrence and Mayo) was used to graphically measure changes in temperature and humidity in 24 hour periods. This instrument was found to be unreliable in the field, especially when placed outdoors in a Stevenson's screen. During rainy conditions, the ink on the needle tended to smudge on the graph paper. This instrument was not used in subsequent seasons. Changes in temperature were measured at half hourly intervals during the observation period by taking a reading from a thermometer at a shaded spot at the observation point.

A plant press, garden clippers, collection jars and containers, formalin and alcohol, a butterfly net, a skinning set, bird bands and pliers, a 2 m tape, two 30 m tapes and a 100 m long marked nylon rope for measuring heights and distances, a stop watch and a hand counter to keep track of the number of occurrences during behavioural observations completed the field equipment. In 1988, sound recordings of the Lesser Florican were made using a Sony Walkman (professional) tape recorder with a uni-directional microphone.

A four wheel drive jeep was used both for transport and as an observation point throughout this study.

Methods

Both the Lesser Florican and the Bengal Florican are difficult birds to study, primarily because the vegetation in the habitat which they occupy hampers free observations. Males, however, are relatively easier to study than females because they are conspicuous and localised within territories. Females are cryptically coloured, shy and secretive and observations on them were few. This dissertation, therefore has very little information on the female florican behaviour.

Attempts were made to colour mark the Lesser Florican, though this remained largely unfruitful. The one male that was captured and colour marked during this study abandoned its territory. Attempts were made to acquire both radio collar equipment and the permission to use them but these too were unsuccessful. Thus this study is based primarily on direct observations of unmarked birds. The methods used to study these species are briefly described here, and any method associated with specific aspects of the study are given in the relevant sections.

The primary problem in studying the floricans is in locating them. Male Lesser Floricans are relatively more easily located when the grass is short. Once sustained display behaviour begins, males are again easily located by their habit of regularly and very frequently jumping above the grass. However, in longer grass, all other activities are hidden from the observer, and data from this period onwards is primarily only on temporal variations in number of display leaps. In the case of the Bengal Florican, males are easily located only when they are present in the display area of their territories which is characterised by short grass. When they move into long grass, as they do during the middle of the day they are not visible at all. Secondly, display in this species is sporadic and infrequent. Thus males are less easily located in this species. However once a male is located all activities are easily observable in the Bengal Florican.

Behavioural observations in the field were made using either binoculars or the telescope. Detailed observations were made from vantage points between 50 and 500 metres from the focal animal. Vantage points included mounds of earth adjacent to wells, the roof of a small house in a crop field, the roof of the Jeep, a convenient branch of a tree, or small 'machans' that were made on trees at suitable locations. Hides made of bamboo and sack cloth, camouflaged with grass, were placed near display sites of selected males, but observations from these were limited by a narrow field of view, particularly when the grass was tall. Dummies made of chicken skins, painted to look like males and females, were used to make close up observations of intraspecific behaviour.

Behavioural observations conformed mainly to the focal animal sampling method (Altmann 1974). No other method was found appropriate in this study, primarily because male floricans are solitary during the breeding season and their territories are widely spaced out. Observations followed two principal methods of data collection, and minor refinements were made in the pattern of data collection as the years progressed. Observational methods for both species of floricans differed slightly, and these are given below.

In 1985 and 1986, a Lesser Florican was located at dawn, and continuously observed until noon. The following day, a male was located at noon (if territorial, the same territory as on the previous day) and observed continuously until dusk. Any major change in activity was noted, and the time recorded to the nearest minute. The total number of jumps in five minute periods were noted. This method was modified in 1988. In that year, observations were made from dawn to 12 noon and resumed at 1400 hours. Observations were made for 20 continuous minutes, followed by a 10 minute interval. During the observation period, the time of every jump was recorded to the nearest second. Similarly, the start and end of every activity was noted to the nearest second. This method of recording observations was found necessary in the Lesser Florican because this species is extremely active and can perform display leaps as rapidly as once every 25 seconds.

The Bengal Florican was observed mainly from machans. Territorial males were observed from dawn until they left their display sites. Observations were continued for a minimum of 20 minutes after the male was last seen in order to ensure that the male had actually left the display site. In the evening the same territory as was studied in the morning was observed. Males generally arrived at the display sites 2.5 to 3 hours before dusk. The observation point was manned at least 20 to 30 minutes prior to the arrival of the territorial male and observation continued until it was too dark to see. Observations were recorded in a similar manner as for the Lesser Florican; however the Bengal Florican being larger, continuous observations were less strenuous. The time of all changes in activity were recorded to the nearest second. Five males were located as target birds and an attempt was made to study each male for one morning and evening session at-least once a week.

The immigration chronology and micro-habitat use patterns of the Lesser Florican were studied by scanning all parts and habitat types of the study site at least 4 to 6 times a week. Data on Lesser Floricans thus flushed, or located, was recorded primarily as to location in study area and micro-habitat i.e. whether in crop field, grass patch or in the main grassland. Two field assistants helped in this task. Within a 350 hectare area, which at the early stages of the breeding season had very little vegetation, locating Lesser Florican was relatively easy. In two or three such attempts a reasonably accurate idea of the number of floricans present at the study site was easily obtained. Habitat use data was based purely on the micro-habitat a florican was using when it was first located. Subsequent movement was not taken into account.

During the early part of the breeding season, such scanning of the study area was done every day, to know the number of new arrivals. Once territories were established and males became localised, such scanning became less frequent and primarily served the function of monitoring territories that were not being actively studied.

Behavioural observations included the identification of the following basic activities. As the floricans are cursorial, foraging activities were essentially difficult to differentiate from walking: whenever a food item is found the florican pauses to eat it. Thus a florican was said to forage whenever it was in motion, irrespective of whether it was actually pecking or not. Display included all courtship activities, and was divided into two. Those displays without the presence of a female were called attraction displays and those directed towards a nearby female were called courtship displays. Agonistic interactions included all aggressive interaction between males. Preening constituted all maintenance activities. Disturbances were regarded as all florican activities emanating from human activity. Detailed notes were made whenever possible on the various postures and sequence of activity (for example sequence of preening) during observations.

Weather data recorded during observations included ambient air temperatures, recorded in the shade every half hour by reading a thermometer at the observation point. Cloud cover was subjectively divided into 0-25, 26-50, 51-75 and 76-100 % of the sky. Similarly, rainfall was classified as light drizzle, moderate drizzle and rain, and wind into light, medium and strong. Every change in the weather condition was noted down to the nearest second in the Lesser Florican study and the nearest minute in the Bengal Florican study. This was because during the monsoon, weather changes are far more rapid and frequent than in the summer. Secondly, activity changes in the Lesser Florican are also far more frequent and rapid than in the Bengal Florican.

Once every 7 days, grass height and orthopteran abundance was measured. Grass height was measured at different sites within each study area. This consisted of a minimum of 30 randomly selected points where measurements of maximum grass length were made at each site. Each study area had between two and five such sampling sites. Additionally, grass height at Lesser Florican 'jumping spots' was measured at 0, 1, 5, 10 and 25 m along 4 directions namely, North, South, East and West, with the jumping spot being the point of their bisection. Orthopteran abundance was measured by using a butterfly net and the 'sweep' method. Four plots, two in the grassland and two in grazed lands, were identified and each plot was measured with 100 'sweeps'. Orthoptera that were either caught in the net or flushed while sweeping were counted.

Detailed maps of territories of focal male Bengal Floricans were made by hand. This was done by measuring the distances of roads, between prominent trees, forest etc. either by a 100 m long marked nylon rope or, where vegetation was too dense to permit penetration, with a range finder. As the grasslands that hold territories were fairly large, it was possible to make accurate maps at lower resolution. Onto these, grassland community types were superimposed. As the areas mapped had a few scattered trees providing prominent points of reference, and distinct borders between grassland types, it was possible using prominent landmarks to accurately draw a profile of the communities. Bengal Florican movements were plotted on copies of these maps. The location of display, line of movement and locations of other salient activities were plotted continuously during observation periods.

In the Lesser Florican study the entire grassland area itself was very small, within which were scattered very small territories of the males. This demanded a very great degree of resolution to do home range and movement pattern studies. Moreover, there were almost no landmarks within each territory and therefore no points of reference. Thus, only overall detailed maps of the study area were made, on which the general location of territories were plotted.

The analysis of data has been done with the help of various computer packages. Some data were entered in Dbase III, especially those with larger data sets, while Lotus 123 was used to enter most data that had been previously sorted and tabulated by hand. Lotus 123 was used to make all calculations, data sorting, data transformation and data standardisation prior to statistical analysis. Most regression analyses were done in Lotus. Finally, tabulated data was imported to Systat where all statistical tests in this dissertation were done. Statistical tests done in this study are based on guidelines laid down by Fowler and Cohen (1986). Graphic representation of the data was done using Harvard Presentation Graphics and to a lesser extent Sygraph. Home range analysis were done in Seas. Wordstar 4 has been used for all word processing.

Additionally, detailed list of reptiles, mammals and birds were maintained. Status, population structure and composition and habitat use of few other species namely the Swamp deer, Hog Deer, Red Jungle Fowl and Peafowl were also studied.

STUDY AREAS

LESSER FLORICAN

Studies on the Lesser Florican were carried out at three main grassland sites. The main study site was at the Naulakha grassland within the Sailana Kharmor Sanctuary in Ratlam district, Madhya Pradesh. A nearby grassland, Hazariya, was monitored regularly. Both Hazariya and Naulakha are within Sailana _tehsil_. In 1988, the Lesser Florican was studied intensively at the Rampura-Movalia-Kalitalai grasslands near Dohad in Panchmahal district, Gujarat.

All three study sites fall within the Malwa plateau. The Malwa plateau covers about 34,600 sq. km and is a wide table-land with a mean elevation of 484 meters above sea level. The plateau is undulating, interspersed with a few hilly regions. The soil can be classified as medium black cotton soil, usually dark brown in colour and not very deep. However, lighter coloured soils, usually red (_murram_), are also seen. The ground is generally stony. The natural drainage is usually from south to north (Raychaudhari _et al._ 1963). All three study sites conform to this description. The land is most steeply undulating at Rampura, least so at Naulakha and intermediate at Hazariya. The valleys (_nullahs_) in these grasslands drain rainwater from the grassland into man-made reservoirs. During heavy rains, these <u>nullahs</u> become torrential rivulets. Black cotton soil occurred rarely at the Naulakha and Hazariya grasslands, as those areas with black cotton soil are all under agriculture. In the Rampura grassland, however, large areas were under black cotton soil, due to the vastness and stability in land use patterns due to Government ownership.

Naulakha (Sailana Kharmor Sanctuary)

The Sailana Kharmor Sanctuary lies on the Tropic of Cancer (23°31' N and 75°01' E), near Sailana town, Ratlam district, western Madhya Pradesh (Fig. 1.2). It was declared a protected area in June 1983 and comprises 354 hectares of grassland, crop-fields and grazing lands. The sanctuary is bounded by three villages, Sailana, Adwanya and Gordhanpura, and the whole area is jointly owned by agriculturists. The grassland area within the sanctuary is about 200 hectares and is known as the Naulakha grass <u>bheed</u> (<u>bheed</u> = protected hay producing grassland), and this study site is referred to as the Naulakha grassland.

The Naulakha grassland has six main ridges and their spurs, all sloping towards the eastern corner of the sanctuary, where lies a perennial reservoir, Gordhansagar. On the banks of this reservoir stand the ruins of a hunting lodge of the erstwhile Maharaja of Sailana, an indication of the non-agricultural use of this area in the recent past. The shallow valleys between the ridges channels rainwater rivulets towards this water body and two other smaller reservoirs (Fig. 1.2).

The Naulakha grassland is a partially grazed grassland. That is, livestock is allowed to graze in the grassland till about four weeks have elapsed after the onset of the monsoon. After this the grassland is protected from grazing until the completion of the hay harvest in November. Once harvest is completed, grazing is once again permitted in the grassland until about four weeks elapse of the following monsoon.

At the Naulakha study site, the habitat available to the Lesser Florican was of three types:

a) Grassland. This was the Naulakha grassland which covered about 200 hectares of pure contiguous grassland.

b) Crop fields. On the periphery of the grassland are the agricultural fields of the nearby villages the predominant monsoon crops being corn, sorghum and soya beans (see crops below).

c) Grass patches in crop areas. These were small isolated patches of grass amidst the cropfields which had not yet been brought under the plough. These patches were small, usually 2 acres or less and totally occupied only about five hectares in 1988.

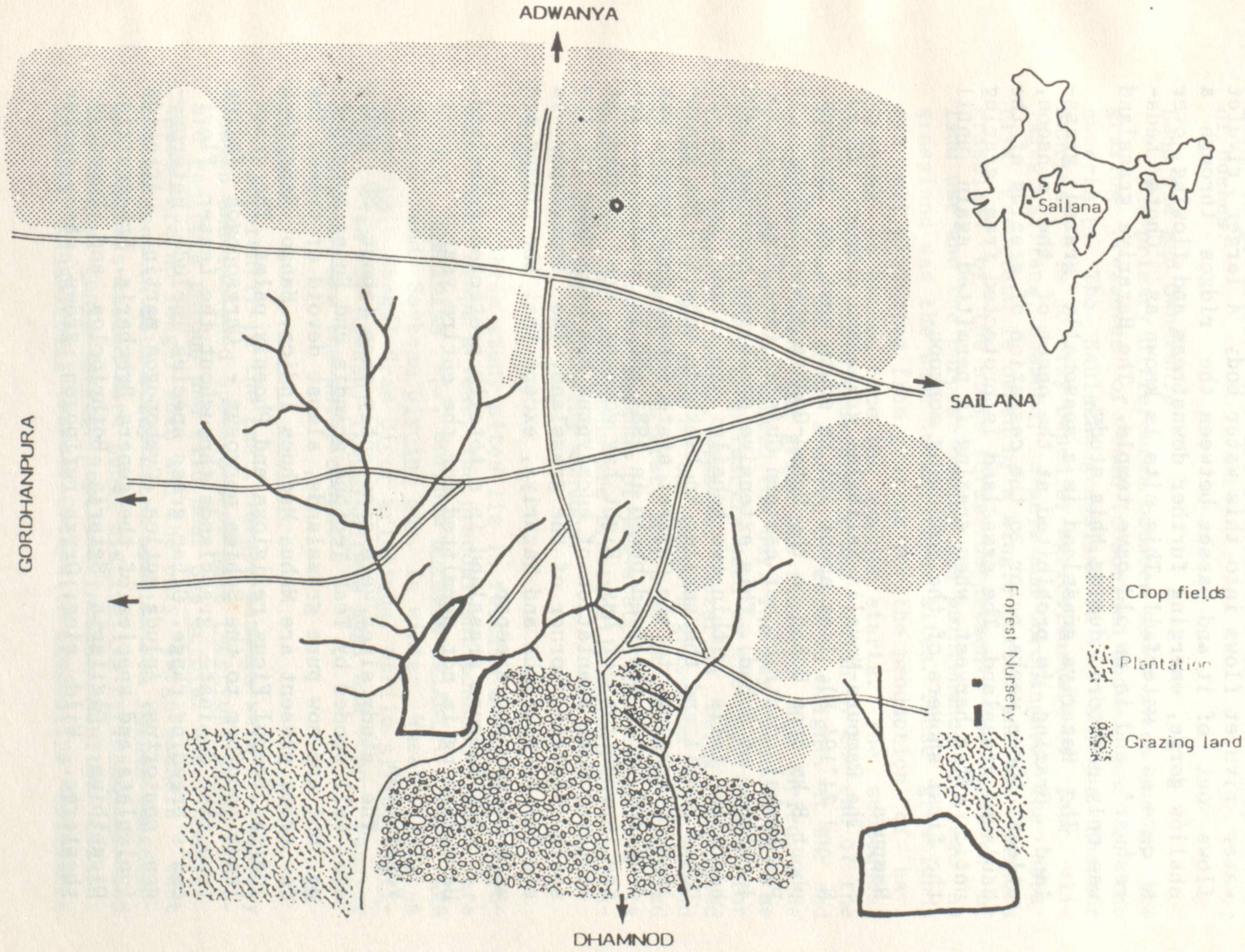


FIG. 1.2. MAIN LESSER FLORICAN STUDY AREA - NAULAKHA GRASSLAND NEAR SAILANA

Hazariya

The Hazariya grass bheed is about 90 hectares in size and lies about 3 km west of the Naulakha grassland, near Sailana town, Ratlam district, Madhya Pradesh. Both Naulakha and Hazariya lie on the same plateau. The Hazariya grass bheed consists of one main ridge and part of another ridge, with a small permanent reservoir between the two. A rain-water rivulet flows into this water body. A larger rivulet flows out of it and passes between the ridges through a shallow gorge, emerging further downstream and flowing over a cave as a waterfall. This site is known as 'Chota Kedareshwar', and is an old cave temple. The Hazariya grassland was only monitored during this study.

The Hazariya grassland is a seasonally grazed grassland. Grazing is prohibited at the onset of the monsoon, atleast three weeks prior to the cessation of grazing at the Naulakha grassland. The grassland is protected from grazing until after harvest, when grazing is permitted again until the first showers of the following monsoon.

Rampura

The Rampura-Movalia-Kalitalai grassland complex (22°53' N and 74°19' E), lies about 125 km south west of Sailana, about 8 km from Dohad on the Dohad-Godhra state highway, in Panchmahal district of eastern Gujarat (see Fig. 1.1 for location of Dohad). This extensive grassland covering 2400 hectares falls within two tehsils: the larger portion in Dohad tehsil and the smaller in Limkheda tehsil. The grassland, belonging to the Gujarat state forest department, was declared as a reserved bheed in 1984 and is protected for the production of hay. Eight hay godowns are located at Rampura. Some plantation of eucalyptus has been done in the south western corner of the grassland. The topography is similar to Naulakha and Hazariya, except that the ridges are much larger and steeper.

The Rampura grassland is a totally protected grassland. Here grazing is not permitted for the entire year.

Vegetation

The study sites were apparently once (about 30 years ago) well wooded by Teak Tectona grandis and Butea monosperma, but are now pure grasslands, almost devoid of trees. The few trees present are Mahua Madhuca indica, Mango Mangifera indica, Peepul Ficus religiosa and Phoenix palms. The grasslands conform to the Sehima nervosum - Chrysopogon fulvus type that dominate grasslands throughout the Lesser Florican's breeding range. Other grass species include Heteropogon contortus, Apluda mutica, Cymbopogon martini, Aristida funiculata and species of the genera Bracharia, Eragrostris, Dicanthium, Digitaria, Setaria, Bothriocloa and Pseudoanthesterea. Wild rice, Oryza rufipogon grows where water accumulates during the monsoon. In both grasslands, Butea monosperma is a common bush, rarely growing into trees. The fibres of the roots are used by the local tribals to make ropes, and this perhaps inhibits growth. At Rampura grassland, perhaps due to the larger size and better protection, greater diversity of vegetation is seen. Like Butea, Teak is seen in profusion, but are stunted and have the appearance of bushes.

Land Use and Ownership

The primary differences between these sites are in the grazing pressures of each (described above) and in the ownership. The Naulakha grassland in the Sailana Kharmor Sanctuary is jointly owned by agriculturists of four villages: Sailana, Dhamnod, Adwanya and Gordhanpura. The Hazariya grassland is owned by a single person and the Rampura grassland by the state forest department. The pattern of land use and the purpose behind the maintenance of these as grassland was the same in all three sites. These grasslands are all protected from grazing for the production of hay. Grazing is banned once the monsoon starts. The subsequent rains cause a rapid growth of grass, which by the end of the monsoon grows to about a metre or more in height. At the end of October, when the grass has flowered and dried, the grasslands are harvested for hay. The hay produce of the Naulakha grassland is primarily used by the individuals for their domestic needs, that of Hazariya being exploited commercially, and that of the Rampura grassland being stored by the Government of Gujarat, and used as and when required to fulfill fodder demands of the state. Once harvesting is completed, the grasslands are practically devoid of vegetation until the following monsoon.

Crops

All three study sites lie in fertile areas which produce two crops a year. The predominant monsoon crops are Cotton Gossypium sp., Sorghum Hordeum vulgare, Maize Zea maize, and Soybean Glycine max. In winter Wheat Triticum aestivum, Bengal Gram Cicer arietinum, Garlic Allium sativum, Ajma (or Ajwain) Trachyspermum ammi and Poppy Papaver somniferum are the chief crops.

Fauna

Apparently in the past, larger mammals were relatively common and included Spotted Deer Axis (=Cervus) axis, Leopard Panthera pardus and Wild Boar Sus scrofa. Now, however, these are no longer seen and the only 'large mammals' that can be seen in both study sites are the Fox Vulpes bengalensis, Rufous-tailed Hare Lupus nigricollis ruficaudatus and the Jackal Canis aureus. Reptiles include Monitor Lizards Varanus bengalensis (rare), Crocodile Crocodilus palustris (very rare), Agama *Agama major*, Garden Lizard *Calotes* sp. Black Cobra *Naja naja oxiana*, Sawscaled Viper *Echis carinata*, Russel's Viper *Vipera russelli*, Checkered Keelback *Xenochrophis piscator*, Striped Keelback *Amphesma stolata*, Olive-green Keelback *Atrecium systotum* (Dohad only) and Common Wolf Snake *Lycodon aulicus*.

For a check list of birds at the Lesser Florican study areas, see appendix in 'Status and Ecology of The Lesser and Bengal Floricans - Final Report' (BNHS).

Climate

The climate is extreme with summers tending to be hot (>40°C) and the winters cold (<10°C). The monsoon usually arrives in these areas in the third or fourth week of June. The major part of the annual precipitation occurs in July and August. The monsoons (June 15 to October 15) usually has 40 to 50 rainy days. Average precipitation during the monsoon at Sailana is about 1100 mm (average of 6 years) while at Dohad it is about 550 mm (average of four years). Temperature during the monsoon varies between 17°C and 38°C.

BENGAL FLORICAN

The Bengal Florican was studied at grassland sites within the Dudwa National Park, between latitude 28°24' and 28°40'N and longitude 80°34' and 80°50'E, in the northern extremity of Lakhimpur Kheri district of Uttar Pradesh (Fig. 1.3). The elevation above sea level slopes down from 182 m in the extreme north to 150 m in the south east. The foothills of the Himalaya in Nepal begin from about 30 km north of the Park. The Mohana and Suheli rivers form natural boundaries, in part, to the north and south respectively. The Park's water system drains into these two rivers, which are tributaries of the river Sharda, which in turn is a part of the Ganges river system. The soil is of the alluvial type, typical to the Gangetic plain, having layers of sand and loam.

The Dudwa Sanctuary (area 212 sq. km) was upgraded to a National Park on 1st February 1977. The Dudwa National Park (DNP) covers an area of 614 sq. km, with a core area of 490 sq. km. At the end of 1987 DNP was brought under Project Tiger, and along with the Kishanpur Wildlife Sanctuary (158 sq. km core area and 43 sq. km buffer) the Dudwa Tiger Reserve now covers 815 sq. km. The two forests are however not contiguous. This dissertation deals only with studies made at the Dudwa National Park, and all data pertains only to the 614 sq. km area.

Florican Sites

Three main florican areas are present in the Park: grassland areas around the Satiana forest rest house (FRH)

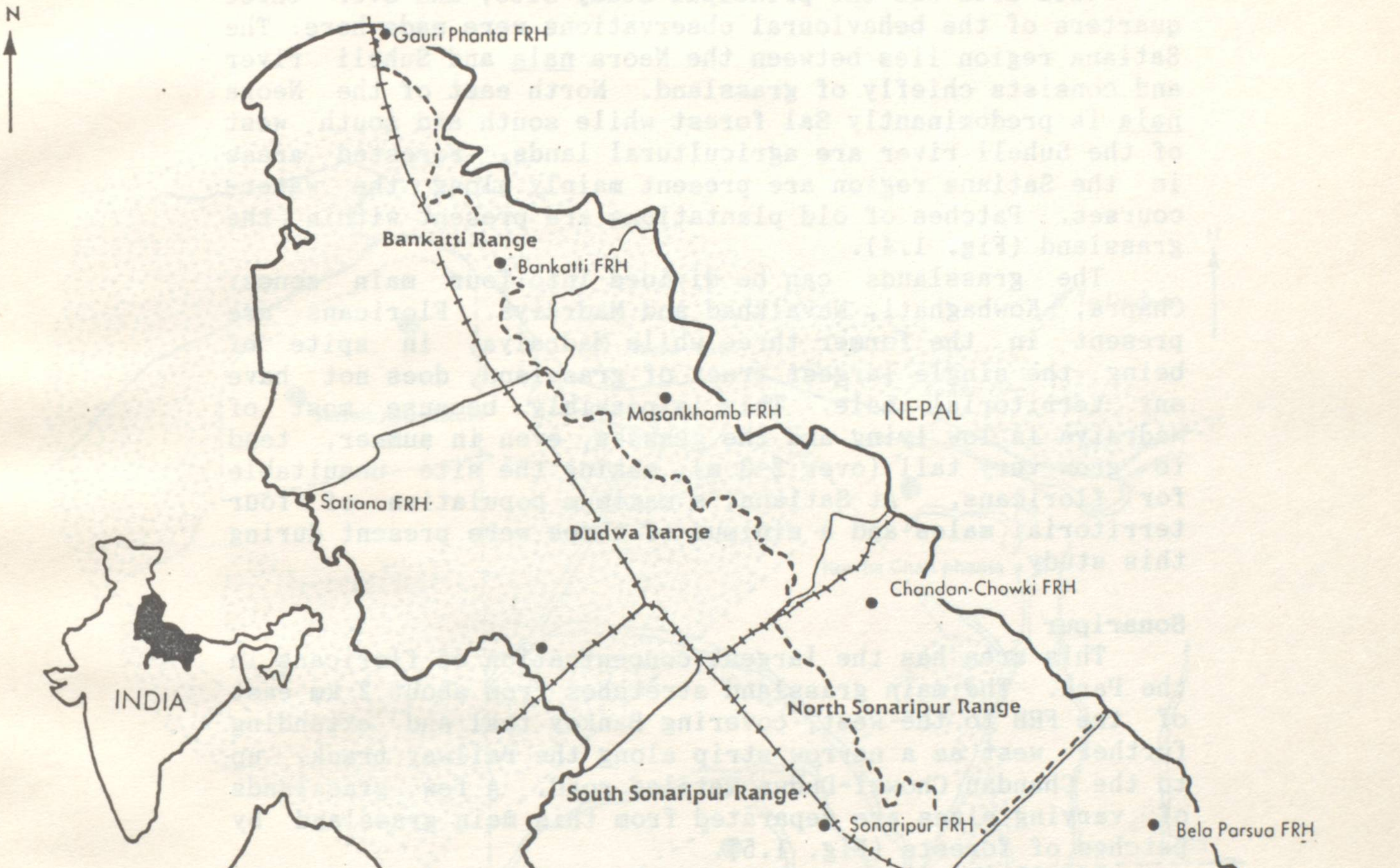


FIG. 1.3. DUDWA NATIONAL PARK

on the border of Dudwa and Bankatti ranges; the rhino enclosure at Kakraha in the South Sonaripur range, and around the Sonaripur FRH on the border of North and South Sonaripur ranges. To simplify matters, the main florican areas are referred to as Satiana, Sonaripur and Kakraha (Salukapur) in this dissertation (Fig. 1.3).

Satiana

This area was the principal study site, and over three quarters of the behavioural observations were made here. The Satiana region lies between the Neora nala and Suheli river and consists chiefly of grassland. North east of the Neora nala is predominantly Sal forest while south and south west of the Suheli river are agricultural lands. Forested areas in the Satiana region are present mainly along the watercourses. Patches of old plantations are present within the grassland (Fig. 1.4).

The grasslands can be divided into four main zones: Chapra, Kowhaghati, Navalkhad and Madraiya. Floricans are present in the former three while Madraiya, in spite of being the single largest tract of grassland, does not have any territorial male. This is possibly because most of Madraiya is low lying and the grasses, even in summer, tend to grow very tall (over 2-3 m), making the site unsuitable for floricans. At Satiana, a maximum population of four territorial males and a minimum of three were present during this study.

Sonaripur

This area has the largest concentration of floricans in the Park. The main grassland stretches from about 2 km east of the FRH to the west, covering Bankey taal and extending further west as a narrow strip along the railway track, up to the Chandan Chowki-Dudwa metaled road. A few grasslands of varying sizes are separated from this main grassland by patches of forests (Fig. 1.5).

Of the five Bengal Florican territories located here, two were in the grasslands around the rest house and the remaining three territorial males were in the Seethagaddai grassland. The three males in the Seethagaddaia grassland were studied in detail in 1989.

Kakraha (Salukapur Rhino Enclosure)

The rhino re-introduction programme was initiated in 1985 and covers an area of 27.4 sq. km, of which about 20 sq. km is grassland. The area is enclosed by an electric fence (Fig. 1.6). The Great Indian One-horned Rhinoceros was last seen in this region in 1878 (Singh, 1985). Presently there are nine rhinos within the enclosure.

Numerous temporary and perennial waterbodies and a few nalas are present within the enclosure. The areas adjoining

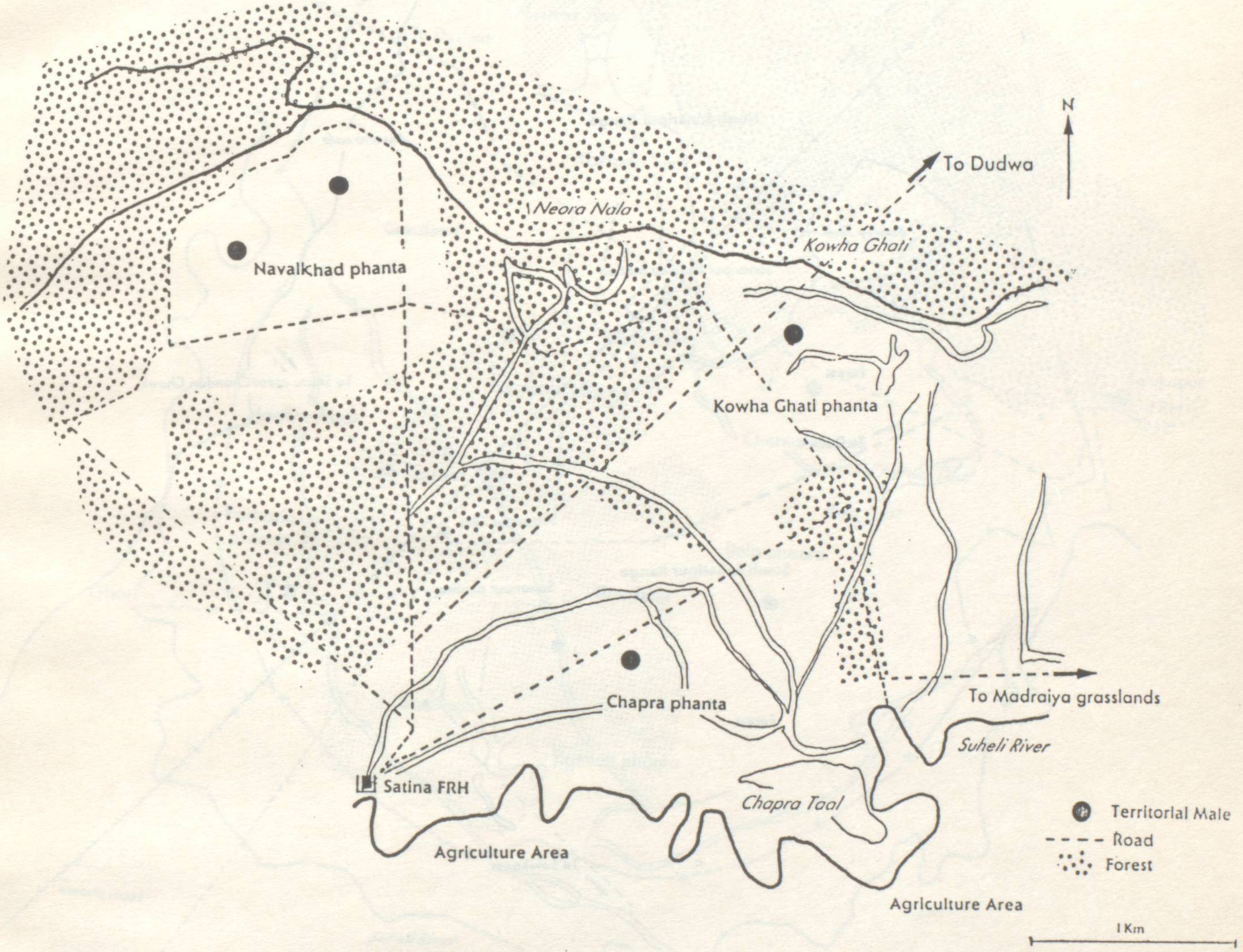


FIG. 1.4. GRASSLAND AREAS AT SATIANA WITH LOCATIONS OF BENGAL FLORICAN TERRITORIES

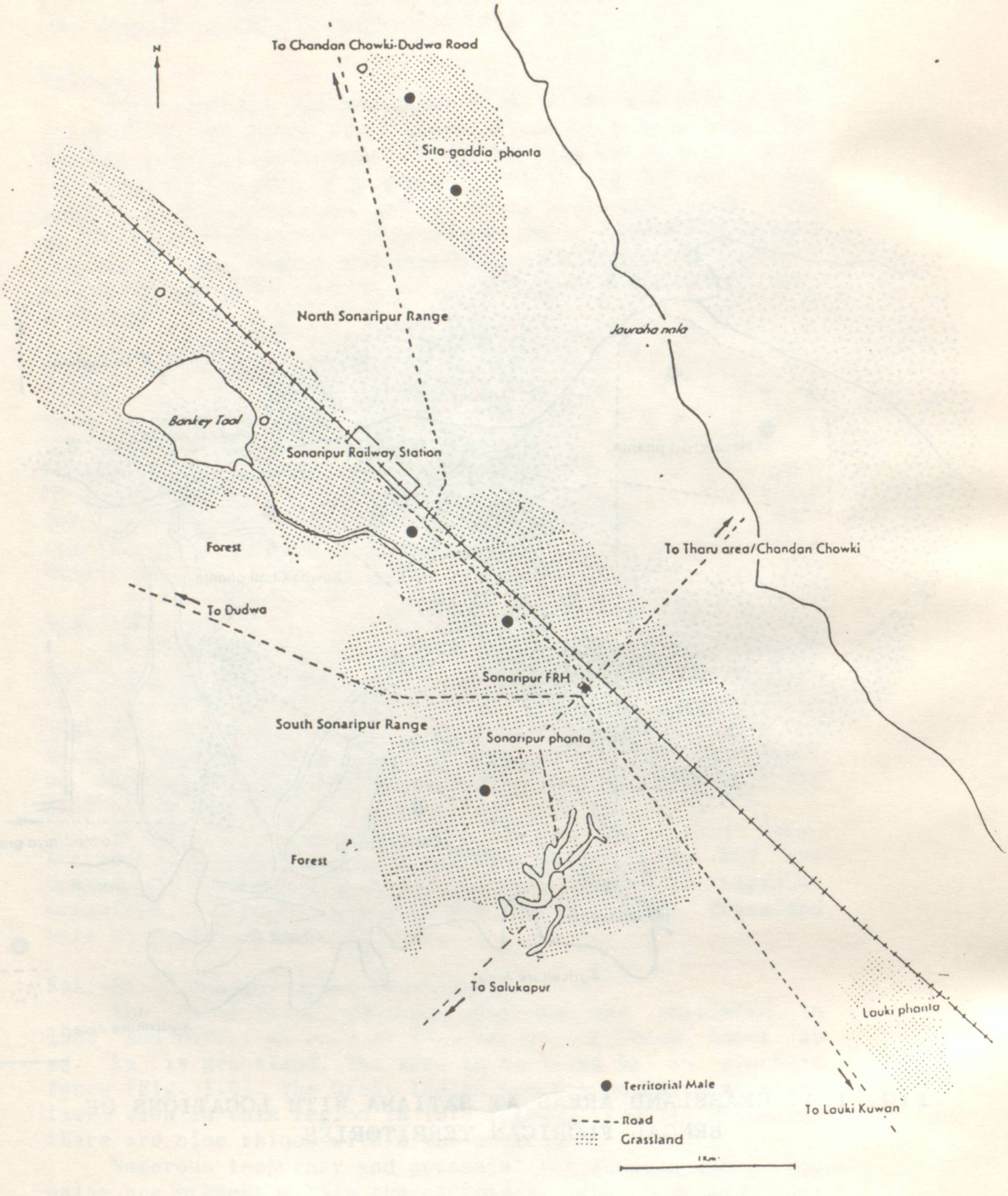


FIG. 1.5. GRASSLAND AREAS AT SONARIPUR WITH LOCATIONS OF BENGAL FLORICAN TERRITORIES

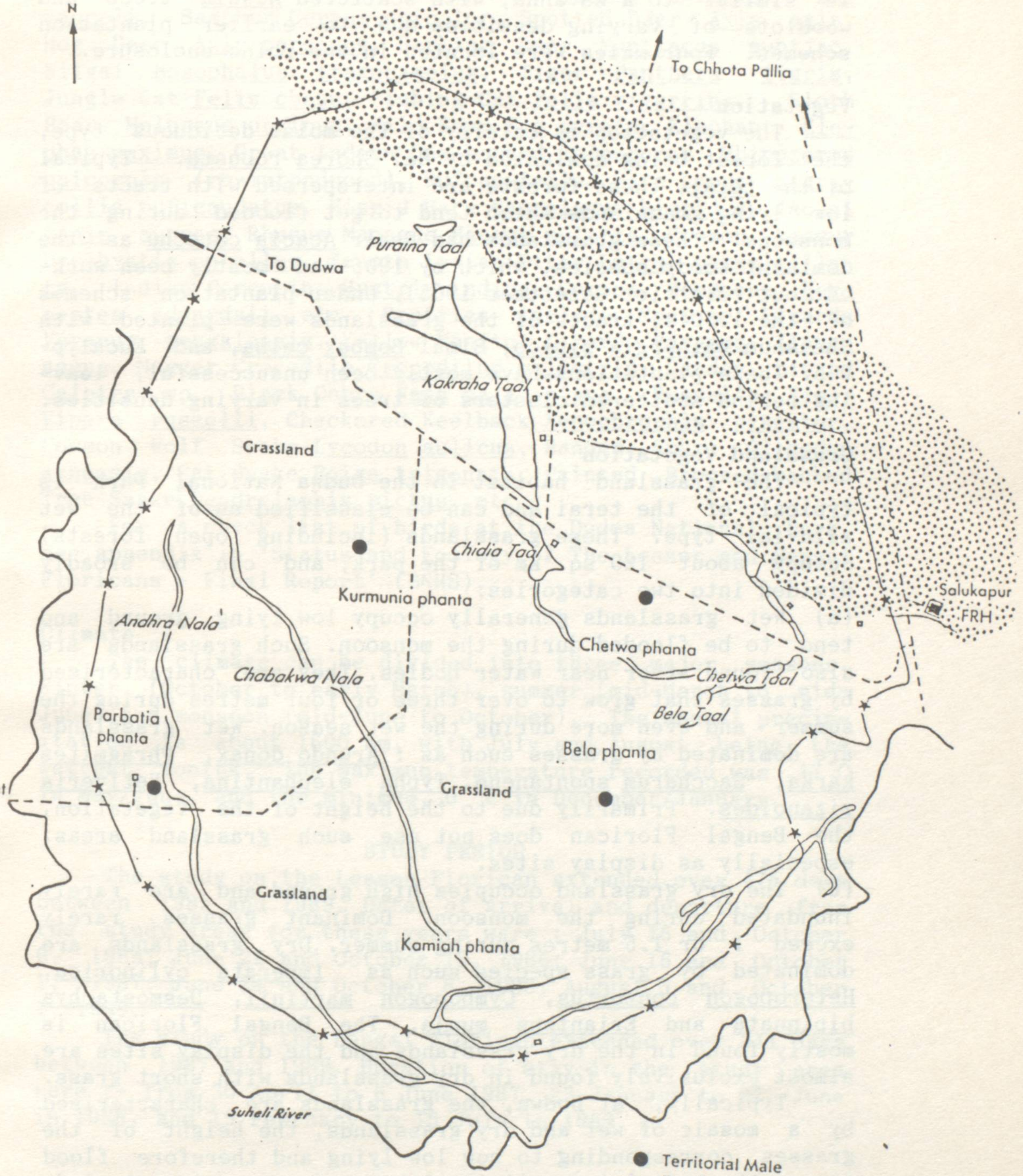


FIG. 1.6. GRASSLAND AREAS AT KAKRAHA WITH LOCATIONS OF BENGAL FLORICAN TERRITORIES

these are covered by tall, dense grasses and hence are unsuitable for the floricans. The Bengal Floricans occupy the higher ground which is covered by short grasses. In fact, the areas suitable for and occupied by the florican is similar to a savanna, with scattered Acacia trees and woodlots of varying densities due to earlier plantation schemes. Four males were located in the rhino enclosure.

Vegetation

The vegetation is chiefly of the moist deciduous type, the forest being dominated by Sal Shorea robusta. Typical of the terai, these forests are interspersed with tracts of low lying grasslands which tend to get flooded during the monsoons. These grasslands had Khair Acacia catechu as the dominant woody species, which by 1905 had mostly been worked out (District Gazetteer 1905). Under plantation schemes of the 1950's, tracts of the grasslands were planted with Sheeshum Dalbergia sissoo, Simul Bombax ceiba, and Eucalyptus. These plantations have mostly been unsuccessful, leaving behind scattered clusters of trees in varying densities.

Grassland Vegetation

The grassland habitat in the Dudwa National Park is typical of the terai and can be classified as of the wet alluvial type. These grasslands (including open forests) occupy about 120 sq. km of the park, and can be broadly divided into two categories:

(a) Wet grasslands generally occupy low lying ground and tend to be flooded during the monsoon. Such grasslands are also found at or near water bodies. They are characterised by grasses that grow to over three or four metres during the summer and even more during the wet season. Wet grasslands are dominated by grasses such as : Arundo donax, Phragmites karka, Saccharum spontaneum, Typha elephantina, Vetiveria zizanoides. Primarily due to the height of the vegetation, the Bengal Florican does not use such grassland areas, especially as display sites.

(b) The dry grassland occupies high ground and are rarely inundated during the monsoon. Dominant grasses rarely exceed 1 or 1.5 metres during summer. Dry grasslands are dominated by grass species such as Imperata cylindrica, Heteropogon contortus, Cymbopogon martinii, Desmostachya bipinnata and Erianthus munja. The Bengal Florican is mostly found in the dry grasslands and the display sites are almost exclusively found in dry grasslands with short grass.

Typically, at Dudwa, the grasslands are characterised by a mosaic of wet and dry grasslands, the height of the grasses corresponding to how low lying and therefore flood prone the underlying soil is. Other grass species include Sacharum narenga, Bothriochloa pertusa, Themeda arundinacea, Perotis indica, Andropogon intermedius, Panicum paludosum, Dactyloctenium aegyptium, Setaria glauca, Cynodon dactylon.

Fauna

Being a Tiger Reserve, the area is rich in fauna. Some of the large mammals are Swamp Deer Cervus duvauceli duvauceli, Sambhar Cervus unicolor, Spotted Deer Axis axis, Hog Deer Axis porcinus, Barking Deer Muntiacus muntjac, Nilgai Bosephalus tragocamelus, Tiger Panthera tigris, Jungle Cat Felis chaus, Fishing Cat Felis viverrina, Sloth Bear Melursus ursinus, Wild Boar Sus scrofa, Elephant Elephas maximus, Great Indian One-horned Rhinoceros Rhinoceros unicornis (re-introduced), Rufous-tailed Hare Lupus nigricollis ruficaudatus, Hispid Hare Caprolagus hispidus, Jackal Canis aureas, Rhesus Macaque Macaca mulatta, Common Langur Presbystis entellus, Smooth Indian Otter Lutra perspicillata, Indian Porcupine Hystrix indica, Common Mongoose Herpestes edwardsii etc. Reptiles include Monitor Lizards Varanus bengalensis, Yellow Monitor Lizard Varanus flavescens, Mugger Crocodile Crocodilus palustris, Garden Lizard Calotes sp. Black Cobra Naja naja oxiana, Russel's Viper Vipera russelli, Checkered Keelback Xenochrophis piscator, Common Wolf Snake Lycodon aulicus, Banded Kukri Oligodon arnensis, Cat Snake Boiga trigonata, Painted Bronzed-backed Tree Snake Dendrelaphis pictus, etc.

For a check list of birds at the Dudwa National Park, see appendix in 'Status and Ecology of The Lesser and Bengal Floricans - Final Report' (BNHS).

Climate

The climate can be divided into three major seasons. Winter (October to early March), summer (mid-March to mid-June) and monsoon (mid-June to October). The annual precipitation is about 1600 mm, with July and August being the wettest months. The maximum temperature recorded was 47°C in May/June, and the minimum, 0° C in December/January.

STUDY PERIOD

The study on the Lesser Florican extended over 475 days between 1985 and 1989. Dates of arrival and departure from the study areas for these years were : July 16 and October 6, 1985; June 22 and October 10, 1986; June 16 and October 1, 1987; June 24 and October 6, 1988; August 5 and October 1, 1989.

The study on the Bengal Florican extended over 341 days between 1987 and 1989. Duration of stay in the study area were :- from 30 April to 6 June 1987, 22 January to 22 June in 1988, and 15 February to 15 July in 1989.

Chapter 2

ENVIRONMENTAL FACTORS INFLUENCING THE BREEDING SEASON

INTRODUCTION

To reproduce successfully, birds should do so when the environmental conditions are most favourable (Earle 1981). Breeding success will not only be determined by the presence of adequate cover for nesting and hiding the young, but also by the availability of adequate food (Lack 1954, 1968, 1973, Perrins 1970, Fogden 1972, Naik and Mistry 1980, Sinclair 1983, Alagar Rajan 1990). Breeding seasons are, however, fixed for most species and the degree of variability in factors determining favourable environmental conditions will play a major role in breeding success.

For instance, for those species which depend on rainfall to breed, poor or no breeding accompanies drought (for e.g. Moreau 1950, Ali and Rahmani 1984, Manry 1985, Rahmani and Manakadan 1987 (a), Vijayan 1987), or where rainfall is highly variable as is the case in South Western Australia, birds may breed whenever there is adequate rainfall (Keat and Marshall 1954, Davies 1979).

Many other species, however, exploit relatively more stable breeding environments than those dependent on highly variable factors like rainfall. The degree of stability or variability in factors determining a species' breeding environment will then govern most breeding responses of that species. Such responses would include, among others, dispersal and/or concentration of populations, fidelity to breeding sites and duration of breeding season. Furthermore, the variability of causative factors may play a role in behavioural divergence of two closely related species.

The Lesser Florican and Bengal Florican are two such closely related species that exploit grassland habitats to breed in. However, the factors that determine the breeding environment are different in that the Lesser Florican's shows marked inter-year variation while the Bengal Florican's is relatively stable. The Lesser Florican breeds during the south west monsoon while the Bengal Florican breeds during the summer (Jerdon 1864, Baker 1921, Dharmakumarsinhji 1950, Inskipp and Inskipp 1982, Inskipp and Collar 1984, Sankaran and Rahmani 1986, 1988, Mukherjee 1986, Narayan and Rosalind 1988, Narayan et al. 1989). Several species of bustards breed during the wet season and the examples include the Kori, Denham's, Arabian, some populations of the Houbara (Morgan-Davies 1965, Cramp and Simmons 1980), most populations of the Great Indian Bustard (Rahmani 1989) and the Australian Bustard (Downes 1981). Fewer bustard species are known to breed during the summer. Apart from the three species that breed in temperate climes (Great, Little and Houbara bustard), only the Bengal Florican and some populations of the Great Indian Bustard are definitely summer breeders.

In this chapter, the theme of stability and variability in factors that determine breeding environments and the corresponding responses of the concerned species is developed. The influence of rainfall on the grassland habitat, the food abundance and the consequent movement patterns of the lesser florican are discussed in detail. The section on Bengal Florican describes the relatively more stable causative factors that reduces the inter-year variation in the breeding of this species.

RESULTS

LESSER FLORICAN

The salient features in the chronology of events in the breeding seasons of the Lesser Florican at the Naulakha Grassland are given in Figures 2.1.a to 2.1.d. These give an overview of the breeding seasons and are referred to as and when necessary. Unless mentioned otherwise, all data pertains to the Naulakha grassland study area.

The time scale of the monsoon has been standardised by fixing the expected commencement date of the southwest monsoon as June 15. All delays in the arrival of the monsoon are expressed as shifts away from this date. The average rainfall for six years, at the Naulakha grassland, from 1984 to 1989 was 1094.85 mm, and normalcy of quantum of rain is expressed in percentage plus or minus that figure. Expressions of the normal distribution of rainfall are based on the average number of rainy days in the monsoon, which for the six years of study was 44 days.

Grass Growth

Grass species at the Naulakha grassland (main study area) are mainly annuals and dependent on rainfall for growth (Figs. 2.2.a & 2.2.b). The relation between rainfall and grass growth is shown only for this grassland. A logistic growth equation was fitted to grass height at different time intervals and the growth rate (r) was estimated. Where ever necessary, grass height at shorter time intervals was estimated using the equation:

$$N_t = N_{t-1}e^{rt}$$

where N_t=grass height (GHT) at time t, N_{t-1} GHT at time t-1, r=growth rate and t=time interval.

While understanding the exact influence of rainfall on grass growth, cumulative rainfall was used in all the calculations. This was for two reasons. Firstly grass height data itself is cumulative, that is, measurement of height during one sample is the increment over the grass height since the previous sample. Secondly, current rainfall has a delayed effect on grass growth, that is, its influence is not discernible immediately, and the use of cumulative rainfall data gave a clearer picture of the grass growth trends.

FIG. 2.1.a. LESSER FLORICAN
CHRONOLOGY OF EVENTS
1985

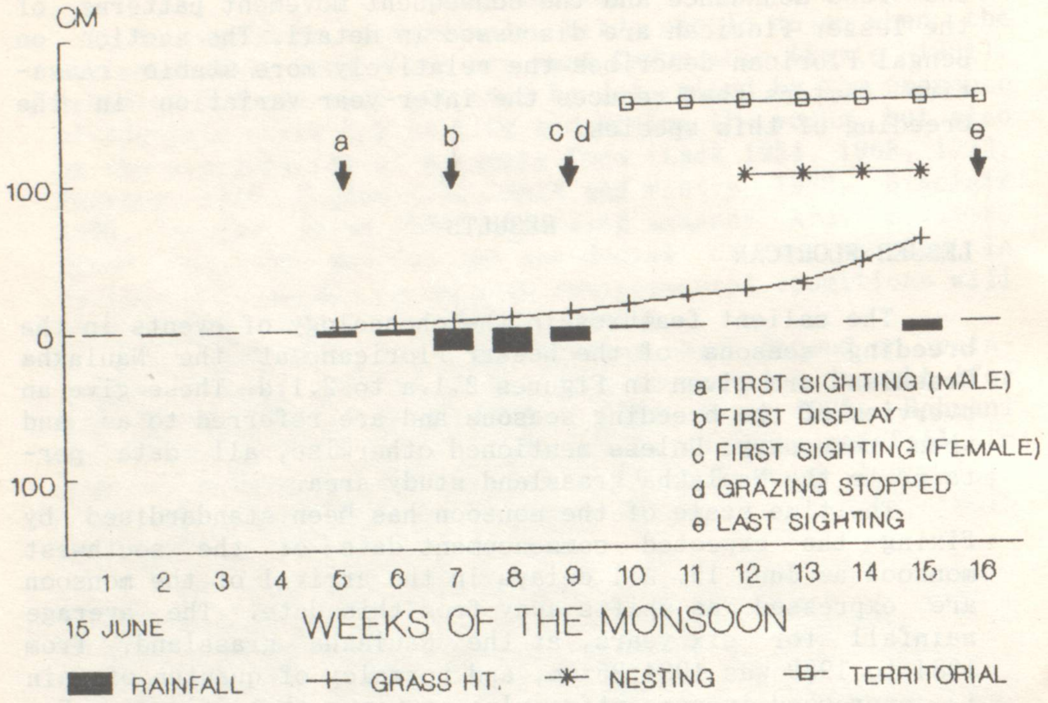


FIG 2.1.b. LESSER FLORICAN
CHRONOLOGY OF EVENTS
1986

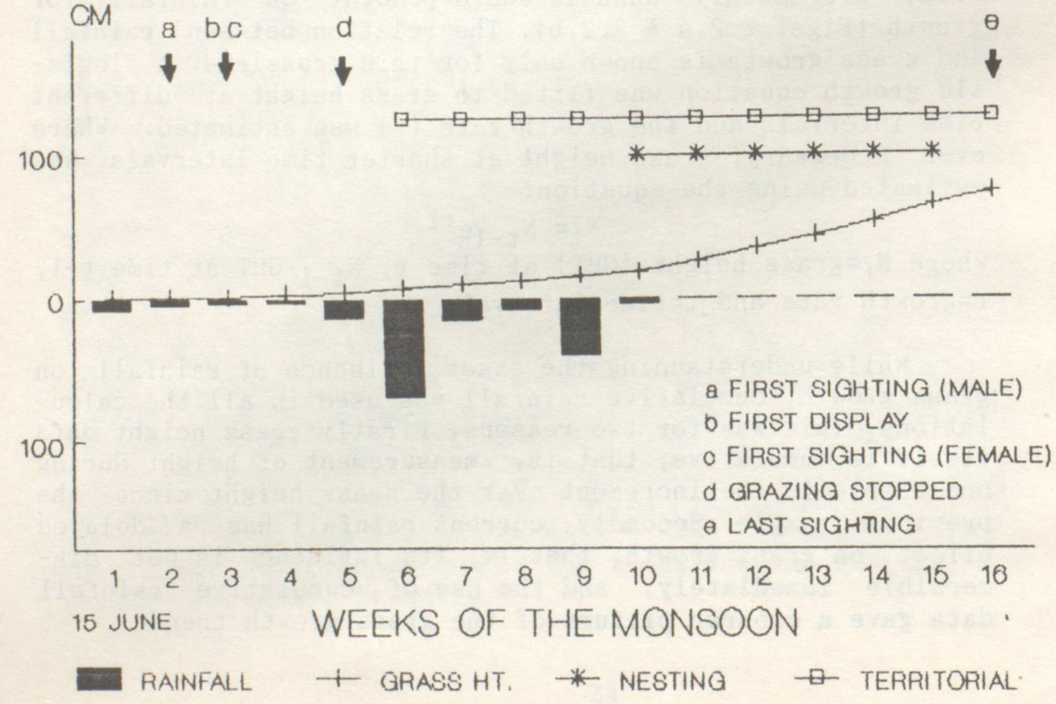


FIG. 2.1.c. LESSER FLORICAN
CHRONOLOGY OF EVENTS
1987

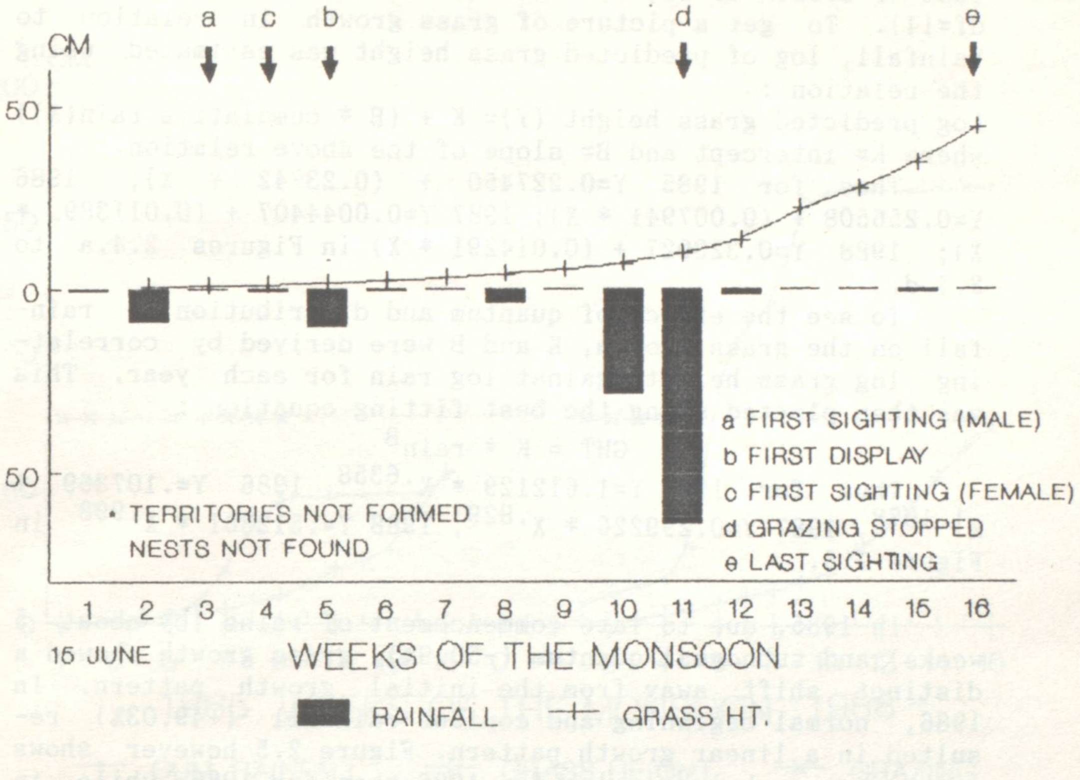
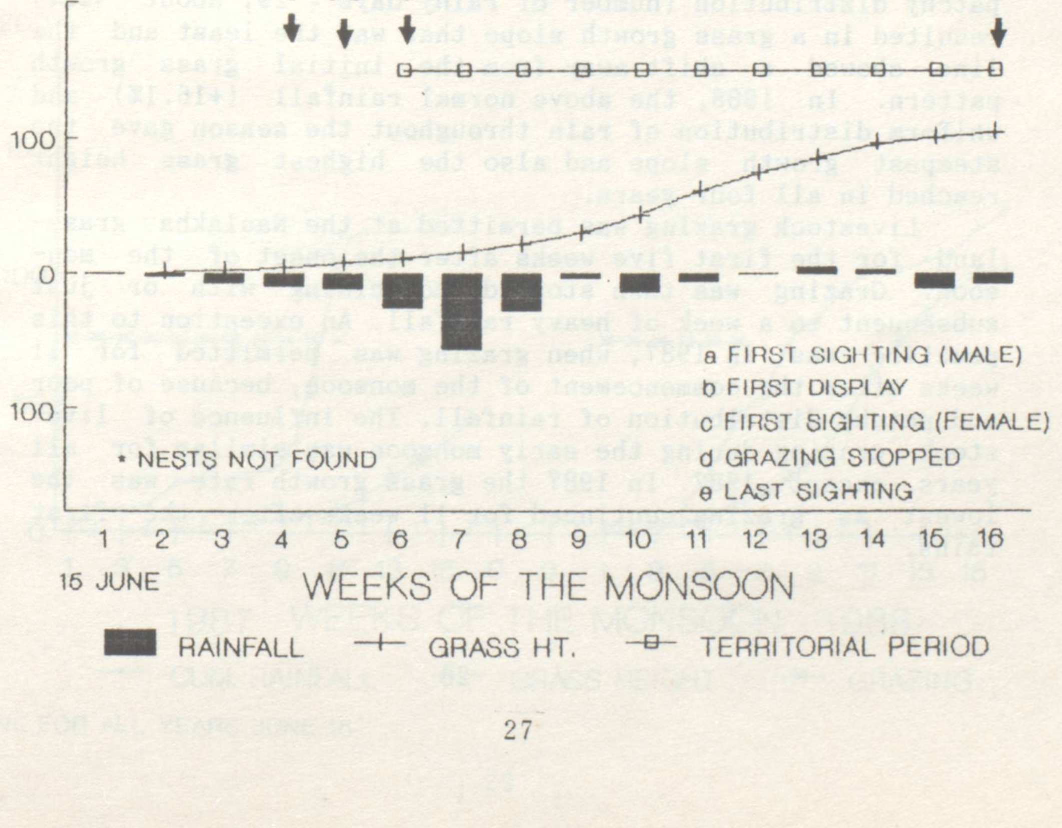


FIG. 2.1.d. LESSER FLORICAN
CHRONOLOGY OF EVENTS
1988



The relation between cumulative rainfall and grass height was found to be significant when log grass height was regressed against cumulative rainfall (1985 r=0.94 df=12, 1986 r=0.929 df=13, 1987 r=0.92 df=14 and 1988 r=0.98 df=14). To get a picture of grass growth in relation to rainfall, log of predicted grass height was estimated using the relation :
Log predicted grass height (Y)= K + (B * cumulative rain(X))
where K= intercept and B= slope of the above relation.

Thus for 1985 Y=0.227450 + (0.23742 * X); 1986 Y=0.256508 + (0.007941 * X); 1987 Y=0.0044407 + (0.011389 * X); 1988 Y=0.323927 + (0.014291 * X) in Figures 2.4.a to 2.4.d.

To see the effect of quantum and distribution of rainfall on the grass growth, K and B were derived by correlating log grass height against log rain for each year. This was then plotted using the best fitting equation :

$$\mathrm{GHT} = K * \mathrm{rain}^{B}$$

Thus for 1985 $Y=1.612129 * X^{.6358}$, 1986 $Y=.107369 * X^{1.1078}$, 1987 $Y=0.299226 * X^{.829}$, 1988 $Y=.512861 * X^{.998}$ in Figure 2.5.

In 1985, due to late commencement of rains (by about 5 weeks) and subnormal quantum (-50.9%), grass growth showed a distinct shift away from the initial growth pattern. In 1986, normal beginning and copious rainfall (+49.03%) resulted in a linear growth pattern. Figure 2.5 however shows a lower grass height value for 1986 than for 1985, while in actual terms maximum grass height reached in 1985 was 23.3% less than that of 1986. However, when the difference in amount of rainfall received in 1986 over 1985 is considered, it becomes apparent that proportionately 1985 had better grass height than 1986. In 1987 though quantum of rainfall was slightly above normal (+8.1%), late commencement and patchy distribution (number of rainy days = 29, about -40%) resulted in a grass growth slope that was the least and the line showed a shift away from the initial grass growth pattern. In 1988, the above normal rainfall (+16.1%) and uniform distribution of rain throughout the season gave the steepest growth slope and also the highest grass height reached in all four years.

Livestock grazing was permitted at the Naulakha grassland for the first five weeks after the onset of the monsoon. Grazing was then stopped, coinciding with or just subsequent to a week of heavy rainfall. An exception to this practice was in 1987, when grazing was permitted for 11 weeks after the commencement of the monsoon, because of poor and patchy distribution of rainfall. The influence of livestock grazing during the early monsoon was similar for all years except 1987. In 1987 the grass growth rate was the lowest as grazing continued for 11 weeks after the first rains.

FIG. 2.2.a. RAINFALL, GRASS GROWTH AND GRAZING - NAULAKHA GRASSLAND

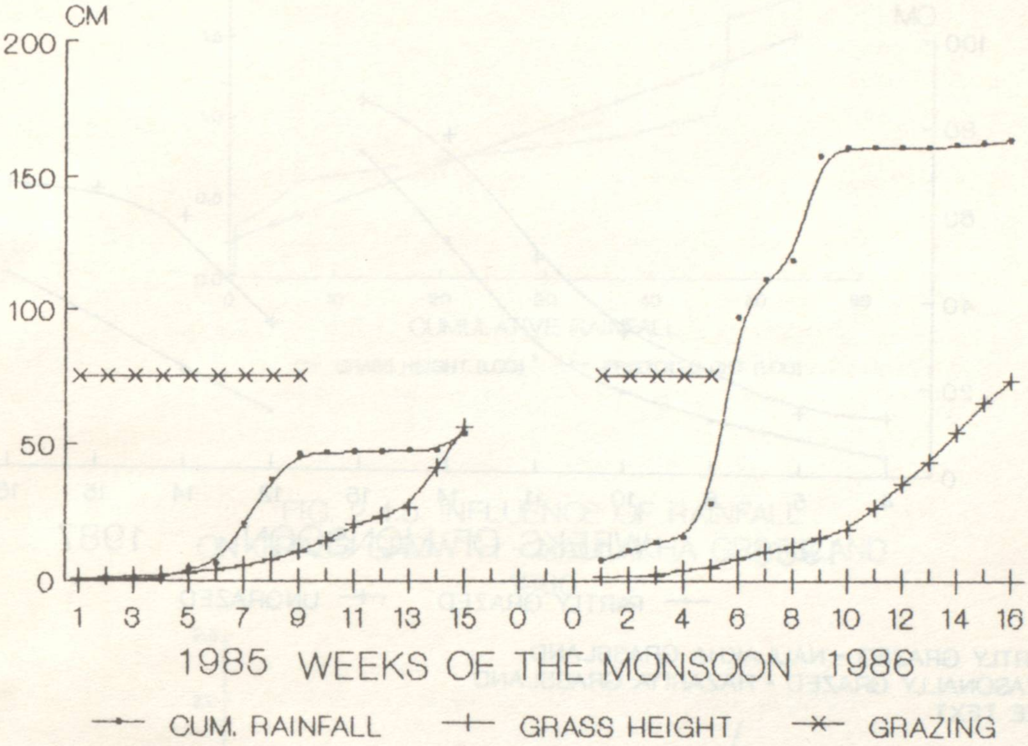
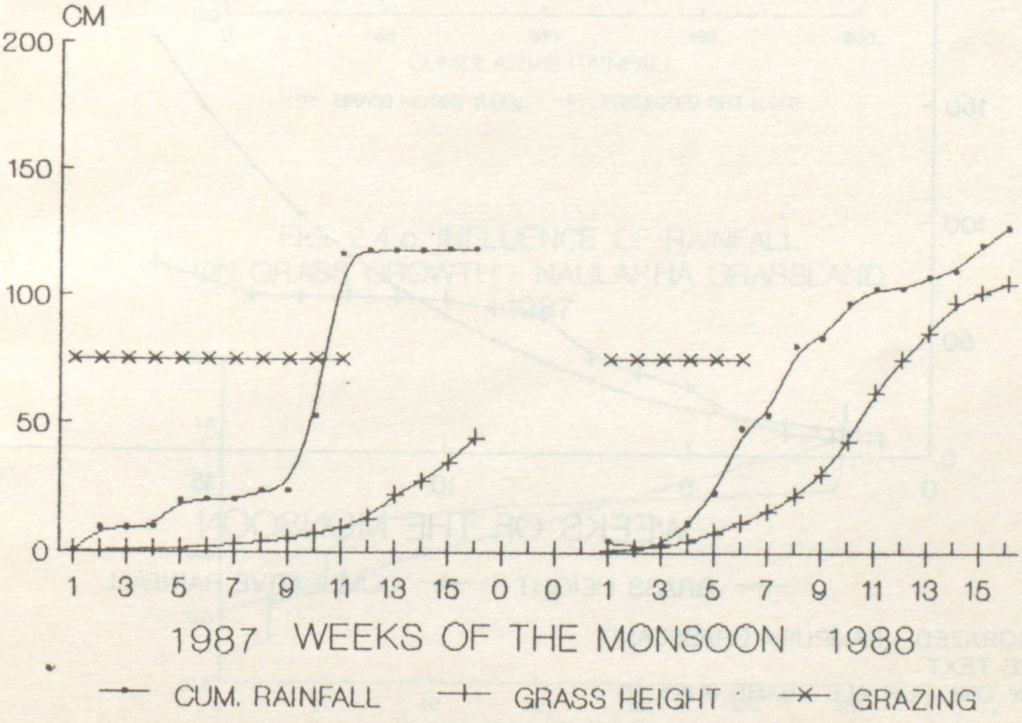
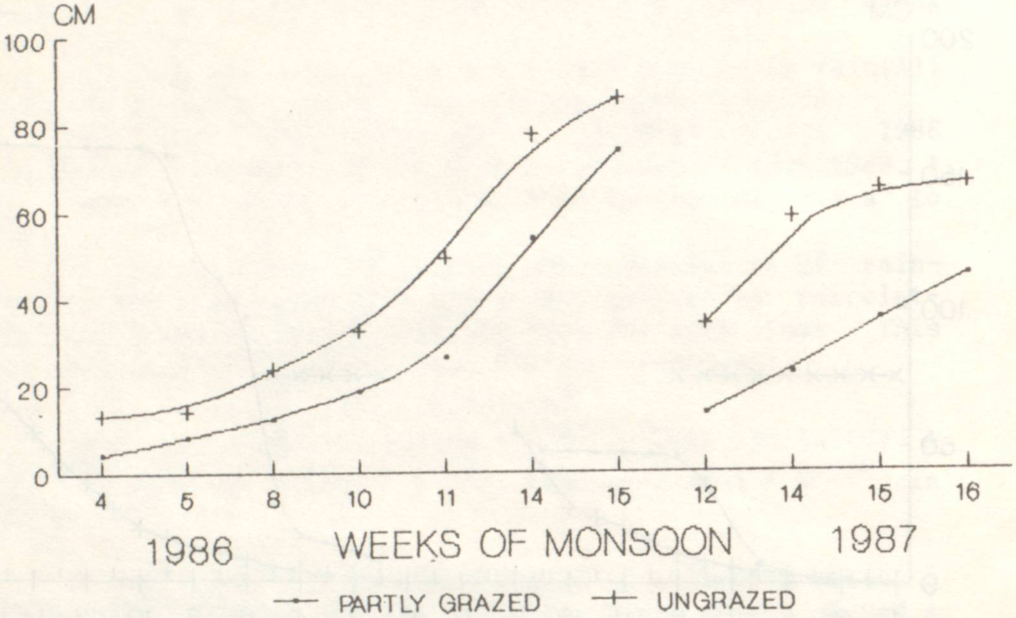


FIG. 2.2.b. RAINFALL, GRASS GROWTH AND GRAZING - NAULAKHA GRASSLAND



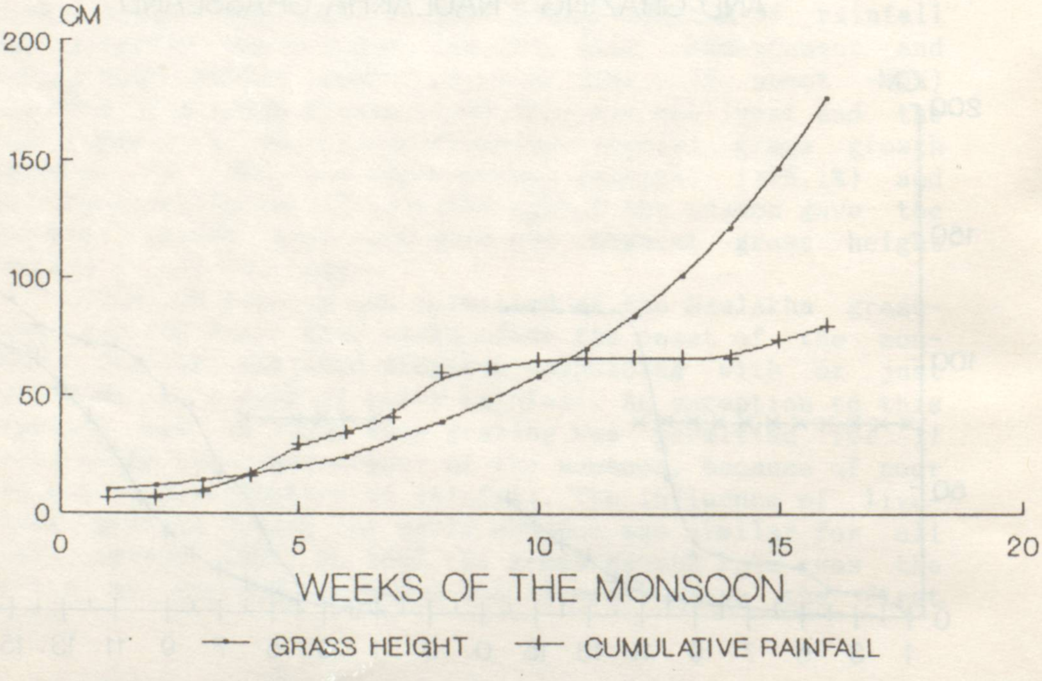
DAY ONE FOR ALL YEARS JUNE 15

FIG 2.3.a. COMPARISON OF GRASS GROWTH BETWEEN SEASONALLY GRAZED AND PARTLY GRAZED GRASSLANDS



PARTLY GRAZED - NAULAKHA GRASSLAND
SEASONALLY GRAZED - HAZARIYA GRASSLAND
SEE TEXT

FIG 2.3.b. GRASS GROWTH AND RAINFALL AN UNGRAZED GRASSSLAND (1988)



UNGRAZED - RAMPURA GRASSLAND
SEE TEXT
DAY ONE FOR ALL YEARS JUNE 15

FIG. 2.4.a. INFLUENCE OF RAINFALL ON GRASS GROWTH - NAULAKHA GRASSLAND 1985

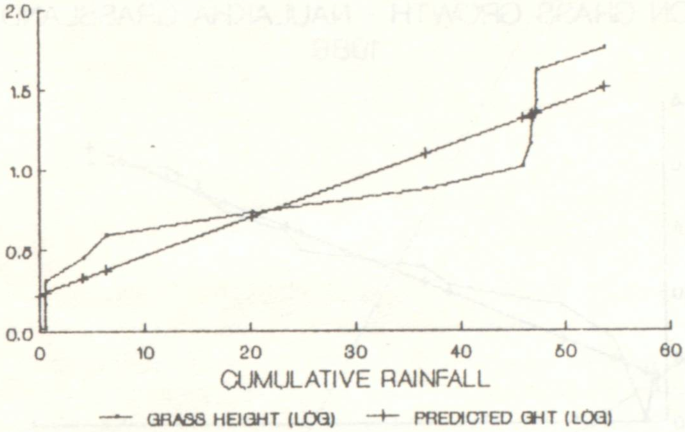


FIG. 2.4.b. INFLUENCE OF RAINFALL ON GRASS GROWTH - NAULAKHA GRASSLAND 1986

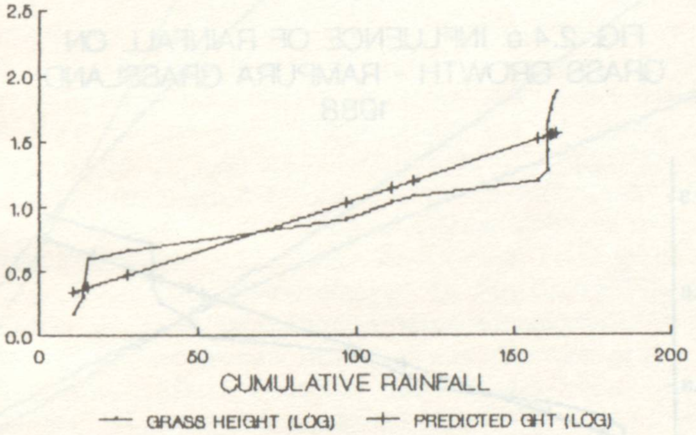


FIG. 2.4.c. INFLUENCE OF RAINFALL ON GRASS GROWTH - NAULAKHA GRASSLAND 1987

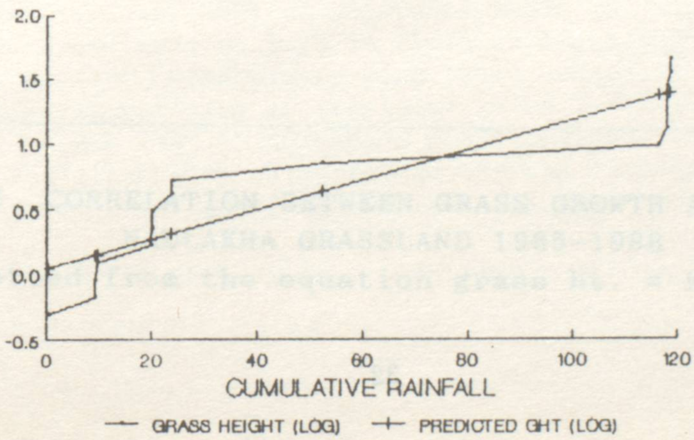


FIG. 2.4.d. INFLUENCE OF RAINFALL ON GRASS GROWTH - NAULAKHA GRASSLAND 1988

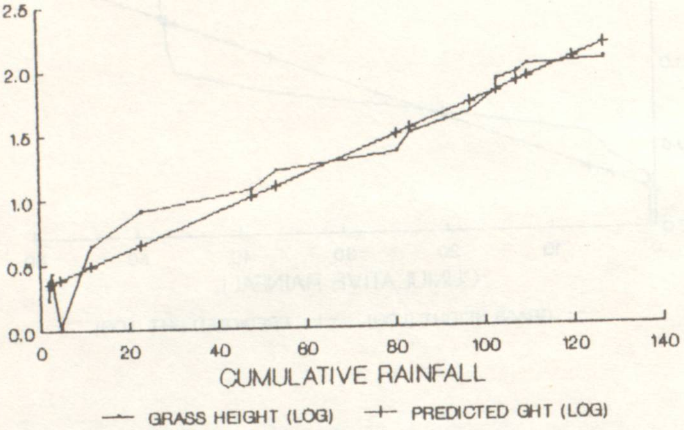
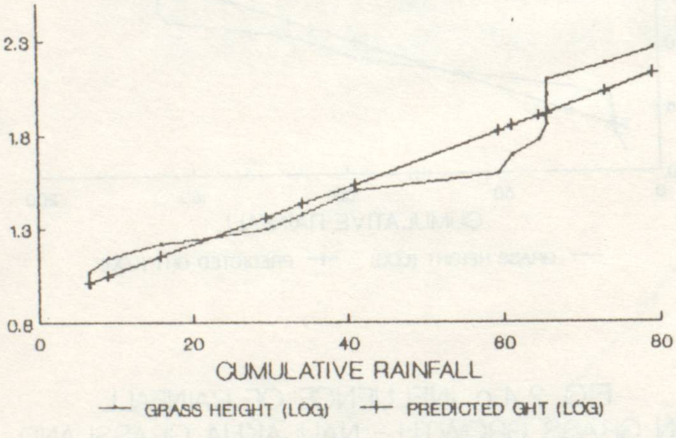


FIG. 2.4.e. INFLUENCE OF RAINFALL ON GRASS GROWTH - RAMPURA GRASSLAND 1988



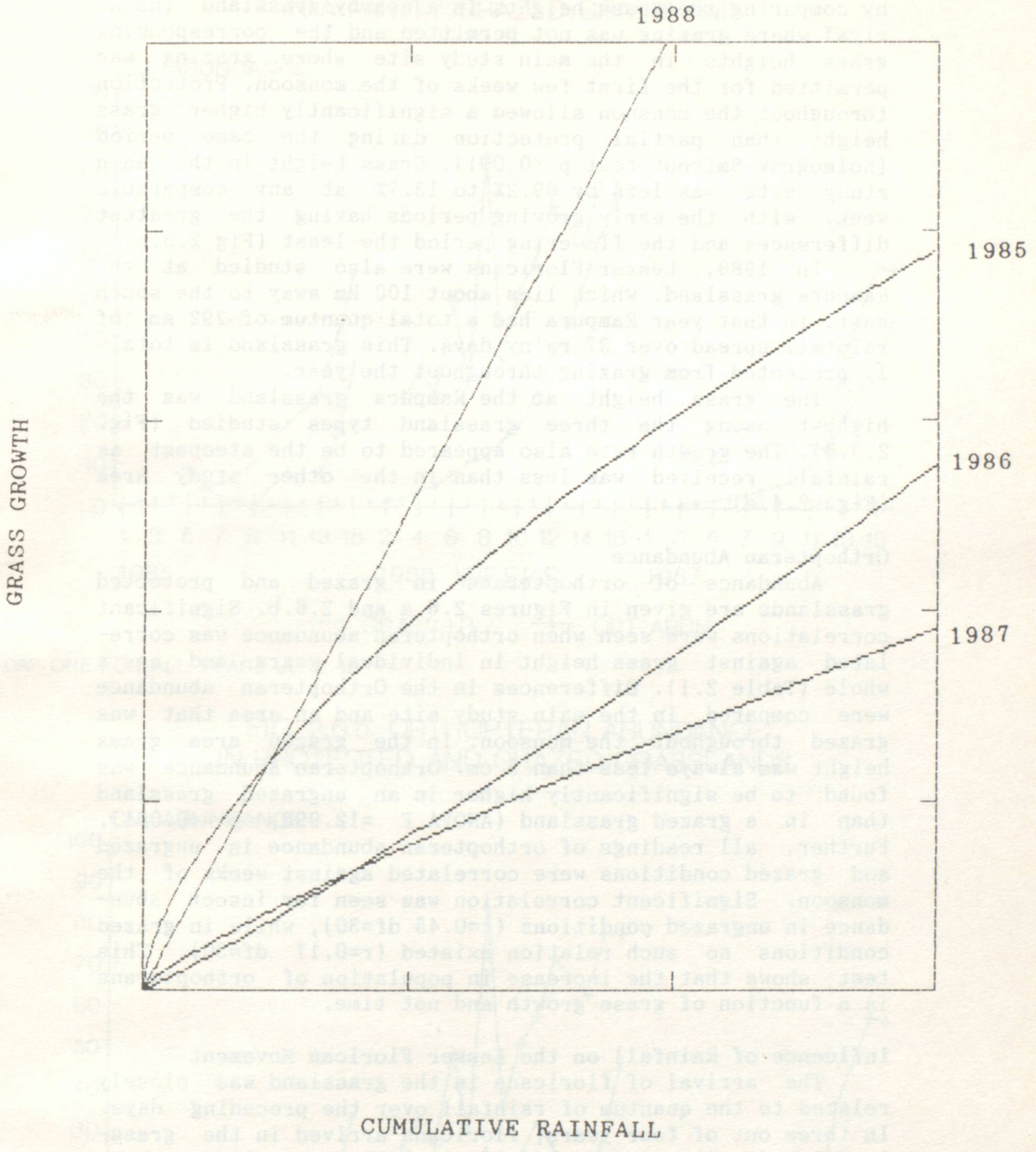


FIG. 2.5. CORRELATION BETWEEN GRASS GROWTH AND RAINFALL NAULAKHA GRASSLAND 1985-1988

(Plotted from the equation grass ht. = $K * rain^{B}$)

The actual reduction in grass growth can be determined by comparing the grass heights in a nearby grassland (Hazariya) where grazing was not permitted and the corresponding grass heights in the main study site where grazing was permitted for the first few weeks of the monsoon. Protection throughout the monsoon allowed a significantly higher grass height than partial protection during the same period (Kolmogrov-Smirnov test $p < 0.001$). Grass height in the main study site was less by 69.2% to 13.7% at any comparable week, with the early growing periods having the greatest differences and the flowering period the least (Fig 2.3.a).

In 1988, Lesser Floricans were also studied at the Rampura grassland, which lies about 100 km away to the south east. In that year Rampura had a total quantum of 792 mm of rainfall spread over 37 rainy days. This grassland is totally protected from grazing throughout the year.

The grass height at the Rampura grassland was the highest among the three grassland types studied (Fig. 2.3.b). The growth rate also appeared to be the steepest as rainfall received was less than in the other study area (Fig. 2.4.e).

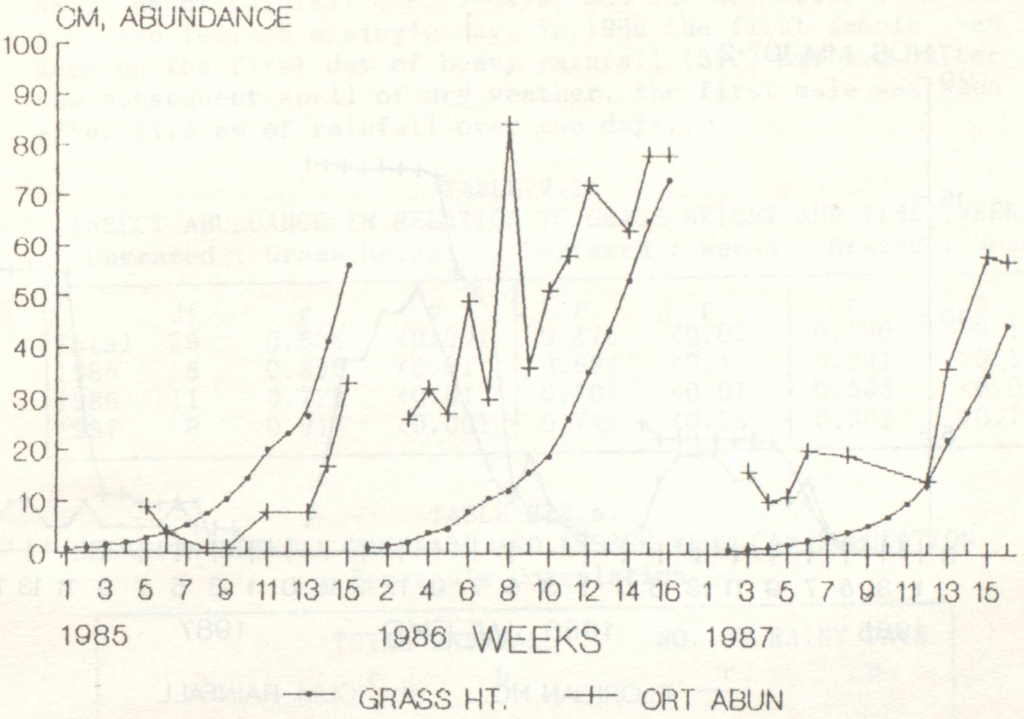
Orthopteran Abundance

Abundance of orthopterans in grazed and protected grasslands are given in Figures 2.6.a and 2.6.b. Significant correlations were seen when orthopteran abundance was correlated against grass height in individual years and as a whole (Table 2.1). Differences in the Orthopteran abundance were compared in the main study site and an area that was grazed throughout the monsoon. In the grazed area grass height was always less than 5 cm. Orthopteran abundance was found to be significantly higher in an ungrazed grassland than in a grazed grassland (ANOVA $F = 12.993$, $p < 0.001$). Further, all readings of orthopteran abundance in ungrazed and grazed conditions were correlated against weeks of the monsoon. Significant correlation was seen for insect abundance in ungrazed conditions ($r=0.45$ $df=30$), while in grazed conditions no such relation existed ($r=0.17$ $df=30$). This test shows that the increase in population of orthopterans is a function of grass growth and not time.

Influence of Rainfall on the Lesser Florican Movement

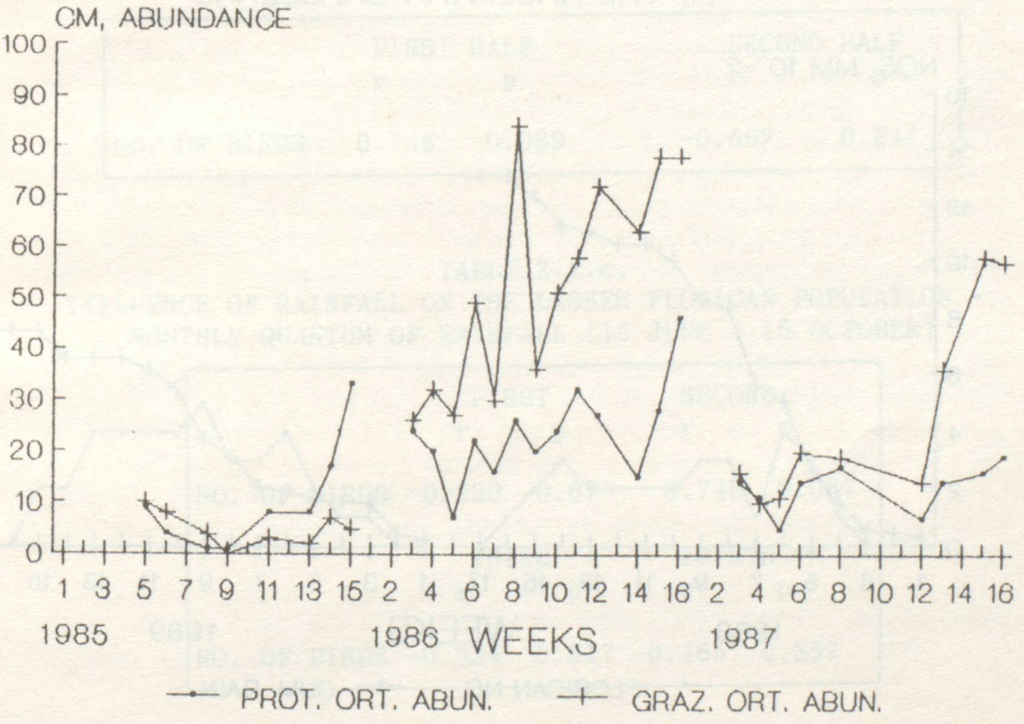
The arrival of floricans in the grassland was closely related to the quantum of rainfall over the preceding days. In three out of four years, floricans arrived in the grassland immediately after rainfall. In 1985, arrival was subsequent to scattered rainfall of 77.2 mm over about 10 days. In that year, the first male was sighted in the morning after a night of heavy rainfall. As meteorological data in 1985 were obtained from a station 17 km away, relation between rainfall and arrival patterns on a daily basis could not be accurately ascertained. In 1986, the exact arrival

FIG. 2.6.a. ORTHOPTERAN ABUNDANCE IN A PARTLY GRAZED GRASSLAND



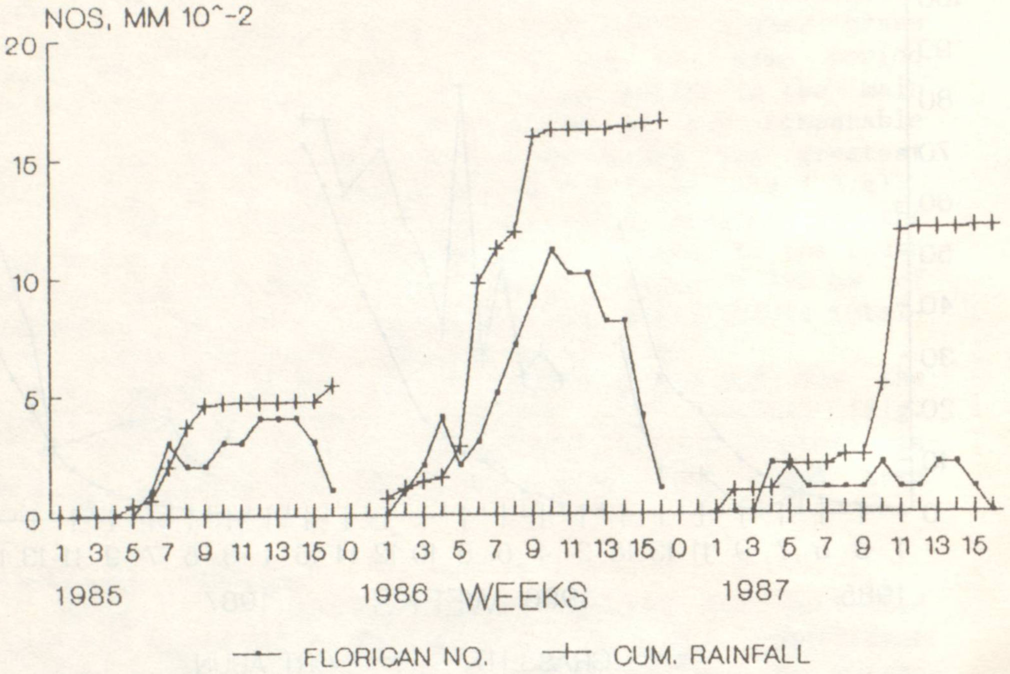
DAY ONE FOR ALL YEARS JUNE 15

FIG. 2.6.b. ORTHOPTERAN ABUNDANCE IN PROTECTED AND GRAZED GRASSLANDS



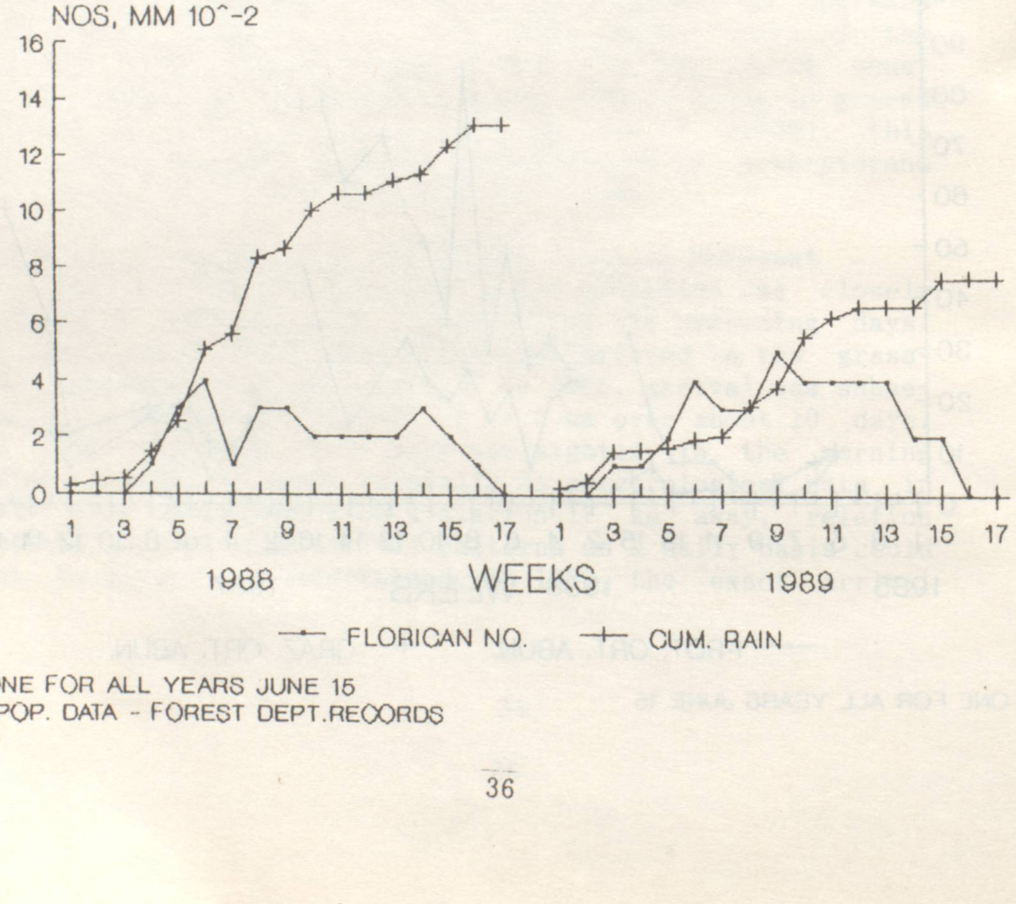
DAY ONE FOR ALL YEARS JUNE 15

FIG. 2.7.a. INFLUENCE OF RAINFALL ON POPULATION OF MALE LESSER FLORICAN IN THE NAULAKHA GRASSLAND



DAY ONE FOR ALL YEARS JUNE 15

FIG. 2.7.b. INFLUENCE OF RAINFALL ON POPULATION OF MALE LESSER FLORICAN AT THE NAULAKHA GRASSLAND



DAY ONE FOR ALL YEARS JUNE 15
1989 POP. DATA - FOREST DEPT.RECORDS

date could not be determined, but the arrival of floricans coincided with the first week of the monsoon, when 70.4 mm of rain fell. In 1987 the first arrival was subsequent to 88.2 mm of rainfall over 5 days, and the day after 44.5 mm of rain fell on a single day. In 1988 the first female was seen on the first day of heavy rainfall (31.2 mm) and after the subsequent spell of dry weather, the first male was seen after 61.5 mm of rainfall over two days.

TABLE 2.1

INSECT ABUNDANCE IN RELATION TO GRASS HEIGHT AND TIME (WEEKS)

	Ungrazed : Grass Height			Ungrazed : Weeks		Grazed : Weeks	
	df	r	p	r	p	r	p
Total	29	0.628	<0.001	0.476	<0.02	0.190	>0.1
1985	6	0.896	<0.01	0.692	<0.1	0.381	>0.1
1986	11	0.725	<0.01	0.782	<0.01	0.565	<0.05
1987	8	0.917	<0.001	0.747	<0.05	0.362	>0.1

TABLE 2.2.a.

RELATION BETWEEN RAINFALL AND LESSER FLORICAN POPULATION

Pearson's Correlation

	TOTAL RAINFALL		NO. OF RAINY DAYS	
	r	p	r	p
NO. OF BIRDS	0.359	0.485	0.742	0.091

TABLE 2.2.b.

INFLUENCE OF RAINFALL ON THE LESSER FLORICAN POPULATION - QUANTUM OF RAINFALL IN THE FIRST HALF VERSUS THE SECOND HALF

	FIRST HALF		SECOND HALF	
	r	p	r	p
NO. OF BIRDS	0.746	0.089	-0.567	0.241

TABLE 2.2.c.

INFLUENCE OF RAINFALL ON THE LESSER FLORICAN POPULATION - MONTHLY QUANTUM OF RAINFALL (15 JUNE - 15 OCTOBER)

	FIRST		SECOND	
	r	p	r	p
NO. OF BIRDS	0.220	0.675	0.748	0.087
	THIRD		FOURTH	
	r	p	r	p
NO. OF BIRDS	-0.334	0.517	-0.465	0.352

In all the years excepting 1988, arrival of male(s) preceded that of female(s) by 11 (1986, 1987) and 15 days (1985). In 1988 a female was sighted 8 days prior to the first sighting of a male. Males are, however, more easily sighted as females are far more cryptically coloured. With the exception of 1987, in other years, the last sighting of males was in the first week of October. In 1987 however the last sighting was on 23 September about, 10 days earlier than usual.

Figures 2.7.a and 2.7.b show the maximum number of male Lesser Floricans seen and the cumulative rainfall in the study area. It is clear that as the rainfall increases the number of birds also increases, reaching a peak in the ninth to eleventh week of the monsoon (i.e. August 10 to 30). This was most visible in 1986 when more floricans arrived than in any other years. Within the grassland, most spells of heavy rainfall in the early monsoon resulted in an increase in the florican population, while an extended sunny or rainless period often had the reverse effect. By the fourteenth week, the males began disappearing from the grassland and no males were seen after the sixteenth week (Figs 2.1.a to 2.1.d).

Total rainfall was found not to have an influence on the number of birds which settle to breed in the study area (Table 2.2.a). For instance, though 1987 had almost twice as much total rainfall as 1985, the number of birds in 1987 were less than half of the earlier year. A positive correlation was seen between the number of rainy days and the maximum number of birds seen in a season (Table 2.2.a). When the season was segmented and the influence of the quantum of rainfall within a segment was considered, positive correlations were seen. Quantum of rainfall in the first half of the season (June 15 to August 15) strongly influenced the number of birds that visited a grassland (Table 2.2.b). Though in 1987 nearly 1200 mm of rainfall was recorded, most of it was received during the second half of the season (after August 15) and hence very few birds arrived in the grassland. As the rainfall regime varied between years, with each year receiving most of the rainfall in different months, the season was segmented into months, to find out which rainfall pattern had the greatest influence on the population of Lesser Florican immigrating into the Naulakha grassland. It was found that the quantum of rainfall in second month (i.e. 16 July to 15 August) had the greatest influence on the number of birds that were seen during a breeding season (Table 2.2.c).

Habitat Use

A description of habitats available to the Lesser Florican during the breeding season is given in the section on Study Areas.

Shifts in fortnightly habitat use under different rainfall patterns are given in Figures 2.8.a to 2.8.c. Data for 1985 have not been included as in that year crop areas were not adequately studied.

As habitat classes occurred in different proportions over the study area, the data for all habitats used have been normalised by dividing the values with weights proportionate to the area under different habitats. Thus grasslands were quantitatively weighted as 15, crop as 5 and grass patches as 1. This was then standardised by converting values into percentage of all sightings in a fortnight between habitats so as to make the data set comparable between years. Standardisation was found to be necessary as number of birds which are sighted varied between years and to eliminate bias that arose because of this.

In 1986 normal rainfall distribution and above normal quantum resulted in good grass growth in the study area. Overall, Lesser Floricans used grasslands, grass patches and crop fields in the descending order of preference (Table 2.3). Fortnightly shifts in habitat use showed maximum use of grasslands in the first fortnight. In the second fortnight, floricans used all three habitats similarly. In the following five fortnights both grass patches and the main grassland, were used the most and crop fields the least (Table 2.5.a; Fig. 2.8.a).

In 1987 subnormal distribution of rainfall resulted in poor grass growth in the study area. Overall, all three habitats were used similarly (Table 2.3). In the first fortnight of the season grassland was used more than grass patches while crop fields were not used at all. In the second fortnight all three habitats were used similarly. In the third and fourth fortnights, crop fields were used almost exclusively while the grassland and grass patches were hardly used. In the fifth fortnight all three habitats were used similarly, and in the sixth fortnight the grassland was used almost exclusively (Table 2.5.b, Fig. 2.8.b).

In 1988 normal distribution and above normal quantum of rainfall resulted in good grass growth. Overall, the grassland was used the most while grass patches and cropfields were used similarly (Table 2.3). In the first two fortnights all the three habitats were used equally. In the third, fourth and fifth fortnights grasslands were used the most. In the sixth fortnight a shift was seen towards croplands, and in the seventh fortnight cropfields were used the most (Table 2.5.c, Fig. 2.8.c).

Overall habitat use was similar in 1986 and 1988. The pattern in 1987 was different, with crop areas being used most frequently and grassland less frequently than in '86 and '88 (Table 2.4). In all these years grass patches did not show significant variation in intensity of use.

FIG. 2.8.a. LESSER FLORICAN HABITAT USE UNDER DIFFERENT RAINFALL PATTERNS NAULAKHA GRASSLAND 1986

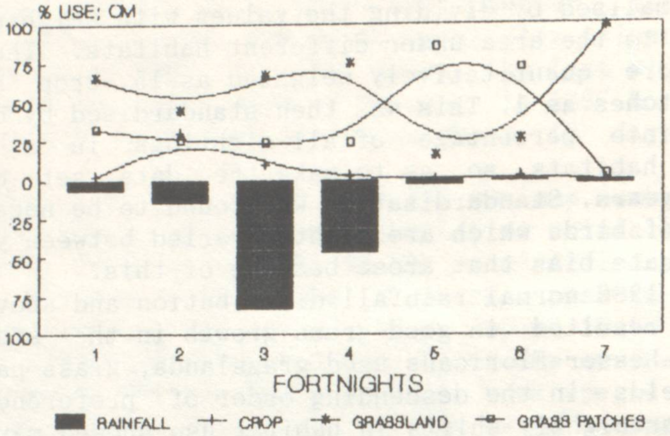


FIG. 2.8.b. LESSER FLORICAN HABITAT USE UNDER DIFFERENT RAINFALL PATTERNS NAULAKHA GRASSLAND 1987

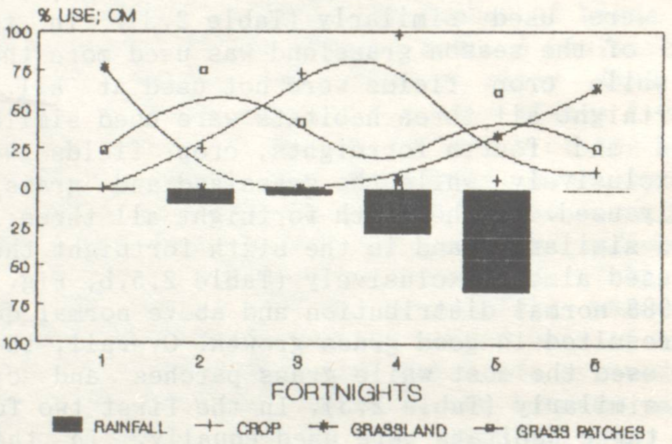
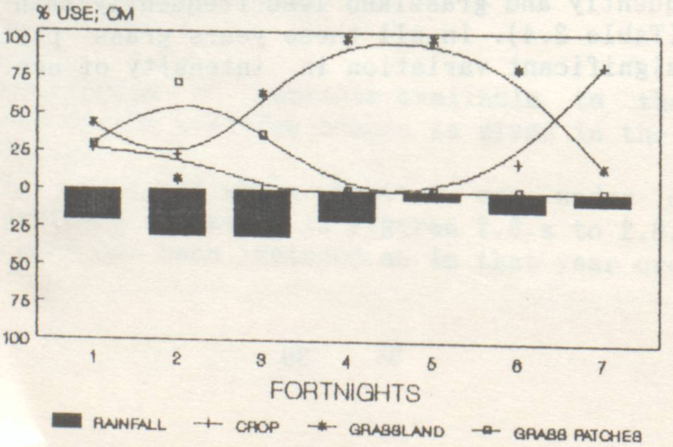


FIG. 2.8.c. LESSER FLORICAN HABITAT USE UNDER DIFFERENT RAINFALL PATTERNS NAULAKHA GRASSLAND 1988



Key for tables 2.3 to 2.5.c.
Crop = Cropfields
Grass = Grassland (Naulakha)
GPC = Grass patches amidst cropfields

TABLE 2.3
VARIATION IN INTRA-YEAR HABITAT USE : 1986 TO 1988
KOLMOGROV-SMIRNOV TWO SAMPLE TEST RESULTS

		GRASS		GPC	
		MD	P	MD	P
1986	CROP	0.791	<0.001	0.418	<0.001
	GRASS			0.478	<0.001
1987	CROP	0.244	0.121	0.267	0.072
	GRASS			0.111	0.921
1988	CROP	0.639	<0.001	0.194	0.448
	GRASS			0.611	<0.001

TABLE 2.4
VARIATION IN INTER-YEAR HABITAT USE : 1986 TO 1988
KOLMOGROV-SMIRNOV TWO SAMPLE TEST RESULTS

	CROP 87		CROP 88	
	MD	P	MD	P
CROP 86	0.422	<0.001	0.139	0.832
CROP 87			0.444	<0.001

	GRASS 87		GRASS 88	
	MD	P	MD	P
GRASS 86	0.644	<0.001	0.167	0.640
GRASS 87			0.667	<0.001

	GPC 87		GPC 88	
	MD	P	MD	P
GPC 86	0.178	0.440	0.111	0.961
GPC 87			0.167	0.640

TABLE 2.5.a.
1986
LESSER FLORICAN HABITAT USE PATTERNS (FORTNIGHTLY)
KOLMOGROV-SMIRNOV TWO SAMPLE TEST RESULTS

		GRASS		GPC	
		MD	p	MD	p
FORTNIGHT 1	CROP	0.875	<0.001	0.375	0.520
	GRASS			0.625	0.049
FORTNIGHT 2	CROP	0.300	0.664	0.200	0.962
	GRASS			0.500	0.112
FORTNIGHT 3	CROP	0.700	0.006	0.300	0.664
	GRASS			0.700	0.006
FORTNIGHT 4	CROP	0.857	0.006	0.286	0.919
	GRASS			0.714	0.047
FORTNIGHT 5	CROP	1.000	<0.001	1.000	<0.001
	GRASS			1.000	<0.001
FORTNIGHT 6	CROP	0.900	<0.001	0.900	<0.001
	GRASS			0.800	<0.001
FORTNIGHT 7	CROP	0.909	<0.000	0.091	1.000
	GRASS			0.909	<0.001

TABLE 2.5.b.
1987
LESSER FLORICAN HABITAT USE PATTERNS (FORTNIGHTLY)
KOLMOGROV-SMIRNOV TWO SAMPLE TEST RESULTS

		GRASS		GPC	
		MD	p	MD	p
FORTNIGHT 1	CROP	1.000	<0.001	0.250	1.000
	GRASS			0.750	0.125
FORTNIGHT 2	CROP	0.250	1.000	0.500	0.500
	GRASS			0.750	0.125
FORTNIGHT 3	CROP	0.900	<0.001	0.600	0.030
	GRASS			0.300	0.664
FORTNIGHT 4	CROP	1.000	<0.001	1.000	<0.001
	GRASS			0.100	1.000
FORTNIGHT 5	CROP	0.167	1.000	0.500	0.333
	GRASS			0.333	0.778
FORTNIGHT 6	CROP	0.545	0.063	0.182	0.986
	GRASS			0.545	0.063

TABLE 2.5.c.
1988
LESSER FLORICAN HABITAT USE PATTERNS (FORTNIGHTLY)
KOLMOGROV-SMIRNOV TWO SAMPLE TEST RESULTS

		GRASS		GPC	
		MD	p	MD	p
FORTNIGHT 1	CROP	0.333	0.778	0.167	1.000
	GRASS			0.500	0.333
FORTNIGHT 2	CROP	0.200	1.000	0.600	0.320
	GRASS			0.800	0.080
FORTNIGHT 3	CROP	1.000	<0.001	0.444	0.307
	GRASS			0.556	0.111
FORTNIGHT 4	CROP	1.000	<0.001	0.000	1.000
	GRASS			1.000	<0.001
FORTNIGHT 5	CROP	1.000	<0.001	0.000	1.000
	GRASS			1.000	<0.001
FORTNIGHT 6	CROP	0.750	0.125	0.250	1.000
	GRASS			1.000	<0.001
FORTNIGHT 7	CROP	1.000	<0.001	1.000	<0.001
	GRASS			0.667	0.667

BENGAL FLORICAN

The salient features of the chronology of the breeding season of the Bengal florican are given in Figures 2.9.a and 2.9.b, and will be referred to where necessary.

Burning

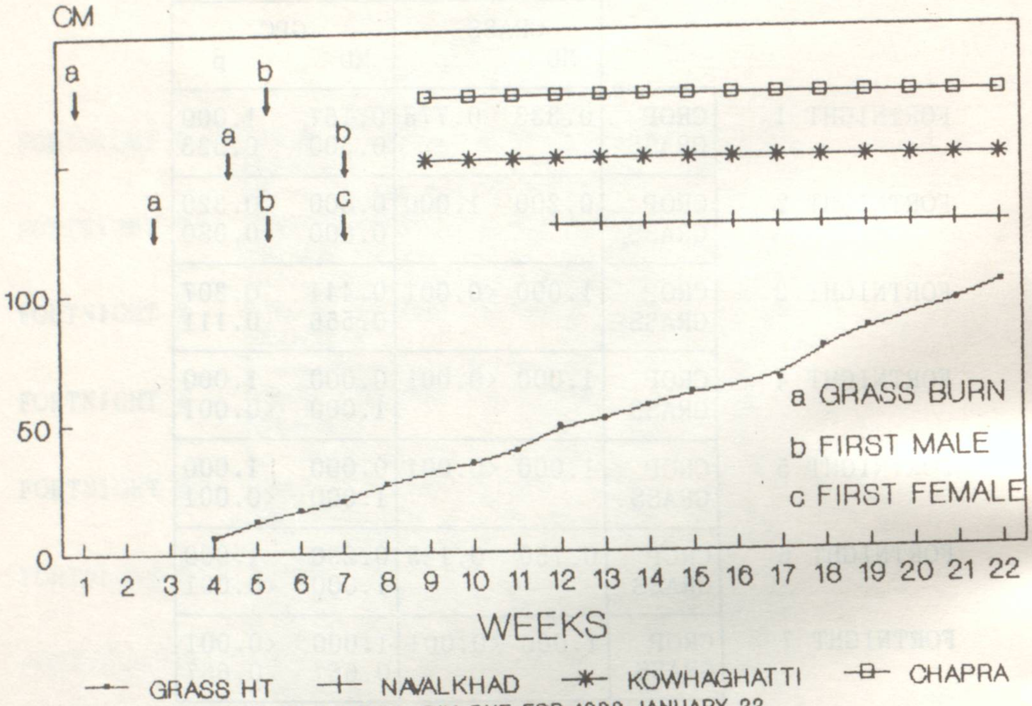
At the end of the monsoon, the grasslands in the Dudwa National Park are covered by dense and very tall grasses (over 3 m in most areas). When these dry up in the subsequent dry season, they form a dense and virtually impenetrable tangle. To clear the grasslands of the previous year's vegetation, and to facilitate fresh growth, the grasslands are burnt between January and March. (see discussion and also Sankaran and Rahmani 1988, Sankaran 1990). This is the only consistent grassland management practice at the Dudwa National park.

Grass Growth

Grasses in the study area are mainly tussock forming perennials, and their growth is determined only indirectly by rainfall. Grass growth begins immediately after the annual grass burn that occurs from January to March. Similar analyses were made with the grass growth in this habitat as of that in the Lesser Florican's.

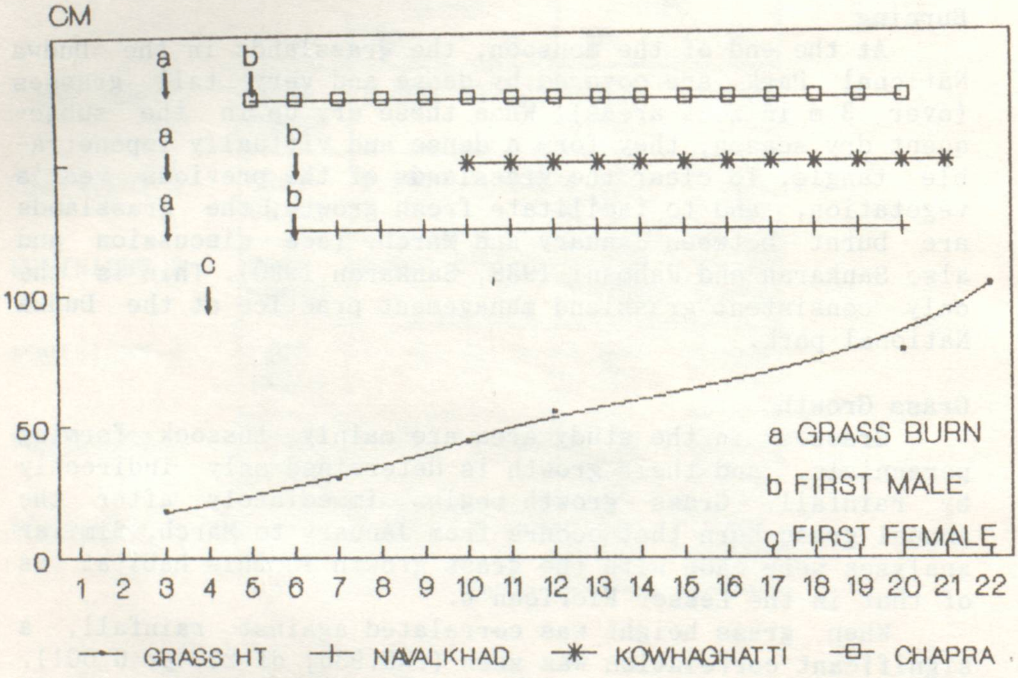
When grass height was correlated against rainfall, a significant correlation was seen ($r=0.935$, $df=20$, $p=<0.001$). However when the log of grass growth and cumulative rainfall

FIG. 2.9.a. BENGAL FLORICAN
CHRONOLOGY OF EVENTS
1988



* STUDY STOPPED BEFORE END OF SEASON; DAY ONE FOR 1988 JANUARY 22

FIG. 2.9.b. BENGAL FLORICAN
CHRONOLOGY OF EVENTS
1989



DAY ONE FOR 1989 FEBRUARY 15

FIG. 2.10.a. COMPARISON OF INFLUENCE OF RAINFALL ON GRASS GROWTH IN TWO HABITATS

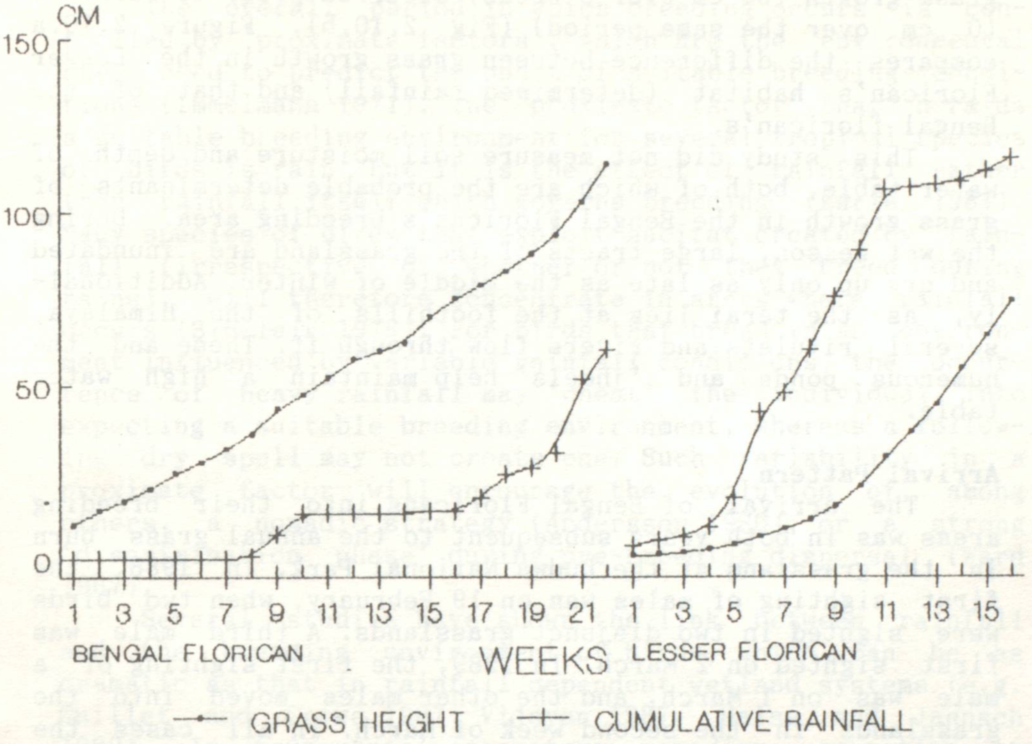
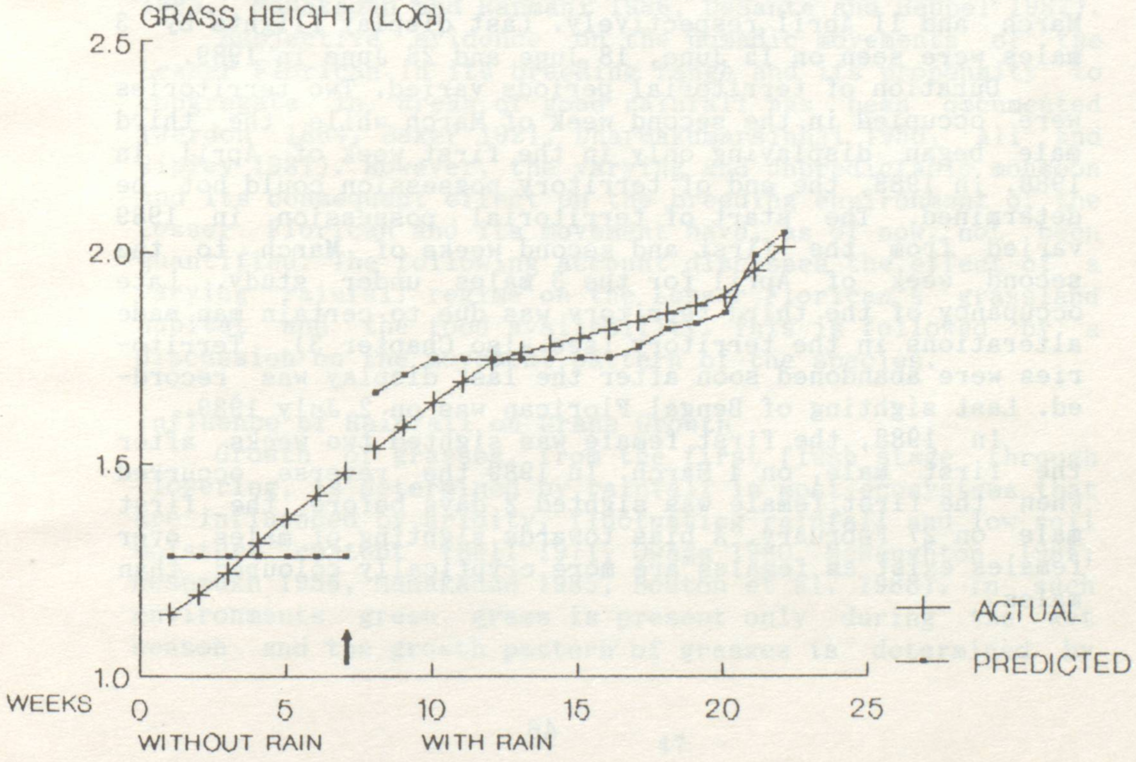


FIG. 2.10.b. BENGAL FLORICAN INFLUENCE OF RAINFALL ON GRASS GROWTH



were correlated and the grass growth slope estimated, it was found that in reality rainfall does not determine grass growth but only influences it. This can be seen when initial grass growth (30 cm over 8 weeks) occurred prior to rainfall (0 cm over the same period) (Fig 2.10.b). Figure 2.10.a compares the difference between grass growth in the Lesser Florican's habitat (determined rainfall) and that of the Bengal florican's.

This study did not measure soil moisture and depth of water table, both of which are the probable determinants of grass growth in the Bengal Florican's breeding area. During the wet season, large tracts of the grassland are inundated and dry up only as late as the middle of winter. Additionally, as the terai lies at the foothills of the Himalaya, several rivulets and rivers flow through it. These and the numerous ponds and 'jheels' help maintain a high water table.

Arrival Pattern

The arrival of Bengal Floricans into their breeding areas was in both years subsequent to the annual grass burn in the grassland at the Dudwa National Park. In 1988, the first sighting of males was on 19 February, when two birds were sighted in two disjunct grasslands. A third male was first sighted on 2 March. In 1989, the first sighting of a male was on 1 March, and the other males moved into the grasslands in the second week of March. In all cases the arrivals at the grassland followed the grass burn by 3 to 4 weeks.

The first display flight in 1988 was on 11 March. The last display flight of the season could not be determined. In 1989, the first display flight at one territory was on 1 March, while in two other territories display was seen on 13 March and 11 April respectively. Last display flights by 3 males were seen on 15 June, 18 June and 26 June in 1989.

Duration of territorial periods varied. Two territories were occupied in the second week of March while the third male began displaying only in the first week of April in 1988. In 1988, the end of territory possession could not be determined. The start of territorial possession in 1989 varied from the first and second weeks of March to the second week of April for the 3 males under study. Late occupancy of the third territory was due to certain man made alterations in the territory (see also Chapter 3). Territories were abandoned soon after the last display was recorded. Last sighting of Bengal Florican was on 2 July 1989.

In 1988, the first female was sighted two weeks after the first male, on 4 March. In 1989 the reverse occurred when the first female was sighted 2 days before the first male on 27 February. A bias towards sighting of males over females exist as females are more cryptically coloured than males.

DISCUSSION

LESSER FLORICAN

The overall period in which breeding occurs is controlled by 'proximate factors', which are the environmental cues used to predict the onset of suitable breeding conditions (Immelmann 1971). The 'proximate factor' that heralds a suitable breeding environment for several tropical species of birds is rain, but it is the effect of rainfall rather than rainfall itself which governs breeding (Earle 1981). Many species of birds that exploit habitat created by rainfall (irrespective of whether or not they breed during rains), will therefore concentrate in areas where rainfall occurs (Sinclair 1978). For birds that breed in an environment influenced by variable rainfall conditions, the occurrence of heavy rainfall may 'cheat' the individual into expecting a suitable breeding environment, whereas a following dry spell may not create one. Such variability in a proximate factor will encourage the evolution of, among others, a nomadic strategy (Andersson 1980), or a strong 'discrimination phase' during pre-breeding dispersal (Ward 1987).

Several studies have shown the link between rainfall and the breeding environment of birds, which can be as dramatic as that in rainfall dependent wetland systems (e.g. Guillet and Crowe 1987, Vijayan 1987, Halse and Jaensch 1989). In terrestrial ecosystems, nomadism, cessation or delays in breeding are characteristic adaptations of species exploiting environments with variable rainfall; the more unpredictable the rainfall, the more extreme the response (Moreau 1950, Thomson 1950, Keat and Marshall 1954, Sinclair 1978, Davies 1979, Earle 1981, Berry and Crowe 1985, Manry 1985, Manakadan and Rahmani 1986, DeSante and Geupel 1987).

Subjective evidence on the nomadic movements of the Lesser Florican in its breeding range and its propensity to congregate in areas of good rainfall has been documented (Jerdon 1864, Baker 1921, Dharmakumarsinhji 1950, Ali and Ripley 1981). However, the varying and unpredictable monsoon and its consequent effect on the breeding environment of the Lesser Florican and its movement have, as of now, not been quantified. The following account discusses the effect of a varying rainfall regime on the Lesser Florican's grassland habitat and the food availability. This is followed by a discussion on the movement pattern of the species.

Influence of Rainfall on Grass Growth

Growth of grasses, from the first flush stage through flowering, is determined by rainfall in most ecosystems that are influenced by aridity, fluctuating rainfall and low soil moisture content (Bell 1971, Owaga 1980 McNaughton 1985, Deshmukh 1986, Manakadan 1985, Bouton et al. 1988). In such environments green grass is present only during the wet season and the growth pattern of grasses is determined by rainfall.

The natural grasslands of western India where the Lesser Florican breeds, are of such a type, with growth of grasses occurring during the wet season (south-west monsoon: June-September). As the terrain is largely undulating and the soil gravelly (Raychaudhari et al. 1963), water retention is poor. While some growth may occur as a consequence of winter rains there is no green biomass in summer. After the flowering and drying of the grass in October, hay harvest is completed in November, leaving behind a stubble at the tussock level. New growth is seen once again only after the onset of the subsequent monsoon.

The Indian monsoon shows considerable inter-annual variation (Shukla 1987) and this was also observed during this study. Corresponding inter-year variations were also seen in grass growth patterns and grass heights. Influence of varying rainfall on grass growth was studied only at the Naulakha grassland. Grasses began sprouting only after the onset of the monsoon; thus starting dates of grass growth varied between years. Growth rates depended mainly on the distribution, and to a lesser extent on quantum of rainfall. Depending therefore on the above factors, grasses grew from 0 cm at the onset of the monsoon to between 50 and 100 cm at the end of the season.

Maximum grass growth rates and net height were seen in those years when the monsoon was on time or early (third week of June), and when rainfall was distributed throughout the season (upto October), as was the case in 1988. Though 1986 had the maximum quantum of rainfall, the distribution was restricted more or less to the first half of the season, with the latter part being dry. This resulted both in lower grass growth rates and net height when compared with 1988. Both 1985 and 1987 were relatively dry years with late commencement of rains and patchy distribution of rainfall. The better net grass height in 1985 over 1987 can be attributed to the rainfall spread over 5 consecutive weeks while in 1987 dry spells of 2-3 weeks occurred between rains. The late flush of growth in 1987 resulted from a few belated heavy showers. This also being compounded by the longer grazing period in 1987 than in 1985.

The grass growth and rainfall data points towards two main conclusions. Firstly, it is rainfall which initiates and determines grass growth in the Lesser Florican's breeding habitat. Secondly, well distributed rainfall bears a stronger influence over growth patterns than total rainfall.

Effect of Grazing

The single biggest inhibitor of grass growth in the study area is grazing. Studies have shown that individual grass species or entire grasslands may be benefited by grazing (depending on which stage of grass growth grazing occurs) or are not affected by light grazing but heavy grazing pressures is detrimental to productivity (Hacker

1984, Geordias and McNaughton 1988, Olson and Richards 1988). These responses of grasses have been largely attributed to evolutionary adaptations by grasses to herbivory pressures.

When grazing pressures are high, as is often the case when grazers are domestic livestock, net loss in productivity and changes in species composition are seen (Owaga 1980, Crawley 1983). For instance Bock et al. (1984) show that exclosure from even very light grazing (1 cow/10 hectares) resulted in a 45% increase in grass cover, a more heterogeneous grass community, significantly more herb cover and more woody and shrub species.

In the grassland areas under study, grazing pressures are considerably higher than that reported by Bock et al. (1984), with approximately 1 head of livestock per hectare. As a measure of comparison, in those areas that are grazed throughout the year (community grazing land) grasses do not grow to more than 5 cm, while in a partially grazed grassland grasses grow to between 50 and 100 cm by the end of the monsoon.

Amongst protected grasslands three levels of grazing pressures were seen, and one grassland of each type was studied. Most of the observations on the Lesser Florican were made in the grassland with the maximum grazing pressure (Naulakha) and the one with no grazing pressure (Rampura). The intermediate type (Hazariya) was only monitored.

1) Partly Grazed Grasslands : Naulakha Grassland

In this type, livestock grazing is usually permitted upto five weeks after the onset of the monsoon, the cattle thus exploit the first flush of vegetation. After this the grassland is strictly protected from grazing until the hay harvest is completed in November. Heavy grazing pressures (c. 1 animal/hectare) during the early monsoon results in a staggered grass growth. Once the harvest is completed, grazing is again permitted in the grassland, the livestock thus exploit the remaining grass stubble. This type of grazing practice yielded the lowest grass heights.

2) Seasonally Grazed Grasslands : Hazariya Grassland

This grassland lies on the same plateau as the Naulakha grassland. Here grazing is stopped at the onset of the monsoon, and the grassland is protected until the harvest is completed in November. Grazing is permitted between the hay harvest and the subsequent monsoon. Under this practice net grass height was more than that of the partly grazed grassland.

Due to their proximity to each other and similarity, both in terrain and soil composition, the patterns of grass growth in these two grasslands can be compared. At every stage, the partly grazed grassland had between 69% and 13% lower grass heights than that in the seasonally grazed grassland, this difference being more at the beginning of the season when grazing pressure is maximum. The difference is least at the end of the season and this may be due to growth compensation as described by Olson and Richards (1988).

3) Totally Protected Grassland : Rampura Grassland

This grassland was studied in 1988 only. It is protected from grazing throughout the year. As this grassland lies well away from the other two, the rainfall patterns and the soil regime vary. The grass growth in Rampura cannot therefore be compared to that in the other two grasslands. However, due to the total absence of grazing, and perhaps also partly due to its richer soil, this grassland had the maximum grass height.

Orthopteran Abundance

A critical factor determining breeding success is the amount of food available; hence selected breeding environments should provide an abundant food supply (Lack 1954, Sinclair 1983). Moreover, females need a sufficiently abundant food supply to initiate egg laying, and the laying must be timed such that the young are hatched when food resources are abundant (Lack 1968, Perrins 1970). Hence birds that breed in a fluctuating breeding environment must, when necessary, postpone or prepone their breeding efforts under certain conditions (Halse and Jaensch 1989) or must place themselves in areas where conditions are better (Sinclair 1983).

As the Lesser Florican is largely insectivorous (Jerdon 1864, Baker 1921, Dharmakumarsinhji 1950, Ali and Ripley 1981), abundance of food in the grassland was measured by the relative abundance of Orthoptera.

Predictably, grasshoppers were more abundant in ungrazed protected grasslands than in grazed areas. A positive correlation was also seen between grass height and orthopteran abundance. In all years orthopteran abundance peaked around the end of September when the grasses were ripening. During years of poor monsoon when grass growth was negatively affected, as in 1985 and 1987, orthopteran abundance was also at the lowest. In contrast, under better monsoon distribution and the resultant better grass growth, as in 1986, orthopteran abundance was at the maximum.

In conclusion, the food availability for the Lesser Florican, as measured by an index of orthopteran abundance, is highest under good grass growth conditions which in turn is dependent on well distributed rainfall.

Influence of Rainfall on the Movement of the Lesser Florican

Some environments that have a superabundance of resources are characterized by unpredictability of both timing and location of the high resource areas; thus the need for animals to place themselves in an environment where there is an abundant resource (Sinclair 1983). The determinant of an optimum breeding environment for the Lesser Florican (i.e., rainfall) is a varying one. It has been shown how grass growth and food abundance varies with rainfall. It should follow that the dispersal and movement patterns of the Lesser Florican will be strongly influenced, if not determined, by those patterns of distribution and quantum of rainfall that determine an optimum breeding environment.

Arrival patterns of the Lesser Florican into the grassland were closely related to rainfall. First arrivals occur in a week of heavy rainfall, and the subsequent arrivals tend to occur immediately after heavy rains. In none of the years under study were Lesser Floricans seen in the study area prior to the onset of the monsoon. Subsequent arrivals were also associated with spells of heavy rain. During the early season, if the intervening period between rainy spells was dominated by dry, sunny weather, birds apparently left the grassland. This is a subjective assessment as the population under consideration is small (3 to 15 individuals in any given year of study), and the number of emigrants were as low as one or two.

How exactly the Lesser Florican follow the rains is uncertain. On one occasion a florican was seen flying towards dense rain clouds. Dharmakumarsinhji (1950) observed that the Lesser Florican does arrive during heavy rain and opined that they tend to follow the main wind currents. Sinclair (1978), based on observations in the Serengeti, suggested that movement of birds to rainfall areas may occur simply by visual guidance (apparently cumulo-nimbus clouds are visible at 150 km distance by day), lightning flashes by night or by simply flying downwind. While a great deal of study is still required before conclusions can be drawn, it is possible that existing wind currents will bring birds into general areas of rainfall, with cloud build ups directing migrating floricans to locales where rain has just fallen or is falling.

The early monsoon movements of the Lesser Florican into the grassland during weeks of heavy rainfall or apparent movements out of grasslands during prolonged dry spells would be in concurrence with Ward's (1987) model of a discrimination phase during dispersal. The movement of floricans into or out of a grassland would be in search of a superior habitat as a result of better rainfall. The lack of continued 'proximate factors' (i.e. sustained rainfall) would cause individuals to abandon it as an inferior habitat and move on.

The Lesser Florican arrival patterns in 1986 support this hypothesis. A steady rise in the population of floricans in the study area was seen with increasing cumulative rainfall. This could be because of the immigration of birds that rejected habitats during the 'discrimination phase' (much of western India was under drought in 1986; this is discussed below) and reached the study site during the search for areas with adequate rainfall. This is further corroborated with the 10 week time lapse between the first and last arrival, the last one presumably after having spent more time in search of optimal habitats. In 1985 and 1988 this time gap was only 7 and 3 weeks respectively. Heavy, widespread rainfall was recorded in 1988 and birds presumably had to spend far less time in locating good rainfall areas. In 1985, the study site did not posses the localized abundance that 1986 did nor was it as widespread as 1988. This may account for it lying between the two extremes of searching out time.

Sinclair (1983) suggested that unpredictable resource availability should select for nomadism rather than fixed migratory patterns. The Lesser Florican shows distinct nomadic movement patterns in relation to varying rainfall patterns within the breeding range. Once breeding is completed, however, birds move away from the breeding areas (Jerdon 1864, Dharmakumarsinhji 1950). Though the wintering areas have not been clearly demarcated, the majority of the population apparently move into southern India (Jerdon 1864), with some birds moving into northern India. Interestingly, a few birds stay on in the breeding range (Jerdon 1864, Dharmakumarsinhji 1950, this study). There is however, a definite pre-breeding migration into western India. Sinclair's (1983) suggestion should then perhaps be modified slightly in the case of the Lesser Florican. This suggests the possibility of a distinct migration from wintering areas into the breeding range, followed by a nomadic dispersal period during which birds search for high rainfall areas.

The overall period in which birds breed is indicated by 'proximate factors' (Immelmann 1971). However, if or when the birds lay eggs will be determined by specific cues like the presence of a mate, adequate nesting habitat and abundant food (Marshall 1959, Krapu 1981), these having been called 'end stimuli' by Marshall (1959). While immediate 'proximate factors' bring floricans into a specific area, a subsequent lack of these will cause the birds to move out in search of better areas. Thus nomadism is an active search for areas that possess or will shortly possess 'end stimuli'. While nomadism is the most important stratagem as a response to the varying 'proximate factors', two alternate passive strategies may be used. A passive strategy could involve waiting at a given location for the 'end stimuli' to come about, even though current 'proximate factors' do not predict this. This is purely speculative due to the absence of sufficient quantitative data, and is merely an attempt at explaining observations made in 1987. That year was a drought year and was characterized by long spells of dry weather followed by scanty rainfall during the early breeding season. Inspite of the sub-optimal breeding environment, one or two birds remained in the study site throughout. Though adequate rainfall did come eventually it was far too late, presumably, for successful breeding.

The passive 'sit and wait' strategy would be less used than an active seeking strategy (nomadism). Both systems would have their costs and benefits. In a year of good rainfall, those birds that adopted a passive strategy and waited in an area which does not receive sufficient rains would fail to breed. Those birds that adopted a nomadic strategy may have, however, found areas with adequate rainfall and bred successfully. In a year when the monsoon fails or is very patchily distributed, a nomadic strategy would greatly increase risk of predation/death (due to increased nomadism), while the passive strategy would reduce this risk because the individual would be familiar with its immediate environment. Thus by being nomadic, birds would greatly increase their possible breeding success by being able to place themselves in suitable conditions while during unfavourable conditions a passive strategy should increase subsequent breeding opportunities by simply reducing risk of mortality.

The third main alternative strategy that the Lesser Florican resorts to is subsequent to a failure in breeding during very poor rainfall. When breeding failure occurs during the regular breeding season, some birds may breed in the wintering grounds presumably on coming across suitable 'end stimuli'. This was seen during the drought year of 1987, when a few birds bred in southern India. The 'proximate factors' that determines breeding during the regular breeding season were absent on wintering grounds and it seems in this instance the presence of 'end stimuli' was sufficient to initiate breeding (Sankaran and Manakadan 1990).

Those rainfall patterns that determine superior breeding environments should also attract the highest number of breeding birds. With the exception of 1988 (discussed below), this was the case at the Naulakha grassland. While the tests were not significant at higher levels of significance (P <0.05, Table 2.2.a to 2.2.c), in this case lesser levels of significance at P <0.1 have been accepted to give an indication of which factor has the greatest influence on Lesser Florican movement patterns. With such a variable factor as rainfall, this is considered to be valid because of two main reasons. First, though the localized distribution and quantum of rainfall will strongly influence the number of Lesser Floricans that immigrate into any given area, the overall dispersal patterns will be governed by the distribution of rainfall over the entire breeding range. This has not been taken into consideration during analysis and will be discussed subjectively later on. Secondly, the data set is small (6 years) and showed considerable inter-year variation. Hence a definite pattern did not emerge as clearly as it presumably would have for a larger data set.

Distribution of rainfall (indicated by number of rainy days) had a stronger influence on the number of Lesser Florican immigrating into the study area than did total rainfall. This is in concurrence with the observation that well distributed rainfall coupled with quantum resulted in better grass growth and subsequently greater food abundance. Concentration of rain during the early part of the season attracted more birds than when rainfall was concentrated during the latter half of the season. An ideal monsoon in terms of breeding environment and Lesser Florican number is when the first month (June 15 - July 15) receives some rainfall, the second month receives heavy rainfall, with the subsequent rainfall well distributed over the rest of the season.

While onset, distribution and quantum rainfall strongly influenced the pattern and number of Lesser Florican immigrating into the study area, this was apparently governed by the distribution and quantum of rainfall over the Lesser Florican's entire breeding range. Due to the size of the breeding range and the consequent absence of sufficient data, this is substantiated by subjective information gathered during this study.

The present breeding range of the Lesser Florican includes western Madhya Pradesh and extreme eastern Gujarat (Malwa plateau), western Gujarat (Kathiawad peninsula), eastern Rajasthan and Kuchch (fringes of the Thar desert). 1987 is not considered in this assessment as drought or semi-drought conditions prevailed over the entire breeding range. Neither is eastern Rajasthan taken into account as there is a lack of sufficient information from that area. For this account only western Madhya Pradesh, eastern and western Gujarat are considered, which comprises the majority of the Lesser Florican's breeding range. (See Fig. 1.1 in Chapter 1).

Both 1985 and 1986 were characterized by drought in most parts of Gujarat. The Kathiawad peninsula was dry and the Lesser Florican was not recorded as breeding in Rajkot, Jamnagar, Kuchch, Junagadh and Bhavnagar districts (Shivrajkumar Khachar, Himmatsinhji pers. comm.). In both years, however, floricans bred in the study area, their numbers varying as a result of local patterns of rainfall. In 1985, few birds bred at the study site, primarily because of the late arrival and sub-normal quantum of rainfall. Presumably most birds had found suitable breeding environments elsewhere in the Malwa plateau. However, in 1986, due to copious rainfall immigration into the study area continued until quite late in the season. This presumably was due to birds not having found adequate breeding areas elsewhere and being attracted to the study area (and the Malwa plateau) due to the good localized rainfall. In 1988 the entire breeding range received good rainfall, in many areas in excess of normal, and floricans were recorded breeding almost everywhere in the breeding range. In fact due to the excessive rainfall, some Lesser Florican even bred in Sind, Pakistan (Roberts, T.J. pers. comm.), which has been rarely documented. The presence of favourable conditions throughout western India apparently resulted in a well distributed breeding population of the Lesser Florican. Hence a super-abundance of resources at the study area did not cause a corresponding greater influx. In contrast, though 1986 had lesser resources, the great degree of localization of rainfall (due to drought in Gujarat) resulted in a high influx of Lesser Floricans into the study site and presumably all over the Malwa plateau.

In summary, the pattern of rainfall that determines optimal breeding conditions of the Lesser Florican also strongly influences its movement patterns. The overall movement pattern, however, is governed by the distribution of rainfall over the entire breeding range. The more widespread the rainfall, the less probable are local concentrations. Patchy but locally abundant rainfall causes high concentration of floricans in areas of good rainfall.

Influence of Rainfall on Habitat use

Habitat use was studied only at the Naulakha grassland. A detailed account of the variations in habitat use, though presented in the results section, is not given here. As an important factor, abundance of food in the different habitat types, was not measured, this discussion on changes in habitat use is based only on two factors: availability of sufficient cover and human related disturbances.

The study area can be classified into two distinct types: crop area and grassland. Within the crop area there are patches of grassland ranging from 0.1 to 1.5 hectares. While grass patches should be classified under grassland, this distinction is made purely on the basis of location and size. Moreover, such a distinction is meant to contrast use between crop fields and areas under grass cover within crop areas.

Overall, the Lesser Florican used areas under grass cover far more than they did those under crop plants. The greater diversity and density of plant species in the grassland areas than in crop fields should result in grasslands possessing a greater diversity and abundance of food. Even in crop areas the floricans preferred grass patches and even preferentially used the grassy bunds that separated crop fields. The relatively greater use of grass patches in 1986 can be attributed to the presence of 2 large grass patches (1 hectare each) on which even territories were established. These patches were ploughed and converted into crop fields in 1987 (see also Fig. 3.4 in Chapter 3).

During the early part of the season, the main grassland was the most disturbed of the three types due to the presence of livestock and graziers. During this period due to heavy and frequent rains, wet slushy soil and freshly sprouting crops prevent farmers from working their fields. Once grazing is stopped the grassland is undisturbed. The cropfields soon become the area of high disturbance with farmers engaging in activities like weeding, spreading fertilizers and spraying pesticides during dry spells. Grass patches are the least disturbed of all three types as these are neither grazed nor worked upon.

During the early part of the season when the grassland was being grazed, floricans were frequently seen in the crop areas. However in the crop areas they are more often seen in the grass patches. A corresponding reversal is seen with the cessation of disturbance in the grassland with the main grassland being the most used among the three types. Another observation which corroborates the suggestion that the Lesser Florican use crop areas primarily due to the disturbance by livestock in the grassland, was their movement away from the grassland into cropfields at about 0800 to 0900 hours, when the cattle start arriving into the grassland. A movement back into the grassland was seen at about 1700 to 1800 hours when the cattle start leaving the grassland.

In 1986 and 1988, both years of adequate rainfall, there was no significant variation in habitat use patterns. On the other hand, 1987 differed significantly due to the dry conditions. This was largely because of the lack of adequate cover and greater disturbance (due to an extended grazing period) in the main grassland. The cropfields had more cover (due to crop growth as a result of irrigation) and relatively less disturbance. The few birds that were present were seen almost exclusively in the cropfields. However once adequate rainfall caused sufficient grass cover in the grassland, the floricans showed a shift towards increased use of the main grassland.

To summarise, areas under grass cover are used significantly more than those under crop cover. In normal years, depending on the intensity and area of disturbance, birds used crop areas or grassland. But even in crop areas they used grass patches more than crop fields. During drought conditions they were, however, more frequently seen in crop fields. This was due to the presence of more cover as a result of irrigation.

BENGAL FLORICAN

The breeding environment of the Bengal Florican differs markedly from that of the Lesser Florican in that it is relatively stable between years. This section demonstrates why this is so. Nineteenth century information on the Bengal Florican is scanty and inaccurate (e.g. Jerdon 1864, Hume and Marshall 1878, Baker 1921). More detailed information is available for Nepal (Inskipp and Inskipp 1982, Inskipp and Collar 1984). The breeding environment and breeding biology of the Bengal Florican has been documented in detail for Assam (Narayan and Rosalind 1988, Narayan et al. 1989) and have been briefly documented for Dudwa National Park (Sankaran and Rahmani 1988). This section outlines the 'proximate factors' determining the breeding environment of the Bengal Florican in the relatively drier part of its range, that is western U.P., where the rainfall is below 2000 mm. Strong variations exist between this and the wetter part of its range, example Assam, where the rainfall is in excess of 3000 mm.

Grass Fire

The single dominant factor in the breeding environment of the Bengal Florican at Dudwa is fire. Before examining the details of fires in the alluvial grassland of the study area, it is would be relevant to examine the historical existence of fire in the terai.

Fire has been an important ecological factor in grassland biomes, and in those grasslands where fire has been an inherent feature plant species show strong adaptive responses to fire (Knapp 1985, Smith and Kadlec 1985, Keeley 1987). Man, especially hunter/gatherers and pastoralists, has used fires to modify, alter or clear areas for his benefit (Vogl 1974, Tainton and Mentis 1984, Rodgers 1986). That pastoralists have used the grasslands of the terai for several centuries is evidenced by, among others things, the names of places (Dudwa probably derived from the Hindi word for milk; Gowdi as in Kaima Gowdi meaning cattle camp) and have used fire to burn grasslands and initiate new growth. The Tharus (a tribal community) of the terai burn grasslands so as to burn away the grass leaves, the remaining charred or unburnt stalks being used for thatching roofs. Forestry operations during both British and Independent India have also burnt grasslands annually, as the risk of grassland fires spreading into valuable timber forests is very high during summer but marginal during spring.

Ecologically too, a very long history (perhaps thousands of years) of annual or periodic fires is evidenced by the presence of fire resistant plant species, significantly Sal which dominates the forest in the terai (Rodgers 1986). This is further corroborated by the behavioural responses of some animal species. For instance the Swamp Deer that form small groups or are solitary in tall grass during the preburn periods form large herds (300 + animals) on recently burnt grass patches (Singh A. 1973, Singh V.P 1984, Sankaran 1990), and the Bengal Florican establishes territories on recently burnt grasslands (Jerdon 1864, Baker 1921, Narayan and Rosalind 1988, Sankaran and Rahmani 1988, Narayan 1990).

The wet alluvial grasslands that typify the terai are dominated by grass species that grow to over two metres in height in most places as a result of the monsoon growth, and in water logged areas to over four metres in height (Hajra and Shukla 198[illegible] Jain and Sastry 1983, Singh V.P. 1984, Sankaran 1990, Dinerstein 1979). By the end of winter these grasses dry up and form a densely matted tangle that makes penetration difficult. Subjective evidence collected during this study indicates that the Bengal Florican does not use areas that are covered by the previous years vegetation. Tainton and Mentis (1984) have shown that in those areas of the South African savanna that are periodically burnt (once in 3 or more years), there is an immediate decline in the francolin populations after burning takes place. This is then followed by a recovery in populations after one to two years and then a decline in numbers in the prolonged absence of burning. They attributed this to the increased difficulty that these essentially terrestrial birds experience in forcing their way through matted, moribund grass and a difficulty in finding food.

Annual grassland fires initiated by man are currently an important management practice in all grasslands throughout the Bengal Florican's range (Rahmani et al. 1988). The primary aim of these grassland fires is to keep away woodland encroachment and to provide nutritional fodder for wild ungulates. At the study area, the annual grass burn is done in January and February by the forest department. These fires are characteristic 'surface fires' that spread swiftly through the grasslands and do not burn live trees; but dead trees do catch fire and may smolder for days after the grassland has been burnt. They do not spread into dense forest, but in open forests may burn the understorey of grass and fallen leaves. The fire stops when it either reaches the edge of the forest, or the coolness and dew of the night puts it out, or when the entire grassland is burnt.

An essential difference between the 'wet' part (i.e. north eastern India) of the Bengal Florican's range and the 'dry' part (terai of U.P.) is in the pattern of burning. In Assam, due to a very high moisture level primarily because of very high precipitation, burning is done in patches (Deb Roy 1986, Narayan and Rosalind 1988). At the Dudwa National Park there is an uniformity in the presence of dry vegetation in most of a contiguous grassland. Therefore, most of, or large tracts of a grassland is burnt in a single fire. The fires leave behind isolated small patches of unburnt grass, and varying densities of burnt/charred grass stalks (depending on the species dominating the grassland, time of burning and intensity of fire). As a rule, by the end of February, all burning is completed at the Dudwa National Park and this marks the very beginning of the Bengal Florican's breeding season in the study area.

Grass Growth

Growth of grass in most grassland biomes, from the first flush through flowering occurs during the wet season and is determined by rainfall (Bouton et al. 1988, Bell 1971, McNaughton 1985, Deshmukh 1986, Owaga 1980, Manakadan 1985, Manakadan and Rahmani 1986). However, in some grasslands that occur in high rainfall areas or swampy areas, green biomass is present most of the year and is only indirectly affected by rainfall. The breeding environment of the Bengal Florican and the Lesser Florican essentially differs in the grass growth patterns and the 'proximate factors' that determine this growth.

The first lush of grass growth began in the Bengal Florican study area within a week of the annual grass burn. In spite of the total absence of rain in the succeeding eight weeks growth continued. Subsequent showers apparently only influenced grass growth rate. Hence the growth of grasses during the summer (the Bengal Florican's breeding season) is not determined by such a variable 'proximate factor' as rainfall, but during this period perhaps is only influenced by it. The growth of grass in summer is determined by far more stable 'proximate factors' than rainfall and these are in all probability the high soil moisture levels and high dew fall during March and April.

The terai is characterized by a very high water table (less than 2 m in most places in the grassland), numerous perennial and seasonal streams, rivulets, rivers, ponds and lakes. Additionally, much of the grasslands are inundated during the monsoon. As a result of this the soil moisture content is high and grass begins growing almost immediately after the annual grass burn despite the absence of rainfall. Consequently, in some areas summer growth can account for as much as 25% or more of the annual grass growth.

The absence of need for rainfall during early growth (summer) is also evidenced when the Bengal Florican and Lesser Florican habitats are compared. In the grassland used by the Bengal Florican a more linear growth is seen, with a marginal acceleration as a response to pre-monsoon showers. In contrast, in the Lesser Florican's habitat grass growth rates are greatly accelerated after heavy rains.

Due to the slightly uneven topography in the grasslands at Dudwa, water retention or duration of inundation varies, with low lying areas being wetter for longer durations than higher ground. Hence a mosaic of grass heights are seen in summer, with high ground areas having shorter grasses (0 to 1 + m growth in summer) and low lying areas having taller grasses (0 to 3 + m growth during summer). As a result of this, adequate cover is available for virtually all aspects of the florican's breeding requirement within a few weeks of the annual grass burn.

In summary, fire has historically been an important factor in the grassland biome. In the terai, annual grassland fires initiated by man have been in existence for at least a few centuries. This is also evidenced by the behavioural or adaptive responses of many species. Grasses begin growing almost immediately after burning is over. Summer grass growth (which may account for as much as 25% of the annual grass growth) is not determined by rainfall but most probably by soil moisture and the heavy dew fall in March and April.

Arrival Pattern of the Bengal Florican in the Study Area

During the non-breeding season, the Bengal Florican is nomadic and/or occupies large home ranges. By inference, at the Dudwa National Park, the species does not use the breeding areas during this season. Similar movement patterns have been documented for some resident populations of the Great Indian Bustard (Rahmani 1989) and the Little Bustard (Cramp and Simmons 1980, Petretti 1985). This has been documented in detail for the latter species (Shulz 1985). Due to the seasonal nature of this study, post breeding movements are poorly known. The Bengal Florican is absent from the study area prior to commencement of breeding and disappears from the study area once breeding is over in the first week of July. Additionally, subjective evidence collected (6-8 sightings outside the National Park in the non-breeding season) indicates that the cropfields and grazing land are used almost exclusively. Though the birds may visit the study site during the non-breeding season, this appears to be sporadic and brief as the grass forms a dense cover on the ground making penetration difficult. However this needs further study for verification.

The populations of breeding males and their arrival times were almost stable between years, and the marginal fluctuations that were seen could not be attributed to inter-year variation in the breeding environment.

The stability between years in arrival patterns, breeding populations and dates can be attributed to the stable breeding environment that this species exploits. The annual grass fire, that helps produce a suitable breeding habitat, has been a regular practice in January and February for as long as evidence is available. The subsequent grass growth patterns, does not show marked inter-year variation in both periodicity and growth rates. This is so because the growth in summer is determined by relatively stable factors (soil moisture and humidity) rather than a variable one (rainfall). Hence the response of the Bengal Florican to this environment is also a stable one. Variations that do occur therefore need explanations other than that of changes in the breeding environment.

Chapter 3

TERRITORIAL BEHAVIOUR

INTRODUCTION

Territories serve varied functions, exclusive feeding areas, nesting and/or pairing sites, or both, or a 'mobile' territory that an individual exhibits to guard a resource that is not spatially fixed (Tinbergen 1957). Correspondingly, the definition of the term territory has varied from 'fixed exclusive area with the presence of defence that keep out rivals' (Brown and Orians 1970), to a less rigid definition 'whenever individual animals or groups are spaced out more than would be expected from a random occupation of suitable habitats' (Davies 1978).

Oring (1982) defined a promiscuous mating system as male dominance polygyny, where male emancipation can emerge from, among others, a superabundance of resources. In those species which exhibit promiscuous mating systems, two main strategies based on the type and function of territories have been documented. 'Leks' are tight clusters of males, each male defending small territories that possess no resource other than the display sites (e.g. Sage Grouse; Gibson and Bradbury 1986). The other form, 'quasi' or 'exploded leks' are characterized by males occupying fairly large, well dispersed territories that are not uniformly distributed, but show some degree of clustering (Bradbury 1981, Oring 1982, Payne 1984). Though these territories possess resources that can be of use to females, these are not necessarily used by them. For instance, females that nest within the territory of a male do so only coincidentally and do not associate with the males during the nesting period except to copulate (Wittenberger 1978, Oring 1982).

In this dissertation the term territory is broadly defined as an area guarded against other individuals of the same species, as has been defined by Odum and Kuenzler (1955) and Hinde (1956). The function of these territories in the Lesser Florican and the Bengal Florican needs further clarification, as all evidence collected during this study points to the existence of an 'exploded lek' mating system in these species. Territories are formed only by males. These are large and widely spaced out, and are defended from the intrusion of other males. Though by virtue of their size the territories possess abundant food resources, these are only coincidentally used by females. The value of a territory is primarily the courtship display sites that it contains.

Virtually all species of bustards that have been studied are territorial during the breeding season, with the males using these territories primarily as display sites (Mendelssohn *et al*. 1979, Cramp and Simmons 1980, Downes

1981, Osborne et al. 1984, White 1985, Shulz 1985, Rahmani 1989). In literature, the territorial behaviour of the floricans has not been documented (Jerdon 1864, Hume and Marshall 1879, Baker 1921). More recent studies have recorded the territorial behaviour of the Lesser Florican in some detail (Dharmakumarsinhji 1950, Ridley et al. 1985, Sankaran and Rahmani 1986). Narayan and Rosalind (1988) have described the territorial behaviour of the Bengal Florican in detail.

The entire section on territorial behaviour is based only on the males of each species. As these were neither banded nor colour marked for individual identification, much of the information is subjective. However, during the pre- or early territorial period some individual males could be identified for a while by the condition of the breeding plumage.

The territorial period is defined as having begun with the commencement of flight displays. Lack of fidelity to display sites was considered as characteristic of the pre-territorial period. Most data on the Lesser Florican are from 1986, as it was in that year that the maximum number of males were seen.

RESULTS

LESSER FLORICAN

Establishment of Territories

The prominent activities and the number of male Lesser Florican present during the early part of the breeding season are given for three grasslands with varying grazing pressures in Table 3.1.

At the Naulakha grassland (which is partially grazed; see Chapter 2), considerable movement of floricans is seen in the weeks subsequent to arrival. This early period is characterized by an absence of site fidelity. The Lesser Floricans also cover large distances, moving from one ridge to another, or between cropfields and grassland. Sporadic display jumps are performed wherever the bird is, but these lack site fidelity. The individual often leaves the location where it displayed to forage or roost on another ridge or area. During the pre-territorial period, when a male is flushed, it usually flies well away from the site of disturbance. Gradually an increase in site fidelity is seen. This increase is marked by periods of sustained display at some locations, with males tending to return there. However, during this period males still tend to move away from the site either while foraging or when flushed.

Localization at a site and sustained display occurs only when grazing is stopped at the Naulakha grassland. In all years of study, territory occupancy and sustained display began only after grazing had stopped (Figs. 2.1.a to 2.1.d).

The chronology of territory formation at both Hazariya and Rampura grasslands (where there is no grazing during the monsoon) differed significantly from those at Naulakha. The pre-territorial period, which is characterized by considerable movement of the Lesser Florican at Naulakha was greatly shortened at the other two study sites. At both Hazariya and Rampura grasslands, males apparently established territories soon after their arrival. Thus, by the time territory occupancy occurred at Naulakha, floricans were displaying from established sites at both Hazariya an Rampura for some weeks (Table 3.1). Once grazing had stopped at the Naulakha grassland, those males present established territories almost immediately. The territorial period is characterized by males landing close to or within its territory on being flushed.

There were two areas of territory concentration at the Naulakha grassland (Fig. 3.2). In all years of study, three locations that were centrally located in the two areas of concentration were the first to be occupied, and these formed the cores of the concentration. There were, however, variations between years as to which area of concentration had the most birds. In 1984, one area had most territories, while in 1986, the other had the maximum number of territories. In both 1985 and 1988 this was not as clearly discernible due to a smaller population size in those years (Fig. 3.1 & 3.2).

Once these three main locations were occupied, subsequent arrivals positioned themselves in nearby or adjacent sites. The later arrivals apparently establish territories swiftly, and the degree of movement seen in the pre-territorial period was absent (Table 3.1). Some males established territories in the crop area during the early part of the breeding season, when disturbance from grazing the grassland was maximum. These males shifted their territories into the main grassland once grazing was stopped. These were also positioned near already established territories.

The changes in crop field coverage in the Naulakha grassland area between 1984 and 1988 is given in Figure 3.4. Approximately 25 hectares of grassland was converted to cropfields during this study.

TABLE 3.1

SALIENT ACTIVITIES OF MALE LESSER FLORICAN IN THE PRE-TERRITORIAL AND EARLY TERRITORIAL PERIOD AT THE THREE GRASSLANDS

Weeks June 22 ->	Salient Activities		
	Naulakha Grassland Partly grazed	Hazariya grassland Seasonally grazed	Rampura grassland Ungrazed
1	No site fidelity; No displays; Agonistic behaviour 2 males seen	No data	No data
2	No site fidelity; Few display jumps seen; Agonistic interactions; 4 males seen	Sustained display; Males territorial; 2 males seen	No data
3	No site fidelity; Sporadic periods of display; Agonistic interactions; 3 males seen	Sustained display; Males territorial; 2 males seen	Sustained display; 5-7 Males territorial; 1-2 males no site fidelity
4	1 male sustained display and territorial; Others no site fidelity; 2-3 males seen	Sustained display; Males territorial; 3 males seen	Sustained display; Males territorial; >10 males
5	1 male territorial; Others partial site fidelity; Sustained display; 3 males	Sustained display; Males territorial; 3-4 males seen	Sustained display; Males territorial; >10 males
6	Sustained display; 6 males territorial; 7 males seen	Sustained display; Males territorial; 3-4 males seen	Sustained display; Males territorial; >10 males
7	Sustained display; 8 males territorial; 1 male no site fidelity; 9 males	Sustained display; Males territorial; 3-4 males seen	Sustained display; Males territorial; >10 males

For grazing pressures see Chapter 2

N.B. Naulakha and Hazariya data of 1986; for Rampura of 1988.

Location, Size, Duration of Possession, and Distance between Territories

The topography was undulating in all the three study areas and male Lesser Floricans occupied territories on ridge tops. As displays are performed from the ridge tops, these were the most used areas within the territory. For instance, in 1986, three males occupied territories along the length of one ridge (Fig. 3.2). Often the territorial boundaries of males on adjacent ridges were the streams that flow between the ridges, paths or roads.

FIG. 3.1. LOCATION OF LESSER FLORICAN TERRITORIES AT NAULAKHA IN 1985 & 1988

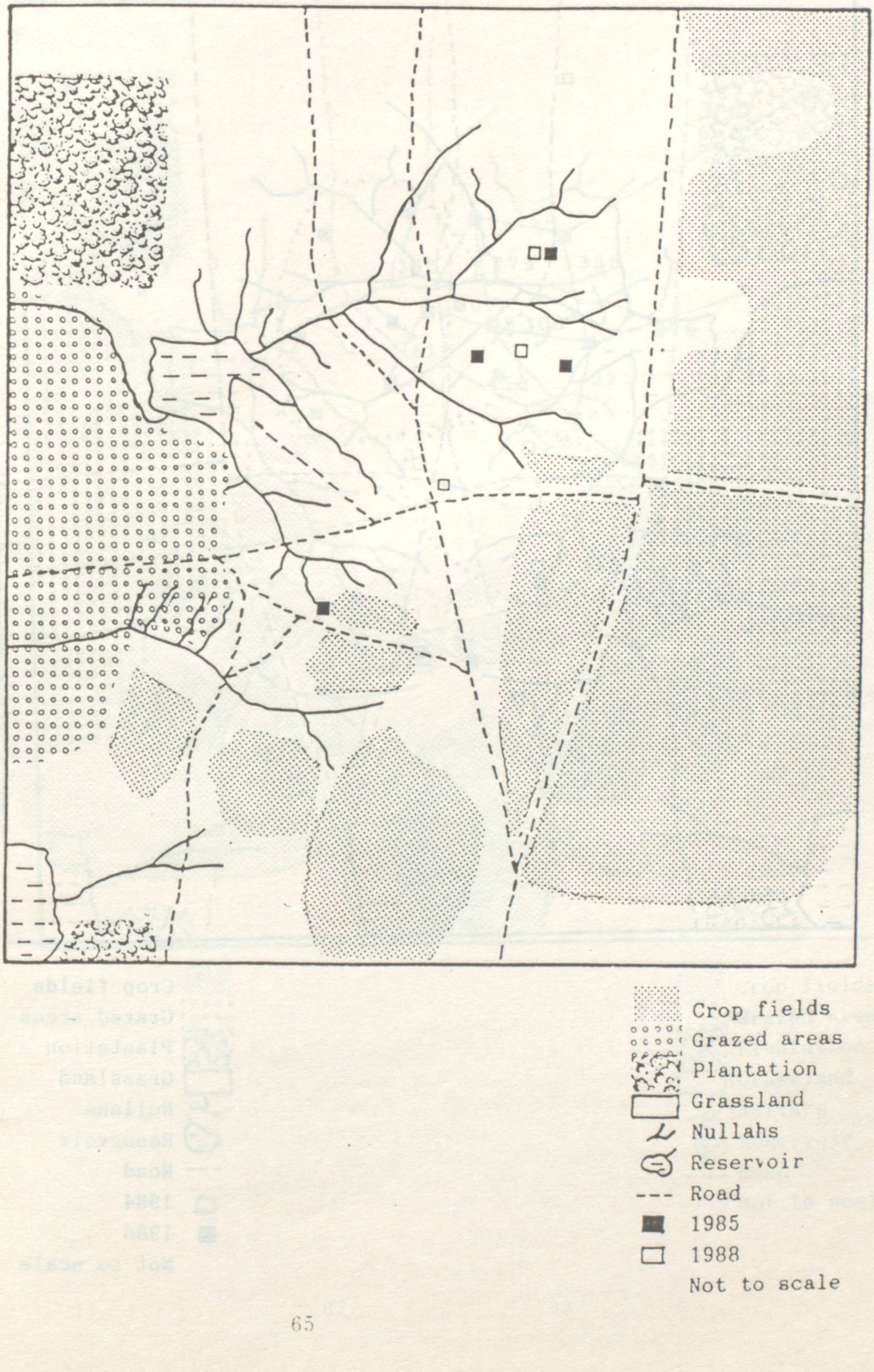


FIG. 3.2. LOCATION OF LESSER FLORICAN TERRITORIES AT NAULAKHA AND AREAS OF THEIR CONCENTRATION IN 1984 & 1986

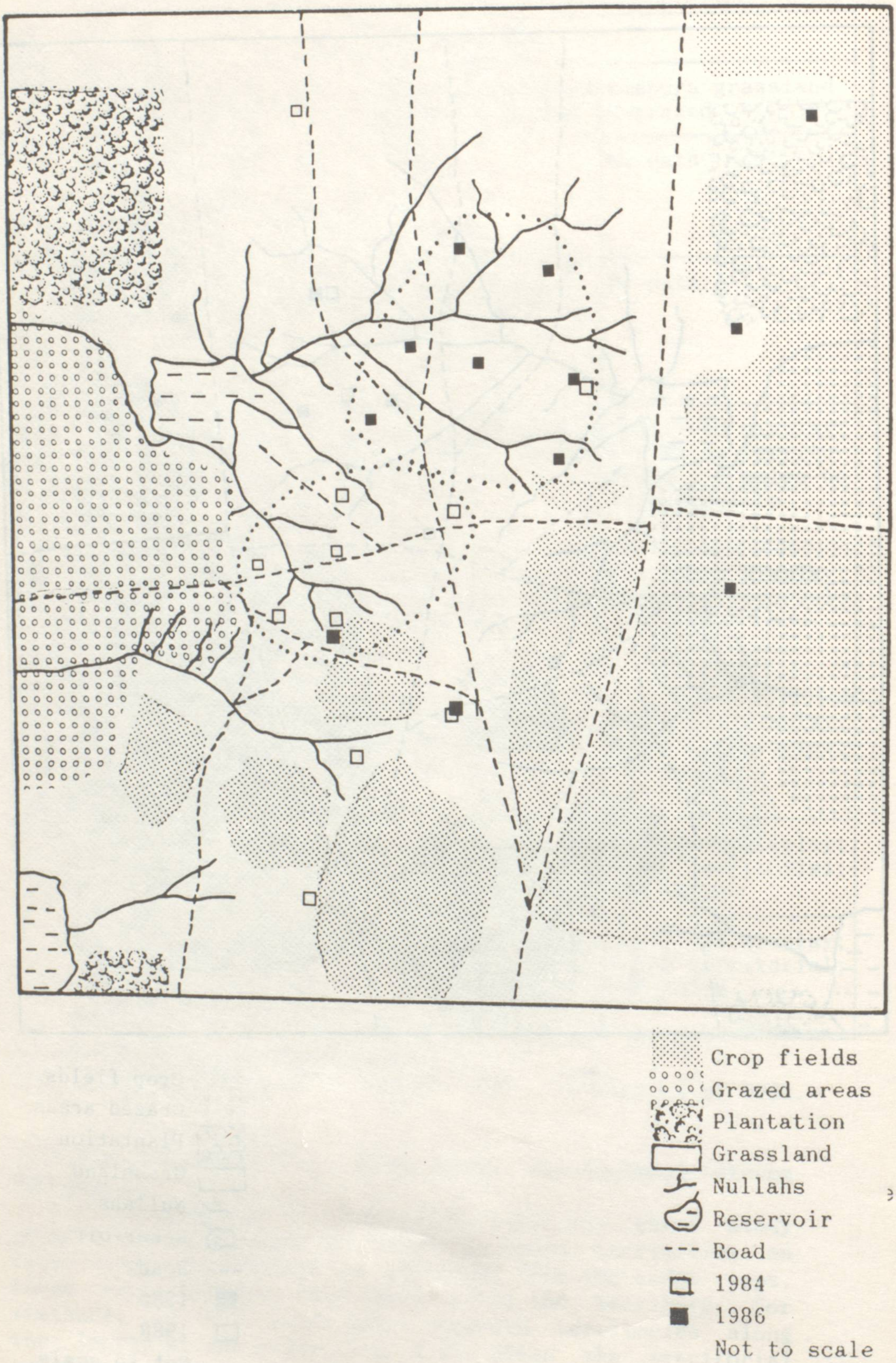


FIG. 3.3. DISTANCE BETWEEN MALE LESSER FLORICAN 'JUMPING SPOTS' AT NAULAKHA IN 1986

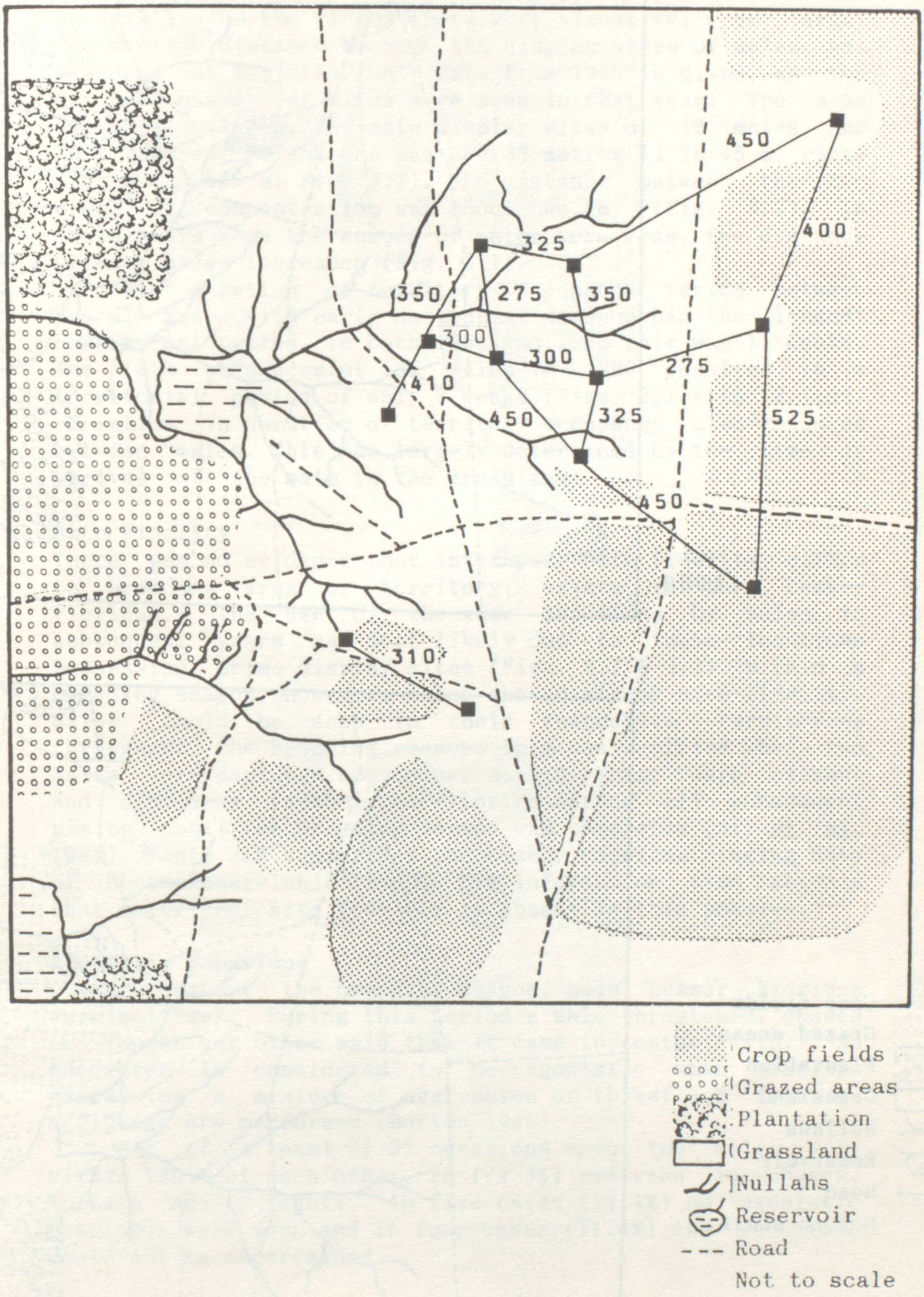
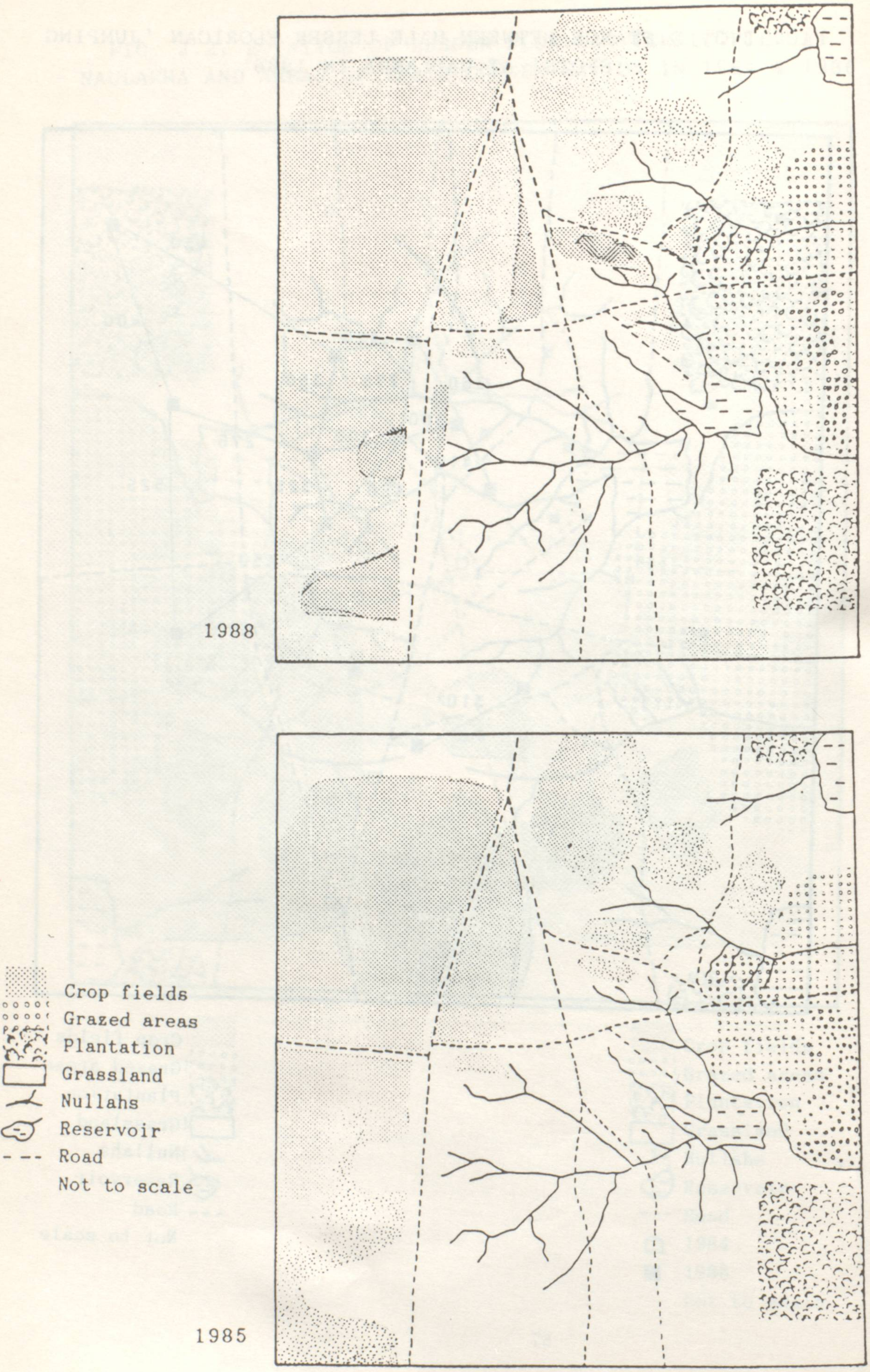


FIG. 3.4. AREA UNDER CROP AT NAULAKHA IN 1985 AND 1988



The size of each territory was about 2 hectares, though this varied between males. The area used for display was smaller as only the ridge tops were used for display. The inter-male distance was greater at Rampura than at Naulakha or Hazariya as the ridges there were almost twice as large. The average distance between the display sites of males was measured at Naulakha. Only data from 1986 is given, as the maximum number of birds were seen in that year. The mean distance between the main display sites of 12 males and their nearest neighbours was 366.33 metres (± 76.45 m, range 275 m to 525 m; Fig. 3.3). The distance between the two areas of concentration was about two km. (Fig. 3.2). In those years when the number of males were less, the distance between males increased (Fig. 3.1).

The duration of territory occupancy varied between years; years with early and normal monsoon had the longest territorial period. In both 1986 and 1988 this was 11 weeks. The late commencement of rains in 1985 resulted in a territorial period of only 7 weeks (Figs. 2.1.a to 2.1.d). Variation in duration of territory occupancy also existed between males. This was largely determined by the time of arrival of the male in the grassland.

Site Fidelity

There was no evidence that inter-year site fidelity, either to breeding area or territory, exists in the Lesser Florican. The use of the same locations by males in subsequent years was most likely due to those locations possessing prime display sites (Figs. 3.1 & 3.2). Within a breeding season, however, males showed strong site fidelity. Males could be seen in their respective territories throughout the breeding season. This was verified when two males were captured and colour marked. These were present and displayed in their territories during all subsequent visits until the breeding season was completed (Ali et al. 1984). Table 3.2 summarises the Lesser Florican ringing data of Dharmakumarsinhji (1950). His information also reveals that inter-year site fidelity is absent in this species.

Agonistic Behaviour

Throughout the breeding season, male Lesser Florican were solitary. During this period a male threatened, chased or fought any other male that it came in contact with. An encounter is considered to be agonistic when displays expressing a mixture of aggression or threat and fear or avoidance are performed (Burton 1985).

Out of a total of 35 occasions when two males were within 50 m of each other, 26 (74.3%) resulted in chases, threats and/or fights. In five cases (14.4%) no agonistic reactions were seen and in four cases (11.4%) the reactions could not be ascertained.

TABLE 3.2
Summary of Lesser Florican ringing data *

Year	No. Ringed	No. Recov.	Year Ringed	Location Same	Location Other
1943	100	-	-	-	-
1944	99	2	1943	0	2
1945	111	0	-	-	-
1946	100	2	1944	1	2
		1	1945		
1947	67	1	1944	5	4
		1	1945		
		7	1946		
1949	11	1	1945	0	2
		1	1947		
1950	0	1	1949	0	1
Total	488	17		6	11

Total birds ringed : 499   Overall recovery : 3.48%
No. of males : 488   From same location : 1.23%
No. of females : 1   From other location: 2.25%
The one female ringed has been omitted from calculation.
* Source Dharmakumarsinhji (1950)

While most agonistic interactions (76.9%) ended in chases and/or threat displays, these culminated in physical fights only occasionally (23.1%). The average duration of threat and/or chase was 6.5 minutes (± 5.21 min., range 1 to 15 min., n = 20). The duration of fights was on average twice as long (avg. = 13 min., ± 3.37 min., range 9 to 17 min., n = 4) as the duration of the threat component was quite prolonged. These values are all from observations when both the start and finish of encounters were seen.

Almost all encounters were between two males. There were only two exceptions to this, once each in 1985 and 1986, when three males threatened and chased each other.

Description of Agonistic Behaviour

The agonistic behaviour of the Lesser Florican can be differentiated into chases, threat displays and physical fights.

Chases

Prolonged 'chases' were seen mainly during the pre-territorial period. The males were not localized during this phase and tended to wander about. On coming across another male, one usually began chasing the other with or without performing threat displays (described below). Such chases varied in duration and ranged from 1 to 15 minutes. The chase consisted merely of an aggressive male running behind another male. None of the displays that are performed during threat were seen (see below). During chases, both males frequently stopped to catch insects which were flushed, resuming chasing or running away immediately after that. Such chases stopped when the aggressor lost sight of the male or apparently lost interest.

At no stage of the breeding season did males chase each other aerially. When chases did occur they only occurred on the ground. When one male flies off after threat displays or fights, or flies over or near another male's territory, it is not pursued by the other.

Condition of breeding plumage (stage of moult) did not determine the degree of aggression. For instance, in 1986 one male that had moulted only partially into the breeding plumage was far more aggressive and usually was the 'chaser' in all encounters with other males who were either in complete breeding plumage or at a later stage of moult.

Threat Display and Physical Fights

Most physical fights seen were during the period when territories were being established or had just been established. Once males had occupied territories and were displaying consistently, intruding males left the territory when they were threatened and/or chased. The sequence of events that lead upto a fight is as follows.

An intruding male displays once or twice at the edge of another male's territory (this was not always the case). On seeing or hearing this, the territorial male responds by displaying vigorously a few times before running towards the intruding male. When both males are within about 15 m of each other they slow down and assume threat postures. This involves deliberate walking abreast of each other with the tail cocked, the mantle feathers raised and the head held low. This 'parallel walking' last about 8-10 minutes. During this period males mostly display their sides to each other. An individual may sit down or peck vigorously on the ground. When the back of one male is shown, the other male may make mock rushes and/or jump towards it with wings partly outstretched. These rushes are apparently signals of increased aggression, and become more frequent as the birds draw closer to each other. The first physical contact is usually in the air as both jump towards each other, but most of the subsequent tussle is on the ground. This consists of a great deal of pushing with the breast, attempted pecking on the head, beating each other with wings (though not always). The birds may break away and rush again at each other and on one occasion such contact was made thrice.

The fights are usually brief - one to two minutes in duration - and end when one of the contestants is pushed to the ground. The loser runs away, or flies for a few metres before running away, with the winner chasing it for a few metres. Immediately after this, the winner starts displaying vigorously at the location of the fight. The loser usually moves away to a nearby location where it also displays, sometimes intensively and sometimes only sporadically.

Once male Lesser Floricans have established territories they do not chase intruders beyond the boundaries of the territory. There were, however, two exceptions to this, once each in 1985 and 1986. In the former case, the territorial male pursued an intruding male from its territory to an adjacent ridge. In the latter, a territorial male left its territory and fought a male that had landed on the opposite ridge.

Distribution of Agonistic Behaviour through the Breeding Season

Distribution of agonistic behaviour over the weeks of the breeding season has been plotted in Figure 3.5. Agonistic interactions are clustered in the first few weeks and show a peak in the very beginning of the breeding season. To see whether there are any significant differences in the distribution of agonistic interactions, the breeding season was divided into three equal parts (Table 3.3). While the frequency of agonistic interactions in the first and second parts of the season did not vary statistically, both the initial and middle parts had a significantly higher frequency of interactions than the last part of the breeding season. Higher frequencies of agonistic interactions are associated with the arrival patterns of the males, who tend to immigrate into the grasslands until mid-August. The downward trend would then be related to the increasing proportion of males that have already established territories. Only on one occasion (1985) was agonistic interaction seen at the end of the season, and this was when an unusually late arrival emigrated into the grassland.

Non-Agonistic Interactions

Only infrequently do two males come in contact without it resulting in fights, chases or threats. Of the five observed occasions, four were in the pre-territorial period. These instances were when two males foraged as close as 20 m to each other (one occasion) or in the same crop field. Only in one instance did a male forage through the territory of another while the occupant male was displaying, without it being threatened or chased off by the occupant.

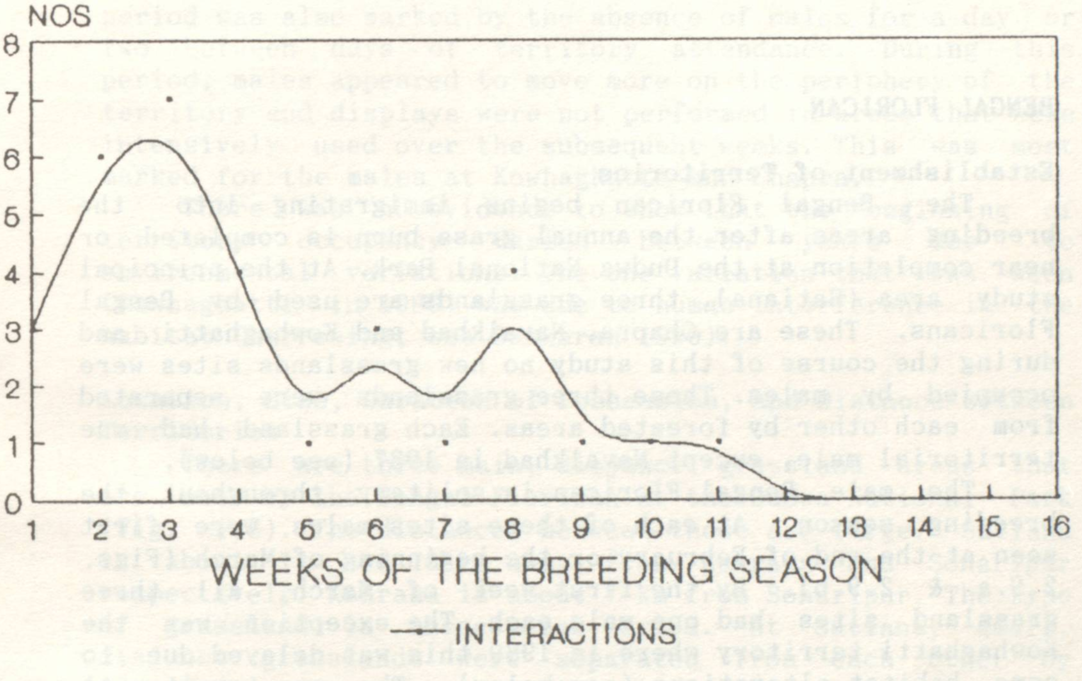


FIG. 3.5. LESSER FLORICAN
DISTRIBUTION OF AGONISTIC INTERACTIONS
IN THE BREEDING SEASON

TABLE 3.3
LESSER FLORICAN
SEASONAL DISTRIBUTION OF AGONISTIC INTERACTIONS
Kolmogorov-Smirnov Two Sample Test

	SECOND		THIRD	
	MD	P	MD	P
FIRST	0.400	0.820	0.800	>0.080
SECOND			0.800	>0.080

N.B. Breeding season divided into three equal parts.

BENGAL FLORICAN

Establishment of Territories

The Bengal Florican begins immigrating into the breeding areas after the annual grass burn is completed or near completion at the Dudwa National Park. At the principal study area (Satiana), three grasslands are used by Bengal Floricans. These are Chapra, Navalkhad and Kowhaghatti and during the course of this study no new grasslands sites were occupied by males. These three grasslands were separated from each other by forested areas. Each grassland had one territorial male, except Navalkhad in 1987 (see below).

The male Bengal Florican is solitary throughout the breeding season. At each of these sites males were first seen at the end of February or the beginning of March (Figs. 2.9.a & 2.9.b). By the first week of March, all three grassland sites had one male each. The exception was the Kowhaghatti territory where in 1989 this was delayed due to some habitat alterations (see below). The pre-territorial period was brief, and merely consisted of a few days between arrival and display. This, however, varied both between males and years.

In 1988, at Kowhaghatti, the time gap between first sighting and first display was 9 days. At Chapra, though this time gap was 24 days, there was a lapse of 13 days between the first and second sighting, and display started 11 days after the male was regularly sighted in that grassland. At Navalkhad the time gap was 40 days and the time lapse between first and second sighting was 22 days. The male was seen regularly over 18 days before display was first recorded. However, at all three sites, occupant males defended the grasslands against intrusion by other males before they began displaying.

In 1989, the pre-territorial period was non-existent.

At both Chapra and Navalkhad display was seen on the first day of sighting itself (Figs. 2.9.a & 2.9.b). This gap, between the first sighting and first display, was prolonged at Kowhaghatti (31 days). In that year, the Kowhaghatti grassland was harrowed as a management experiment (see also Sankaran 1990). Though the male was first sighted on 11 March, it moved away soon after that to a location adjacent to the Navalkhad male's territory. It displayed there on two consecutive days and then was seen returning to the Kowhaghatti grassland and subsequently began displaying there.

During the pre-territorial period, when flushed, males flew away from the grassland and as fidelity increased began landing within the grassland itself. The pre-territorial period was also marked by the absence of males for a day or two between days of territory attendance. During this period, males appeared to move more on the periphery of the territory and displays were not performed in areas that were intensively used over the subsequent weeks. This was most marked for the males at Kowhaghatti and Chapra.

There was no evidence to show that the beginning of territory occupancy varied between years due to environmental variations. The one variation that was seen (Kowhaghatti in 1989) was due to human interference in the habitat (harrowing; see Sankaran 1990).

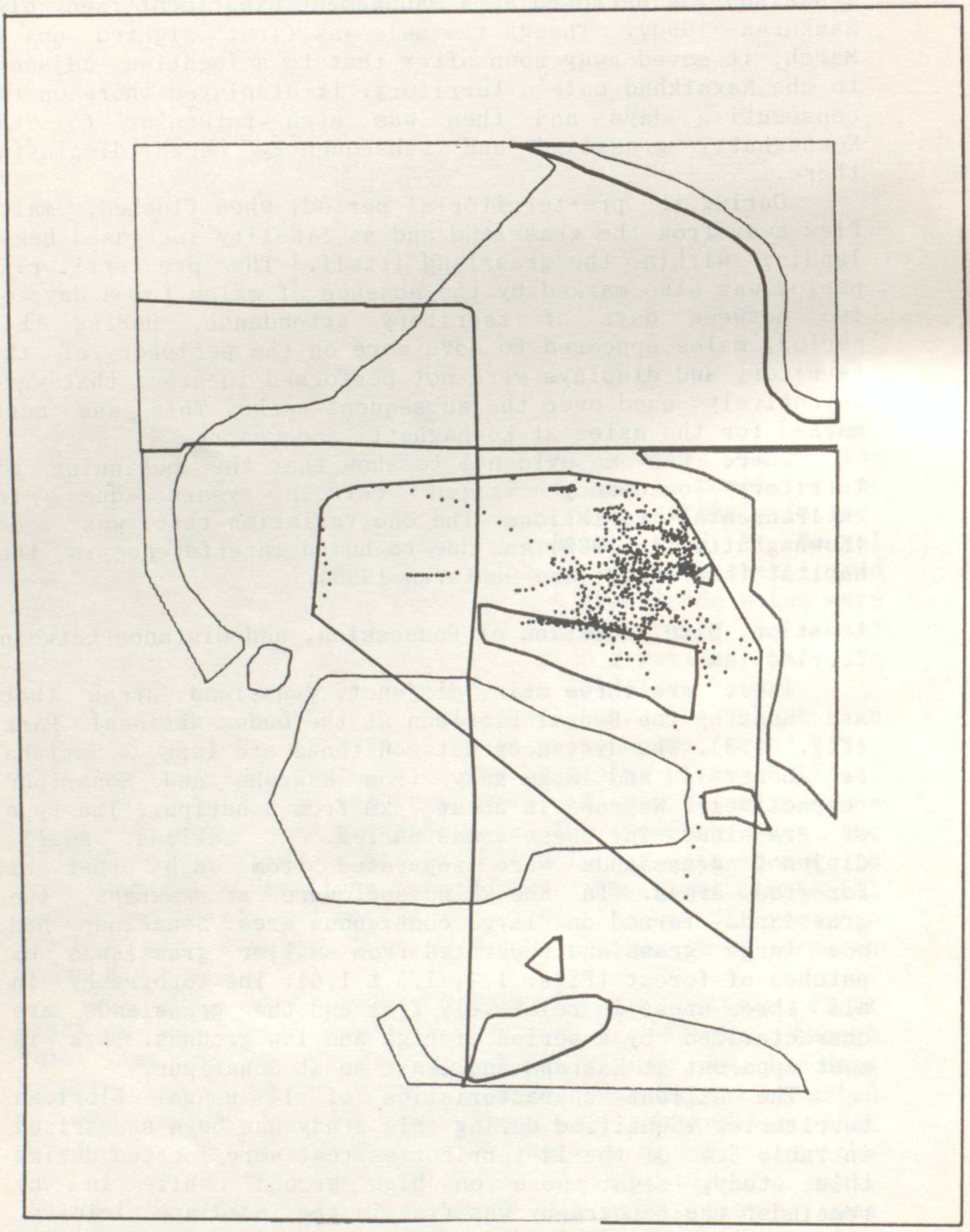
Location, Size, Duration of Possession, and Distance between Territories

There are three main, disjunct, grassland areas that are used by the Bengal Florican at the Dudwa National Park (Fig. 1.3). The distances between these are large. Satiana is about 14 and 18 km away from Kakraha and Sonaripur respectively. Kakraha is about 7 km from Sonaripur. The type of grassland in these areas varied. At Satiana, small, disjunct grasslands were separated from each other by forested areas. In the Rhino enclosure at Kakraha, the grasslands formed one large contiguous area. Sonaripur had one large grassland separated from smaller grasslands by patches of forest (Figs. 1.4, 1.5 & 1.6). The topography in all three areas is relatively flat and the grasslands are characterized by a series of high and low grounds. This is most apparent at Kakraha and least so at Sonaripur.

The salient characteristics of 14 Bengal Florican territories identified during this study has been summarized in Table 3.4. Of the 14 territories that were located during this study, eight were on high ground, while in the remainder the topography was flat in the immediate vicinity. Almost all territories were situated well away from forested areas. However, some males had display sites close to forested or thinly wooded areas. This was largely due to patches of thin forest that exists in the grasslands at

FIG. 3.6. TERRITORY OF MALE BENGAL FLORICAN IN THE KOWHAGHATTI GRASSLAND AT DUDWA N.P. 1989

Foraging area within territory



Area of use = 26.44 hectares

Method : Minimum-perimeter polygon (Mohr 1947)

(n = 25 observation periods)

scale 1cm = 0.096km

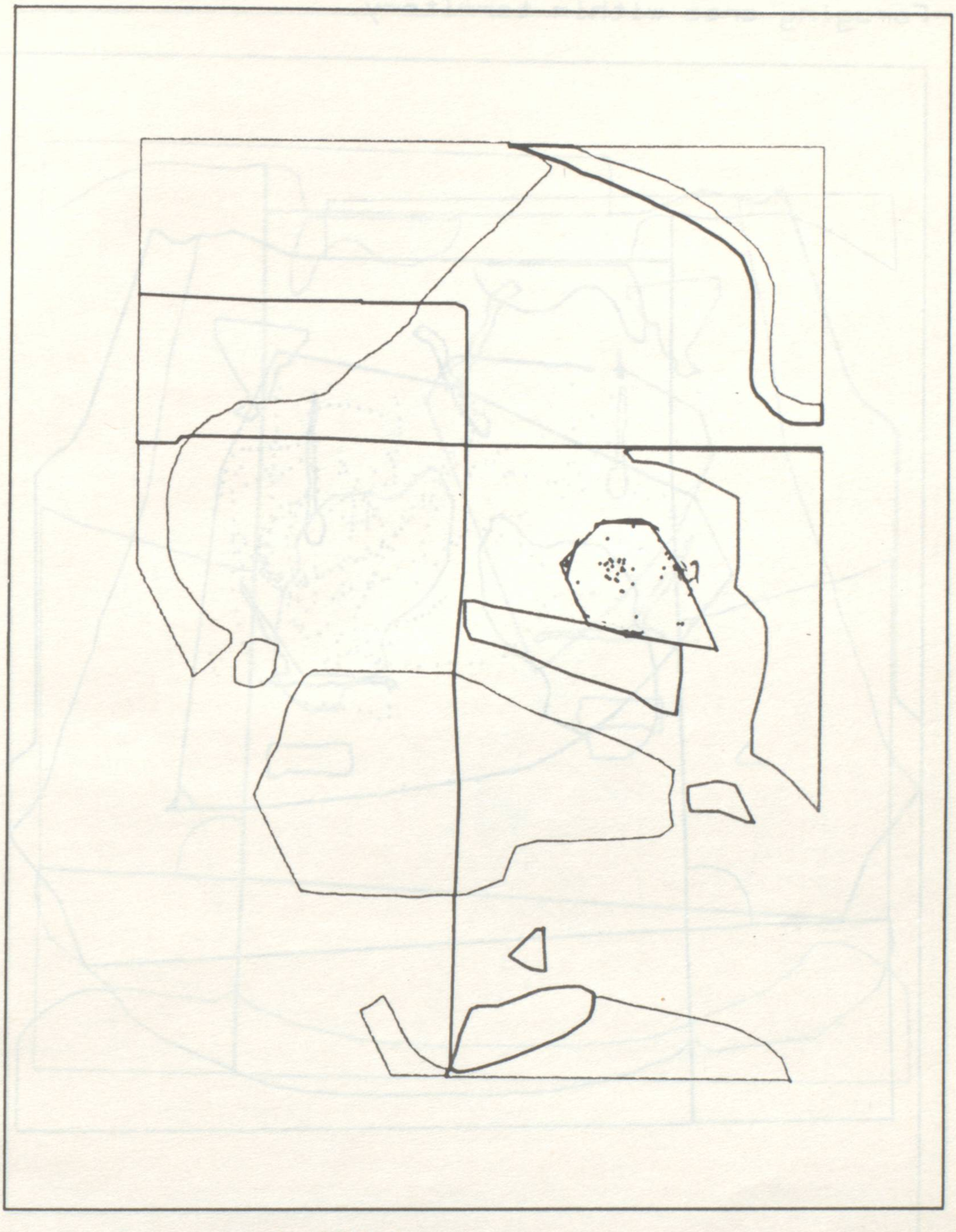
Dense forest

Open forest

Neora river

FIG. 3.7. TERRITORY OF MALE BENGAL FLORICAN IN THE KOWHAGHATTI GRASSLAND AT DUDWA N.P. 1989

Display sites within territory



Area of use = 2.076 hectares

Methods : Minimum-perimeter polygon (Mohr 1947)

(n = 60 displays)

scale 1cm = .096km

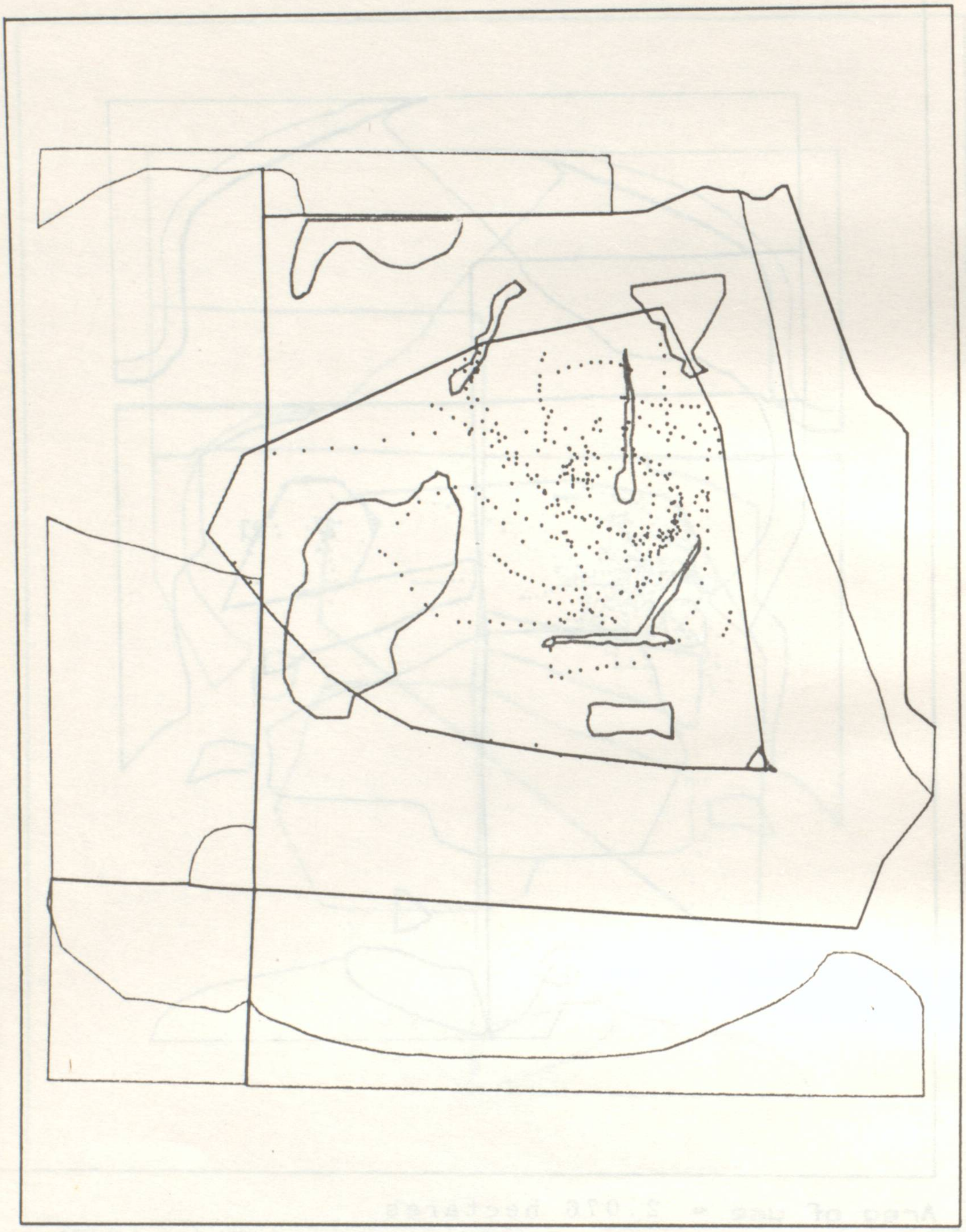
Dense forest

Open forest

Neora river

FIG. 3.8. TERRITORY OF MALE BENGAL FLORICAN IN THE NAVALKHAD GRASSLAND AT DUDWA N.P. 1989

Foraging area within territory



Area of use = 28.01 hectares

Method : Minimum-perimeter polygon (Mohr 1947)

(n = 17 observation periods)

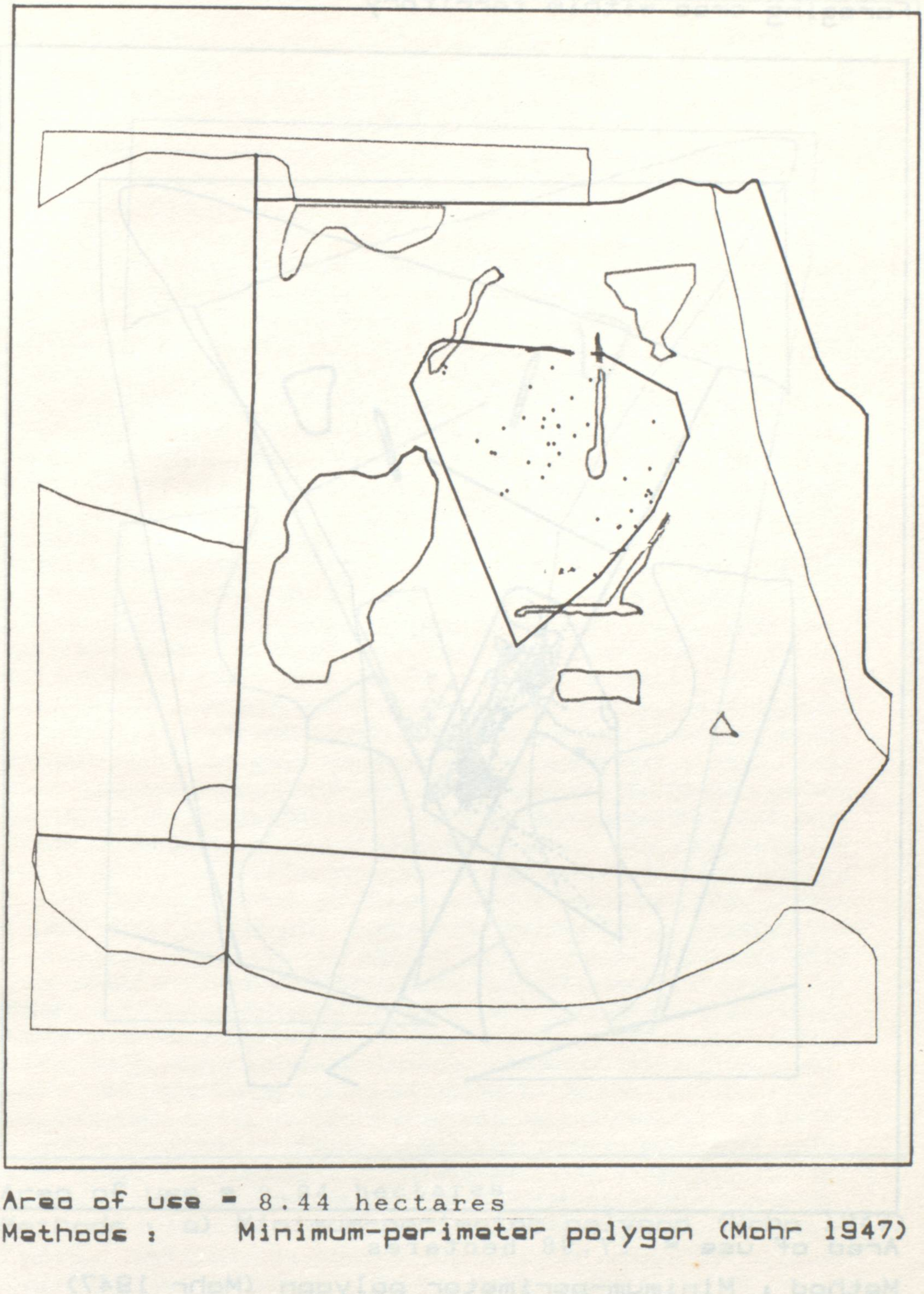
scale 1cm = 0.086 km

Dense forest

Open forest

FIG. 3.9. TERRITORY OF MALE BENGAL FLORICAN IN THE NAVALKHAD GRASSLAND AT DUDWA N.P. 1989

Display sites within territory



Area of use = 8.44 hectares

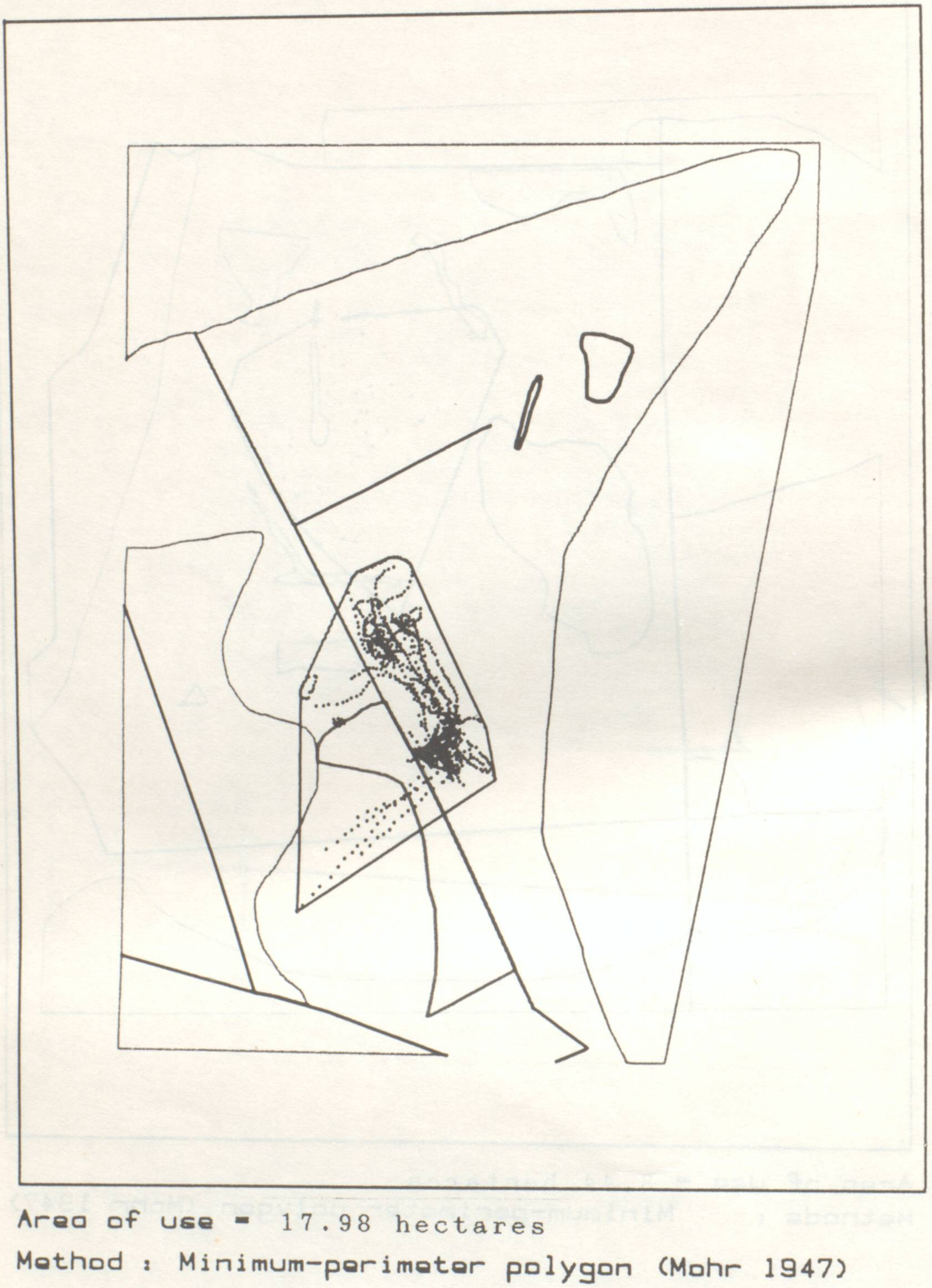
Methods : Minimum-perimeter polygon (Mohr 1947)

(n = 55 displays)

scale 1cm = 0.086km
Dense forest
Open forest

FIG. 3.10. TERRITORY OF MALE BENGAL FLORICAN IN THE CHAPRA GRASSLAND AT DUDWA N.P. 1989

Foraging area within territory



Area of use = 17.98 hectares

Method : Minimum-perimeter polygon (Mohr 1947)

(n = 22 observation periods)

scale 1cm = 0.135km

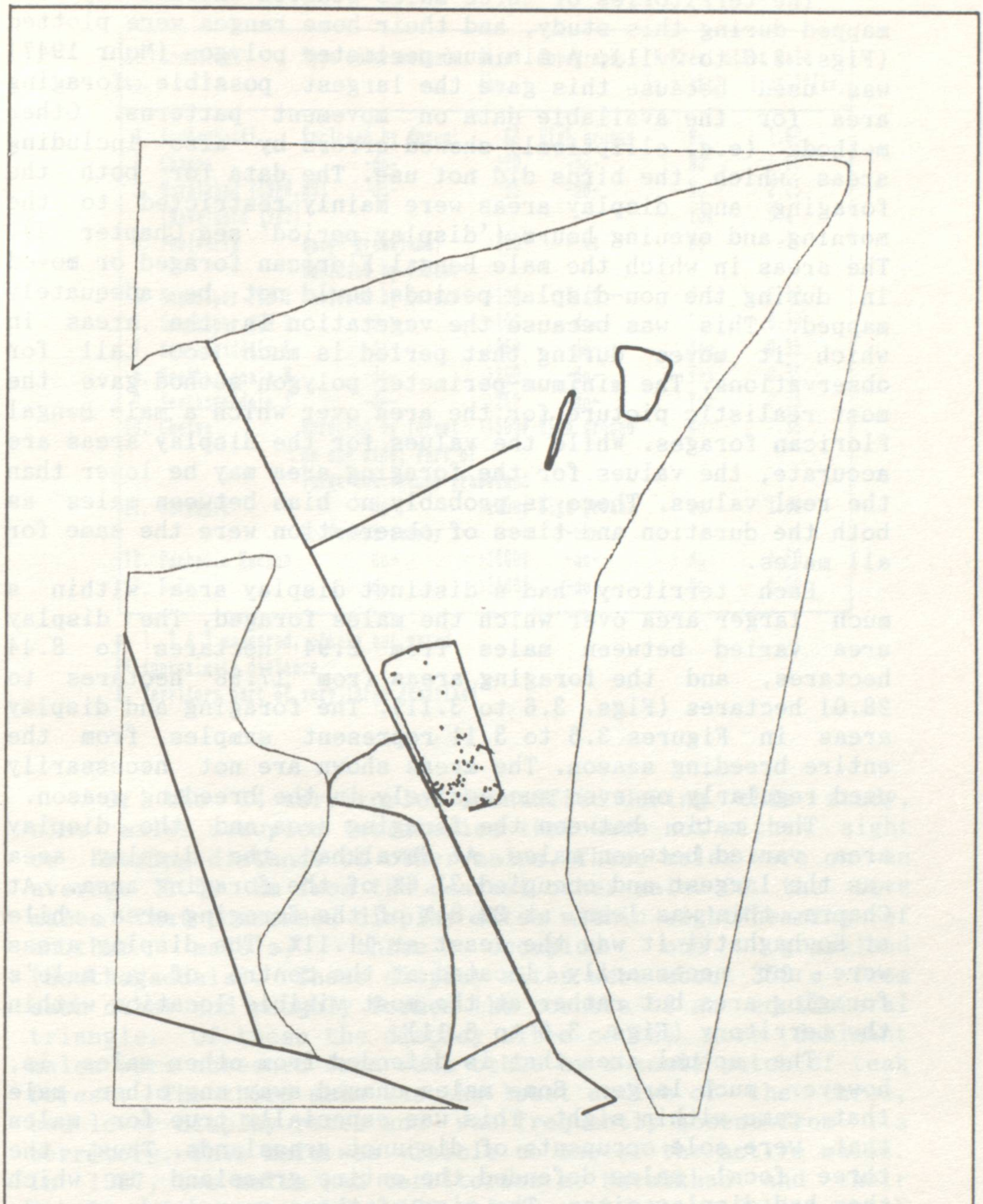
Dense forest

Open forest

Chapra 'taals'

FIG. 3.11. TERRITORY OF MALE BENGAL FLORICAN IN THE CHAPRA GRASSLAND AT DUDWA N.P. 1989

Display sites within territory



Area of use = 2.94 hectares

Methods : a) Minimum-perimeter polygon (Mohr 1947)

(n = 63 displays)

scale 1cm = 0.135km
Dense forest
Open forest
Chapra 'taals'

Dudwa as a result of earlier plantation programmes (see Study Areas).

The territories of three males studied intensively were mapped during this study, and their home ranges were plotted (Figs. 3.6 to 3.11). A minimum-perimeter polygon (Mohr 1947) was used because this gave the largest possible foraging area for the available data on movement patterns. Other methods (e.g. elliptical) showed errors by also including areas which the birds did not use. The data for both the foraging and display areas were mainly restricted to the morning and evening hours ('display period' see Chapter 4). The areas in which the male Bengal Florican foraged or moved in during the non-display periods could not be adequately mapped. This was because the vegetation in the areas in which it moves during that period is much too tall for observations. The minimum-perimeter polygon method gave the most realistic picture for the area over which a male Bengal Florican forages. While the values for the display areas are accurate, the values for the foraging area may be lower than the real values. There is probably no bias between males as both the duration and times of observation were the same for all males.

Each territory had a distinct display area within a much larger area over which the males foraged. The display area varied between males from 2.94 hectares to 8.44 hectares, and the foraging areas from 17.98 hectares to 28.01 hectares (Figs. 3.6 to 3.11). The foraging and display areas in Figures 3.6 to 3.11 represent samples from the entire breeding season. The areas shown are not necessarily used regularly or even successively in the breeding season.

The ratio between the foraging area and the display area varied between males. At Navalkhad, the display area was the largest and occupied 31.6% of the foraging area. At Chapra, this was less, at 22.81% of the foraging area, while at Kowhaghatti it was the least at 11.11%. The display areas were not necessarily located at the centre of a male's foraging area but rather at the most visible location within the territory (Figs. 3.6 to 3.11).

The actual area that is defended from other males is, however, much larger. Some males chased away any other male that came within sight. This was especially true for males that were sole occupants of disjunct grasslands. Thus, the three focal males defended the entire grassland in which they had display sites. The size of these grasslands varied. The grassland area of Navalkhad was 85.1 hectares, Chapra 120.3 hectares, and Kowhaghatti 62.7 hectares. There was apparently no relation between the size of grassland and the area used for foraging.

TABLE 3.4
SALIENT CHARACTERISTICS OF TERRITORIES OF BENGAL FLORICAN

S. no.	Location	Type of grassland	Size* (ha.)	Topography	Nearest other male	
					In sight?	Dist.**(km)
1.	Kowhaghatti	Enclosed by forest	63	High ground	No	1.60
2.	Chapra	-do-	120	-do-	No	1.60
3.	Navalkhad (1988,89)	-do-	85	-do-	No	2.25
	(Navalkhad 1987)				Yes	0.4
4.	Phulvaria	Large grassland; Enclosed by forest	›300	Flat	No	-
5.	Sonaripur FRH 1	Enclosed by forest	›100	Flat	?	0.90
6.	Sonaripur FRH 2	-do-	›100	-do-	?	0.90
7.	Seethagaddaia E.	-do-	›250	-do-	Yes	0.35
8.	Seethagaddaia W.	-do-	›250	-do-	Yes	0.35
9.	Seethagaddaia 3	-do-	›250	-do-	Yes	0.35
10.	Chetwa	Bordered by forest on one side; Part of large contiguous grassland	›1500‡	High ground	No	1.85
11.	Kurmunia	-do-	›1500‡	High ground	No	1.60
		No forest nearby		-do-		
12.	Parbatia Machan	-do-	›1500‡	-do-	No	1.60
13.	Bela	-do-	›1500‡	-do-	No	2.00

* 1, 2 & 3 measured, others estimated

** Approximate distance

‡ Territory part of very large grassland

Of the 14 territories identified during this study, nine males occupied territories that were not within sight or hearing distance of other males. These males were on an average 1.59 km from the nearest other male. Of the five males that possessed display sites within sight/hearing of another male's, three occupied one grassland (Seethagaddaia). Their display sites were about 350 m from each other and roughly formed the corners of an equilateral triangle. Of these the display sites of the more dominant males were screened from each other by a small patch of teak forest. The third male was the least active of the three, had lower display rates and was frequently absent from its territory. This male was visible to one of the active males. In 1987, two males had territories at Navalkhad and their display sites were about 400 m from each other. But in both 1988 and 1989 this grassland was occupied by only one male. In 1988, a second male tried establishing a territory, but was not allowed to do so by the occupant male.

The duration of territory possession varied between males, and could be ascertained only for 1989. This period ranged from between 12 weeks (Kowhaghatti) to 16 weeks (Chapra) (Fig. 2.9.b). The latter figure appears to be more realistic as in 1989 the late establishment and shorter occupancy period by the male at Kowhaghatti was due to man made changes to the territory.

Movement Patterns within Territories

While the area that the Bengal Florican defends is large and usually covers the whole grassland in those locations where only one male is present, the area in which it forages is usually much smaller. The entire defended area can be defined as that male's territory and in this section, the area within which it is seen to move is called its foraging area.

Males used the display areas only during the display periods. This was restricted to the morning and evenings. In between, the males foraged in longer grass away from the display site. They generally moved away from the display site between 0700 and 0900 hours depending on the time of sunrise and usually returned between 1530 and 1730 hours (see also Chapter 4). They roosted at or near the display sites. Such fixed patterns of movement were most marked at the Kowhaghatti territory and least at the Navalkhad territory. For example the Kowhaghatti male preferentially moved into the grassland area south of its display site in the non-display period. At Chapra, the male used to move into the area east of its display site, while the Navalkhad male would either move into one corner of its display area or move elsewhere within the grassland.

Site Fidelity

There was strong evidence to show that the display sites of the Bengal Florican are traditional sites, and that this species shows site fidelity to both breeding area and territory. However, this could not be proved due to the absence of individual marking of birds in this study.

The same display sites were in use between 1985 and 1989. In 1985, three display sites were located and these three were also used in 1987, '88 and '89. In 1987, eight display sites were identified, which were again re-occupied in 1988 and '89. In 1988, 14 display sites were located, of which at least 12 were re-occupied in 1989. The other two locations were visited infrequently and their status could not be determined.

The existence of traditional display sites was also corroborated by subjective information gathered during this study. Some display sites, that were conspicuous to man due to their locations, are known to have been in use for the last 45 years. For instance, the Kowhaghatti and Chapra grasslands and the grasslands adjacent to and west of the Sonaripur Forest Rest House, have had territorial males since 1942-43 for the last and since at least 1950 for the first two (Naresh Singh; Balram Singh pers. comm.).

Some behaviour patterns, especially in the choice of display sites and similarity in movement patterns between years within the territory, also indicated that a male will re-occupy its old territory in subsequent years as long as it is physically capable of doing so.

Agonistic Behaviour

During the breeding season, male Bengal Floricans are solitary. Most often, the coming together of two or more males results in threats, chases or fights.

Totally, 40 encounters between males were recorded during this study, of which 35 (87.5%) resulted in threats, chases or fights. Two males were together continuously over a period of four days and this has been taken as four encounters. (This behaviour is believed to be unusual - see below). In only other one encounter (2.5%) did a male fly over another territory without it resulting in a chase.

Of the 35 encounters that resulted in agonistic interactions, 5 (14.29%) developed into fights, 5 (14.29%) ended in threat displays, 7 (20%) resulted only in aerial chases, while 18 (51.43%) resulted in a combination of both threats and aerial chases.

Of the five fights recorded, one was brief (3.5 minutes) and consisted only of the physical fight. This occurred when one male landed at the display site of another male. One fight followed a period of threat (totally 15 minutes). Three fights were after a combination of threats and aerial chases and lasted seven, 21 and 30 minutes. Though the average duration of encounters that resulted in fights was 15.3 minutes (± 10.69 min.; range 3.5 to 30 min., n = 5), the period of actual physical contact was brief and lasted only between one and four minutes. The average duration of 6 encounters which resulted only in aerial chases was 14 minutes (± 16.13 min., range 1 to 45 min., n = 6). Most encounters resulted in a combination of threat and aerial chases and the average duration of such encounters was 19.54 minutes (± 25.17 min., range 3 to 99 min., n = 18). The values for all encounters with aerial chases are only for that period when the birds were visible, because sometimes the birds flew out of sight and did not return to the territory.

Out of the 35 agonistic interactions seen, 24 (68.57%) were between two males, 10 (28.57%) were between three males, and one (2.80%) was between four males. Of the five encounters that developed into physical fights, four were between two males and one was between three males.

Description of Agonistic Behaviour

The agonistic behaviour of the Bengal Florican can be differentiated into threat displays, aerial chases and physical fights. Though this behaviour has been described in detail (Narayan and Rosalind 1988, Narayan 1990), a description is made here based on observations made during this study.

Threat Displays

This agonistic behaviour is performed on the ground. When an intruding male (or males) enters the territory of another male, a period of threat follows. The occupant male may chase the intruder on the ground, or if the intruder is aggressive, walk abreast of it. During threat, the males cock their tails, slightly raise their mantle feathers and may partly fluff out their neck feathers. The latter two are not displayed in all encounters. The degree of intensity of the first varies, with greater aggression apparently resulting in a more cocked tail. During threat, the males constantly vocalize with varying volume. This call, 'chik', is emitted every few seconds, and is delivered with an opened beak and an abrupt forward thrust of the head. Generally the intruding male flies off after a period of threat.

If more than one male intrudes, the occupant male chases or threatens whichever male is closest to it. In one instance, two males entered the territory of a third male which threatened and chased both males in turn. However, it seemed that the two intruding males were more intent on chasing and threatening each other, with one of them being more aggressive. The two flew off shortly.

Aerial chase

Most agonistic interactions of the Bengal Florican also include an aerial chase. An aerial chase involves one male flying behind another, and usually occurs whenever a male flies into the grassland or within sight of the territorial male. Or, an aerial chase ensues after the territorial male has threatened an intruding male into flight. Both may also occur alternately for a while, with periods of threat on the ground followed by brief aerial chases. During an aerial chase, the males also call 'chik' every few seconds, though one or both males may stop calling during prolonged aerial chases.

While some aerial chases end once the territorial male has 'escorted' the intruding male outside the confines of the territory or grassland, some carry on beyond the territorial boundaries. Though aerial chases are usually done only over grasslands, some may carry on over dense forest. Such chases are prolonged and can even last upto 100 minutes. For instance, in one aerial chase both males had flown so far off that they were not visible through a telescope.

Often an aerial chase that begins at one territory is carried on to another territory. The occupant male of that territory may join in and so on. During this study period a maximum of four males were seen chasing each other.

Sometimes during an aerial chase, especially while landing, one male may attempt striking the other in the air.

Fights

Rarely do agonistic interactions develop into physical fights and when they do, the actual fight itself is brief. After aerial chase and threat displays have occurred, males may attack each other. The first contact is usually in the air as males leap at each other. Some pushing and pecking is seen, but beating the opponent with the wings appears to be the main tactic during offense. This beating of wings can be vicious, and in one such fight the wing beating could be heard from nearly 400 metres away. Males repeatedly break away and again rush or jump at each other. For instance, in one fight that lasted three minutes, the males attacked each other seven times, five times within the space of one minute. Fights ended when one male was either beaten or pushed off balance. The loser usually flies away, sometimes followed by the winner. In the above instance, the fight was apparently not decisive. At dusk one male flew off and roosted about 100 metres away. At dawn, the other male flew to where it had landed, and both males fought again. The loser then flew away from the grassland itself.

Of its own volition, a male would leave its territory, fly to another male's territory and fight and/or threaten that male before returning. Some such interactions were initiated by the male under observation, while some were by other males who had presumably left their territory to intrude into the focal male's territory. The presence of a floating or non-territorial male greatly increases the frequency of agonistic interactions. For instance, in about twelve hours of observation over two days when one such male tried establishing a territory at Navalkhad, the resident male spent about two hours and 15 minutes in threatening and chasing the intruding male. This period also had a number of interactions at the territories of other males under observation, as during aerial chases, these males would often enter the territories of other males.

Distribution of Agonistic Interaction

Distribution of agonistic interactions in the Bengal Florican have been plotted in Figure 3.12. Agonistic interactions show an initial peak in the first week of arrival when males are as yet mobile and not restricted to their territories. Following this, the subsequent few weeks do not have a high frequency of interactions. By the middle of the season frequency of interactions peaks and is more or less evenly distributed until the very end of the season. This is largely due to a greater frequency of movement of males between territories, which results in aerial chases and/or fights. To see if there was any statistical difference in the distribution of agonistic interactions the season was divided into three equal parts (Table 3.5). No difference was seen in the frequency of agonistic interaction in any part of the breeding season.

FIG. 3.12. BENGAL FLORICAN
DISTRIBUTION OF AGONISTIC INTERACTIONS
IN THE BREEDING SEASON

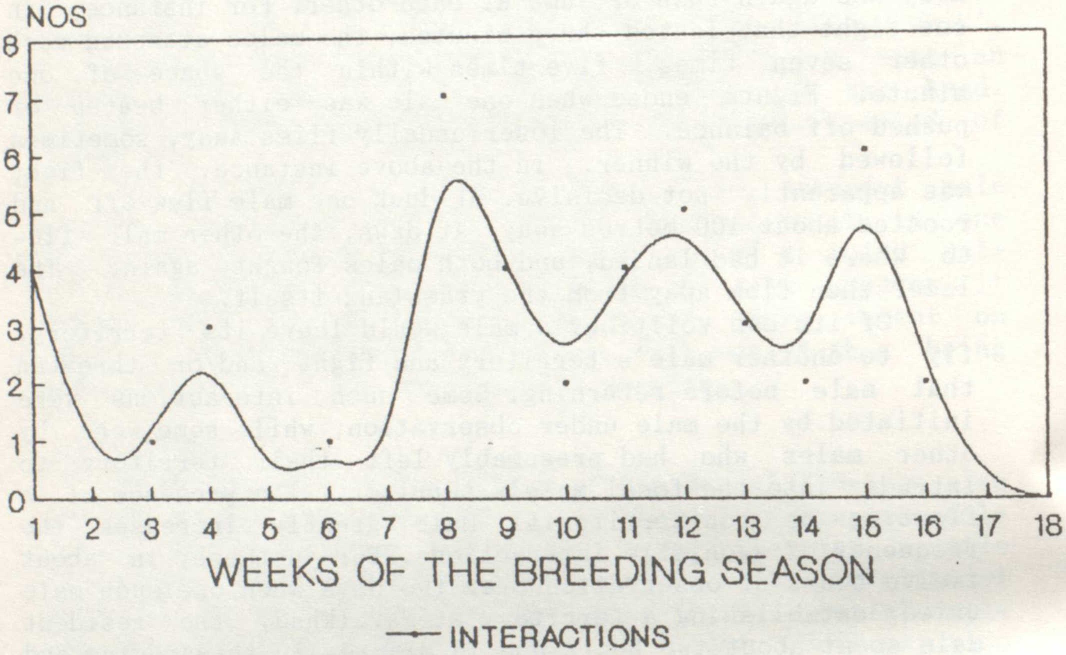


TABLE 3.5
BENGAL FLORICAN
SEASONAL DISTRIBUTION OF AGONISTIC INTERACTIONS
Kolmogorov-Smirnov Two Sample Test

	SECOND		THIRD	
	MD	P	MD	P
FIRST	0.500	0.333	0.167	1.000
SECOND			0.333	0.778

* NB Breeding season divided into three equal parts.

Non-Agonistic Interactions

While most interactions between males are agonistic, a few are not. On one occasion, a male flew over the territories of two males at Seethagaddaia without eliciting an aerial chase from the occupant males.

The other instances occurred over a five day period in the first week of March 1989. This interaction was both unusual and difficult to explain. At the Chapra grassland a male had just established its territory and had begun displaying sporadically. This male, called 'black male', was almost in the complete breeding plumage, though some buff patches were present on the head and neck. On third March, at 1741 hours a male flew into the territory of the black male. This male, called the 'buff male', was easily differentiated from the occupant by being larger and having considerably more buff on the head and neck. The black male immediately threatened the buff male, which reciprocated the displays. By 1754 hrs they were about two to four metres apart and had stopped threat displays. Over the next 10 minutes they threatened each other sporadically. These threats were only partial and mainly the 'chik' call was made. Mostly, their backs were to each other and at 1820 hours the black male roosted, followed by the buff male at 1823 hours. They were only two or three metres apart.

Until the morning of seventh March, these males were together in the Chapra grassland. They either sunned themselves in close proximity to each other, or foraged within five or 10 metres of each other, without showing undue aggression. Occasional mild aggression by the black male was seen, with the buff male invariably moving away a few metres from the aggressor. However, these instances were sporadic and brief, and soon after both males would again resume activities with apparent indifference to the presence of the other. During this period, the black male performed the flight display at least twice; displaying an increased level of aggression towards the buff male immediately after.

By the ninth of March, the buff male had left Chapra and only the black male remained. On the eleventh of March, the buff male was seen in the Kowhaghatti grassland where it later established its territory.

DISCUSSION

The observations on the territorial behaviour of the Lesser Florican and the Bengal Florican show two major differences. The existence of site fidelity in the Bengal Florican and its the absence in the Lesser Florican raise the question as to why this is so. Secondly, distribution of agonistic interactions over the breeding season of the two species varies, with the Lesser Florican having most of the interactions in the early part of the season, while in the Bengal Florican it is more or less well distributed throughout the breeding season. In this section mainly these two aspects are discussed, and for convenience both species are dealt with together.

Site Fidelity

Fidelity to breeding area, territory, nesting site, or lek has been documented in a number of studies over a wide spectrum of avian taxa (Hilden 1965, Kruijt and Hogan 1967, Lack 1968, Graul 1973, Lenington and Mace 1975, Wittenberger 1978, Harvey et al. 1979, Ferguson 1981, Avery and Sherwood 1982, Cairns 1982, Greenwood and Harvey 1982, Oring 1982, de Vos 1983, Dunn and Braun 1985, Lanyon and Thompson 1986, Parmelee and Pietz 1987, Atwood and Massey 1988, Haig and Oring 1988). Among promiscuous species, where males display either from leks or dispersed leks, fidelity to site or breeding area is common. This is also true for some species of bustards, with males returning to traditional display sites and females returning to sites where they had successfully nested the previous year (Great Bustard, Cramp and Simmons 1980; Little Bustard, Shulz 1985; Bengal Florican, Narayan and Rosalind 1990; Great Indian Bustard, Rahmani 1989).

Explanations for the existence of site tenacity include knowledge of terrain, food sources and ease in locating predators. Lack (1968) suggested that traditional display sites are used by males because they have proven safe from predators. However, Wittenberger (1978) argued that the location of traditional sites can just as easily be learnt by predators. Gullion and Marshall (1968) found that male Ruffed Grouse having perennial drumming logs have a lower life expectancy than those displaying from transient sites. However, in the Blue Grouse males occupying traditional sites had a longer life expectancy, with a greater mating success than males occupying transient sites (Lewis and Zwickel 1981). Wittenberger (1978) provided an alternate explanation in that females can more safely approach and mate at traditional sites even though their longevity is reduced. He concludes that "The use of traditional sites should evolve whenever the propensity for females to mate at familiar sites offsets any reduction in male life expectancy". The knowledge, however, of traditional sites must have followed the initial occurrences of males returning to their old display sites, as any such knowledge must be through a process of learning. The propensity for females to mate at traditional sites, superior food or nest site location abilities or better predator avoidance will be advantages that follow the establishment of territory, breeding area or lek fidelity.

The emphasis of current research has been on the effect of more readily quantifiable characters (e.g. quality of territory or reproductive success) on breeding dispersal. Stability in the breeding environment has been dealt with only briefly in most previous studies (e.g. McNicholl 1975, Morse 1980, Haig and Oring 1988). Based on studies on gulls and terns, McNicholl (1975) argued that nest site tenacity is strongly developed in stable habitats and that it is much reduced in unstable ones. Only a species with low nest site tenacity could colonize unstable areas such as marshes (Morse 1980).

Other, more basic, conditions must be met before fidelity to areas can form. Using the Lesser Florican, Bengal Florican and the Great Indian Bustard as examples, it is argued that stability or instability in a species' breeding environment between years is the basic factor which results in fidelity or the lack of it to the breeding area or site.

In this section, breeding area fidelity is defined as a propensity for individuals to return to the previous year's breeding area. The old territory or display sites need not be used, but an individual can establish territory in an adjacent or nearby site. Site fidelity is defined as, when an individual reoccupies its old territory in subsequent years. Traditional sites are those location that are used as territories by successive males over a number of years. Hence, site fidelity is a more extreme form of breeding area fidelity. 'No site fidelity' is when individuals do not return to previous years breeding area or sites.

As a response to strong inter-year variation in the breeding environment (due to a varying south west monsoon), the Lesser Florican has a nomadic breeding strategy, in which individuals seek out areas of adequate rainfall. Hence considerable fluctuations are seen in the number of breeding individuals in an area between years (see Chapter 2). Based on his data Dharmakumarsinhji (1950) concluded that "(Lesser) Floricans are not particular about returning to the same area for breeding in which they did the previous year, though we have had some such recoveries". A recapture rate of only 1.2% at old breeding sites does not indicate any site or area fidelity.

The Bengal Florican, on the other hand, appears to show both breeding area and site fidelity. Barring a few exceptions, most territories were re-occupied by males in subsequent years. Due to an absence of colour marked individuals, site fidelity could not be conclusively established. However, circumstantial evidence indicates that fidelity to site or area exists. This was evidenced by the behaviour of the Kowhaghatti male which re-established its territory in spite of the habitat being altered. Hilden (1965) suggested that old birds that have learnt site tenacity tolerate more disturbance in their breeding places without abandoning them. The return to the former territory, in spite of a deterioration of the habitat, indicates that site tenacity represents a return to a geographical locality which has become familiar and not towards a certain type of environment. There were no significant variations in the total number of territories seen at Dudwa National Park and this was also true for the population in Manas Wildlife Sanctuary (Narayan 1990).

At least three populations of the Great Indian Bustard show site and breeding area fidelity (pers. obs., Rahmani 1989). These are the central Indian, south central and the southern Indian populations. The western Indian population that inhabits the Thar desert is as yet unstudied. It is highly probable that this population has a nomadic strategy as a response to fluctuating and erratic rainfall. In the central Indian population, one colour marked individual re-occupied its old territory for three successive years. The same location continues to be used as a territory (for 8 consecutive years) despite an overall deterioration in the habitat (in terms of disturbance) and a disappearance of most of the females after a hailstorm in 1986 (pers. obs.). This site fidelity and the use of traditional display sites was also evidenced at both the south central Indian and south Indian populations where particular sites have been used as display sites for a number of years now (Manakadan and Rahmani 1986).

Why then do some species, or populations of some species, show site or breeding area fidelity while others do not? This can be explained, in part, by considering the behavioural responses to varying levels of stability in environmental conditions by the Lesser Florican, the Bengal Florican and the Great Indian Bustard.

As a response to the strong inter-year variation in the breeding environment (due to a varying south west monsoon), the Lesser Florican has a nomadic breeding strategy. That is, individuals follow existing rainfall cues to arrive at suitable breeding environments (see also Chapter 2). In this species site fidelity is absent, because the probability of finding optimal breeding conditions in the previous year's breeding area is lower than the probability of conditions being sub-optimal there. Hence a better strategy would be to seek out a geographical condition, that is seek out an area of good rainfall rather than returning to a fixed geographical location.

In the Bengal Florican, which breeds during the summer, grass growth is initiated by annual fires. These annual fires have occurred for at least the last 100 years and are more or less regularly timed, that is between late January and early March. Subsequent grass growth is determined by environmental conditions that are far more stable than rainfall, these being ground water, dew and humidity (see also Chapter 2). Thus there is little inter-year variability in the breeding environment, which results in insignificant fluctuations in the number of territorial males. As a result, Bengal Floricans can return to a fixed geographical location, as the probability of suitable breeding habitat being present there every year is much greater than the probability of conditions being unsuitable at that location. Depending on the manner of burning and the wetness of the area, the fidelity responses shown by two different populations differ. Dudwa is relatively drier than grasslands of Assam, and as a result, a fire burns most of a grassland in a single day. Hence there is little or no changes in the availability and location of suitable breeding habitat for the floricans between years. In Assam, however, it is far wetter and burning occurs only in patches (Deb Roy 1986, Narayan and Rosalind 1988). Hence suitable breeding sites are available at differing locations within the breeding area. At Dudwa, males can return to their old sites simply because these sites will provide optimal conditions. Whereas at Manas (in Assam), barring those sites which are cleared of vegetation every year, fluctuations are seen within the grassland as to where the locations of territories are in subsequent years (Narayan and Rosalind 1988, Narayan 1990). At Dudwa the existence of traditional sites is a result of very stable breeding habitat, whereas at Manas, site fidelity is seen for those locations which do not vary between years, and breeding area fidelity is seen for those areas where locations of suitable breeding habitat varies within the grassland. Hence Bengal Florican individuals will return to their previous year's breeding area or site as under conditions of low inter-annual variability of the breeding environment this is the best stratagem. In this species breeding area fidelity should not only be present, but the urge to re-occupy the previous years breeding territory should also be high.

In the three populations of the Great Indian Bustard that have been studied (Ali and Rahmani 1984, Manakadan and Rahmani 1986, Rahmani 1989), one population is resident within the breeding area, while the other two are nomadic in the non-breeding season. All three populations show site fidelity and use traditional display sites. The central Indian population is a summer breeder, and thus there is only marginal variation in the breeding environment between years. Both the south central and south Indian populations are monsoon breeders and both show site fidelity. In this species, males apparently establish territories irrespective of environmental conditions during the breeding season. For example, in the South Central Indian population, even though 1982 was a drought year the territorial male displayed from the traditional site throughout the breeding season (Ali and Rahmani 1984). In the South Indian population, males establish territories twice a year, for a prolonged period during the south west monsoon, and a shorter period during the summer. Site fidelity in the Great Indian Bustard is most likely due to an ability to tolerate far greater variations in environmental conditions in the south and south central Indian populations, while under extreme arid conditions nomadism must be the favoured stratagem.

Site fidelity was shown for one population of the Little Bustard, which was resident throughout the year near the breeding locations. Males not only returned to their old sites but contested fiercely to repossess the previous year's territories (Shulz 1985). In this area also, inter-year variation in the breeding environment was low.

To summarise this section, the existing hypotheses on causative factors of site fidelity include greater mating success, better knowledge of food sources, location of predators and terrain. These hypotheses, however, deal with advantages that accrue as a result of site fidelity, and do not point out the basic conditions that must be fulfilled before the initiation of area or site fidelity and the use of traditional sites.

The Lesser Florican, the Bengal Florican and the Great Indian Bustard are used as examples to highlight the hypothesis that degree of inter-annual variation in the breeding environment determines the existence or absence of site fidelity. For breeding area fidelity, there must be insignificant variations in the overall environment of the breeding area between years. In areas where conditions are even more stable, site fidelity to the previous year's territories will come about and develop into the use of traditional sites. Hence breeding area and site fidelity will occur under those conditions when the probability of finding suitable breeding conditions in the previous year's site or area is much greater than the probability of it not being so. Absence of fidelity to area or site is a result of strong inter-annual variations in the breeding environment. Hence the probability of finding optimal or suitable breeding conditions in the previous year's breeding area is lower than the probability of it not being so. The best stratagem then is to follow environmental conditions rather than returning to a geographical location, and this results in an absence of both site and breeding area fidelity.

Distribution of Agonistic Interaction

Another major difference seen in the territorial behaviour of the Lesser Florican and Bengal Florican is in the distribution of agonistic interactions. In the Lesser Florican most such interactions are clustered in the early part of the breeding season, and tapers down by the time all territories have been established. In the Bengal Florican, agonistic interactions, occur more or less throughout the breeding season. In this section an attempt is made to find plausible explanations for these differences.

Aggressive behaviour appears to be an important element of initial territory establishment in many birds (e.g. Young 1956, Mundahl 1982, Shulz 1985). In the Lesser Florican, males arrive in the breeding area singly (see Chapter 2). Arrival is followed by a period of wandering before territories are established. Agonistic interactions are mainly seen during this period when males frequently come in contact with other males. Interactions also occur during early territorial periods, when recent arrivals that have still not established territories intrude into established territories. Once all males have established territories, agonistic interactions cease (this pattern is similar for the Little Bustard as well, Shulz 1985).

Wittenberger (1978) suggested that the use of traditional display sites should evolve whenever the propensity for females to mate at familiar sites offsets any reduction in male life expectancy. Conversely, the lack of site fidelity and therefore the absence of traditional display sites will result in females mating with 'attractive' males rather than those that have occupied specific locations. If this is true, then it could explain why agonistic interactions are clustered in the early territorial period of the Lesser Florican.

It has already been shown that site and breeding area fidelity and traditional display sites are absent in the Lesser Florican. First arrivals apparently settle at prime locations and other males arrange themselves in adjacent or nearby locations. Once established, males appear to effectively repulse any intrusions into their territories. Moreover, the habitat in the study area was more or less homogeneous, and possible display sites always exceeded the number of displaying males. If females are not particular about mating with males at specific locations, as an absence of traditional display sites would indicate, then males should attempt to establish their own territories rather than attempt taking over an established territory. They would then increase their mating chances by advertising themselves, as females would be seeking attractive males rather than specific locations. This would further result in an absence of an adult male 'floating' population, the absence of which was also observed during this study. All these factors would contribute to swift establishment of territories, with agonistic interactions being clustered in the pre- and early territorial phases.

The distribution of agonistic interactions in the Bengal Florican has a different pattern, occurring throughout the breeding season. The pre-territorial period is short, and most males occupy territories within the first ten days or so of the commencement of the breeding season. This pattern of distribution of agonistic interaction can be explained by two phenomena, namely hierarchy and floating population of males. It is likely that in this case both of these result due to site fidelity and traditional display sites.

Hierarchial social orders have been documented for a number of species. This is especially true among birds where quality and/or location of territory plays a strong role in mating success (e.g. Davies 1978, Gibson and Bradbury 1986, Avery and Ridley 1988). This should result in a constant jostling for better positions in the hierarchy, as males attempt to improve their spatial position. Thus, constant agonistic interactions would be expected. Such a system could also explain why males leave their territories and fly to another territory apparently only to fight.

The other explanation, that could function either in tandem with or alternative to the above is the presence of 'floating' males. Floating males can be defined as males who though capable of breeding or holding territories, do not do so for some reason. Floating males need not necessarily be inferior to territory owners (e.g. Eckert and Weatherhead 1987). Floaters have been documented in a number of studies (Jenkins <u>et</u> <u>al</u>. 1967, Zwickel and Bendell 1967, Ellison 1971, Rippin and Boag 1974, Gullion 1981, Hunter 1987, Smith and Arcese 1989). In the Bengal Florican evidence was obtained of a floating population of adult males in addition to non-territorial young males. Floaters frequently intruded into territories of established males. For instance, in 1988, one such male frequently intruded into the Navalkhad territory, which resulted in chases, threats and fights.

Whenever there is a propensity for females to mate at traditional sites, then males unsuccessful in occupying such locations could either occupy transient territories or exist as floaters. Gullion (1981) speculated that in the Ruffed Grouse, floaters may prefer to await their turn to occupy an activity centre rather than use a poorer quality habitat. The existence of a floating population would also result in the occurrence of agonistic interactions throughout the breeding season.

Both the suggestions are as yet mere speculation and a long term study is required before definite conclusions can be drawn.

Chapter 4
COURTSHIP BEHAVIOUR

INTRODUCTION

Courtship displays in the bustard group are as spectacular as they are diverse, and can be broadly classified into four categories (Osborne _et al_. 1984). The 'balloon' type display is seen amongst the heaviest members of this group and is the prevalent form of display in the genera _Ardeotis_, _Neotis_ and _Otis_ (Mattingley 1929, Cramp and Simmons 1980, Osborne _et al_. 1984, Hellmich 1988, Rahmani 1989). The second type is the running type of display which is seen in the Houbara bustard (Mendelssohn _et al_. 1979). The last two categories are both aerial displays and are performed by the smaller members of the bustard group. One of these is a display leap or jump as is seen in the Little Bustard and the Lesser Florican (Shulz 1985, Ridley _et al_. 1985, Dharmakumarsinhji 1950). The other is an aerial display flight and is seen in small African bustards such as the Black Bellied, Buff Crested and Black bustards (Osborne _et al_. 1984) and in the Bengal Florican (Narayan and Rosalind 1988).

Considerable literature is available on the general behaviour of the Lesser Florican and Bengal Florican as they were popular game birds. While descriptions of courtship displays of the Lesser Florican are reasonably accurate (Jerdon 1864, Baker 1921, Dharmakumarsinhji 1950), those of the Bengal Florican are inaccurate (e.g. Baker 1921, Hume and Marshall 1879, Ali and Ripley 1969). It was not until 1988 that an accurate and detailed description of the Bengal Florican's flight display was published (Narayan and Rosalind 1988). A detailed study on some aspects of the display leap of the Lesser Florican is also available (Ridley _et al_. 1985).

In this chapter the base line information required to compare these closely related species is given. The displays of both species is described and analysed. In the discussion, the species are dealt with individually and only those aspects relevant to each are covered.

The displays related to breeding of the Lesser Florican have been differentiated into attraction display and courtship display (Dharmakumarsinhji 1950). This justifiable division is retained in this account for both species. The displays are categorized according to the source of stimulation. Attraction displays are aerial displays performed irrespective of the presence or absence of females or rival males. The courtship display on the other hand is performed only in the presence of females and directed towards them.

RESULTS

LESSER FLORICAN

Description of the Attraction Display

The attraction display of the Lesser Florican is an aerial one, taking the form of a 'vertical' display leap. It is performed almost throughout the day, and depending on the height of the grass (see below) and the period of the breeding season, either at fixed locations or at randomly chosen sites or from wherever the bird may be. At the peak of the breeding season, a male Lesser Florican may perform its aerial display well over 500 times in a single day.

The first indication of arousal is evidenced by the bird standing, with its neck and head craned up. The white feathers of the throat and chin are erected and appear in some large males as a sort of white 'bib'. The neck feathers may be slightly fluffed up but this is not always discernible as these feathers are not unusually elongated. The bird while standing thus shuffles or stamps its feet. When completely aroused it faces the wind, abruptly retracts its head, crouches and leaps into the air by flexing its legs. Take off is followed by about 10 or more very rapid wing beats, which enables the male to reach a height of about 1.5 - 2 m, vertically above the spot of take off. The height of the display leap is apparently determined by the height of the surrounding vegetation. During the ascent, the head is arched back, the neck feathers are slightly fluffed, and the auricular plumes are partly thrown forward. On reaching the peak of the ascent in this manner, the male drops back to the ground. Its wings are held partly closed and kept away from the body, thus acting as a sort of parachute to reduce the impact of landing. The legs are usually paddled a few times for balance. The bird crouches on landing, and then gradually raises itself up until fully erect, scanning the grassland around itself before performing the next display leap.

Each display jump lasts on average 1 second (min. = 0.8 s, max. = 1.1 s). During the peak of the breeding season, a male Lesser Florican may spend 70 - 80 % of the daylight hours in performing the aerial display and related display activities. On average, inter display leap duration is 40.23 seconds (SD = 40.06 s, max. = 613 s, min. = 4 s, n = 2396). Time lag between displays varies to some extent depending on the degree of spot specificity and the weather conditions (see below). The period in between display leaps is spent either in walking or foraging or standing and looking around.

All display leaps are performed facing the wind, so much so that a male on being aroused will pivot around and display into the wind. This appears to have some sort of aerodynamic function. On those few occasions when the male did display at an angle to the wind it was invariably pushed off balance.

Auditory signals of the Display Leap

The display jump is accompanied by a loud rattling or clapping auditory signal. This sound lasts about 0.4 to 0.5 seconds and is produced only during the ascent of the display flight. The sound consists of 7 or 8 individual sounds all similar in pitch and intensity (evidenced from sonography; not presented here). This auditory signal of the display leap is made by the wings and is not a vocalization or produced by the clicking of the tongue as has been suggested by others (Dharmakumarsinhji 1950, Osborne *et al*. 1984, Ridley *et al*. 1985). To produce this sound, the wings of the males have specialized pointed primaries which are not present in the female (Table 4.1). The exact mechanism by which this auditory signal is produced from the pointed primaries is not known. (The pointed primaries are also present in the wings of the non-breeding males and sub-adult males. Their presence differentiates without doubt males in the non-breeding plumage from females).

During the period just prior to the peak of the breeding season, when males fly into their territories, they often land in the typical display flight pattern, i.e. with arched neck and head. Similarly, when flushed, the males often take to flight as in the display leap, even producing the auditory signal before easing into regular flight.

Display Patterns

Changes in display patterns are perhaps best quantified by the nature of display leaps performed. Display leaps by the Lesser Florican are performed along two patterns. Spot specific display (SSD) is when birds display continuously from a single spot without moving between jumps. Non-spot specific display (NSS) is when the bird moves between jumps and when consecutive jumps are not performed from the same spot.

The breeding season of the Lesser Florican can be broadly classified into two phases, namely pre-territorial and territorial periods. The territorial period can be further classified into early, peak and end territorial periods.

Figure 4.1 shows the changing activity patterns of the Lesser Florican at Sailana. After arrival and until the establishment of territories (i.e. pre-territorial period), the males are not site specific and spend most of the day foraging. Occasionally males may display, but this is an inconsistent activity, and usually occurs in the form of sporadic bursts of display leaps. However, towards the end of the pre-territorial period, such display becomes consistent and some degree of site specificity is also seen.

TABLE 4.1
INFORMATION ON PRIMARY FEATHERS OF THE LESSER FLORICAN

Male			Female		
Wing length = 195 mm 11 primaries; overall narrow & pointed. First primary normal; Eleventh primary minute; Outer primaries narrower than inner primaries.			Wing length = 233 mm 11 primaries; overall slightly narrow. Primaries 1 to 5 normal Primary 6 slightly narrowed; 7 to 10 distinctly tapered; Outer primaries narrower than inner.		
Prim. Nos.	Length (mm) of Notched Part	Width (mm)of Notched Part (at middle)	Prim. Nos.	Length (mm) of Notched Part	Width (mm)of Notched Part (at middle)
1	normal	-	1	normal	-
*2	46.0	8.3	2	normal	-
3	45.5	7.7	3	normal	-
4	51.1	7.7	4	normal	-
5	62.7	7.2	5	normal	-
6	56.7	6.7	*6	45.5	12.5
7	55.5	4.4	7	50.5	10.0
8	54.4	4.4	8	45.5	9.5
9	52.8	3.8	9	52.2	7.5
10	51.0	2.9	10	53.3	5.5
11	minute	-	11	minute	-

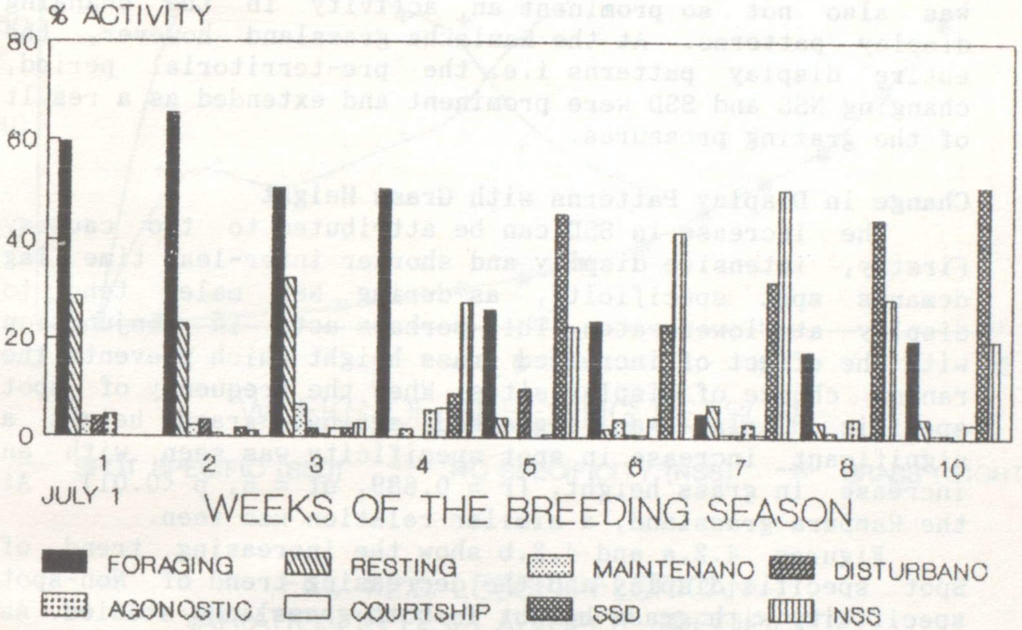
* Notch not distinctive
(Data from one skin each of male and female from the BNHS collection. For description of the pointed primaries in males see Jerdon 1864, Baker 1921, Ali and Ripley 1969).

The territorial period occupies most of the Lesser Florican's breeding season. In 1985, male floricans were present in the grassland for 71 days, of which they were recorded displaying for 42 days (59.15%). In 1986, display was seen on 66 of 101 days (66.3%).

Initially, after the establishment of territories the major diurnal activity is 'Non-spot specific display'. The males spend most of their time foraging, constantly interrupting their foraging with display leaps. 'Spot specific display' is relatively low during this period (Fig 4.1). As the season progresses, NSS becomes less and SSD soon becomes the major diurnal activity.

Throughout the early and peak territorial periods, male Lesser Floricans display throughout the day, but more so in the mornings and evenings. This is especially true during cloudy days, when males display with very brief breaks throughout the day. Towards the end of the breeding season,

FIG. 4.1. LESSER FLORICAN
CHANGES IN ACTIVITY PATTERNS
AT THE SAILANA KHARMOR SANCTUARY



SSD - SPOT SPECIFIC DISPLAY
NSS - NON SPOT SPECIFIC DISPLAY
(SEE TEXT)

due to an increase in day temperatures and a waning of display intensities, males display almost exclusively in the mornings or evenings. However, even during the waning of the breeding season males tend to display for brief periods in the afternoon. In all years display stopped by the first week of October.

This pattern varied between grassland sites, and between years, due to the effects of varying rainfall and grazing pressures. For instance, at the ungrazed Rampura grassland, the pre-territorial period was brief and the NSS was also not so prominent an activity in the changing display patterns. At the Naulakha grassland however, the entire display patterns i.e. the pre-territorial period, changing NSS and SSD were prominent and extended as a result of the grazing pressures.

Change in Display Patterns with Grass Height

The increase in SSD can be attributed to two causes. Firstly, intensive display and shorter inter-leap time lag demands spot specificity, as during NSS males tend to display at lower rates. This perhaps acts in conjunction with the effect of increased grass height which prevents the random choice of display sites. When the frequency of spot specific display was regressed against grass height a significant increase in spot specificity was seen with an increase in grass height, ($r = 0.889$, $df = 6$, $p < 0.01$). At the Rampura grassland, a similar relation was seen.

Figures 4.2.a and 4.2.b show the increasing trend of Spot specific display and the decreasing trend of Non-spot specificity with grass height in both grasslands studied. As the study at Rampura started later in the season, early display specificity patterns could not be ascertained there. Percentage of spot specificity in relation to non-specific display was higher at Rampura than at Naulakha for the same time scale. This was probably due to the longer grass at Rampura than at Naulakha (see also Chapter 2).

When rainfall is below normal, less dense vegetation may result in greater time spent in non-spot specific jumping than spot specificity. Similarly, those males which display from or close to the edge of crop fields are less prone to be spot specific and tend to display from various locations within their territories.

Time lags between two consecutive jumps were measured and their differences were tested. Time lags between consecutive jumps was significantly shorter when males displayed from a specific spot than when displaying from different spots (T-Test $t = -7.100$, $p < 0.0001$; mean SSD = 36.20 secs. SD= 28.63; mean NSS = 58.13, SD = 62.62).

Jumping Spots

Depending on the grass height and the time of

FIG. 4.2.A LESSER FLORICAN
VARIATION IN DISPLAY SPOT SPECIFICITY
WITH GRASS HEIGHT (NAULAKHA 1985 & 1986)

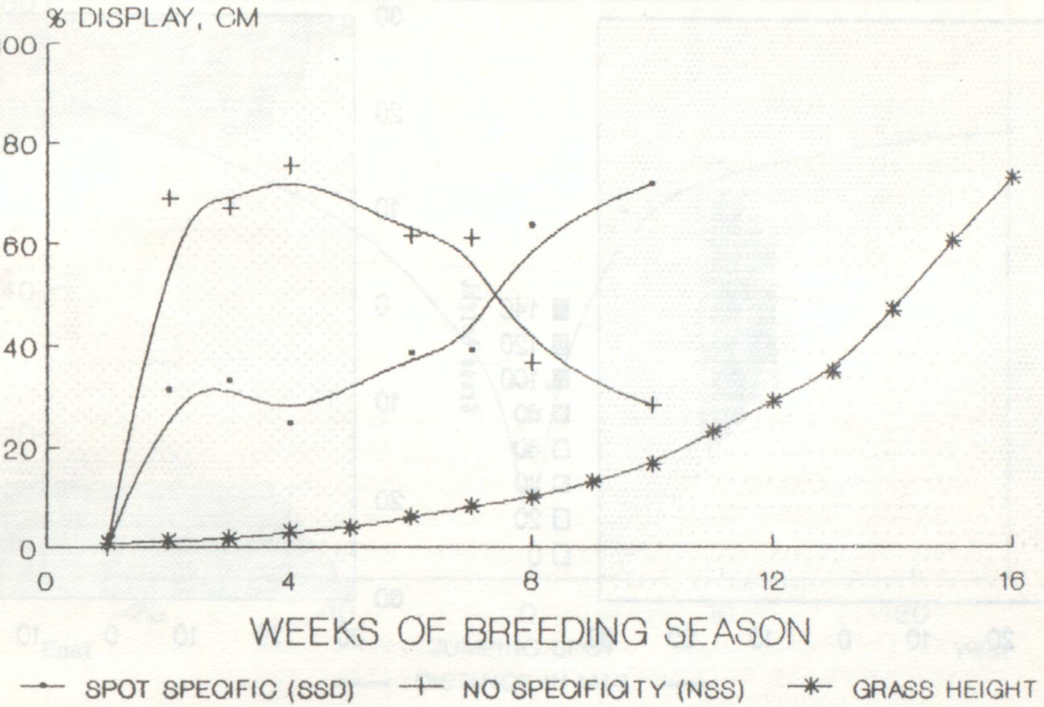


FIG. 4.2.b. LESSER FLORICAN
VARIATION IN DISPLAY SPOT SPECIFICITY
WITH GRASS HEIGHT - RAMPURA 1988

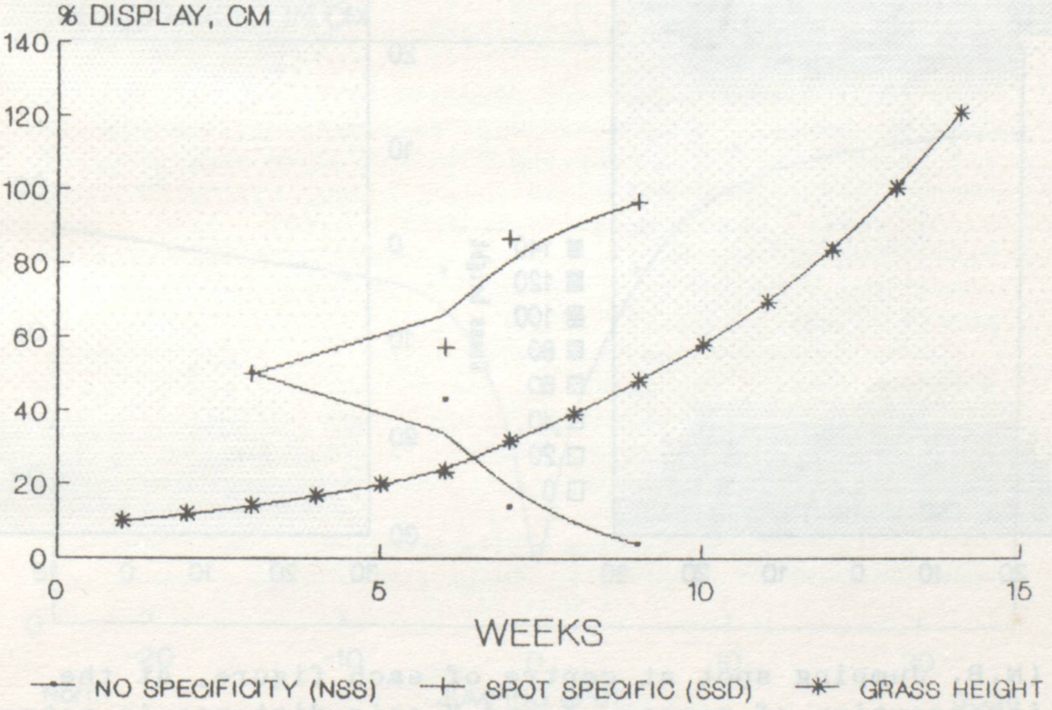
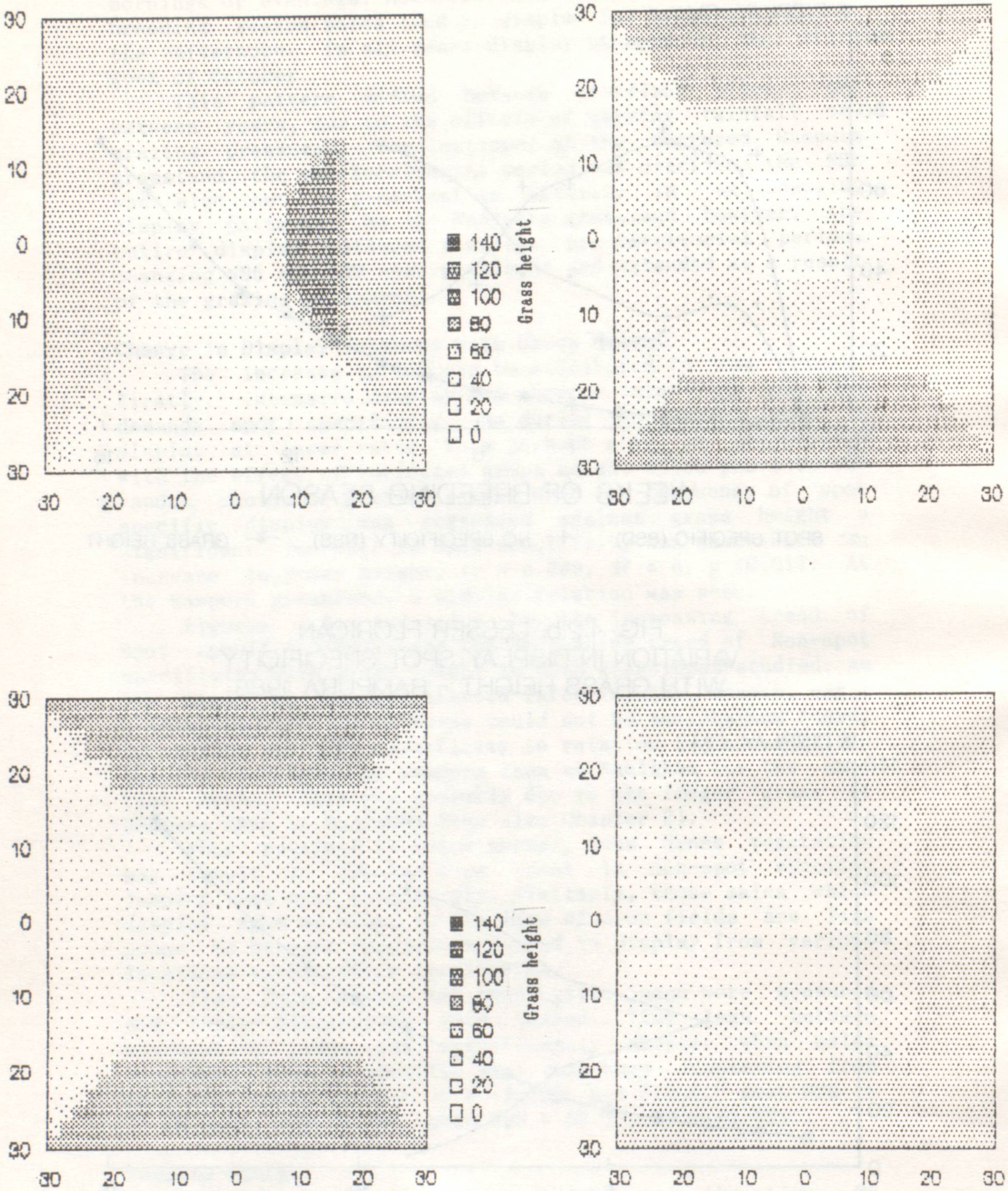


FIG. 4.3. GRASS HEIGHT CONTOURS OF FOUR MALE LESSER FLORICAN JUMPING SPOTS AT THE RAMPURA GRASSLAND - AUGUST 1988



(N.B. Jumping spot at centre of each figure, at the intersection of zeroes. X and Y axis distance in metres from jumping spot).

FIG. 4.4.a. LESSER FLORICAN
GRASS HEIGHT AT JUMPING SPOTS

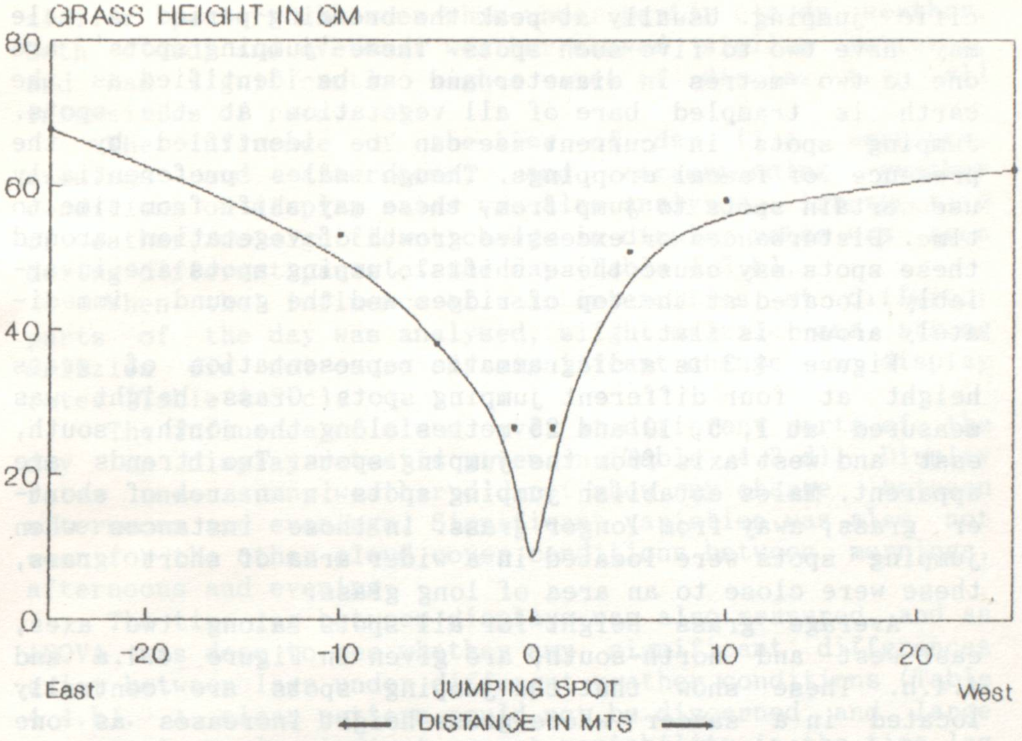
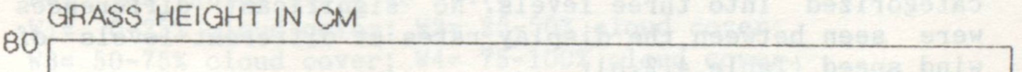


FIG. 4.4.b. LESSER FLORICAN
GRASS HEIGHT AT JUMPING SPOTS



establishment of territories, males increasingly begin using a few selected locations from which they perform spot specific jumping. Usually at peak the breeding period a male may have two to five such spots. These 'jumping spots' are one to two metres in diameter and can be identified as the earth is trampled bare of all vegetation at the spots. Jumping spots in current use can be identified by the presence of faecal droppings. Though males preferentially use certain spots to jump from, these may shift from time to time. Disturbances or excessive growth of vegetation around these spots may cause these shifts. Jumping spots are invariably located at the top of ridges and the ground immediately around is flat.

Figure 4.3 is a diagrammatic representation of grass height at four different jumping spots. Grass height was measured at 1, 5, 10 and 25 metres along the north, south, east and west axis from the jumping spots. Two trends are apparent. Males establish jumping spots in an area of shorter grass, away from longer grass. In those instances when jumping spots were located in a wider area of short grass, these were close to an area of long grass.

Average grass height for all spots along two axes, east-west and north-south, are given in Figure 4.4.a and 4.4.b. These show that the jumping spots are centrally located in a 'saucer' where grass height increases as one moves away from the centre towards the periphery.

Influence of Weather on Display Rates

The display rate (displays per minute), was measured in different weather conditions.

The influence of different wind speeds on display rates are given in Table 4.2.b. Wind speeds were tentatively categorized into three levels. No significant differences were seen between the display rates at different levels of wind speed (Table 4.2.b).

Cloud cover, however, caused significant changes in display rates. Cloud cover was qualitatively categorized into four levels; sunny having 0 to 25% cloud cover, partly cloudy having 25 to 50% cloud cover, cloudy having 50 to 75% cloud cover and overcast having 75 to 100% cloud cover. Male display was at its highest under cloudy or overcast conditions. Lower rates of display were seen under sunny or partly cloudy conditions (Table 4.2.c).

Rainy conditions were categorized into light drizzle, strong drizzle and rain. Of the three conditions, males displayed at highest rates during light drizzles, while strong drizzles and rainy weather caused males to reduce significantly the display rates or to cease displaying totally (Table 4.2.d).

A comparison between rates of display and cloud and rain intensities is given in Table 4.2.e. Display rates were similar in sunny weather and slight drizzle conditions, lower in strong drizzle and lowest in rainy conditions. A similar pattern was seen when under partly cloudy weather. Both cloudy and overcast weather showed similar patterns, and had significantly higher rates of display than all intensities of rain.

The influence of the time of day (i.e mornings, evenings and afternoons) and corresponding weather conditions on display rates was also analysed. Irrespective of weather, no significant change in display rates was seen during different parts of the day (Table 4.3.b).

When the influence of rain intensities at different parts of the day was analysed, slight drizzle and strong drizzles did not cause any significant change in display rates (Table 4.3.c).

The influence of cloud cover at different parts of the day on display rates is given in (Table 4.3.d). Display rates under sunny weather did not show any change between afternoons and evenings. Significant variation was also not seen for the other cloud cover conditions between mornings, afternoons and evening.

The time lag between displays was also measured, and an ANOVA was done to see whether any significant differences exist between lags under different weather conditions (Table 4.4.b). A clear pattern could not be discerned and large error values also indicate great variability in the time lag between two display jumps.

When display rates were correlated against temperature, a significant decrease in the rate of display was seen as temperature increased ($r= -0.52$, $df=24$, $p<0.02$) (Fig. 4.5).

Key for Tables 4.2.a to 4.4.b
W1= 0-25% cloud cover; W2= 25-50% cloud cover;
W3= 50-75% cloud cover; W4= 75-100% cloud cover.
B1= breeze; B2= moderate wind; B3= strong wind;
R1= light drizzle; R2= strong drizzle;
R3= rain; R4= No rain or drizzle

TABLE 4.2.a.
BASIC STATISTICS FOR DISPLAY RATES (LEAPS/MINUTE)
UNDER DIFFERENT WEATHER CONDITIONS

	W1	W2	W3	W4	R1	R2	B1	B2	B3
Minimum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Maximum	1.93	2.30	3.00	3.70	2.00	1.39	3.08	1.93	2.25
Mean	0.75	0.92	1.29	1.39	0.92	0.45	1.06	1.14	1.01
SD	0.75	0.79	0.95	0.79	0.57	0.51	0.86	0.60	0.65

Bartlett's test for homogeneity :
Chi Square = 58.959, P < 0.0001 (For W1,W2,W3,W4,R1,R2,R3,R4)
Chi Square = 7.236, P < 0.027 (For B1,B2,B3)

TABLE 4.2.b.

EFFECT OF 3 LEVELS OF WIND SPEED ON DISPLAY RATES

	B2		B3	
	F	P	F	P
B1	0.276	0.60	0.071	0.79
B2			0.400	0.53

TABLE 4.2.c.

EFFECT OF 4 LEVELS OF CLOUD COVER ON DISPLAY RATES

	W2		W3		W3	
	F	P	F	P	F	P
W1	0.172	0.68	3.275	0.071	6.041	0.015
W2			2.953	0.087	7.138	0.008
W3					0.324	0.570

TABLE 4.2.d.

EFFECT OF 4 LEVELS OF RAIN ON DISPLAY RATES

	R2		R3		R4	
	F	P	F	P	F	P
R1	2.753	0.098	10.898	0.001	3.257	0.072
R2			1.778	0.183	9.637	0.002
R3					25.707	0.512

TABLE 4.2.e.
COMPARISON BETWEEN DISPLAY RATES UNDER 4 LEVELS OF CLOUD COVER AGAINST 4 LEVELS OF RAINFALL

	R1		R2		R3	
	F	P	F	P	F	P
W1	0.431	0.512	4.112	0.043	12.360	0.001
W2	0.000	0.989	2.724	0.100	10.794	0.001
W3	3.119	0.078	9.018	0.003	22.094	0.001
W4	7.675	0.006	14.410	0.001	32.776	0.001

ALL TESTS (TABLE 4.2.b TO 4.2.e) ANALYSIS OF VARIANCE

TABLE 4.3.a.
BASIC STATISTICS FOR DISPLAY RATE (LEAPS/MINUTE) UNDER DIFFERENT WEATHER CONDITIONS FOR DIFFERENT TIMES OF THE DAY

	W1	W2	W3	W4	R1	R2	OVERALL
0600-1000 h							
Mean	*	0.15	1.44	1.39	1.02	0.95	1.14
SD	*	0.16	1.19	0.60	0.59	0.63	0.66
1000-1500 h							
Mean	0.55	1.06	1.53	1.41	1.03	0.86	0.91
SD	0.55	0.74	1.01	0.98	0.62	0.43	0.67
1500-1900 h							
Mean	0.99	1.13	1.01	1.43	0.76	0.09	1.09
SD	0.93	0.86	0.90	0.87	0.52	0.14	0.86

TABLE 4.3.b.
VARIATION IN RATES OF DISPLAY BETWEEN DIFFERENT TIMES OF THE DAY

	1000-1500 P	1500-1900 P
0600-1000 h	0.101	0.588
1000-1500 h		0.777

TABLE 4.3.c.
VARIATION IN RATES OF DISPLAY IN DIFFERENT RAIN CONDITIONS

	R1		R2	
	1000-1500 P	1500-1900 P	1000-1500 P	1500-1900 P
0600-1000 h	0.982	0.769	0.650	0.418
1000-1500 h		0.777		0.168

TABLE 4.3.d.
VARIATION IN RATES OF DISPLAY UNDER DIFFERENT CLOUD COVER

	W1		W2		W3		W4	
	10-15	15-19	10-15	15-19	10-15	15-19	10-15	15-19
	P	P	P	P	P	P	P	P
06-10	-	-	0.114	0.117	0.968	0.623	0.767	0.827
10-15		0.372		0.568		0.113		0.997

ALL TESTS (TABLE 4.3.b TO 4.3.d) ANALYSIS OF VARIANCE

TABLE 4.4.a.
BASIC STATISTICS FOR THE TIME LAPSE (IN SECONDS) BETWEEN DISPLAYS UNDER DIFFERENT WEATHER CONDITIONS

	W1	W2	W3	W4	R1	R2
Minimum	5	13	8	4	9	10
Maximum	613	456	330	609	326	185
Mean	42.8	49.4	43.5	39.6	45	46.9
SD	56.8	45.1	36.6	37.2	42.4	37.5

Bartlett's Test for Homogeneity of group variance:
Chi Square = 80.533; $P < 0.0001$

TABLE 4.4.b.
TIME LAPSE BETWEEN DISPLAYS UNDER DIFFERENT WEATHER CONDITIONS

	W2		W3		W4		R1		R2	
	F	P	F	P	F	P	F	P	F	P
W1	2.355	0.125	0.026	0.872	1.019	0.313	0.250	0.617	0.414	0.520
W2			2.73	10.099	10.393	0.001	1.131	0.288	0.155	0.694
W3					2.899	0.089	0.180	0.671	0.346	0.557
W4							3.106	0.078	1.721	0.190
R1									0.096	0.756

ANALYSIS OF VARIANCE

Key for Tables 4.2.a to 4.4.b
W1= 0-25% cloud cover; W2= 25-50% cloud cover;
W3= 50-75% cloud cover; W4= 75-100% cloud cover.
B1= breeze; B2= moderate wind; B3= strong wind;
R1= light drizzle; R2= strong drizzle;
R3= rain; R4= No rain or drizzle

FIG. 4.5. LESSER FLORICAN
DISPLAY RATES AND TEMPERATURE

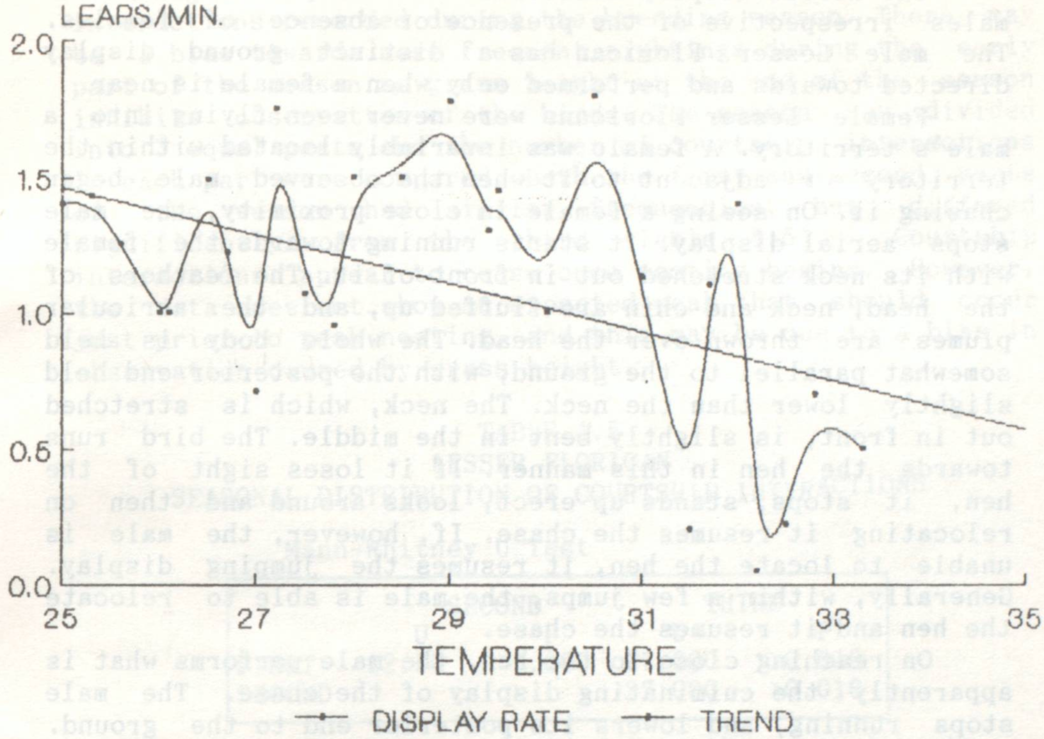
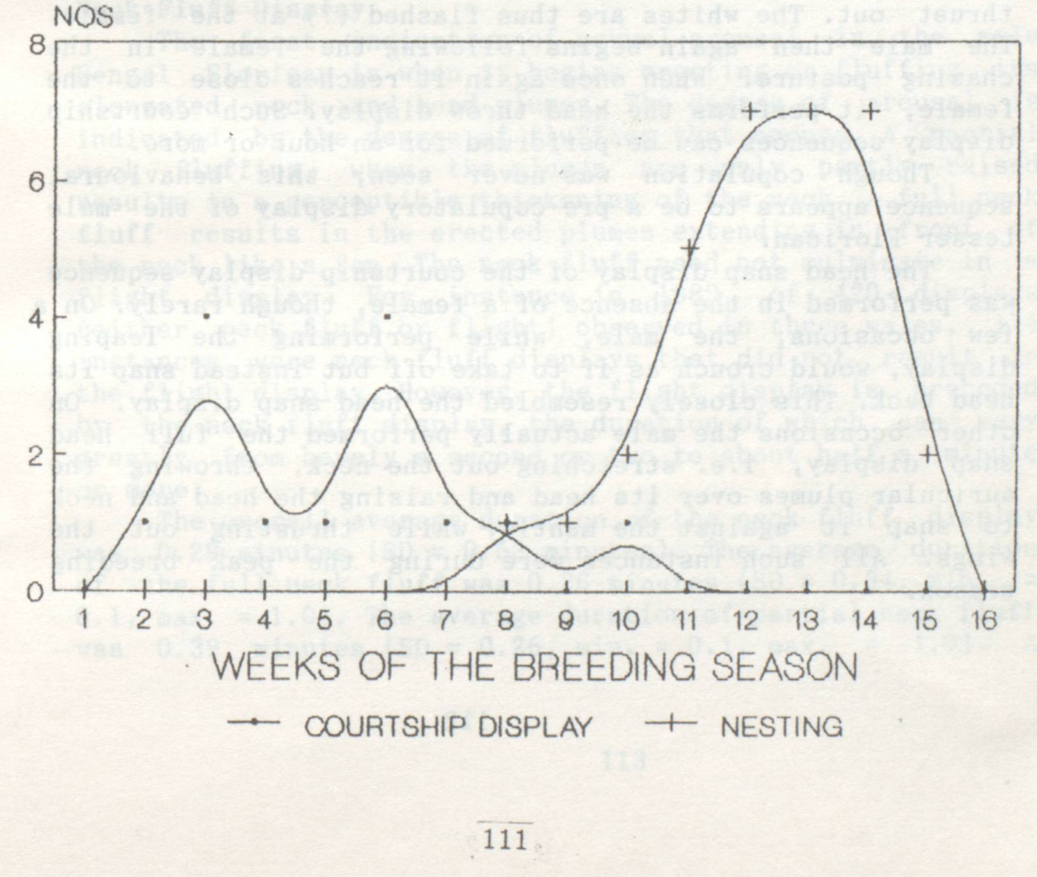


FIG. 4.6. LESSER FLORICAN
COURTSHIP DISPLAY AND NESTING



Description of Courtship Display

The aerial display described above is performed by the males irrespective of the presence or absence of females. The male Lesser Florican has a distinct ground display directed towards and performed only when a female is near.

Female Lesser Floricans were never seen flying into a male's territory. A female was invariably located within the territory or adjacent to it when the observed male began chasing it. On seeing a female in close proximity, the male stops aerial display. It starts running towards the female with its neck stretched out in front of it. The feathers of the head, neck and chin are fluffed up, and the auricular plumes are thrown over the head. The whole body is held somewhat parallel to the ground, with the posterior end held slightly lower than the neck. The neck, which is stretched out in front, is slightly bent in the middle. The bird runs towards the hen in this manner. If it loses sight of the hen, it stops, stands up erect, looks around and then on relocating it resumes the chase. If, however, the male is unable to locate the hen, it resumes the jumping display. Generally, within a few jumps, the male is able to relocate the hen and it resumes the chase.

On reaching close to the hen, the male performs what is apparently the culminating display of the chase. The male stops running, and lowers its posterior end to the ground. At the same time it raises its head, the neck retaining the characteristic posture of the prior display (feathers fluffed and the auricular plumes thrown over as earlier). The head is then thrown back onto the mantle, with a jerky motion. At the instant of the head snap, the wings which were upto this time folded normally against the body are thrust out. The whites are thus flashed (?) at the female. The male then again begins following the female in the chasing posture. When once again it reaches close to the female, it performs the head throw display. Such courtship display sequences can be performed for an hour or more.

Though copulation was never seen, this behavioural sequence appears to be a pre-copulatory display of the male Lesser Florican.

The head snap display of the courtship display sequence was performed in the absence of a female, though rarely. On a few occasions, the male, while performing the leaping display, would crouch as if to take off but instead snap its head back. This closely resembled the head snap display. On other occasions the male actually performed the full head snap display, i.e. stretching out the neck, throwing the auricular plumes over its head and raising the head and neck to snap it against the mantle, while thrusting out the wings. All such instances were during the peak breeding season.

Distribution of Courtship Display through the Season

Figure 4.6 shows the distribution of courtship interactions recorded during the breeding season. There may be a bias towards more frequent sightings during the early part of the season as grass height at the end of the season inhibits observation of the birds. The season was divided into 3 equal parts and the number of courtship interactions in each part were compared. Both the first and second parts of the season had similar frequencies, but differed significantly from the third (Table 4.5). Courtship interactions appear to cease once nesting begins. However, the data does not show an expected peak that should occur just prior to peak nesting, and this may be due to a bias in observation caused by grass height.

TABLE 4.5
LESSER FLORICAN
SEASONAL DISTRIBUTION OF COURTSHIP INTERACTIONS
Mann-Whitney U Test

	SECOND		THIRD	
	U	P	U	P
FIRST	12.50	1.000	27.000	>0.010
SECOND			27.000	>0.010

N.B. Breeding season divided into three equal parts.

BENGAL FLORICAN

Description of Attraction Display

Neck Fluff Display

The first indication of sexual arousal in the male Bengal Florican is when it begins erecting or fluffing its elongated neck and head plumes. The degree of arousal is indicated by the degree of fluffing that occurs. A partial neck fluffing, when the plumes are only partly raised results in a perceptible thickening of the neck. A full neck fluff results in the erected plumes extending in front of the neck like a fan. The neck fluff need not culminate in a flight display. For instance in 1989, of 420 displays (either neck fluff or flight) observed in three males, 174 instances were neck fluff displays that did not result in the flight display. However, the flight display is preceded by the neck fluff display, the duration of which can vary greatly, from barely a second or two to about half a minute or more.

The overall average duration of the neck fluff display was 0.29 minutes (SD = 0.53 minutes). The average duration of the full neck fluff was 0.26 minutes (SD = 0.54, min. = 0.1, max. = 1.0). The average duration of partial neck fluff was 0.39 minutes (SD = 0.26, min. = 0.1, max. = 1.0). A significant difference existed between the duration of full neck fluff and partial neck fluff displays (Mann-Whitney U test, $U = 4179$, $P < 0.002$).

Flight Display

When completely aroused, usually indicated by a period of complete neck fluffing, the male Bengal Florican performs its spectacular flight display. The male crouches slightly and assists take off by flexing its legs. The ascent is made with about 15 - 18 wing flaps, the initial few being strong and rapid with the wings being folded and brought almost against the body during each flap. Towards the apex of the first ascent, the wing flaps are more regular and less rapid and the wings are not folded as much as during the initial phase of the ascent. The angle of the initial rise into the air is about 65° and the bird rises to a height of about 3 to 4 metres until it reaches the first peak. The wings are now flapped evenly and less rapidly, very like the wing flapping during normal flight. The legs are also stretched out behind the bird (as in normal flight) and do not dangle as was the case during the ascent. The male now descends, the wings being flapped evenly and like normal flight, and is sustained until the bird reaches within a metre or so of the ground. During the first descent the wings are flapped about 8 to 10 times, and the angle of descent is a little more gradual than the angle of ascent. The male now ascends a second time. The angle of the second ascent is steeper than that of the first one. The wings are not flapped as was the case during the first ascent, but are held outstretched and 'quivered' rapidly from a more or less fixed outstretched wing position. The wing thus 'quivers' 18 - 20 times until the peak of the second ascent, which is slightly lower than that of the first ascent. Once it reaches the second peak, the wings are half folded but held away from the body. The whole bird tilts downwards, with the head pointing towards the ground and the tail up. The legs dangle forward until almost touching the neck. It then descends to the ground at a steep angle, almost vertically. When about 1 to 2 metres from the ground, the body is held horizontal once more while the wings are flapped a few time to break the fall. The legs may be paddled a few times for balance. With the momentum of landing, the bird usually runs forward a few steps.

Throughout the display flight, the neck feathers remain fluffed and give the male's head and neck the appearance of an inflated elongated balloon. This is maintained until after landing, when the bird usually stands still for a few seconds, de-fluffs its neck, and then either walks back to the point of take off or to another spot or begins foraging. The average duration of normal flight displays was 6.1 seconds (SD. = 0.59, min. = 5.4, max. = 8.1, n = 64). The distance covered by the display flight varies between 15 and 25 metres.

Auditory signals of the flight display

The display flight is accompanied by auditory signals. The one unique to the display flight is a loud clapping sound that is produced by the wings during the first ascent. This lasts about 1 - 1.2 seconds and consists of between 12 and 15 individual claps (evidenced from Sonography - not presented here). Once the first peak is reached, the bird then begins vocalizing. This is the 'chik' call that is not unique to the flight display as it is made during normal flight and during threat displays as well. Between 4 and 6 individual 'chik' calls are made during each display flight (mean = 5.49, SD. = 0.56 n = 33). About 1 'chik' is made for every 1.1 seconds of display flight. At the Dudwa Tiger Reserve, the second ascent is not accompanied by the wing clap sound. This shows some form of dialectic difference with the population of the Bengal Florican at the Manas Tiger Reserve, where a softer wing clap sound is heard during the second ascent (G. Narayan, pers. comm.).

Extended Flight Displays

While the above descriptions are for normal displays, some (8.5%) are different in that the male, after the first ascent and descent, may carry on flying for a distance before landing in a display 'dive' (i.e. the second ascent and descent). In a further variation, the display begins in the typical manner, but then ends in a normal landing.

Extended flight displays sometimes occur when a female lands in the territory of a male. However, very frequently the male performs the extended flight displays without the stimulus of a female. Differences of frequency of extended flight displays existed between males. In both the Navalkhad and Chapra males, a far higher proportion of their total display flights were extended flight displays, whereas this was significantly lower in the Kowhaghatti and Seethagaddaia males (Table 4.7).

TABLE 4.7

EXTENDED FLIGHT DISPLAY AND NORMAL DISPLAYS IN DIFFERENT MALE BENGAL FLORICANS

Males	Norm. disp.	Ext. Flight	%
Kowhaghatti	189	7	3.7
Navalkhad	142	23	16.2
Chapra	82	14	17.1
Seethagaddaia	179	6	3.4

The average duration of the extended flight display was 16.5 seconds (SD. 7.4 sec. max.=34 sec. min.=9 sec. n=8).

Other aberrant displays which were not extended flight displays included some flights which did not end in a display dive (2.2%), or flights in which the wing clapping sound was not heard (6.8%).

Arousal

Intensity in arousal was seen to vary; mild arousal would result in a fluffing of the neck feathers. This frequently ends in the male de-fluffing its neck feathers. When arousal is maximum then it culminates in the male performing a flight display. In such cases, the duration of neck fluffing was significantly lower than when arousal did not culminate in the flight display ($t = -3.406$, $p < 0.001$).

Display Periods

The display activity of male Bengal Floricans is restricted to the early morning hours and the late evening hours. These parts of the day can be called the display periods for this species.

When the influence of sunrise and sunset on display frequencies were considered, a strong correlation was seen (Fig 4.7.a and 4.7.b). 70 % of displays were seen to occur within 70 minutes after sunrise and 70 % of display occurred within 50 minutes of sunset. In both cases peaks in number of displays occurred at about 20 minutes after sunrise and 20 minutes before sunset.

Table (4.8) summarises morning and evening display frequencies of 5 males. Overall, there was no difference in the frequency of displays between the mornings and evenings (Mann-Whitney U test $P > 0.8$). Excepting the Chapra male, which displayed significantly more often in the morning than in the evening, the other four males showed no such differences (Table 4.8).

TABLE 4.8
NUMBER OF DISPLAY FLIGHTS
IN THE MORNING AND EVENINGS FOR DIFFERENT MALES

	Chapra		Kowhaghatti		Navalkhad		Seetha. E.		Seetha. W.	
	M	E	M	E	M	E	M	E	M	E
Mean	3.2	0.7	2.6	3.0	2.5	2.2	8.3	7.2	3.0	4.3
SD	2.8	0.9	2.9	2.0	3.2	2.4	1.5	4.3	1.9	3.0
Max.	9	3	15	8	13	10	10	14	6	9
Min.	0	0	0	0	0	0	6	1	1	0
p	0.003		0.161		0.972		0.761		0.391	

Display Frequency Patterns in the Breeding Season

Male Bengal Floricans are rather erratic as to the number of flight displays they perform on any given day in the breeding season (Figs. 4.8.a to 4.8.c). Though there is

FIG. 4.7.a. BENGAL FLORICAN
DISTRIBUTION OF FLIGHT DISPLAY
IN RELATION TO SUNRISE

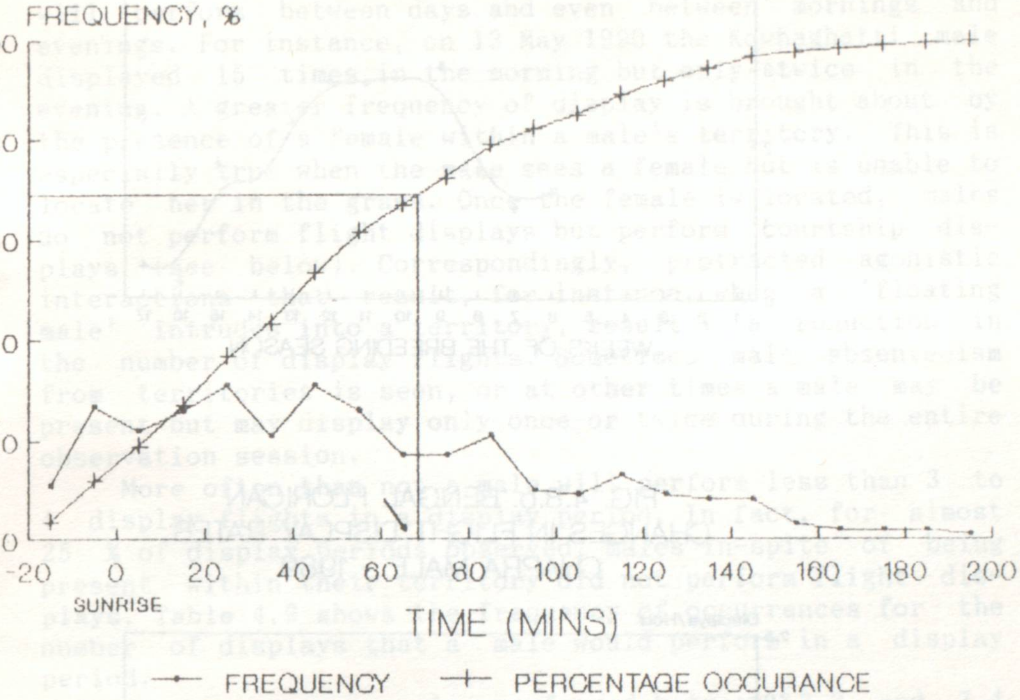


FIG. 4.7.b. BENGAL FLORICAN
DISTRIBUTION OF FLIGHT DISPLAY
IN RELATION TO SUNSET

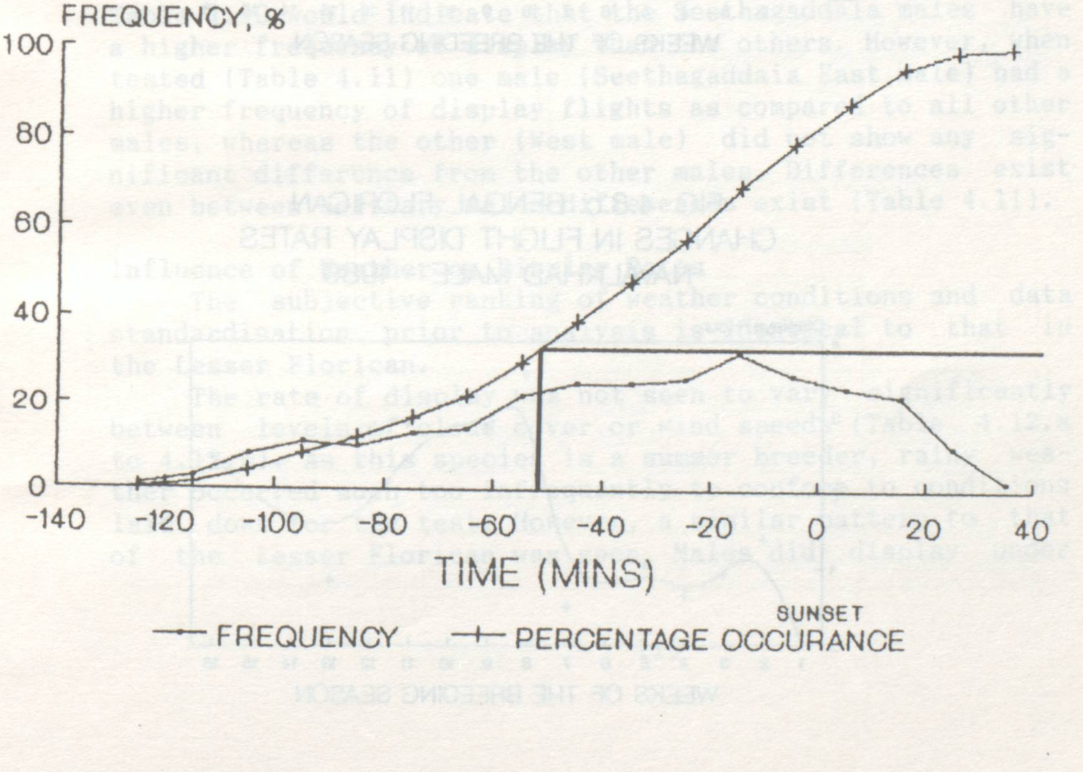


FIG. 4.8.a. BENGAL FLORICAN
CHANGES IN DISPLAY RATES
KOWHAGHATI MALE - 1989

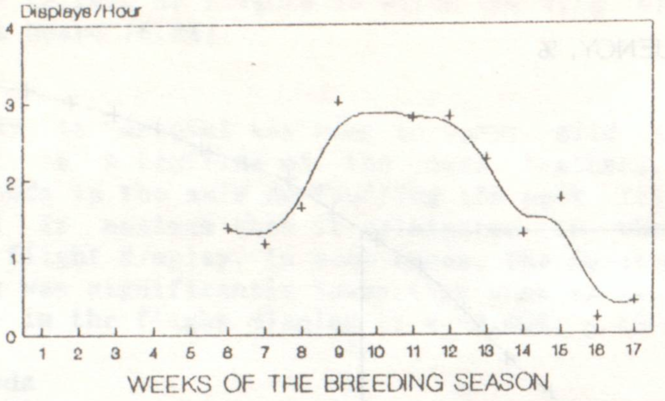


FIG. 4.8.b. BENGAL FLORICAN
CHANGES IN FLIGHT DISPLAY RATES
CHAPRA MALE - 1989

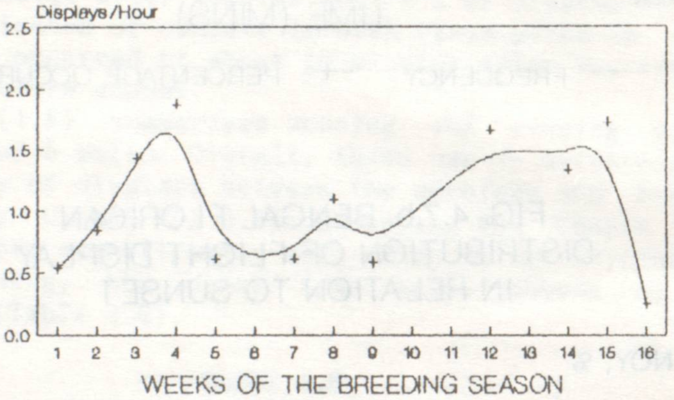
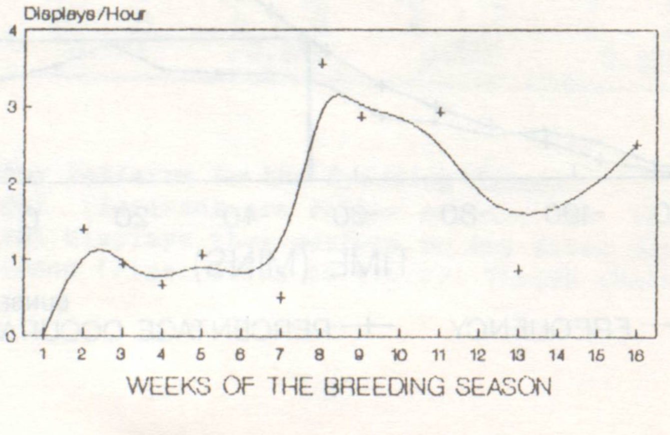


FIG. 4.8.c. BENGAL FLORICAN
CHANGES IN FLIGHT DISPLAY RATES
NAVALKHAD MALE - 1989



a trend towards a peak in display rates during April and May in some males, this is not evident in others. There is considerable variation in the number of displays that a male will perform between days and even between mornings and evenings. For instance, on 13 May 1990 the Kowhaghatti male displayed 15 times in the morning but only twice in the evening. A greater frequency of display is brought about by the presence of a female within a male's territory. This is especially true when the male sees a female but is unable to locate her in the grass. Once the female is located, males do not perform flight displays but perform courtship displays (see below). Correspondingly, protracted agonistic interactions that result, for instance, when a 'floating male' intrudes into a territory, result in a reduction in the number of display flights. Sometimes male absenteeism from territories is seen, or at other times a male may be present but may display only once or twice during the entire observation session.

More often than not a male will perform less than 3 to 4 display flights in a display period. In fact, for almost 25 % of display periods observed, males in-spite of being present within their territory did not perform flight displays. Table 4.9 shows the frequency of occurrences for the number of displays that a male would perform in a display period.

On an average, males performed between 2.2 and 7.4 display flights per display period (Table 4.9). Two types of territorial males were present (see also Chapter 3). The Seethagaddaia males were within sight and acoustic distance of each other whereas the other three were not. The display frequencies were tested between these males to see whether any correlation existed between proximity of other males and number of display flights that an individual would perform. Table 4.10 would indicate that the Seethagaddaia males have a higher frequency of display than the others. However, when tested (Table 4.11) one male (Seethagaddaia East male) had a higher frequency of display flights as compared to all other males, whereas the other (West male) did not show any significant difference from the other males. Differences exist even between solitary males differences exist (Table 4.11).

Influence of Weather on Display Rates

The subjective ranking of weather conditions and data standardisation prior to analysis is identical to that in the Lesser Florican.

The rate of display was not seen to vary significantly between levels of cloud cover or wind speeds (Table 4.12.a to 4.12.b). As this species is a summer breeder, rainy weather occurred much too infrequently to conform to conditions laid down for the test. However, a similar pattern to that of the Lesser Florican was seen. Males did display under light and strong drizzles but not under rainy conditions.

TABLE 4.9

FREQUENCY OF DISPLAY FLIGHTS PER DISPLAY PERIOD

Dis/per.	0	1	2	3	4	5	6	7	8	9	>9
Chapra	14	8	4	4	0	3	1	2	1	1	0
Kowha.	12	15	12	11	9	7	4	0	1	1	1
Nav.	21	12	9	5	3	7	1	1	1	0	3
See.E.	0	2	1	0	1	0	2	1	2	2	5
See.W.	3	1	1	1	4	1	1	2	1	1	0
Totals	50	38	27	21	17	18	9	6	6	5	9
%	24.3	18.5	13.1	10.2	8.3	8.7	4.4	2.9	2.9	2.4	4.4

TABLE 4.10

BASIC STATISTICS FOR NUMBER OF FLIGHT DISPLAYS IN A DISPLAY PERIOD FOR FIVE MALE BENGAL FLORICANS

	Seethagaddaia		Kowhaghatti	Chapra	Navalkhad
	East	West			
Minimum	1	0	0	0	0
Maximum	14	9	15	9	10
Mean	7.4	4.0	2.8	2.2	2.3
SD.	3.8	2.8	2.5	2.6	2.8
N Obs Per.	16	16	73	39	62

N.B. A display period is either the morning or evening. Males display upto 2-3 hours after sunrise and from 2 hours before sunset to dusk (see below).

TABLE 4.11

COMPARISON OF NUMBER OF DISPLAYS PER OBSERVATION PERIOD BETWEEN FIVE MALES

Mann-Whitney U Test

	SEE.W.		KOW.		NAV.		CHA.	
	U	P	U	P	U	P	U	P
SEE.E.	195.5	0.01	171.5	0.01	125.5	0.06	218.5	0.001
SEE.W.			125.0	0.59	83.0	0.80	169.0	0.12
KOW.					1816.5	0.06	1097	0.07
NAV.							1199.0	0.84

N.B. Tested from comparable periods of the breeding season.

One factor believed to restrict display to the mornings and evenings was temperature. Figures 4.9.a to 4.9.c show different temperatures when display was recorded during the study. Though the trend shows a decrease with increasing temperature, when display was correlated against temperature it was not found to be statistically significant. The data was then classified monthly and according to morning and evenings, to help account for seasonal variation in maximum temperatures. In no combination was display found to significantly decrease with temperature.

TABLE 4.12.a.
BENGAL FLORICAN
BASIC STATISTICS FOR
DISPLAY RATES UNDER DIFFERENT WEATHER CONDITIONS

	W1	W2	W2	W4	B1	B2	B3	B4
MINIMUM	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MAXIMUM	17.50	12.50	17.14	15.30	13.30	7.41	3.64	17.40
MEAN	3.93	3.93	5.67	3.99	4.06	4.33	1.79	4.91
SD	4.06	4.12	5.04	4.49	4.54	2.71	1.73	4.53

W1= 0-25% cloud cover; W2= 25-50% cloud cover;
W3= 50-75% cloud cover; W4= 75-100% cloud cover
B1= breeze; B2= slight wind; B3= strong wind

TABLE 4.12.b
EFFECT OF CLOUD COVER ON BENGAL FLORICAN DISPLAY RATES
T - TEST

	W2		W3		W4	
	t	p	t	p	t	p
W1	-0.002	0.998	-1.361	0.179	-0.051	0.959
W2			-1.030	0.312	-0.042	0.967
W3					-1.014	0.318

TABLE 4.12.c.
EFFECT OF 4 LEVELS OF WIND SPEED ON
BENGAL FLORICAN DISPLAY RATES
T - TEST

	B2		B3		B4	
	f	p	f	p	f	p
B1	-0.126	0.902	-1.059	0.312	-0.470	0.641
B2			-1.802	0.105	-0.301	0.765
B3					-1.431	0.162

FIG. 4.9.a. BENGAL FLORICAN
TEMPERATURE AND DISPLAY

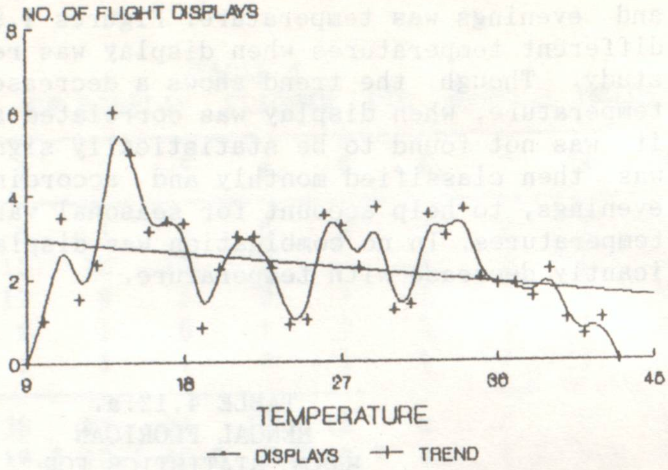


FIG. 4.9.b. BENGAL FLORICAN
TEMPERATURE AND FLIGHT DISPLAYS
IN THE MORNING

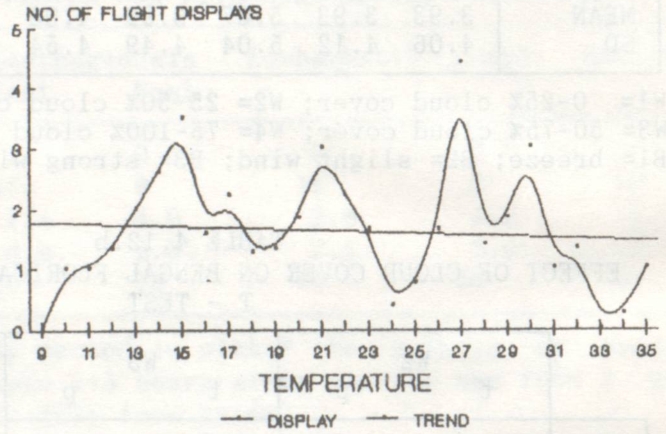
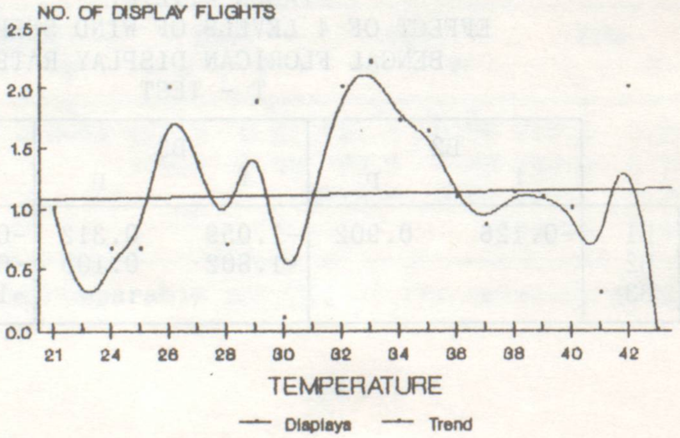


FIG. 4.9.c. BENGAL FLORICAN
TEMPERATURE AND FLIGHT DISPLAYS
IN THE EVENINGS



Stimuli and Triggers

Of the 14 known territories of male Bengal Floricans in the study area, only 3 males were within acoustic and visual range of each other. All other males occupied territories in disjunct grasslands. In the case of males which occupied adjacent territories, tests were made to understand the influence of display by one male on another.

Figure 4.10 is a representation of the time lag between displays of three males and the frequency of occurrences. The highest frequency of displays by males were performed in a narrow time range from the displays by another male. It would then appear that displays by one male tends to cause another to display. However, as maximum display tended to be in a narrow range of time at sunrise and sunset, it seemed probable that the pattern arrived at in Fig 4.10 might be simply due to an overlap in display times.

To understand the exact influence of displays by one male on another a multiple regression analysis between the time lag of displays from sunrise or sunset for two males was done. In the evenings, males appear to stimulate one another to display (influence of male B on male A, $p < 0.022$ and influence of male A on male B, $p < 0.022$). By partitioning out the effect of sunset on the birds a similar relation was seen (influence of males A and B on each other, $r = 0.559$, $df = 14$, $p < 0.05$). However in the mornings, a weaker correlation exists (multiple correlation for influence of male B on male A, $p > 0.2$ and influence of male A on male B, $p > 0.1$). When the effect of time lag from sunrise was partitioned out a similar relation was seen ($r = 0.2293$, $df = 14$, $p > 0.1$).

Displays of Bengal Floricans are more often than not triggered by the calls of unrelated species of birds, chiefly Peafowl, and to a lesser extent the jungle crow. During this study, out of a total 611 display flights recorded, 65.63 % were released by sound triggers and 33.72 % were not. Of those flight displays released by triggers, 72.32 % were released by peacock calls while 27.68 % were released by crow calls. Of 58.74 % of instances of neck fluffing not followed by flight display (n = 509), 86.6 % were caused by peacock calls while 13.4 % were released by crow calls.

A trigger was said to have set off a display when the time lag between the source sound and the display was 0 seconds (Fig. 4.11). Time lapse was measured only for peacock calls. Of the 196 instances when time lapse was measured from peacock calls, 81.63 % occurred at 0 seconds time interval, i.e while the peacock was calling. A uniform distribution of calls at all other intervals shows that there is no lag effect by peacock calls on the Bengal florican's display.

FIG. 4.10. BENGAL FLORICAN
TIME LAPSE BETWEEN FLIGHT DISPLAYS OF
3 ADJACENT TERRITORIAL MALES

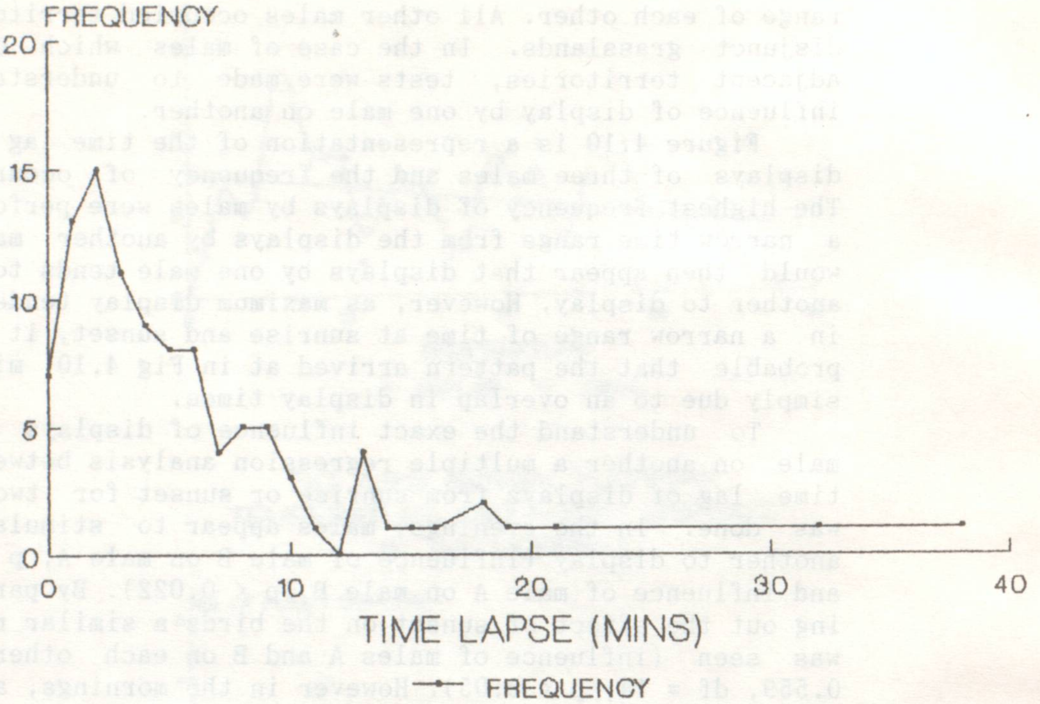


FIG. 4.11. TIME LAPSE BETWEEN
PEACOCK CALLS AND
BENGAL FLORICAN FLIGHT DISPLAYS

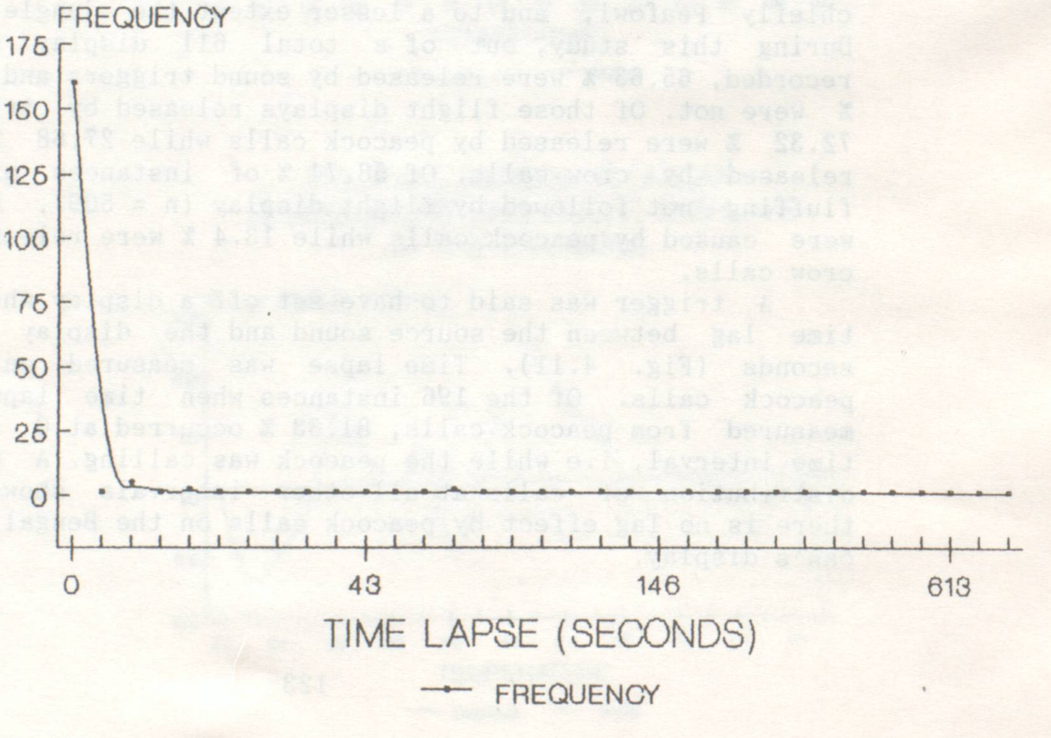


FIG. 4.12.a. FREQUENCY OF PEACOCK CALLS IN RELATION TO SUNRISE

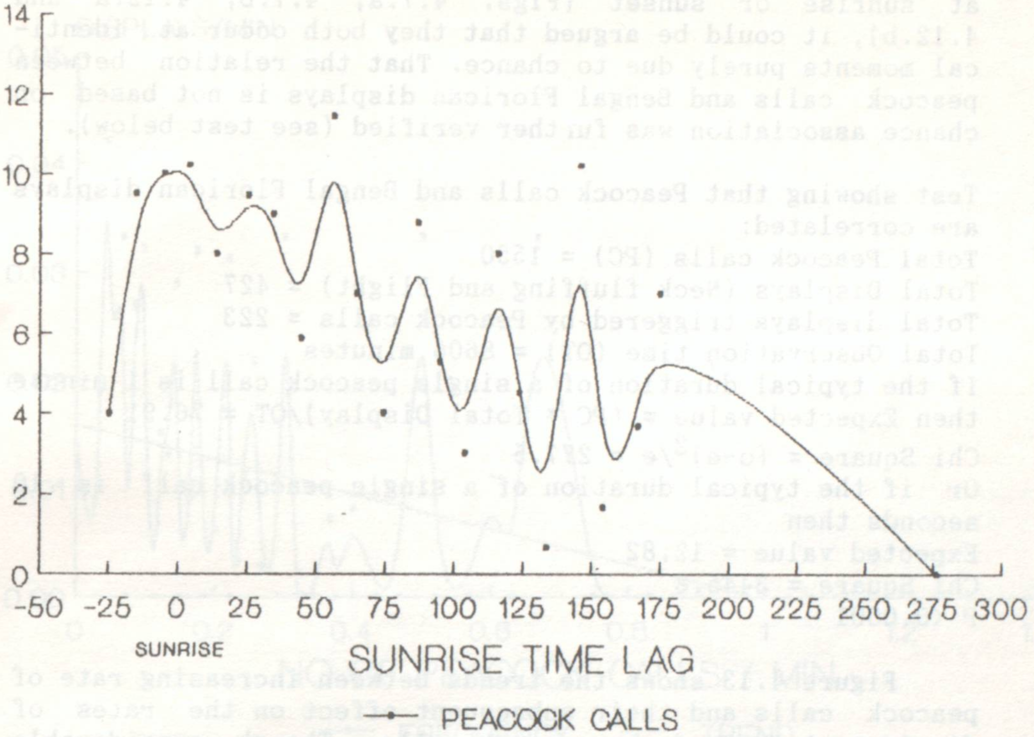
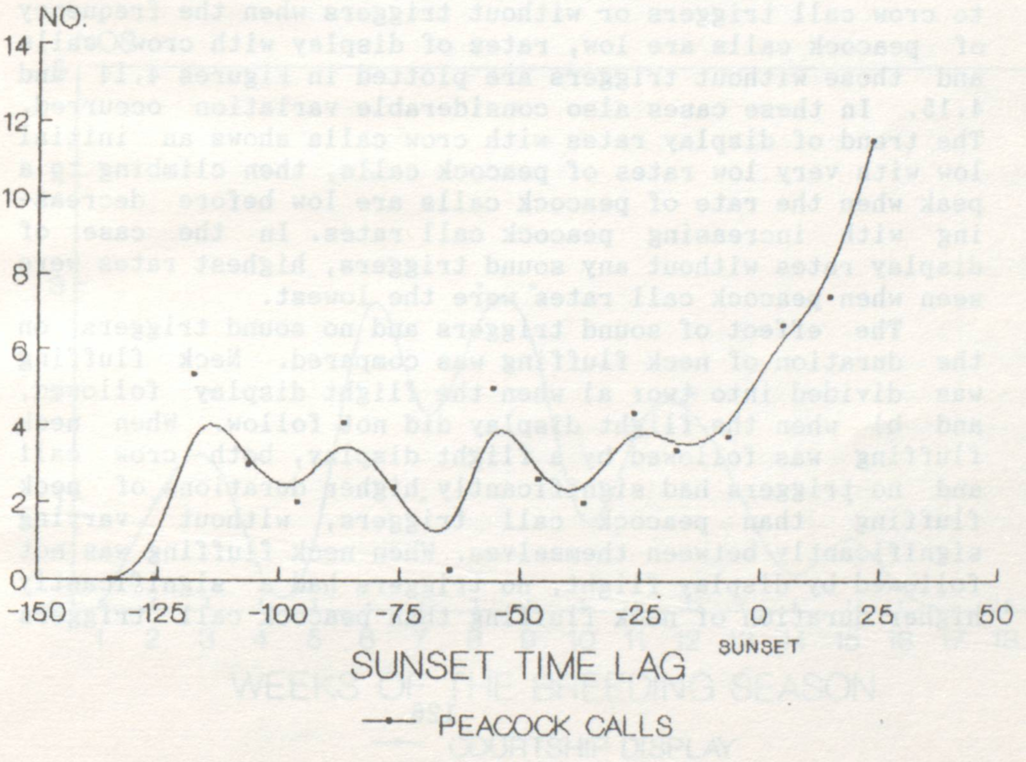


FIG. 4.12.b. FREQUENCY OF PEACOCK CALLS IN RELATION TO SUNSET



However, as both peacock calls and Bengal Florican displays occur at greatest intensity in a narrow time range at sunrise or sunset (Figs. 4.7.a, 4.7.b, 4.12.a and 4.12.b), it could be argued that they both occur at identical moments purely due to chance. That the relation between peacock calls and Bengal Florican displays is not based on chance association was further verified (see test below).

Test showing that Peacock calls and Bengal Florican displays are correlated:
Total Peacock calls (PC) = 1550
Total Displays (Neck fluffing and Flight) = 427
Total displays triggered by Peacock calls = 223
Total Observation time (OT) = 8606 minutes
If the typical duration of a single peacock call is 1 minute then Expected value = (PC * Total Display)/OT = 76.91
Chi Square = $(o-e)^2/e$ = 277.5
Or if the typical duration of a single peacock call is 10 seconds then
Expected value = 12.82
Chi Square = 3445.8
$P < 0.0001$

Figure 4.13 shows the trends between increasing rate of peacock calls and their subsequent effect on the rates of displays triggered by peacock calls. Though considerable variation exists, the trend is that of an increase of display rates with that of peacock calls. This trend apparently is maintained only upto a point, beyond which the high rates of peacock calls fail to act as a trigger.

To see whether male floricans display more frequently to crow call triggers or without triggers when the frequency of peacock calls are low, rates of display with crow calls and those without triggers are plotted in Figures 4.14 and 4.15. In these cases also considerable variation occurred. The trend of display rates with crow calls shows an initial low with very low rates of peacock calls, then climbing to a peak when the rate of peacock calls are low before decreasing with increasing peacock call rates. In the case of display rates without any sound triggers, highest rates were seen when peacock call rates were the lowest.

The effect of sound triggers and no sound triggers on the duration of neck fluffing was compared. Neck fluffing was divided into two: a) when the flight display followed, and b) when the flight display did not follow. When neck fluffing was followed by a flight display, both crow call and no triggers had significantly higher durations of neck fluffing than peacock call triggers, without varying significantly between themselves. When neck fluffing was not followed by display flight, no triggers had a significantly higher duration of neck fluffing than peacock call triggers

FIG. 4.15. RATE OF DISPLAY WITHOUT SOUND TRIGGERS AND RATE OF PEACOCK CALLS

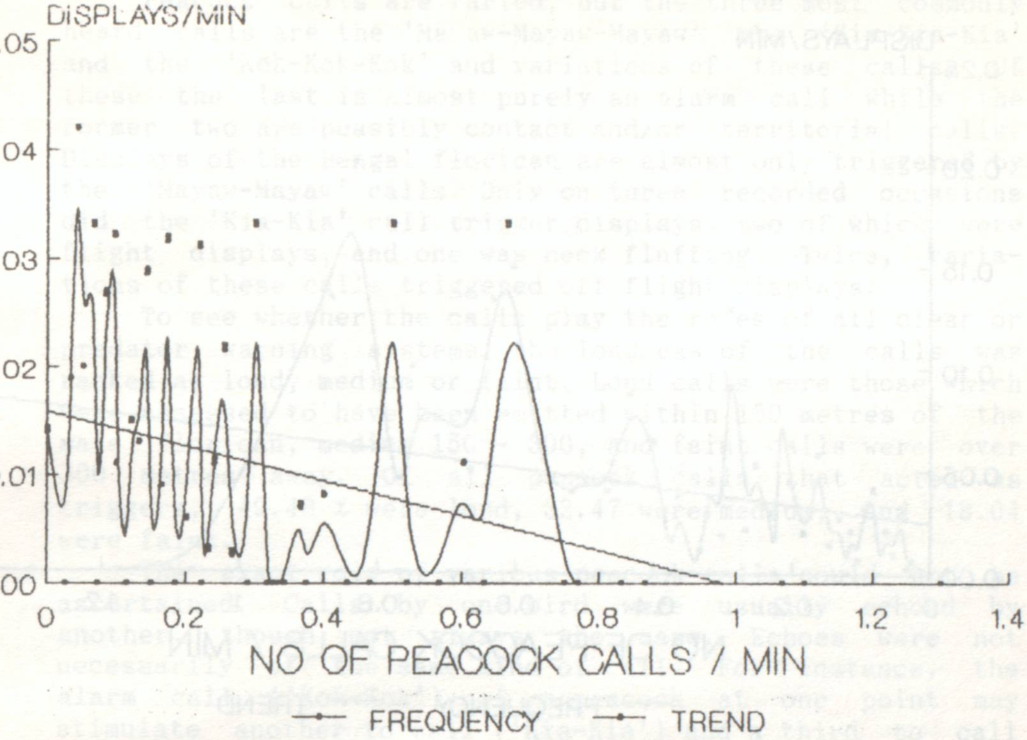


FIG. 4.16. BENGAL FLORICAN DISTRIBUTION OF COURTSHIP DISPLAY

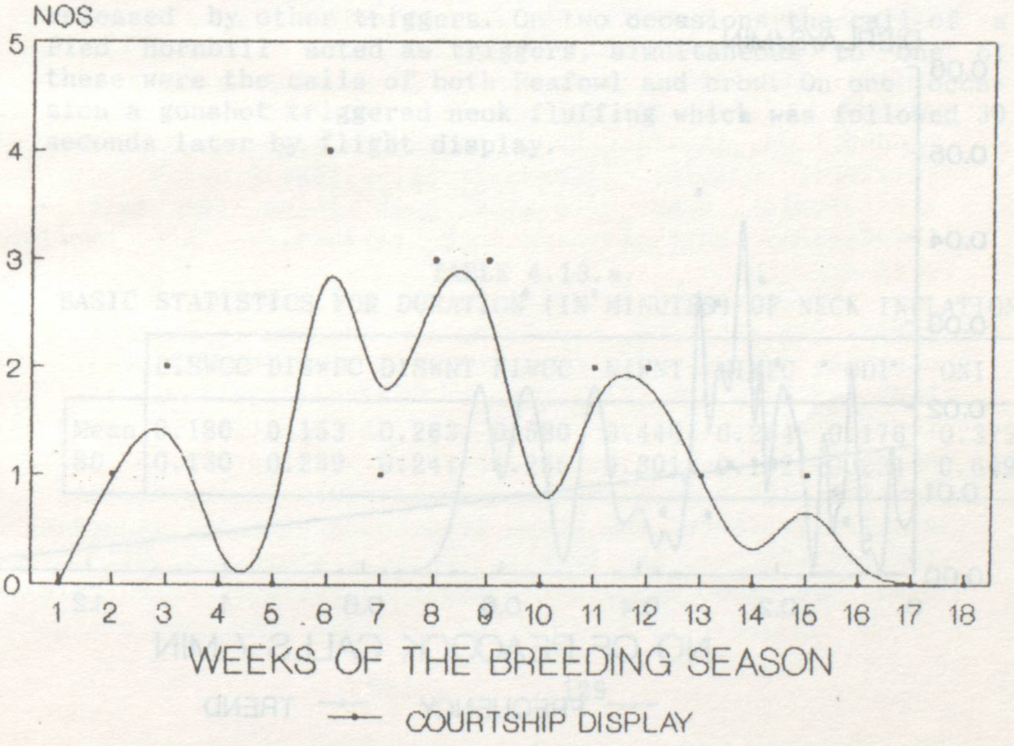


FIG. 4.13. BENGAL FLORICAN
RATE OF PEACOCK CALLS AND RATE OF
DISPLAYS TRIGGERED BY PEACOCK CALLS

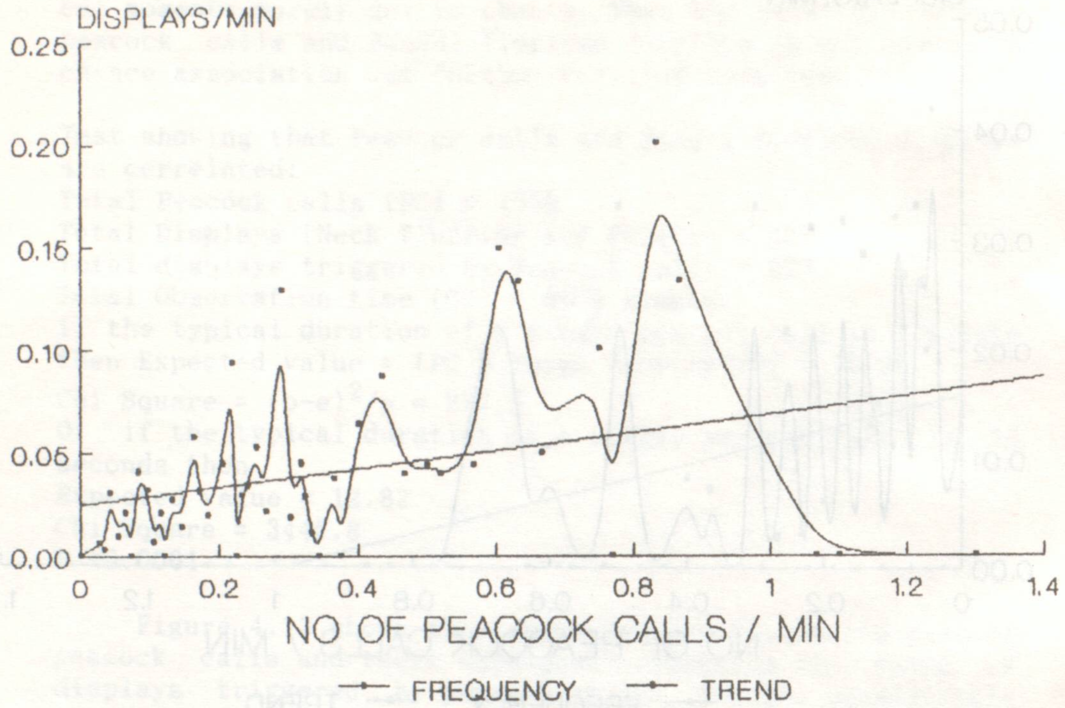
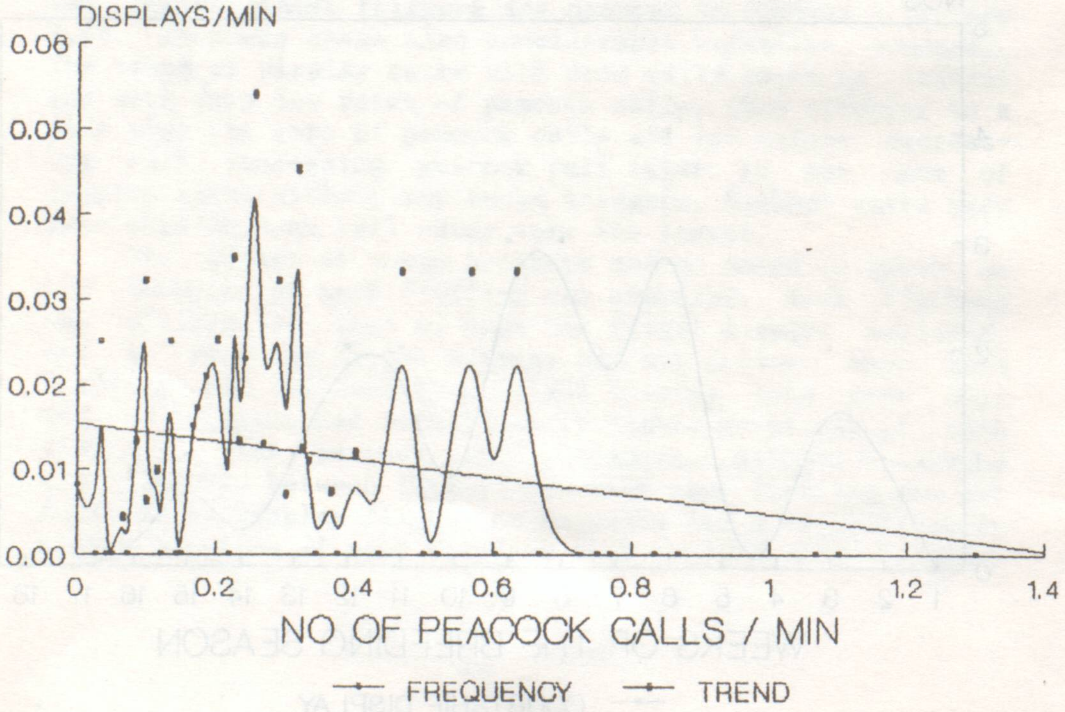


FIG. 4.14. BENGAL FLORICAN
RATE OF DISPLAYS TRIGGERED BY CROW CALLS
AND RATE OF PEACOCK CALLS



(Table 4.13.b). Crow call triggers did not vary significantly from both peacock calls and no triggers.

Peacock calls are varied, but the three most commonly heard calls are the 'Mayaw-Mayaw-Mayaw' the 'Kia-Kia-Kia' and the 'Kok-Kok-Kok' and variations of these calls. Of these the last is almost purely an alarm call while the former two are possibly contact and/or territorial calls. Displays of the Bengal florican are almost only triggered by the 'Mayaw-Mayaw' calls. Only on three recorded occasions did the 'Kia-Kia' call trigger displays, two of which were flight displays, and one was neck fluffing. Twice, variations of these calls triggered off flight displays.

To see whether the calls play the roles of all clear or predator warning systems, the loudness of the calls was ranked as loud, medium or faint. Loud calls were those which were assessed to have been emitted within 150 metres of the male florican, medium 150 - 300, and faint calls were over 300 metres away. Of all peacock calls that acted as triggers, 49.48 % were loud, 32.47 were medium, and 18.04 were faint.

The exact role of various peacock calls could not be ascertained. Calls by one bird were usually echoed by another, though not always the case. Echoes were not necessarily of the same kind of call. For instance, the alarm call ('Kok-Kok') of a peacock at one point may stimulate another to call ('Kia-Kia') and a third to call ('Mayaw-Mayaw') or their variations and any such combination. A loud sound may also result in Peafowl calling. It is most probable that non-alarm calls of the peacock are in some way connected to territorial and/or social displays.

Displays by Bengal Floricans were on rare occasions released by other triggers. On two occasions the call of a Pied Hornbill acted as triggers, simultaneous to one of these were the calls of both Peafowl and crow. On one occasion a gunshot triggered neck fluffing which was followed 30 seconds later by flight display.

TABLE 4.13.a.

BASIC STATISTICS FOR DURATION (IN MINUTES) OF NECK INFLATION

	DISWCC	DISWPC	DISWNT	NIWCC	NIWNT	NIWPC	ODI	ONI
Mean	0.180	0.153	0.263	0.580	0.448	0.264	0.176	0.373
SD	0.130	0.259	0.241	1.255	0.301	0.192	0.234	0.649

TABLE 4.13.b.
DIFFERENCES IN DURATION OF NECK FLUFF DISPLAY WHEN TRIGGERED BY PEACOCK CALLS, CROW CALLS AND WITHOUT SOUND TRIGGERS

	Neck Fluff followed by flight display				Neck fluff not followed by Flight display			
	WPC		WNT		WPC		WNT	
	T	P	T	P	T	P	T	P
WCC	2.433	0.021	-1.214	0.240	1.668	0.103	0.681	0.501
WNT	2.387	0.028			2.539	0.017		

ALL TESTS = T - TEST

Key to Tables 4.13.a and 4.13.b
DISWCC = Flight display triggered by crow calls
DISWPC = Flight display triggered by peacock calls
DIWNT = Flight display without sound triggers
NFWCC = Only neck fluff display triggered by crow call
NFWPC = Only neck fluff display triggered by peacock call
NFWNT = Only neck fluff display without sound triggers
DI = Neck fluff display followed by flight display
ONI = Neck fluff display not followed by flight display

Description of Courtship Display

In the absence of a female, males perform the neck fluff and flight displays described above. However, on seeing a female within its territory, or in close proximity, the male performs a distinct ground display. Approach of a female into a territory occurred usually in two manners. Firstly, a female would fly in and land in some part of the male's territory. The male would usually respond with an extended flight display and land near where the female had landed. On locating the female, the male would begin the courtship display. Alternatively, a female would walk into the display area of a male, upon which the male would immediately move towards her performing the courtship display.

The courtship display can be differentiated into two parts. The approach, i.e. when the male moves towards or is chasing the female, consists of a head pumping walk. The neck feathers are fully fluffed. The male retracts its head to almost against its shoulders, the fluffed up elongated neck plumes hanging before its legs, similar to an inflated balloon. The male runs, or walks rapidly in the direction of the female. Every few steps or more, apparently depending on the proximity of the female, the male stops, abruptly erects its neck and head, looks about jerkily before abruptly retracting its head and commencing chasing the female. The sequence of this head pumping chase apparently facilitates location of the female in the grass, as often the male orients, or realigns itself towards the female after erecting the head and neck.

On reaching within a metre or two of the female, the male begins swaying its head (still retracted) for a few steps and then stops. The head is now fully erected, and the fully fluffed neck plumes extend before it like an opened fan. The head is jerked from side to side, causing the neck plumes to sway to and fro. Observations on courtship displays stopped at this stage, as in all observed encounters of this display, the females invariably flew or ran away at this point.

During the courtship display, males often lost sight of the female. When this occurred, the male would perform flight display, extended or normal, over the area where the female was seen last. On relocating the female, the entire sequence of the courtship display, i.e. the chase with the 'head pump' sequence, and culminating in the fanning and swaying of the neck feathers. The last stage is least often seen as females rarely permitted males to approach so closely.

Distribution of Courtship Interactions

Figure 4.16 shows the distribution of courtship interactions recorded during the breeding season. Courtship interactions are seen virtually throughout the season with a peak in the middle (Fig 4.16). When the season was divided into 3 equal parts and the frequency of occurrence in each part compared, the first part did not vary significantly between the second and the third (Table 4.14). The second part had a significantly higher frequency of courtship interactions than the third part of the breeding season.

TABLE 4.14
BENGAL FLORICAN
SEASONAL DISTRIBUTION OF COURTSHIP INTERACTIONS
Mann-Whitney U Test

	SECOND		THIRD	
	U	P	U	P
FIRST	12.00	0.323	23.000	>0.368
SECOND			31.000	>0.029

N.B. Breeding season divided into three equal parts.

DISCUSSION

Aerial displays have been described in several species of birds (e.g. Storor 1940, Van Tyne and Berger 1959, Ali and Ripley 1969, Sutton 1981). Amongst, bustards aerial displays have been recorded for most of the smaller species and this form of display can be categorized into two types (Osborne _et al_. 1984). That of the Lesser Florican comes under the 'jumping', i.e. the display consists of a very brief vertical leap followed by a drop to the spot of take off. Osborne _et al_. (1984) erroneously categorized the Bengal Florican's display as a 'jumping display' largely due to it having been likened to the Lesser Florican in nineteenth and twentieth century literature (Baker 1921, Ali and Ripley 1969; see also Narayan and Rosalind 1988). The Bengal Florican's display can be classified as a display flight (or 'aerial display'), though similarly classified displays of African bustards are apparently more prolonged (Osborne _et al_. 1984).

An important component in the understanding of a species breeding behaviour, is a knowledge of the displays that are performed in connection with breeding. This discussion deals with some aspects of the attraction and courtship displays that were dealt with in the results section. For convenience, each species is dealt with separately independently. Those aspects of the breeding behaviour that are better discussed together are dealt with in Chapter 6. This discussion deals with two aspects of the Lesser Florican's behaviour, namely display patterns in the breeding season and the influence of weather on display rates. In addition to these two aspects, the role of stimuli and triggers in the Bengal Florican display behaviour are also discussed.

LESSER FLORICAN

Display patterns in the Breeding Season

The onset of attraction displays in the breeding season is a phased affair. Until the establishment of territories, males display with decreasing sporadicity. Initially, after arrival, males display very rarely, perhaps less than eight or 10 times in a day or even not at all. Soon display is seen at greater frequencies and the onset of territorial behaviour is characterised by sustained attraction display. Once territorial behaviour sets in, the time spent in display does not appear to vary significantly between days. Males spend 70% or more of the day in display activities for most of the territorial phase. Variations in the number of display leaps in a day, or the time spent in display, can just as easily be attributed to fluctuations in daily weather conditions (see also below). On a predominantly rainy or sunny day, males display less irrespective of whether they are in the early or peak display phase.

What does vary, however, is the nature of the display leap, i.e. whether the male moves between leaps or preferentially displays from a fixed spot. During the early territorial phase, males move constantly between display leaps. A decrease in such movement between leaps is simultaneous to an increase in spot specificity in display, until most displays are performed from a few spots only. This change can be attributed to different reasons, and the degree of influence of each is yet to be determined.

First, the period of lowest spot specificity coincides with lower availability of food resources. In this period would have to spend more time in foraging over a wider area to fulfill nutritional needs and perhaps to build up a certain amount of energy reserves as well. Dharmakumarsinhji (1950) opined that 'when the birds have newly arrived, when they are in lean condition, they feed at all times of the day.' As the season progresses, insect life becomes considerably more abundant, and individuals would have to spend less and less time to fulfill nutritional requirements.

Secondly, if fitness of a male is advertised by frequency of display and thus enhances mating success, then as the breeding season progresses males should attempt to display at maximum frequencies. (The time lag between leaps was significantly lower in spot specific display than that of no spot specificity, i.e. males displayed at higher frequencies when they did spot specific display than when they were not spot specific). Thus a peak in display rates should be evident in early to mid August when females become receptive. Males may achieve this, not by increasing time spent in display but by reducing movement between display which results in an increase in frequency of jumps. Therefore a change is seen in the kind of display i.e. from no spot specificity to spot specificity as the season progresses.

The third possibility, the only one which has been directly substantiated, deals with grass height. A strong positive correlation is seen between spot specific display and increasing grass height. This correlation can have three explanations. a) On arrival of the floricans, the grassland is bare of vegetation. Sustained display at fixed sites, in the absence of sufficient cover, could greatly increase predation risks. Thus with increasing grass cover, males can display with relatively greater safety from fixed sites for longer durations. b) As insect abundance is directly related to increasing grass height, the second reason may be merely concomitant to that of nutritional demands (see above). c) The third explanation is rather simplistic but has evidence to support it when different grassland sites are compared. Arbitrarily chosen display sites occur at a time when the grass height is short and free movement is possible. Once the grass grows taller, about 20 cm or more, arbitrary choice of jumping spots will be hampered by the grass. So males return to fixed spots as these are trampled bare of vegetation, and are also set in patches of shorter grass.

Thus the height of the grass does not hamper display. This is evidenced by the fact that in years of lower rainfall and the resultant shorter grasses, males tend to spend more time in non spot specific display than in spot specific display than in years of greater grass heights. Also, in grasslands with greater grass heights, as in Rampura, males spend far more time in spot specific display than in grasslands that have shorter net grass heights (like Naulakha).

It is likely that all the above reasons, i.e. nutritional demands, advertisement of fitness and grass height, play a role in the observed change in display patterns from non-spot specific display to spot specific display.

Effect of Weather on Display Rates

A consistent observation in all literature on the Lesser Florican is its preference to display in cloudy or overcast weather conditions (Jerdon 1864, Baker 1921, Dharmakumarsinhji 1950), this preference having been quantified by Ridley et al. (1985). The display leap of the Lesser Florican communicates both acoustic and visual signals over longer distances and should logically be performed most frequently during weather conditions that maximize the range of such signals. That the leaps of the Lesser Florican are performed maximally during weather conditions that do not maximize the range over which these signals are communicated is of particular interest. For instance, audibility is high when an inversion is present and may account for the high levels of bird song on clear calm mornings (Elkins 1983). Similarly visibility is higher on clear days, and sunshine would better contrast the black and white plumage of the male Lesser Florican during its display leap. Yet males display at higher rates under overcast conditions when presumably both auditory and visual ranges are reduced. Then again, turbulence during strong winds reduce the audibility of acoustic signals (Elkins 1983), yet there is no significant differences in display rates under different wind speeds.

Several species of birds display mainly at dawn and dusk or at night and include among others the Sage Grouse (Gibson and Bradbury 1987), Little Bustard (Cramp and Simmons 1980, Shulz 1985), the Great Snipe (Avery and Sherwood 1982, Hoglund and Robertson 1990), and the Kakapo (Merton et al. 1984). Other species of birds have been specifically associated with particular types of weather. For instance, the Mistle Thrush or 'Storm Cock' and the Red Flanked Blue Tail are both persistent songsters in rainy and windy weather, and damp cloudy days with drizzle have been typically associated with the 'reeling' of the Grasshopper Warbler and the drumming display of the snipe. Elkins (1983) suggests that the rather unique sounds of those species associated with inclement weather may carry further under cloudy or overcast conditions.

When contrasted with the above examples, the Lesser Florican stands out as an anomaly. It is neither nocturnal nor crepuscular in its display behaviour and hence light intensity cannot be the reason why it prefers to display in overcast conditions. Neither can its display be typically associated with cloudy weather as males display in sunny weather, albeit at lower rates. The tendency of the male to display in all weather conditions indicates that even if the acoustic quality of the display rattle is enhanced in cloudy weather, it does not play a significant role in the marked preference to display at higher rates in inclement weather.

The frequency of bird song, rather than the audible range is possibly of greater biological significance (Elkins 1983). For instance, in the Sage Grouse, 'males that mated attended the lek more often, strutted (displayed) at higher rates and scored higher on acoustic component than those that did not mate (Gibson and Bradbury 1985). If a similar correlation is present in the Lesser Florican, then it could explain why males display at higher rates in cloudy weather. Males should display at higher rates in those environmental conditions that require the least expenditure of energy, or more important, cause least stress to the individual. Ridley et al. (1985) suggested that male Lesser Floricans avoid displaying in direct sunshine because the sun heats up the black body of the bird too much, or because females are perhaps more active in overcast conditions.

If display rates are associated with mating success (as seems plausible - see also display patterns), then males should display for as long a duration and at as high a rate as possible to maximize success. However, display rates should peak under certain conditions that causes least stress to the individual. A high display rate in hot sunshine should cause thermo-regulatory stress on the individual. This is also indicated by the inverse correlation between display rates and temperature. Hence males display at higher rates in cloudy conditions, when heat stress must be least, than in sunny conditions when heat stress should be most.

Under strong windy conditions, a male displaying as close as 50 m or less down wind is often inaudible to the human observer. Conversely, a bird displaying in strong up wind can be heard as much as 500 m away or more. Perhaps such compensations in open country result in the absence of a significant variation in display rates under different wind speeds. Secondly, if display frequency is of more importance than auditory range, then a similar reason as given earlier should also hold true. Except that as wind does not create any perceptible stress, there is no variation in display rates. Lastly and more trivially, in the monsoon it is almost always windy. Hence males would have little option but to display in all wind conditions.

BENGAL FLORICAN

Display Patterns

The strong variation in the number of displays that a male Bengal Florican performs between the morning and the evening of a single day and between days and the resultant lack of a distinct peak in the display behaviour in the breeding season is difficult to explain. This is compounded by the fact that males, on an average, perform three or four flight displays per display period. What mate attraction value can such sporadic display have? There are two possible solutions to this puzzle. The first deals with whether duration of presence in the display area or the frequency of display is of greater importance and carries on to cover the rather ephemeral 'degree of arousal'. The second deals with seasonality of nesting.

Adult male Bengal Floricans weigh 1.5 kg or more. This appears to be at the size threshold of bustards, above which males exhibit only ground displays and below which the species perform aerial displays (see Chapter 6). A Lesser Florican like display leap, and at similar frequencies, is obviously not possible for the Bengal Florican to perform due to its body size. As a result there is greater diversity in attraction displays that range from ground displays to the aerial display.

The displays of males are restricted to the early morning and the late evening hours. They are also confined to distinct display areas within each male's territory, these being characterised by short grass. Thus once males enter their display area, they are easily visible. Males attempt to make themselves even more conspicuous by standing on mounds of sand (caused by rodents?) that raises them a few more centimetres over the surrounding flat land. A considerable part of each display period is spent in the male just standing in such open patches. Should such exposure be considered as a display itself. By just placing itself prominently at a traditional site, a male passively advertises itself, or advertises occupancies of the site. If this is true, then just presence in a prominent open patch, or the duration of such presence could be of greater importance than the actual number of displays that the male performs.

The displays of the Bengal Florican can be related to the degree of arousal that an individual experiences at a given moment. The most passive of these displays is the male just standing or being present in an open patch within its territory. Slight arousal results in a partial neck fluff display, with greater arousal resulting in the complete neck fluff display. Total arousal culminates in the flight display. When the kind of display performed is considered in terms of arousal, then the seemingly inexplicable fluctuations in display numbers begins to make sense. A male will perform its neck fluff or flight display the number of times it gets aroused. The number of times a male gets aroused will depend both on extrinsic and intrinsic factors. The presence of a female for instance, causes it to display more often (see also Narayan and Rosalind 1988). However, levels of arousal appear to be determined by predominantly intrinsic factors. Thus variations in the frequency of displays will occur due to a variation in intrinsic levels of arousal between display periods and between days.

An alternative explanation is based on the patterns of nesting and receptivity of the females. Only one nest was found during this study (see also Narayan and Rosalind 1988, Narayan 1990). However, data sifted from Baker (1921) indicates that egg laying and nesting occurs over most of the breeding season (see Chapter 5). This is an expected breeding response to the habitat in this species. In Chapter 2 it was shown that growth of grass is primarily determined by factors like ground water, dew and humidity. As some parts of the grassland are wetter than others, it results in a mosaic of grass patches of varying heights throughout the breeding season. Consequently, optimal nesting conditions are available from a few weeks of the annual grass burn onwards. When the distribution of courtship interactions of the Lesser Florican (where there is a distinct nesting period) and the Bengal Florican (where there is presumably no distinct nesting phase) are contrasted, it is evident that females solicit males throughout the breeding season in the Bengal Florican. The absence of a peak in female receptivity could result in the absence of distinct peaks in male courtship activity, resulting in the display patterns that were seen in this study.

Effect of Weather and Temperature on Display

The absence of significant variation in display rates under different weather conditions in the Bengal Florican is easily explained. During the summer, when this species breeds, cloudy skies are quite the exception. Evolution of a preference must result from the existence of sufficient choice. The absence of sufficient cloudy conditions and the presence of a relatively homogeneous weather condition appears to have resulted in this species not having any preference to display under particular weather conditions. Nevertheless males tend to spend longer periods in the display area during cloudy mornings, resulting in a longer time range when displays may be performed. However, there is insufficient data to quantify this.

The absence of a significant correlation between display rates and temperatures is less easily explained. The breeding season of the Bengal Florican begins at the end of winter, carries on through summer and ends at the onset of the monsoon. During this period the minimum ambient temperature ranges from 6° C to 25° C and the maximum ambient temperature ranges from 20° C to 45° C. Thus males have a wide range of temperatures at which they may display during the breeding season. For instance, on a typical summer day males are present in the display area until about 0830 hours when the ambient temperature is about 35°C. When they return to the display area at about 1630 hours, the temperature is about 42°C. Thus on a typical summer day, males display over a temperature range from 27°C to 42°C. This results in the absence of a significant variation in display rates with temperatures, both within days and through the breeding season. That temperature is not a critical factor in this species is also seen in that the males can display at high temperatures (42°C), yet do not display in the afternoon on days when the temperature is 35°C or less.

Display Periods

The restriction of display to the early morning and late evening hours are is related to factors other than temperature. Two plausible explanations are available. First, it is possible that light intensity (not measured in this study) is a limiting factor, and hence the restriction of display to certain times of the day. This, however, does not seem true as at 1630 hours when the males start display, the glare is far greater than at 0830 hours when they stop display. Furthermore, a preference for displaying in dimmer light conditions should result in a preference for displaying in cloudy conditions, which was not observed in this study.

The most plausible explanation for the observed periodicity in male display is that the female Bengal Floricans are most active in the early morning and late evening hours. The choosing of the males by females would then be restricted to the same periods, with the resultant evolution of males displaying at the same periods. Though not corroborated in this study, some other species have shown that it is so. For instance, out of seven mating observed in the Great Indian Bustard most were in the late evening hours (Rahmani 1989). In the Sage Grouse, females mate mainly in the mornings and less frequently at dusk or on moonlit nights (Wiley 1973, Gibson and Bradbury 1986). In the Little Bustard, certain courtship displays are restricted to dawn and dusk, while others are restricted to the mornings and evenings. Though males chased females all through the day the 3 observed matings were in the morning and late evening (Shulz 1985). Such observations have been made in other studies as well and it is likely that such marked preference for choosing and mating with males at certain periods of the day has led to males displaying almost exclusively in those periods. However, it can be argued that females solicit males in the mornings and evenings because males display only at those periods and clearly more research is needed to arrive at a better understanding.

Stimuli and Triggers

At first glance, the most curious aspect of the behavioural repertoire of the Bengal Florican is its display response to certain sounds, primarily the 'mayaw' call of the peacock and secondarily the 'caw' of the jungle crow. Why do such sounds elicit an immediate display response from the Bengal Florican? What biological significance, if at all, can such calls have on the breeding behaviour of the Bengal Florican? The analysis and descriptions of display responses to external stimuli leads us first to the definition and classification of the sources that elicit such behavioural responses. These sources can be classified as those that stimulate and those that trigger a behavioural sequence.

(a) A stimulator is of biological importance to the individual in that it acts as a releaser of a behavioural sequence. For instance, the presence of a female stimulates a male to display. A stimulus has a longer effect in terms of time duration in that it can elicit both an immediate as well as a delayed response. For example, the tendency of males to display in a narrow time range after the display of a rival male.

(b) A trigger, on the other hand need not be of any biological significance to the species and to the behavioural sequence that it releases. A trigger releases the response immediately. In this case, the time lag between the trigger and the response was zero seconds i.e. the behavioural sequence (display) was released when the trigger (peacock or crow call) was actually being sounded. A time lapse of two or more seconds from a possible trigger did not influence a male to display.

The correlation between peacock calls and the Bengal Florican was first documented by Narayan and Rosalind (1988). One possible explanation for this correlation, also suggested by Narayan and Rosalind (1988), is that apart from acting as a stimulus, the 'mayaw' call of an unalarmed peacock acts as an all clear signal to the Bengal Florican. Thus a male displays in response to the peacock call because the call signals the absence of predators in the vicinity. This hypothesis however, has insufficient evidence for to support and does not answer the following arguments.

(a) Peafowl have a wide repertoire of calls, but the exact function of many calls are to be adequately defined (see

Johnsingh and Murali 1980). The 'mayaw' call, which triggers display in the Bengal Florican, is a social call (Johnsingh and Murali 1980), that apparently has some breeding connotations as it is most often made during that season. It is certainly not an alarm call, but that does not necessarily mean that it is an all clear signal is. Often the utterance of this call is an echo to an alarm call of another peacock, or some commotion in the forest.

An alarm call is an honest signal, i.e. the announcement of a predator that the individual has seen, and the advantage of such signals to both conspecifics and other species has been documented extensively in literature. However, an all clear signal is not a reliable one, as it simply indicates that the source has not seen a predator. Dependency on such a signal, especially that of another species, for display does not fit.

Even distant (500+ m) peacock call trigger display. The value of an all clear signal over such a distance is doubtful, especially in long grass.

(b) Though peacock calls are the predominant releasers of display, calls of the Jungle Crow and very rarely that of the Indian Pied Hornbill and (once) of a gunshot also release displays. This also indicates that it is the sound rather than any message that the sound may be signaling.

(c) Lastly and more significantly, the Peacock call elicits an immediate behavioural response from the Bengal Florican. It does not have any lag effect and acts purely as a trigger. If the peacock call is an all clear signal, and thus of biological significance to the Bengal Florican, then a call at one instant will be of value for some time after that instant. This would result in males clustering their displays near an all clear signal. However, the observations do not reveal this, and instead show that only the instant of the call is of significance and the period following it.

It is rather improbable that the Peacock call signals any particular message to the Bengal Florican that results in the latter's display.

What then are the reasons behind the observed display responses of the Bengal Florican to the peacock and Jungle Crow calls? This question is easily answered when these calls are considered purely as triggers and not as stimuli (see above). Early ethological literature succinctly describes and explains such phenomenon (see Gould 1982 for a review). Tinbergen (1951) demonstrated the release of complex behavioural sequences by very simple and crude stimuli in a number of species of animals. He explained this by identifying complex behavioural sequences as 'fixed-action pattern' (FAP), an innate and highly schematic filter that released the FAP when anything stimulated its criteria for that behaviour as the 'innate releasing mechanism' (IRM), while the features of the stimulus essential in triggering it were termed as 'releasers' or 'sign stimuli'. His experiments demonstrated that the criteria of the IRM in filtering stimuli are very crude and often is just one basic aspect of the object. For instance, any object that is concave and does not have sharp edges fulfills the criteria for 'eggness' that triggers the egg rolling behaviour in geese. Thus a goose performs the egg rolling behaviour (fixed-action pattern) when the IRM is triggered by any object (e.g. a volley ball - releaser or sign stimuli) that fulfills its criteria for 'eggness'. Similarly, the removal of eggshells from the nest (FAP) is triggered by any object (sign stimuli) that fulfills the IRM's criteria for 'eggshellness'. In both cases, complex behavioural patterns that have strong survival implications on the eggs and chicks are released by very simple 'sign stimuli that fulfill the criteria for 'eggness' and 'eggshellness'. Other examples of 'releasers' have implications on breeding and in all cases the releasers are directly related and have direct beneficial implications on the species in some way or other (Tinbergen 1951, 1972).

It is shown below that the display response of the Bengal Florican to sound stimuli is similar to the examples given above. However, before that a point needs to be raised. In the case of the Bengal Florican, the trigger (or releaser), i.e. peacock or crow call, does not have any biological implications of either survival or breeding. This then raises the question of why and how this particular trigger/response syndrome came into existence.

Tinbergen's (1951) studies revealed the existence of 'super normal sign stimuli'. For instance, the egg rolling behaviour of the Oystercatcher was triggered by an enormous egg over its own egg, when a choice of both was made. Similarly, a goose was triggered by a volleyball rather than its own egg, and in the Grayling butterfly, models of much greater size than normal got more responses than models of normal size. Thus in such cases, it was evident that the bigger the 'sign stimuli', the greater the trigger effect.

The evolution of the peacock and crow calls as a releaser of the Bengal Florican's displays can be attributed to the linkage of a 'super normal sign stimuli' to a complex behavioural action. Male Bengal Florican are stimulated to display on hearing the acoustic signal (wing clap) of the flight display of a rival male. This is evident because males that are not within sight but are within hearing range display soon after a rival's display. It is suggested that the wing clap sound, or some component of it, is the 'sign stimuli' that stimulates the innate release mechanism to induce the bird to display (FAP). However, during the evolution of this behavioural sequence, 'super normal stimuli', i.e. louder sounds, got linked to the display patterns of the Bengal Florican. Further fixation in the behavioural sequence resulted in certain calls like the peacock's 'mayawe' or the jungle crow's 'caw' acting as triggers, while the original source of this, the display sound of a rival male continuing to act as a stimulus.

The major factor in the fixation of a 'super normal' stimuli triggering the displays of male Bengal Florican, lies in the nature of the displays themselves. In nature, 'sign stimuli' like for instance eggness have remained crude and simple, primarily because the probability of being repeatedly 'cheated' is very low. (Only an ethologist would keep placing a volley ball next to a goose's nest!). Whenever the probability of such 'cheating' becomes high, then the innate-release mechanism would necessarily become more complex, and 'sign stimuli' that are not of biological significance to the species would be filtered out.

The neck fluff display and the flight display of the Bengal Florican are attraction and territorial displays of the Bengal Florican. These displays though directed towards females are rarely made in the presence of one and are meant as signals for longer distances. Thus these displays are not measured in terms of responses elicited as is typical in such mating systems. Thus the fixation of the 'super normal sign stimuli' as a trigger for display could never be measured in terms of effectivity or even of direction and thus could never be weeded out as a worthless 'sign stimuli'.

The other factor which has resulted in the fixation of a 'super normal stimuli' as a trigger is the sporadicity of displays in the Bengal Florican. For instance some other species of birds have been known to display to stimuli that have no biological significance, but such instances are rare. The Great Indian Bustard has been recorded displaying to quail (Rahmani and Manakadan 1987b). Bouts of display have been triggered in the Black Grouse by a flying Woodcock (Koivisto 1965), the barking of a dog and explosive sounds from a mine (Hohn 1953). In both these examples, displays occupy time and are not individual acts. (Koivisto 1965, Rahmani 1989). Constant display as in the Great Indian Bustard and bouts of display that perform an act repeatedly as in the Lesser Florican should not have any fixed triggers. A 'sign stimuli' may release a bout of display but as the display occupies time each individual display act cannot be triggered simply because it is being performed too frequently. In the Bengal Florican however a male may display 10 or 15 times in a display period of 3 hours. Such sporadicity has resulted in each display act being a single independent unit. Thus the fixation of unrelated triggers also appears to be a function of the sporadicity of an act.

It is of considerable interest to see that this complex behaviour pattern has varied release mechanisms that do not necessarily resemble each other. For instance a female will elicit a display response and the display of a rival male does likewise. Display is triggered by a peacock or crow call. Arousal in the absence of such stimuli still results in the male displaying. It is evident that in this species that only if a male is at some degree of arousal will a trigger cause it to display. Thus for instance, most peacock calls do not trigger display as the male is not intrinsically aroused. But when aroused or ready to display, a peacock call triggers the display. Absence of a peacock call when the male is aroused results in it being triggered by a crow call if such is sounded, or occurring without any sound triggers. Thus, arousal is essential before a male will display. Triggers only release the display in an aroused male.

One aspect that has been not covered in this study due to a lack of equipment is whether there is some component in the wing flapping sound of the Bengal Florican's display with the calls of the peacock and crow. An understanding of this would result in a better knowledge of the role of this behavioural sequence.

Chapter 5

NESTING BEHAVIOUR

Both the Lesser Florican and the Bengal Florican are ground nesters as are all other species of bustards. The nest itself is a simple scrape in the ground without any nesting material added, and the behaviours associated with nest building are absent in this family (Osborne et al. 1984).

Primarily due to the nesting habitat, long grass, florican nests are very difficult to find. This is made more so by the shy secretive behaviour and the cryptic colouration of the hens (see also Narayan and Rosalind 1988). Once nests were found, however, detailed studies on the nesting behaviour were not made, primarily because these species are currently threatened. The information on nesting behaviour gathered during this study is therefore limited.

RESULTS

LESSER FLORICAN

The Lesser Florican usually lays between 3 and 6 eggs (Baker 1921). Of the 9 nests recorded in this study, one had five eggs, four had four eggs and four had three eggs each (Table 5.1). There was a distinct nesting phase in the breeding season of the Lesser Florican (Fig. 4.6). Nesting began in the first week of August and all nests had hatched by the last week of September.

The incubation period was ascertained from one nest and was 21 days. The male played no role in the incubation of the eggs. The chicks, were precocial, nidifugous and covered in a short, plush-like, highly cryptic down.

The nest locations were either at the periphery or well away from male territories (Table 5.1). All nests found, were in the grassland, barring one which was found in a stunted, unweeded maize field. This (the only one to be) was preyed upon, possibly by crows.

While on the nest, female Lesser Floricans, did not flush unless almost trampled upon. They preferred to avoid detection by sitting tight on the eggs and relying upon the effective camouflage. Thus a nest with an incubating female is unnoticeable, even when the location is known, from as close as five feet or less. The tendency of the females not to flush or move away at the sound of approaching danger enables the tribals of the area in trapping females by throwing a net or a basket over an incubating hen.

The female with the young stay on in the grassland until mid- or end November as evidenced by stray sighting and/or flushing records.

TABLE 5.1
NESTING DATA OF THE LESSER FLORICAN

Year	Date found	Date laid (last egg)	Date hatched	No. of eggs	Dist.(m) from male	Habitat
1985	16 Sept.	2 Sept.	23 Sept.	4	115	Grassland
1985	19 Sept.	31 Aug.	21 Sept.	3	>150	,,
1986	28 Aug.	30 Aug.	20 Sept.	4	114	,,
1986	30 Aug.	-	-	3	>500	Cropfield
1986	5 Sept.	21 Aug.	14 Sept.	4	100	Grassland
1986	17 Sept.	6 Aug.	27 Sept.	4	75	,,
1989	16 Sept.	27 Aug.	17 Sept.	5	>500	,,
1989	16 Sept.	27 Aug.	17 Sept.	3	>500	,,
1989	2 Aug.	1 Aug.	22 Aug.	3	>150	,,

N.B. For 1989, all dates estimated from an assumed hatching date of one day after unhatched clutch last seen

BENGAL FLORICAN

Only one nest was found of this species during this study. On 24 April 1988, a nest with two eggs was found. On the following morning when the nest site was visited the eggs had been preyed upon, probably by a crow. The absence of blood vessels indicated that the eggs were fresh and the embryo had not yet formed.

DISCUSSION

The major difference between nesting in the Lesser Florican and the Bengal Florican is in the presence of a short and distinct nesting phase in the former and an absence of it in the latter. Data sifted from Baker (1921) shows that though there is a two month peak egg laying phase, nesting is spread between late February and early June. Whereas nesting in the Lesser Florican occurs between early August and end September.

This difference can be explained, in part, as a result of factors in the breeding environment. The onset of laying in the Lesser Florican should be limited by two primary factors, the availability of food and nesting habitat. Depending on the degree of protection from grazing that the habitat receives, and the onset of the rains, these prime requisites vary between years and locations. Both at the Naulakha and in Kuchch nesting occurred in August (Table 5.1). Moreover, though rains began fully a month late in 1985, nesting was not postponed, but occurred in exactly the same phase as during 1986, in which year the monsoons were on time. Thus while food and nesting site are the prime requirements for nesting, a third factor which influences nesting period exists.

In normal south west monsoon conditions, the rains peak in the last two weeks of July. Until early August there are frequent spells of rains when for two or three days it rains continuously. Thus the risk of inundation of the nest is high until mid-August. Females should therefore have evolved the commencement of laying at such a time that the risk of loss of eggs through inundation or by bad weather is reduced. Thus females begin laying only in early August, with a peak a little later, and thus avoid majority of the rains of the south west monsoon. Heavy rains are brief from mid-August, and barring the early nesters, most others effectively minimise the risk of nest inundation.

This appears to be a plausible explanation as several studies have shown that inundation or bad weather comprises a significant proportion of factors that destroy eggs and nests (Boyd 1972, Morton 1978, Shipley 1984, Warriner et al. 1986). Thus the evolution should be such that females nest when the probability of bad weather is least.

As the Bengal Florican is a summer breeder, the risk of inundation of the nests is largely absent. However, they should time themselves such that incubation and hatching are completed and the chicks have been partly reared before the onset of the south west monsoon for the same reasons as that of the Lesser Florican. The availability of a mosaic of grassland habitat throughout the summer enables the Bengal Florican to nest at most times in the breeding season.

Thus while the monsoon influences the date from which female Lesser Florican can begin nesting, the onset of the rains influences the date by which time female Bengal Floricans should have completed nesting.

Chapter 6

SOME CONSIDERATIONS ON ADAPTIVE DIFFERENCES IN THE LESSER FLORICAN AND BENGAL FLORICAN

INTRODUCTION

The final chapter of this dissertation is primarily discussive. It attempts exploring certain areas that have emerged as of particular interest when both species of floricans are compared. The first of these is a speculation on the affinities between the Lesser Florican and Bengal Florican, two species that at first glance are obviously closely related. The next is an attempt at understanding the kind of breeding systems that the Lesser Florican and Bengal Florican follow. The last deals with the primary feature that sets both the florican species distinctly apart from all other species of bustards. Why are female Lesser Floricans and Bengal Floricans larger than the males?

Prior to dealing with these three topics, two analyses are presented. These analyses do not actually fit into any of the previous chapters, but are necessary for a better understanding of the two species. A reference to the correlation between bustard body size and display type has already been made in chapter 4. The vulnerability to aerial predation is referred to while discussing the displays of the two species.

Relation between Bustard body size and display types

The family Otididae is comprised of 22 species. The variation in body size within the group is quite remarkable. The smallest species (Lesser Florican) weighs about 0.5 kg (wing length 180-248 mm) while the largest species (Kori) weighs over 10 kg (wing length 629-761 mm). Correspondingly, bustard displays vary, from ground to aerial displays.

In this analysis, all data has been extracted from Ali and Ripley (1969), Cramp and Simmons (1980), and Collar et al. (1986). The use of body weights in the analysis has proved unsatisfactory primarily because the variation in available data is large (±50% of the mean). Body weights are variable and dependent on several factors such as season, availability of food and condition of the bird. Wing length, however shows less variation (±20% of the mean). Moreover, once birds reach adulthood, wing length becomes more or less fixed and will not vary in response to extrinsic factors. Both wing length and body weight are indicators of body size, and body weight is directly correlated to wing length (Fig 6.1). Thus in this analysis, which attempts relating display types with body size, wing length is used as a measure of body size.

Bustard attraction displays are divisible into two groups, namely aerial displays and ground displays. Aerial displays can be further classified into two types based on

FIG. 6.1. BUSTARDS
WING LENGTH AND BODY WEIGHT

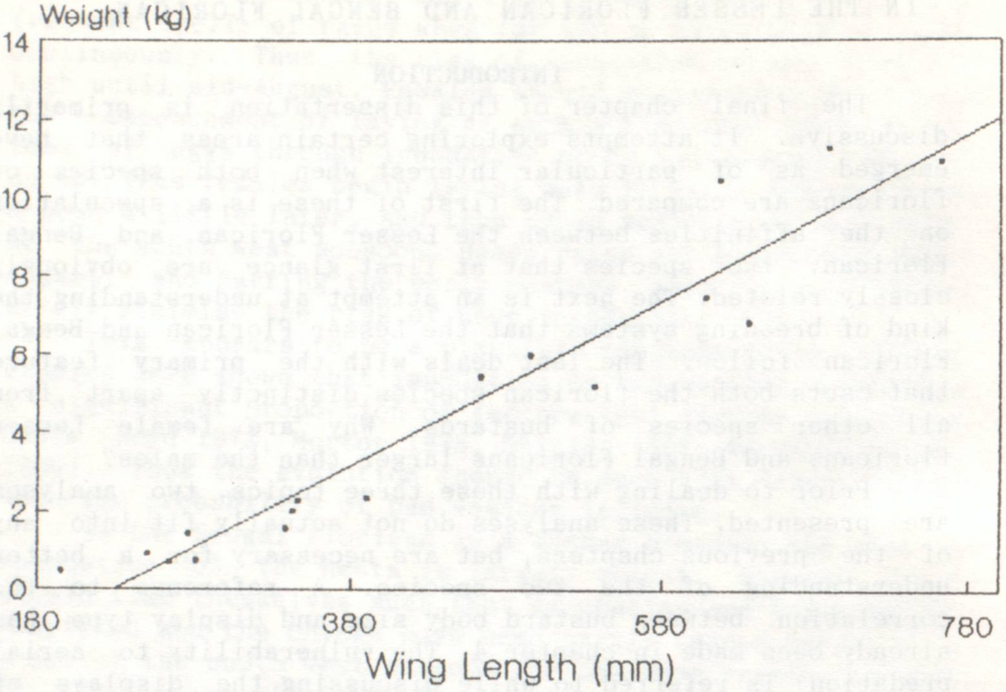
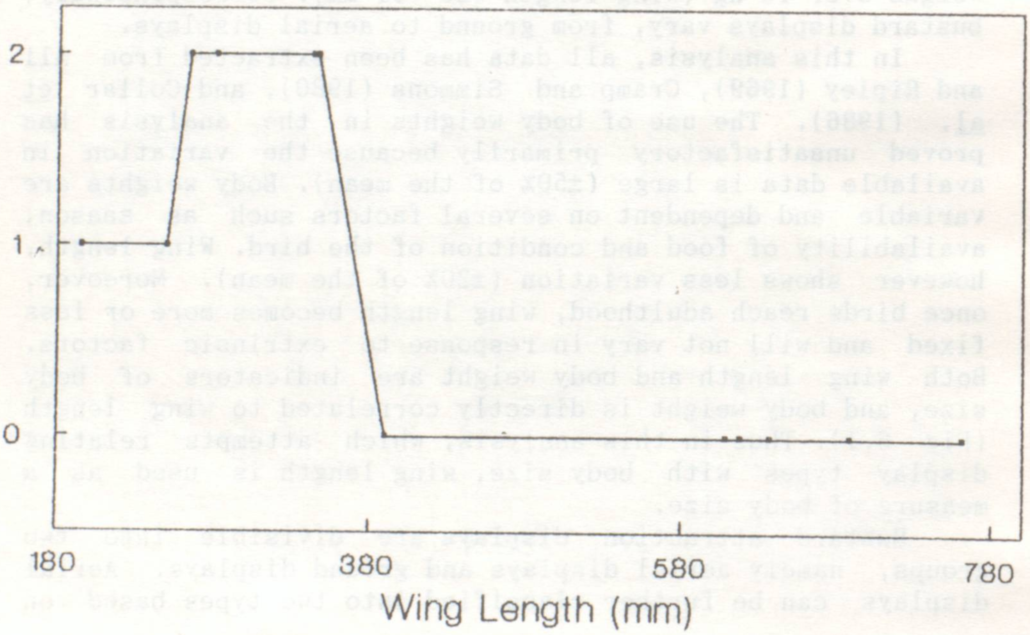


FIG. 6.2. BUSTARDS
WING LENGTH AND DISPLAY TYPES



1 - Jumping display; 2 - Flight display;
0 - Ground display

the duration and the type of display. The first is the jumping type of display. This is of very short duration (e.g. Lesser Florican one second jump; Little Bustard half second jump, Shulz 1985), and consist of a brief vertical display leap. The other type of aerial display is a display flight that lasts for 6 or more seconds and consists of a short or extended flight from one point to another. This type of display is seen in the Black, Buff Crested (?) and Black Bellied Bustards (Osborne et al. 1984) and the Bengal Florican.

A distinct correlation is seen between body size and display types. The small bustards have aerial displays, with the smallest of these having a jumping type of display, those species with an increased body size having flight displays, and beyond this body size all bustards have ground displays (Fig 6.2). This analysis also shows that the Bengal Florican and the Black Bellied Bustard are at the size threshold beyond which all bustards have ground displays. The next larger species i.e. the Houbara is 12 - 15 % larger than the Black Bellied Bustard and only has a ground display.

The Bengal Florican, being at the body size threshold of aerial displays, has few and sporadic displays (see also Chapter 4). This bustard also has a distinct ground display, the neck fluff display. A ground display is also seen in the Black Bellied Bustard (pers. obs., Cramp and Simmons 1980). At the other extreme of the size scale is the Lesser Florican, which has very frequent display jumps and no distinct ground displays. It is most probable that in bustards body size plays a strong role in the type of displays seen. The smallest bustards have short display leaps that are made very frequently, larger species have longer flight displays, and as body size increases, frequency of displays reduces. Ridley et al. (1985) also suggest that a short leap is associated with greater frequency. Beyond a certain size threshold, all bustards have ground displays.

Vulnerability to Aerial Predators

The necessity to escape or avoid predators is a major requisite for a species' survival. Thus most life history requirements and the corresponding behavioural responses must have evolved in such a way as to minimise such risks. The vulnerability to aerial predation is an important factor to be considered when the significance of behavioural traits in a species is examined; this is particularly important when that species performs aerial attraction displays. The following analysis lists diurnal aerial predators that occupy the same geographical range as the floricans, and indicates whether each raptor species is capable of killing either species of florican. This was done by finding out the largest prey species that each species of raptor has been recorded as killing from Ali and Ripley (1969). If a prey species is of equivalent size to either of the floricans, then that raptor is said to be capable of killing that species of florican. The analysis does not claim to indicate preference or regularity (or even if ever killed) of predation by raptors on either species of florican. It merely compares the number of raptor species that can potentially kill the Lesser Florican and Bengal Florican.

Of the 43 species of raptors listed in Table 6.1, 20 (46.5%) are capable of killing adult Lesser Florican, but only 4 (9.5%) can prey upon an adult Bengal Florican. Clearly the degree of vulnerability from aerial predators is a function of body size. Thus the Lesser Florican which is about a quarter the weight of the Bengal Florican is vulnerable to about 5 times the number of aerial predator species.

Morphological and Behavioural Affinities between Floricans

Taxonomic classification within the family Otididae has generated confusion, with the result that relationships within the family are still poorly understood (Cramp and Simons 1980, Osborne et al. 1984). So much so, the species that comprise this family have been classified into a number of genera that have varied from 8 to 11. Currently, 22 species subdivided into 47 subspecies are classified into 8 genera, five of which are monotypic (Osborne et al. 1984). This confusion in taxonomic classification over the years is typified by the changes in placement in systematics that the floricans have gone through. The Lesser Florican has been variously classified as Otis fulva, Otis indica, Otis aurita, Otis marmota, Sypheotides auritus, Eupodotis aurita, Sypheotis aurita and Sypheotides indica. Similarly, the Bengal Florican has been variously named as Otis deliciosa, Otis himalayana, Otis bengalensis, Sypheotides bengalensis, Sypheotis bengalensis, Eupodotis bengalensis, and Houbaropsis bengalensis.

The placement of these two species in separate genera in modern classification has been based primarily on one character. The male Bengal Florican was believed not to have an eclipse plumage while the Lesser Florican was known to have a female like eclipse plumage (Baker 1921, Ali and Ripley 1969, but see also Jerdon 1864). This resulted in the placement of these two species in separate genera causing Ali and Ripley (1969) to comment '...but separation of the genus on this character alone inconsistent with other similar cases and seems doubtfully necessary'.

That the Bengal Florican does have a female-like eclipse plumage has now been established. All males arriving at the onset of the breeding season in the Dudwa National Park were moulting into the breeding plumage, a process that

TABLE 6.1
VULNERABILITY OF FLORICANS FROM DIURNAL AERIAL PREDATORS

RAPTOR	LENGTH OF WING (MM)	PREDATION LF	BF	LARGEST PREY RECORDED
Blackwinged kite	260-283	N	N	-
Blyth's Baza	327-360	N	N	-
Blackcrested Baza	227-243	N	N	-
Crested Honey Buzzard	382-445	Y	N	Chicken
Pariah Kite	420-499	N	N	-
Brahminy Kite	359-403	N	N	-
Eastern Goshawk	290-362	Y	?	Pheasant
Shikra	176-222	N	N	-
Crested Goshawk	230	Y	?	Pheasant
Sparrow Hawk	204-257	Y	N	Chicken
Besra Sparrow Hawk	165-210	N	N	-
Long Legged Buzzard	415-431	N	N	-
Buzzard	374-454	N	N	-
White Eyed Buzzard	278-314	N	N	-
Hodgson's Hawk-eagle	475-491	Y	?	Pheasant
Changeable Hawk-eagle	400-438	Y	Y	Imm. Peafowl
Crested Hawk-eagle	351-462	Y	Y	Imm. Peafowl
Bonelli's Hawk-eagle	458-550	Y	Y	Houbara
Booted Hawk-eagle	370-423	Y	?	Chicken
Rufousbellied Hawk-eagle	380-433	Y	?	Khaleej
Imperial Eagle	575-630	N	N	-
Tawny Eagle .	500-560	N	N	-
Greater Spotted Eagle	485-545	Y	N	Coot
Lesser Spotted Eagle	470-508	N	N	-
Black Eagle	520-610	Y	?	Jungle Fowl
Ringtailed Fishing Eagle	555-598	Y	Y	Demoiselle crane
Greyheaded Fishing Eagle	450-515	Y	N	Jungle Fowl
Himalayan Greyheaded F.E	426-495	Y	N	Jungle Fowl
Hen Harrier	341-392	Y	N	Chicken
Pale Harrier	332-360	N	N	-
Montagu's Harrier	334-395	N	N	-
Pied Harrier	344-387	N	N	-
Marsh Harrier	385-430	Y	N	-
Short Toed Eagle	520-571	N	N	-
Crested Serpent Eagle	472-484	Y	N	Chicken
Osprey	452-537	N	N	-
Laggar Falcon	316-370	Y	N	Partridge
Peregrine Falcon	297-379	Y	?	Khaleej
Hobby	247-379	N	N	-
Indian Hobby	211-248	?	N	Imm. Chicken
Redheaded Merlin	190-232	N	N	-
Lesser Kestrel	222-244	N	N	-
Kestrel	230-270	N	N	-

Total Raptors 45
Total Raptors capable (Y) of preying on Lesser Florican 20,
Total Raptors capable of preying on Bengal Florican 4

N.B. (a) Source of all data - Ali and Ripley 1969. (b) Raptors of same geographical range, but irrespective of habitat. (c) Table must not be misconstrued as indicating regular or preferential predation by raptors. (d) Approx. weights of adults (kg) : Bengal Florican 1.4-2.2; Lesser Florican 0.45-0.75; Grey Partridge 0.20-0.34; Pheasants :- Monal 1.80-2.4, Khaleej (all sub sp.) 0.8-1.7, Red Jungle Fowl 0.8-1.36, Koklas 1.03-1.42, Chir 1.25-1.7, Peafowl 2.75-4.0. (e) Approx. wing lengths (mm) : Bengal Florican 338-368; Lesser Florican 180-248; Grey Partridge 134-160; Pheasants : Monal 259-320, Khaleej 198-236, Red Jungle Fowl 177-244, Koklas 180-244, Chir 225-270, Peafowl 400-500.

lasted about two weeks, in both years of study, The patterns of the final stages of the moult were similar to that of the Lesser Florican when the latter were moulting into the breeding plumage at the onset of the monsoon (Sankaran and Rahmani 1986). A far more detailed observation on an identical process was made on the Bengal Florican in the Manas Tiger Reserve in Assam (Narayan under prep. Narayan 1990). Thus the one reason why these two species were classified into separate genera does not hold true any longer. Further, when contrasted with other species of the Otididae, two characters place them apart from the rest while indicating a very close affinity between the two species. Firstly, they are the only two bustard species in which the females are larger than the males, a difference which is more marked in the Lesser Florican and less so in the Bengal Florican. Secondly, and equally significantly, while all other bustards have a wing-tarsus ratio of 3.5 or more, the Lesser Florican and the Bengal Florican have a ratio of about 2.5 or less. Thus the placement of the Lesser Florican and the Bengal Florican in separate genera is most probably an erroneous one.

The discussion that follows is based on the assumption that the previous argument is true, that is, both the Lesser Florican and the Bengal Florican deserve placement in the same genera. The placement of the two species in a common genera would indicate a common ancestor prior to speciation. The reasons behind this speciation, and whether both radiated from a now extinct common ancestral form or whether one diverged from the other is in the absence of fossil records a matter of speculation, and of little significance to this discussion. (However, it seems most probable that the Lesser Florican has evolved more recently as it shows highly adapted characters, primarily the pointed primaries that produce the display sound, whereas such an adaptation is not seen in the Bengal Florican).

It would appear that the ancestral form of the Lesser Florican and Bengal Florican had two basic characters apart from possessing similar plumages. It must have had an aerial attraction display, and females must have been larger than the males. This section explores the similarities and the underlying causes of differences in the attraction displays of the two species.

There are two primary components in the aerial displays of both the Lesser Florican and Bengal Florican. The first is the visual component whereby the whites on the wings are flashed while the wings are flapped during the display. During display, the birds are made even more conspicuous by the contrast in the whites of the wings and the black body, neck and head. The second component is acoustic, that is, the clapping sound produced by the wings during the aerial display. These are essentially the two similarities in the aerial displays of the two species. (The Bengal Florican has in addition a 'chik' call. This however is not purely an aerial display call as it is produced during aggressive interactions as well as during normal flight, indicating that it acts as an all purpose signal.)

The differences lie in two sets of characters. Firstly, while the Bengal Florican's display lasts on average for 6 seconds, the Lesser Florican's lasts only for one second. The other major differences that are related to aerial display are morphological. The entire wing of the Bengal Florican is white, while in the Lesser Florican the white of the wing is reduced to a band that covers approximately the secondary feathers and which joins the whites of the other wing by a narrow band that runs over the shoulder like a white collar. The second major difference is that the primaries of the Lesser Florican are emarginated, narrow and stiff, specialized to produce the display sounds. In the case of the Bengal Florican a very slight emargination is seen but on the whole the primaries are unspecialized.

The adaptive differences in both morphology and duration of display, that have retained the two essential characters of the ancestral display, i.e. flashing of white and the wing clap sound, is explained through one readily quantifiable limiting factor i.e. predation. 'The location of a communicator performing visible displays is apparent if the displays are seen. The likelihood of detection by predators can be reduced, however by limiting the amount of time during which the display renders the communicator conspicuous' (Smith 1977). It has already been shown that due to its body size, the Lesser Florican is far more vulnerable to aerial predation than the Bengal Florican. This could have been among the underlying reasons of the evolution of so brief a display in the Lesser Florican. In an almost tree-less habitat, leaps of such short duration, which are repeated unpredictably and with a frequent change of location would reduce risk of aerial predation (Ridley <u>et al</u>. 1985). The duration of the time spent in the air (one second) itself greatly reduces the vulnerability from aerial predation during the leap. Any danger from predation would essentially be on the ground. Thus the evolution of a reduced body size in the Lesser Florican would have resulted in a simultaneous reduction in the duration spent in the air during the display. This process must have accelerated once the species fell below a size threshold below which predation risks were greatly increased, with an end result of a one second display leap.

The morphological adaptations, that is, the reduced white on the wings and the stiff and pointed primaries has probably been an evolutionary result of the reduction in the duration of the aerial display. With so brief a duration in which to convey its signals, the acoustic component of the aerial display must have had an increasingly greater role to play in the displays. In a one second aerial display, an observing individual would have to be looking at the location of the communicator to actually see the display. A strong acoustic signal would therefore have been imperative to attract the attention of conspecifics in the first place. Assume that the ancestral form of the Lesser Florican had a simple wing clap sound. However, an acoustic signal made from simple wing flapping in so short a duration was probably weak in amplitude. It is suggested that as a result of this, the primaries of the Lesser Florican evolved to produce the loud wing sound and thus enhance the acoustic signal of the display. To the human observer, the loud display rattle is a far more effective advertisement than the visual impact which often goes unnoticed. Perhaps as the duration of display was further reduced, the acoustic component became the single most attention attracting factor of the Lesser Florican's aerial display. If true, then the aerial display which must have originated as a visual signal, now serves the more important function of delivering the acoustic signal, with the visual component taking second place.

Primarily due to its size, the Bengal Florican's aerial display is an extended one that lasts for six or more seconds. With a longer duration in which to signal, the display is primarily visual with a strong acoustic component. The wing 'clapping' sound caused by the rapid flapping of wings during the take off of the display serves to attract attention of an observer who then can easily watch the rest of the display flight. The visual component, that is, the white wings contrasted against the black body is often perceivable over greater distances than the sound of the wing flapping itself.

It is interesting to note that these two species, of greatly differing size, have a display sound that is produced by the wings and can be heard over approximately the same distances. However to communicate this signal, the Lesser Florican had to evolve specialized primaries, whereas the Bengal Florican did not.

Mating System

Avian mating systems can be classified into four categories namely promiscuous, polygynous, monogamous and polyandrous (Mock 1983). Though the promiscuous system is essentially a sub-division of the polygynous system, Mock's (1983) distinction is preferred here over Emlen and Oring's (1977) classification. This is because of the primary difference in both systems in male investment in offspring and the consequent criteria in female choice of males. Mock (1983) has defined each of these as :

a) Promiscuity. A commonly used term for polygynous systems in which no pair bonds form, and males contribute only gametes to the production of offspring.

b) Polygyny. Occurs when one male mates with two or more females, more or less concurrently. The essential distinction from promiscuity is that the polygynous male has some kind of social relation with the females and contributes post zygotically to the offspring, whereas the promiscuous male does not.

c) Monogamy. May be defined as a prolonged association and essentially exclusive mating relationship between one male and one female.

d) Polyandry. A female mates with two or more males, which then perform most of the parental care.

Each of these, however, can be further sub-divided according to ecological and/or temporal classifications (Emlen and Oring 1977, Wittenberger 1979).

Primarily due to an absence of sufficient mating and nesting data, the kind of mating system that the Lesser Florican and the Bengal Florican follow is difficult to empirically substantiate. That they follow one of two mating systems, that is promiscuous or polygynous, is obvious because males defend dispersed territories from which they display and indiscriminately court visiting females. Males of either species were never seen in protracted association with females or with young. For this reason alone both monogamous and polyandrous systems are ruled out, because in both these systems males must exhibit parental care.

By defining and understanding the types of polygynous and promiscuous systems, the mating system of the Lesser Florican and the Bengal Florican are arrived at primarily through a means of rejection of systems.

Polygynous systems can be further broadly classified into two systems namely resource defense polygyny and Female (or harem) defense polygyny (Emlen and Oring 1977).

In resource defense polygyny, males defend resources essential to females. When resources that are critical to female reproduction are unevenly distributed or spatially clumped, then competition among males revolves around subdividing and monopolizing these resources. Female choice of mate should be influenced both by the quality of resources in a male's territory (perhaps primarily), and the quality of the defending male. Such a system comes into play when the degree of resource clumping is sufficiently high that a female mating with an already paired male will have equal or greater reproductive success than if she mated with an unpaired male on a poorer quality territory (Orians 1969).

Female (or harem) defense polygyny occurs when females are gregarious for reasons unrelated to reproduction. Their self clumping tendencies facilitate direct monopolization by males, with the result that males forcibly accumulate females and herd them in harems.

Promiscuous mating systems occur when resources critical to female reproduction or females cannot be economically monopolised (Oring 1982). Males in these systems compete for females by sorting out positions of dominance and/or directly demonstrating quality through display (Oring 1982). Within this system two types of mating strategies are present, that is the lek system and the dispersed (or exploded) leks system (Bradbury 1981).

A lek can be described as a communal display ground where several males aggregate and display from small territories. Inter male distances are small, the territories within the lek possess no resources other than the display sites and only this is defended (Bradbury 1981, Oring 1982, Payne 1984).

The dispersed lek system is intermediate to the classical lek and the resource defense system (Bradbury 1981). In this system, males occupy territories that possess resources other than display sites and almost all requirements are fulfilled within the territories. Inter-male distances are large, often males are not within visual range of each other. Essentially, in the dispersed lek system, male territories are not uniformly dispersed over suitable habitat, but show some degree of clustering (Bradbury 1981). Often this clustering is apparent only as a result of careful mapping. The dispersed lek is distinct from resource defense in that though male territories possess resources of value to females, these are not necessarily used by them. Females that nest within a male's territory do so only incidentally (Wittenberger 1978).

The classification of mating systems of the Lesser Florican and Bengal Florican is a question between resource defense and dispersed lek. As males do not herd females or display from tight clusters, both female defense and lek mating systems can be ruled out. The differentiation between resource defense and dispersed lek is made complicated because in both cases males defend territories that possess resources of value to females.

The grassland ecosystems that the Lesser Florican and the Bengal Florican exploit are both superabundant in resources, namely food and nesting sites, that are critical to female reproduction. Wide distribution of such resources results in females not being dependent on male territories to fulfill these requirements. Though males possess territories which have these resources, all available resources are not monopolized. Additionally, the absence of a nest and nest building activities, and precocial young, results in male emancipation from parental care and a lack of female dependence on males for the same. Thus males display throughout the breeding season, and females come into association with males only briefly for the purpose of mate assessment and mating.

Other characteristics of the breeding biology of the Lesser Florican and the Bengal Florican provide strong indications that the mating systems is the dispersed lek system. These are :

1) By definition, a dispersed lek system should show a degree of clustering of male territories. This is immediately apparent in the Lesser Florican in years of higher breeding populations when dispersal of male territories was not uniform, but showed clustering. This is not as obvious in the Bengal Florican probably because male territories are very large, and the overall scale on which such mapping should have been done is correspondingly larger. Only indications of this existed at the Dudwa Tiger Reserve, and this needs verification at areas where the population of Bengal Florican is substantially larger.

2) Prolonged association between males and females was absent in both species. Every encounter between males and females was a brief courtship encounter. In the resource defense system, a prolonged association is seen once females settle in a male's territory. In the case of the floricans, females appeared to have large home ranges and visited a series of territories. Even after commencing nesting, female Lesser Floricans were not restricted to a single territory but tended to move between territories (see also Shulz 1985 for similar observations on the Little Bustard).

3) Of the six nests studied and monitored in the Lesser Florican at the Naulakha grassland, 2 were well away from the territory of any male. The remaining four were on the periphery or just outside the territories of males. (See also Wittenberger 1978). In the Bengal Florican only one nest was found which was well away from any male's territory. In Assam, all nests found by Narayan (1990) were well away from male territories.

Thus it appears certain that both the Lesser Florican and the Bengal Florican follow the dispersed lek mating system. Females interact with males only for mate selection and copulations, after which they are not dependent on males for any resource. Though nesting may occur on the periphery of a male's territory, this is only incidental and females use resources outside that male's territory and even in another male's territory. Further research on the floricans becomes of particular interest as the dispersed lek mating system is still poorly understood.

Why are Female Floricans Larger than Males

Spectacular courtship displays, sexual dimorphism and exaggerated physical traits have been observed in many species of animals. The evolution of such traits has been largely attributed to selection pressures exerted through female choice (e.g. Trivers 1972, Emlen and Oring 1977, Halliday 1978, Maynard-Smith 1978, Andersson 1982, Payne 1984). Selection pressures through female choice are most intense when mating success of males is highly skewed and this has been observed in two kinds of polygynous mating systems (Hedrich 1988). In the resource based mating system, sexually selected behaviour may be an advertisement of resource quality (Searcy 1979). The advantages of female choice in non-resource based systems (e.g. leks) is not as obvious. It has been suggested that viability differences between males may be advertised through body condition, vigorous displays or even tail length (Andersson 1986).

The focus of recent research on sexual selection in the lek mating system has generated considerable information on differences between individuals in terms of physical traits, display qualities and display location and the highly skewed mating success that is present in such mating systems (e.g. Wiley 1973, Shephard 1975, Trail 1985, Gibson and Bradbury 1986, Clutton-Brock 1988, Beehler 1988). While shorter inter-male distances have resulted in the lek system being better understood (Bradbury and Gibson 1983), considerably greater inter-male distances in dispersed lek mating systems has resulted in the latter system being poorly understood. The dispersed lek mating system is of particular interest as it is a midway stage between resource defence and the lek mating systems (Bradbury 1981).

Most bustard species that have been studied in some detail appear to follow the dispersed lek mating system (Cramp and Simmons 1980, Ridley _et al_. 1985, Shulz 1985, Rahmani 1989) though variation can occur within and between populations (Caranza _et al_. 1989). Amongst bustards, which follow the dispersed lek mating system, the floricans are of particular interest. While males of other species are slightly to considerably larger than females, in the floricans this sexual size dimorphism is reversed (Table 6.2).

One explanation that could answer this is a hypothesis proposed by Jehl and Murray (1986), who suggested that in the Charadrii and Scolopaci (shore birds), reversed sexual dimorphism has evolved as a result of selection for small sizes in males for agility in aerial displays (see Hoglund 1989, for a similar conclusion in polygynous mating systems). Mueller (1989) contested this hypothesis primarily because aerial agility was implied to be the underlying cause of all expressions of reversed sexual dimorphism, including for instance, bill length.

Assume instead that selection for aerial agility influenced only one aspect of sexual dimorphism, namely size. Then this could explain why males are smaller in the Lesser Florican and Bengal Florican as males in both these species have aerial displays. But, males of other species of bustards that have aerial displays do not exhibit a reversed sexual size dimorphism. It would, therefore, indicate that this hypothesis does not reveal the primary cause of reversed size dimorphism, but rather points out to a preferred male trait that could, among others, result in a reversed sexual size dimorphism.

An appealing explanation lies in what qualities are selected for by females. A speculative exploration of this area points out the conditions under which reversed sexual size dimorphism can occur, but still does not explain the exact mechanisms of the same.

In a comprehensive study to test several predictions of sexual selection, Payne (1984) suggested that if sexual selection is effected largely through combative competition among males, then males should be relatively larger than females. If however, sexual selection is effected largely through female choice, then there is no reason to expect males to be larger than females. Females may then choose smaller males for agility, or brighter males for beauty, rather than large males, successful in combat. The following attempt in answering reversed sexual size dimorphism in the floricans is based primarily on the above hypothesis.

TABLE 6.2

WING LENGTH OF MALE & FEMALE BUSTARDS AND MALE DISPLAY TYPES

Species	Wing length (mm) Male	 Female	Display type
Otis tarda	617	486	G
Ardeotis kori	761	629	G
A. arabs	636	542	G
A. nigriceps	688	500	G
A. australis	?	?	G
Neotis denhami	608	511	G
N. heuglinii	495	423	?
N. ludwigii	536	452	G (?)
N. nuba	463	395	?
Eupodotis afra	281	270	A
E. caerulescens	336	331	?
E. senegalensis	276	269	?
E. ruepelli	329	313	?
E. vigorsii	351	329	?
E. humilis	253	246	?
E. ruficrista	264	255	A
E. melanogaster	346	319	A
E. hartlaubi	338	309	?
Houbaropsis bengalensis	339	344	A *
	345	365	**
Sypheotides indica	194	228	A
	195	233	*
Tetrax tetrax	249	247	A
Chlamydotis undulata	389.5	353	G

G = Ground display; A = Aerial display; ? = Undescribed

* measurement of skins from the BNHS collection

Source of all data: Ali and Ripley (1969); Cramp and Simmons (1980); Osborne *et al*. 1984; Collar *et al*. 1986.

** Hume and Marshall (1878)

Sexual selection theory predicts that males are under more intense sexual selection pressure than females in promiscuous systems. Males mate indiscriminately, whereas females are selective in their choice of mates. This is primarily because males in these systems, provide only their gametes towards reproduction; incubation and care of young being entirely borne by the female (e.g. Oring 1982). Thus females choose males based on expressions of quality that males display through different means; quality itself being the possession of superior traits that enhance, for instance, survival or mating success (Trivers 1972, Halliday 1978, Andersson 1982).

Quality or fitness is expressed by different means, and female choice of males is essentially based on these expressions which vary from species to species (see for example Bradbury and Gibson 1983 for a review on leks). In some species age and/or dominance and spatial position of males determines mating success (e.g. Lill 1974, Hill 1988). In others it may be based on plumage quality (e.g. Johnson and Marzlutt 1990, Hoglund et al. 1990, Moller 1990), while in still others female choice of males is based on a particular physical character like spurs or supra-orbital combs that indicate dominance (e.g. Brodsky 1988, Goransson et al. 1990). In yet other species mate choice may be base purely on components of courtship display (e.g. Gibson and Bradbury 1985).

From these and several other studies, two basic traits on which female choice is based emerges. First are those in which expressions of male dominance hierarchies, inter-male competition, spatial position of males and the physical characters that demonstrate these are used as measures of male quality by females. Thus, in this system, males prominent in inter-male competition are the most successful in mating. The second is based on characters which are not related to or do not express strength or success inter-male conflict. In this case females use 'beauty' as a measure of male quality. In this system, though male competition and dominance is of importance, it is of value in as much as an aggressive male will repel any intrusion into its territory. But, merely by being a strong or dominant male need not confer an advantage in mating success. For instance, a female could choose a male who is not necessarily dominant but who possesses the longest tail or who displays at the greatest frequencies.

As a rule, during disputes over resources, dominant or stronger males emerge victorious. When contestants differ in fighting ability, this asymmetry when perceived by both contestants should be used to resolve the contest quickly (Parker 1974, Wells 1988). Size is often a good predictor of fighting ability, with the result that the larger of the two opponents usually wins (Wells 1988). (But see also Greenwood and Adams 1987 for counter argument).

Thus in those mating systems where dominance and fighting ability of males determines mating success, evolution should result in males that are large and dimorphic. In those systems where male dominance and fighting does not influence female choice of mates (i.e. females choose 'beauty' and not strength), males can be smaller, equal to or larger than females because selection will not favour any one size trait. If for example, females then use aerial agility as a criteria for male quality, then one would expect the evolution of reversed sexual size dimorphism in that species.

It is suggested that in both the Lesser Florican and Bengal Florican, female choice is based on male characters other than strength. The favoured character(s) is obviously one that has resulted in the evolution of a reversed sexual size dimorphism in these species.

There are strong behavioural evidences that the above hypothesis is true. These indications emanate from another hypothesis that if male mating success is based primarily on its ability to dominate other males, then in that species, the courtship displays will have strong aggression-like components. On the other hand if male success in mating is unrelated to dominance, then aggressive components should be absent from courtship displays. For instance, many species exhibit aggressive behavioural components in courtship displays (Smith 1977), and a cursory glance at species described by Payne (1984) reveals that in those species where males that have aggressive components to courtship displays show normal sexual size dimorphism, thus lending credence to this hypothesis.

In both the Lesser Florican and the Bengal Florican, the courtship displays (i.e. pre-copulatory display, not aerial display) do not have agonistic or aggressive components. In both species, agonistic displays are based on a cocking of the tail and a raising of mantle feathers. In the Bengal Florican, the 'chik' call is also rendered. In both species, courtship displays do not have components of agonistic or aggression displays. Courtship displays do not have cocked tails and raised mantles. The posturing of wings, body, neck and the fluffing of feathers are unique to the courtship display and do not in any way resemble aggressive displays. (See Chapters 3 and 4 for detailed descriptions).

Thus it is tentatively suggested that the reversed sexual size dimorphism in these species originated because choice of traits that expressed male quality were based on 'beauty' rather than strength. What traits of 'beauty' that are selected for in the Lesser Florican and the Bengal Florican is yet to be determined.

BIBLIOGRAPHY

Alagar Rajan, S. 1990. The ecology of the Indian Ring Dove Streptopelia decaocto decaocto (Frivaldszky) and the Indian Spotted Dove Streptopelia chinensis suratensis (Gmelin) at Point Calimere Wildlife Sanctuary, Tamil Nadu. M. Sc. Thesis, Univ. of Bombay.

Ali, S. & Ripley, S.D. 1969. Handbook of the birds of India and Pakistan. Vol II. Oxford Univ. Press, New Delhi.

Ali, S. & Rahmani, A.R. 1984. Study of ecology of certain endangered species of wildlife and their habitats. The Great Indian Bustard. Annual report 2. Bombay Natural History Society, Bombay.

Ali, S., Daniel, J.C., Rahmani, A.R., Bhutia, U. & Haribal, M. 1984. Study of the ecology of some endangered species of wildlife and their habitats. The Lesser Florican in Sailana (M P). Technical report no. 24. Bombay Natural History Society, Bombay.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behavior 48: 227-265.

*Alvi, M.A. & Rahman, A. 1968. Jehangir the naturalist. Monograph series 3. National Institute of Sciences of India. New Delhi.

Andersson, M. 1980. Nomadism and site tenacity as alternate reproductive tactics in birds. J. Anim. Ecol. 49: 175-184.

Andersson, M. 1982. Sexual selection, natural selection and quality advertisement. Biol. J. Linn. Soc. 17: 375-393.

Andersson, M. 1986. Evolution of condition dependent sex ornaments and mating preferences: Sexual selection based on viability differences. Evolution 40: 804-816.

Atwood, J.L. & Massey, B.W. 1988. Site fidelity of Least Terns in California. Condor 90: 389-394.

Avery, M. & Sherwood, G. 1982. The lekking behaviour of the Great Snipe. Ornis Scandinavica 13: 72-78.

Avery, M.I. & Ridley, M.W. 1988. Game bird mating strategies. Pp 159-176 in Ecology and management of game birds (Hudson P.J. & Rands, M.R.W. eds.). BSP Professional Books, Oxford.

Baker, E.C.S. 1921. The game birds of India, Burmah and Ceylon. Vol. 2. Bombay Natural History Society, Bombay.

Bannerman, D.A. 1931. The birds of tropical west Africa. Vol. II. Publ. by Crown Agents for the Colonies, London.

Beehler, B.M. 1988. Lek behavior of the Raggina Bird of Paradise. National Geographic Res. 4: 343-358.

Bell, R.A.V. 1971. A grazing ecosystem in the Serengeti. Sci. Amer. 225: 86-93.

Berry, M.P.S. & Crowe, T.M. 1985. Effects of monthly and annual rainfall on game bird population in the northern Cape Province, South Africa. S. Afr. J. Wildl. Res.

Suppl. 1: 116-117.

Blanford, W.T. 1898. The Fauna of British India: Birds. Vol IV. Taylor and Francis, London.

Bock, E.L., Block, J.H., Kenney, W.R. & Hawthorne, M.V. 1984. Response of birds, rodents and vegetation to livestock exclosure in a semi-desert grassland site. J. Range Manage. 37: 239-242.

Bouton, T.W., Tieszen, L.L. & Imamba, S.K. 1988. Biomass dynamics of grassland vegetation in Kenya. Afr. J. Ecol. 26: 89-101.

*Boyd, R.L. 1972. Breeding biology of the Snowy Plovers at Cheyenne Bottoms Waterfowl management area, Barton COunty, Kansas. Unpubl. M.S. Thesis. Kansas State Teachers College, Emporia, Kansas.

Bradbury, J.W. 1981. The evolution of leks. Pp 138-169 in Natural selection and social behaviour: Recent research and theory (Alexander, R.D. & Tinkle, D.W. eds.). Chiron Press, New York.

Bradbury, J.W. & Gibson, R.M. 1983. Leks and mate choice. Pp 109-138 in Mate choice (Bateson, P.B. ed.). Cambridge Univ. Press. Cambridge.

Brodsky, L.M. 1988. Ornament size influences mating success in male Rock Ptarmigan. Anim. Behav. 36: 662-667.

*Brown, J.C. & Orians G.H. 1970. Spacing patterns in mobile animals. Annu. Rev. Ecol. Sys. 1: 239-262.

Burton, R. 1985. Bird behaviour. Granada, London.

Cairns, W.E. 1982. Biology and behaviour of breeding piping plovers. Wilson Bull. 94: 531-545.

Caranza, J., Trucios, S.J.H.D. & Ena, V. 1989. Mating system flexibility in the Great Bustard: a comparative study. Bird Study 36: 192-198.

Collar, N.J., Goriup, P.D. & Osborne, P.E. 1986. Suborder Otides, Family Otididae. Pp 148-179 in The birds of Africa. Vol II. (Urban, E.K., Fry, H.C. & Keith, S. eds.). Academic Press, London.

Clutton-Brock, T.H. 1988. Reproductive success. Pp 473-485 in Reproductive success (Clutton-Broc, T.H. ed). Univ. Chicago Press, Chicago.

Cramp, S. & Simmons, K.E.L. 1980. (Chief eds.) Handbook of the birds of Europe, Middle East and North Africa. Vol II Hawks to Bustards. Oxford Univ. Press, London.

Crawley, M.J. 1983. Herbivory. The dynamics of plant - animal interactions. Blackwell Scientific Publ. Oxford.

Davies, N.B. 1978. Ecological questions about territorial behaviour. Pp 317-350 in Behavioral ecology. An evolutionary approach (Krebs, J.R. & Davies, N.B. eds.). Blackwell Scientific Publ., Oxford.

Davies, S.J.J.F. 1979. The breeding season of birds in south-western Australia. J. Royal Soc. Western Aust. 62: 53-64.

Deb Roy, S. 1986. Fire in wet grassland habitats of Assam.

Indian Forester 112: 914-917.

DeSante, D.F. & Geupel, G.R. 1987. Landbird productivity in central coastal California: the relation to annual rainfall and a reproductive failure in 1986. Condor 89: 636-653.

Deshmukh, I.K. 1986. Primary productivity of a grassland in Nairobi National Park, Kenya. J. appl. Ecol. 23: 115-123.

de Vos, G.J. 1983. Social behaviour of th Black Grouse. An observational and experimental field study. Ardea 71: 1-103.

Dharmakumarsinjhi, K.S. 1950. The Lesser Florican [Sypheotides indica (Miller)]: Its courtship display, behaviour and habits. J. Bombay. nat. Hist. Soc. 49: 201- 216.

Dinerstein, E. 1979. An ecological survey of the Royal Karnali-Bardia wildlife reserve, Nepal. Part 1. Vegetation, modifying factors and successional relationships. Biol. Conserv. 15: 127-150.

District Gazetteer 1905. United Provinces of Agra and Oudh, Vol. XLIII. Govt. Press, Allahabad.

Downes, M. 1981. Re-establishment of the Bustard in Victoria. Pp 227-239 in Proceedings 'wildlife management in the 80's. Field and game federation. Monash University. Monash.

Dunn, P.O. & Braun, C.E. 1985. Natal dispersal and lek fidelity of Sage Grouse. Auk 102: 621-627.

Earle, R.A. 1981. Factors governing avian breeding in Acacia Savanna, Pietermaritzburg. Part 1: Extrinsic factors. Ostrich 52: 65-73

Eckert, G.C. & Weatherhead, P.J. 1987. Owners, floaters and competive asymetries among territorial Red-winged Blackbirds. Anim. Behav. 35: 1317-1323.

Elkins, N. 1983. Weather and bird behavior. T & AD Poyser, Calton.

Ellison, L.M. 1971. Territoriality in Alaskan Spruce Grouse. Auk 88: 652-664.

Emlen, S.T. & Oring L.W. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197: 215-223.

Ferguson, R.S. 1981. Territorial attachment and mate fidelity by Horned Grebes. Wilson Bull. 93: 560-561.

Fogden, M.P.L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114: 307-343.

Fowler, J. & Cohen, L. 1986. Statistics for Ornithologists. BTO Guide 22. U.K.

Geordias, N.J. & McNaughton, S.J. 1988. Interaction between grazers and a cyanogenic grass, Cynodon plectostachyus. Oikos 51: 243-350.

Gibson, R.M. & Bradbury, J.W. 1985. Sexual selection in lekking Sage Grouse: Phenotypic correlates of mating success. Behav. Ecol. Sociobiol. 18: 117-123.

Gibson, R.M. & Bradbury, J.W. 1986. Male and female mating strategies on Sage Grouse leks. Pp 379-398 in Ecological aspects of social evolution (Rubenstein, D.I. & Wrangham, R.W. eds.). Princeton Univ. Press, Princeton.

Gibson, R.M. & Bradbury, J.W. 1987. Lek organization in Sage Grouse: Variations on a territorial theme. Auk 104: 77-84.

Goransson, G., Schantz, T.V., Froberg, I., Helgee, A. & Wittzell, H. 1990. Male characteristics, viability and harem size in the pheasant Phasianus colchicus. Anim. Behav. 40: 89-104.

Goriup, P.D. & Vardhan, H. 1980. Bustards in decline. Tourism and wildlife society of India, Jaipur.

Goriup, P.D. & Karpowicz, Z.J. 1981. An account of the decline of the Lesser Florican Sypheotides indica in north-western India. Unpubl. Rep. I.C.B.P. Cambridge.

Gould, J.L. 1982. Ethology. The mechanisms and evolution of behavior. W.W. Norton & Co., New York.

*Graul, W.D. 1973. Adaptive aspects of the mountain plovers social systems. Living bird 12: 149-151.

Greenwood, P.J. & Harvey, P.H. 1982. The natal and breeding dispersal of birds. Ann. Rev. Ecol. Sys. 13: 1-13.

Greenwood, P.J. & Adams, J. 1987. Sexula selection, size dimorphism and a fallacy. Oikos 48: 106-108.

Guillet, A. & Crowe, T.M. 1987. Monthly and seasonal changes in the aquatic avifauna of Rondevlei bird sanctuary (Cape province, South Africa). Avocetta 11: 1-16.

Gullion, G.W. 1981. Non-drumming males in a Ruffed Grouse population. Wilson Bull. 93: 372-382.

Gullion, G.W. & Marshall, W.H. 1968. Survival of Ruffed Grouse in a boreal forest. Living bird 7: 117-167.

Hacker, R.B. 1984. Vegetation dynamics in a grazed mulga shrubland community: II the ground storey. Aust. J. Bot. 32: 251-261.

Haig, S.M. & Oring, L.W. 1988. Mate, site and territory fidelity in piping plovers. Auk 105: 268-277.

Hajra, P.K. & Shukla, U. 1983. Dudhwa National Park. (Some botanical aspects of the proposed new habitat for Rhino). Botanical Survey of India, Howrah.

Halliday, T.R. 1978. Sexual selection and mate choice. Pp 180-213 in Behavioral ecology. An evolutionary approach (Krebs, J.R. & Davies, N.B. eds.). Blackwell Scientific Publ., Oxford.

Halse, S.A. & Jaensch, R.P. 1989. Breeding seasons of waterbirds in South-western Australia - the importance of rainfall. Emu 89: 232-249.

Harvey, P.H., Greenwood, P.J. & Perrins, C.M. 1979. Breeding area fidelity of the Great Tit (Parus major). J. Anim. ecol. 48: 305-313.

Hedrich, V.A. 1988. Female choice and the heritability of attractive male traits: An empirical study. Amer. Nat. 132: 267-276.

Hellmich, J. 1988. Zum balz-verhalten der Riesentrappe (Ardeotis Kori). Zool. Garten N.F. 58: 345-352.

Hendrickson, H.T. 1969. A comparative study of the egg white proteins of some species of the avian order Gruiformes. Ibis 111: 80-91.

Hilden, O. 1965. Habitat selection in birds. A review. Ann. Zool. Fenn. 2: 53 - 75.

Hill, G.E. 1988. Age, plumage brightness, territory quality and reproductive success in the Black-headed Grosbeak. Condor 90: 379-388.

Hinde, R.A. 1956. The biological significance of the territories of birds. Ibis 98: 340-369.

Hoglund, J. 1989. Size and plumage dimorphism in lek breeding birds. A comparative analysis. Amer. Nat. 134: 72-87.

Hoglund, J. & Robertson, J.G.M. 1990. Female preferences, male decision rules and the evolution of leks in the great snipe Gallinago media. Anim. Behav. 40: 15-22.

Hoglund, J., Eriksson, M. & Lindell, L.E. 1990. Females of the lek-breeding Great Snipe, Gallinago media, prefer males with white tails. Anim. Behav. 40: 23-32.

*Hohn, E.O. 1953. Display and mating behavior of the black grouse (Lyrurus tetrix). Brit. Jour. Anim. Behav. 1: 40-58.

Howard, R. & Moore, A. 1980, A complete checklist of the birds of the World. Oxford Univ. Press, Oxford.

Hume, A.O. & Marshall, A.H.T. 1878. The game birds of India, Burmah and Ceylon. Publ. by authors, Calcutta.

Hunter, L.A. 1987. Acquisition of territories by floaters in cooperatively breeding purple gallinules. Anim. Behav. 35: 402-410.

Immelmann, K. 1971. Ecological aspects of periodic reproduction. Pp 342-389 in Avian biology Vol. I (Farmer, D.S. & King, J.R. eds.). Academic press, New York.

Inskipp, T. & Inskipp, C. 1982. International Council for Bird Preservation project on the Bengal Florican. I.C.B.P. Newsletter 4.

Inskipp, C. & Collar, N.J. 1984. The Bengal Florican in Nepal. Oryx 18: 30-35.

Jain, S.K. & Sastry, A.R.K. 1983. Botany of some tiger habitats in India. Botanical Survey of India and Dep. of Environment, Delhi.

Jehl, J.R. Jr. & Murray, B.G. Jr. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. Pp 1-86 in Current Ornithology (Johnson, R.F. ed.). Plenum Press. New York.

*Jenkins, D., Watson, A. & Miller, G.R. 1967. Population fluctuation in the Red Grouse *Lagopus lagops scotticus*. *J. anim. Ecol.* *36*: 97-122.

Jerdon, T.C. 1864. Birds of India. Vol. 2. Publ. by authors, Calcutta.

Johnsingh, A.J.T. & Murali, S. 1980. The ecology and behaviour of the Indian Peafowl (*Pavo cristatus* Linn.) of Injar. *J. Bombay Nat. Hist. Soc.* *75(suppl)*: 1069-1079.

Johnson, K. & Marzlutt, J.M. 1990. Some problems and approaches in Avian mate choice. *Auk* *107*: 296-304.

Keat, J.A. & Marshall, A.J. 1954. Reproduction in Australian desert birds. *Proc. Zool. Soc. Lond.* *124*: 493-499.

Keeley, J.E. 1987. Role of fire in seed germination of woody taxa in California chaparral. *Ecology* *68*: 434-443.

Knapp, A.K. 1985. Effects of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tall grass prairie. *Ecology* *66*: 1309-1320.

Koivisto, I. 1965. Behavior of the Black Grouse, *Lyrurus tetrix* (L.), during the spring display. Finnish Game Res. 26.

Krapu, A.J. 1981. The role of nutrient reserves in mallard reproduction. *Auk* *98*: 29-38.

Kruijt J.P. & Hogan, J.A. 1967. Social behaviour on the lek in Black Grouse, *Lyrurus tetrix* (L.). *Ardea* *55*: 204-240.

Lachungpa, U.G. & Rahmani, A.R. 1990. Former distiribution of the Lesser Florican. Pp 95-100 *in* Status and ecology of the Lesser Florican and Bengal Florican. Final report. Bombay Natural History Society, Bombay.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen & Co. Ltd., London.

Lack, D. 1973. Population studies of birds. Oxford Univ. Press, London.

Lanyon, S.M. & Thompson, C.F. 1986. Site fidelity and habitat quality as determinants of settlement pattern in male Painted Buntings. *Condor* *88*: 916-919.

Lenington, S. & Mace, T. 1975. Mate fidelity and nesting site tenacity in the Killdeer. *Auk* *92:* 149-151.

Lewis, R.A. & Zwickel F.C. 1981. Differential use of territorial sites by male Blue Grouse. *Condor* *83*: 171-176.

Lill, A. 1974. Sexual behavior of the lek-forming White Bearded Manakin (*Manacus manacus trinitatis* Hartert). *Z. Tierpsychol* *36*: 1-36.

Manakadan, R. 1985. Ecology of Great Indian Bustard *Ardeotis nigriceps* (Vigors) habitats. Unpublished M.Sc. Thesis. Univ. of Bombay, Bombay.

Manakadan, R. & Rahmani, A.R. 1986. Study of ecology of certain endangered species of wildlife and their habitats. The Great Indian Bustard. Annual Report 3. Bombay Natural History Society, Bombay.

Manry, D.E. 1985. Reproductive performance of the Bald Ibis _Geronticus calvus_ in relation to rainfall and grass-burning. _Ibis 127_: 159-173.

Margrath, R.D., Ridley, M.W. & Woinarski, J.C.Z. 1983. Status and habitat requirements of the Lesser Florican, _Sypheotides indica_, in Kathiawar, Western India. Unpubl. Rep. I.C.B.P. Cambridge.

Marshall, A.J. 1959. Internal and environmental control of breeding. _Ibis 101_: 456-478.

Mattingley, A.H.E. 1929. The love display of the Australian bustard. _Emu 28_: 198.

*Maynard Smith, J. 1978. The evolution of sex. Cambridge Univ. Press, Cambridge.

McNaughton, S.J. 1985. Ecology of a grazing ecosystem: the Serengeti. _Ecol. Monogr. 55_: 259-294.

McNicholl, M.K. 1975. Larid site tenacity and group adherence in relation to habitat. _Auk 92_: 89-104.

Mendelssohn, H., Marder, U. & Stavy, M. 1979. Captive breeding of the Houbara (_Chlamydotis undulata macqueeni_) and a description of its display. Pp 265-279 _in_ XIII Bulletin I.C.B.P., Cambridge.

Merton, D.V., Morris, R.B. & Atkinson, I.A.E. 1984. Lek behavior in a parrot: the Kakapo _Strigops habroptilus_ of New Zealand. _Ibis 126_: 277-283.

Mock, D.W. 1983. On the study of Avian mating systems. Pp 55-91 _in_ Perspectives in ornithology (Brush, A.H. & Clark, G.A. Jr. eds.). Cambridge Univ. Press, Cambridge.

*Mohr, C. O. 1947. Table of equivalent populations of North American 'small mammals'. _American Midland Naturalist 37_: 223-249.

Moller, A.P. 1990. Male tail length and female mate choice in the monogamous swallow _Hirundo rustica_. _Anim. Behav. 39_: 458-465.

Moreau, R.E. 1950. The breeding seasons of African birds. 1. Land birds. _Ibis 92_: 223-267.

Morgan-Davies, A.M. 1965. On the Kori bustard, _Ardeotis kori_ (Burchell) in north-western Tanzania. _Bull. Brit. Ornithol. Club 85_: 145-147.

Morse, D.H. 1980. Behavioural mechanisms in ecology. Harvard Univ. Press. Cambridge.

Morton, L.M. 1978. Snow conditions and the onset of breeding in the Mountain White-crowned Sparrow. _Condor 80_: 285-289.

Mueller, H.C. 1989. Aerial agility and the evolution of reversed sexual dimorphism (RSD) in shorebirds. _Auk 106_: 154-155.

Mukherjee, A.K. 1986. The ecology and conservation of Bengal Florican, _Eupodotis bengalensis_ (Gmelin). Pp 305-308 *in* Wildlife wealth of India (Majpuria, T.J. ed.). Teepress Services L.P., Thailand.

Mundahl, J.T. 1982. Role specialization in the parental and territorial behaviour of the Kill Deer. *Wilson Bull 94*: 515-530.

Naik, R.M. & Mistry, L. 1980. Breeding season in a tropical population of the house sparrow. *J. Bombay nat. Hist. Soc. 75 (suppl.)*: 118-1142.

Narayan, G. 1990. General ecology and behaviour of the Bengal Florican. Pp 17-34 *in* Status and ecology of the Lesser Florican and Bengal Florican. Final report. Bombay Natural History Society, Bombay.

Narayan, G. & Rosalind, L. 1988. Ecology of Bengal Florican in Manas Wildlife Sanctuary. Pp 5-42 *in* The Bengal Florican. Status and conservation. Annual Report 3. Bombay Natural History Society, Bombay.

Narayan, G., Sankaran, R., Rosalind, L. & Rahmani, A.R. 1989. The Floricans. *Houbaropsis bengalensis* and *Sypheotides indica*. Annual Report No. 4. Bombay Natural History Society, Bombay.

Odum, E.P. & Kuenzler E.J. 1955. Measurement of territory and home range size in birds. *Auk 72*: 128-137.

Olson, B.E. & Richards J.H. 1988. Tussock regrowth after grazing: Intercalary meristem and axillary bud activity of tillers of *Andropyron desertorum*. *Oikos 51*: 374-382.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. *Amer. Nat. 103*: 589-603.

Oring, L.W. 1982. Avian mating systems. Pp 1-92 *in* Avian biology vol. VI (Farmer S.D., King, J.R. & Parkes, K.C. eds.). Academic Press, Orlando.

Osborne, P., Collar, N. & Goriup, P.D. 1984. Bustards. Dubai Wildlife Research Centre. Dubai, U.A.E.

Owaga, M.L.A. 1980. Primary productivity and herbage utilization by herbivores in Kaputei plains, Kenya. *Afr. J. Ecol. 18*: 1-15.

Parker, G.A. 1974. Assessment strategy and the evolution of fighting behavior. *J. theor. Biol. 47*: 223-243.

Parmelee, D.F. & Pietz, P.J. 1987. Philopatry, mate and nest-site fidelity in the brown skuas of Anvers island, Antartica. *Condor 89*: 916-919.

Payne, R.B. 1984. Sexual selection, lek and arena behaviour, and sexual size dimorphism in birds. *Ornith. Monogr. 33*. Amer. ornithol. Union.

Perrins, C.M. 1970. The timing of birds' breeding seasons. *Ibis 112*: 242-255.

Petretti, F. 1985. Preliminary data on the status of the Little Bustard (*Tetrax tetrax*) in Italy. *Bustard Studies 2*: 165-170.

Priest, C.D. 1934. The birds of southern Rhodesia. Vol II. William Cowles & Sons, London.

Rahmani, A.R. 1989. The Great Indian Bustard. Final report. Bombay Natural History Society, Bombay.

Rahmani, A.R. & Manakadan, R. 1987 (a). Movement and flock composition of the Great Indian Bustard. J. Bombay Nat. Hist. Soc. 83: 17-31.

Rahmani, A.R. & Manakadan, R. 1987 (b). Interspecific behaviour of the Great Indian Bustard. J. Bombay Nat. Hist. Soc. 84: 317-331.

Rahmani, A.R., Narayan, G. & Rosalind, L. 1988. Bengal Florican survey in Uttar Pradesh, Bihar, West Bengal and Assam. Pp 65-109 in the Bengal Florican. Status and ecology. Annual report No.3. Bombay natural History Society, Bombay.

Raychaudhari, S.P., Agarwal, R.R., Datta Biswas, N.R., Gupta, S.P. & Thomas, P.K. 1963. Soils of India. Indian Council for Agr. Res. New Delhi

Ridley, M.W., Magrath, R.D. & Woinarski J.C.Z. 1985. Display leap of the Lesser Florican Sypheotides indica. J. Bombay Nat. Hist. Soc. 82: 271 - 277.

Ripley, S.D. 1961. A synopsis of the Birds of India and Pakistan. Bombay Natural History Society, Bombay.

Rippin, A.B. & Boag, D.A. 1974. The recruitment to populations of male Sharp-tailed Grouse. J. Wildl. Manage. 38: 616-621.

Rodgers, W.A. 1986. The role of fire in the management of wildlife habitats: a review. Indian Forester 112: 845-857.

Sankaran, R. 1990. Status of the Swamp Deer Cervus duvaucelli duvaucelli in the Dudwa National Park, Uttar Pradesh. J. Bombay nat. Hist. Soc. 87: 250-259.

Sankaran, R. & Rahmani, A.R. 1986. Study of ecology of certain endangered species of wildlife and their habitats. The Lesser Florican. Annual report 2. Bombay Natural History Society, Bombay.

Sankaran, R. & Rahmani, A.R. 1988. Status of the Bengal Florican at the Dudwa National Park. Pp 43-64 in The Bengal Florican. Status and conservation. Annual Report No. 3. Bombay Natural History Society, Bombay.

Sankaran, R. & Manakadan, R. 1990. Recent breeding records of the Lesser Florican Sypheotides indica (Miller) from Andhra Pradesh. J. Bombay nat. Hist. Soc. 87: 294-296.

Sankaran, R., Lachungpa, U.G. & Lachungpa, G. 1990. Survey of some wintering habitats of Lesser Florican in south India. Pp 113-116 in Status and ecology of the Lesser Florican and Bengal Florican. Final report. Bombay Natural History Society, Bombay.

Schulz, H. 1985. Grundlagenforschund Zur Biologie Der Zwergtrappe Tetrax tetrax. Braunschweig.

Searcy, W.A. 1979. Female choice of mates: A general model for birds and its application to Red-winged Black Birds. Am. Nat. 114: 77-100.

Shephard, J.M. 1975. Factors influencing female choice in the lek mating system of the ruff. Living Bird: 14 87-111.

Shipley, F.S. 1984. The 4-egg clutch limit in the Charadrii: an experiment with American Avocets. South Western Naturalist 29: 143-147.

Shukla, J. 1987. Interannual variability of monsoons. Pp 399-463 in Monsoons (Fein, J.S. & Stephen, P.C. eds.). John.Wiley & sons, New York.

Sinclair, A.R.E. 1978. Factors affecting the food supply and breeding season of resident birds and movements of Palearctic migrants into a tropical African savannah. Ibis 120: 480-497.

Sinclair, A.R.E. 1983. The function of distance movements. Pp 240-258 in The ecology of animal movements (Swingland, I.R. and Greenwood, P.J. eds.). Clarendon Press, Oxford.

Singh, A. 1973. Tiger haven. Macmillan London Ltd., London.

Singh, R.L. 1985. Management of re-introduced Indian Rhinoceros - A pioneer experiment. Unpubl. report.

Singh, V.P. 1984. Bio-ecological studies on Cervus duvauceli duvauceli, Swamp Deer (Barasingha) in Dudwa forest near Indo-Nepal border. Unpubl. Ph.D. Thesis. Kanpur University, Kanpur.

Smith, J.N.M. & Arcese, P. 1989. How fit are floaters? Consequences of alternate territorial behavior in a non-migratory sparrow. Auk 133: 830-845.

Smith, J.W. 1977. The behaviour of communicating. An ethological approach. Harvard Univ. Press. London.

Smith, L.M. & Kadlec, J.A. 1985. Fire and herbivory in a great salt lake marsh. Ecology 66: 259-265.

Storor, C.R. 1940. Courtship and display among birds. County Life Ltd. London.

Stressman, E. 1959. The status of avian systematics and its unsolved problems. Auk 76: 269-280.

Sutton, G.M. 1981. On aerial and ground displays of the World's snipes. Wilson Bull. 93: 457-609.

Tainton, M.M. & Mentis, M.T. 1984. Fire in grasslands. Pp 117-147 in Ecological effects of fire in South African Ecosystems (Booyen, P.V. & Tainton, N.M. eds.). Ecological studies 48. Springer-Verlag, Berlin.

Thomson, L. 1950. Factors determining the breeding success of birds: an introductory review. Ibis 92: 173-184.

Tinbergen, N. 1951. The study of instinct. Oxford Univ. Press, New York.

Tinbergen, N. 1957. The functions of territory. Bird Study 4: 14-27.

Tinbergen, N. 1972. The animal in its world. Explorations of an Ethologist. Vol I, field studies. Harvard Univ. Press, Cambridge.

Trail, P.W. 1985. Courtship disruption modifies mate choice in a lek-breeding bird. Science 227: 778-780.

Trivers, R.L. 1972. Parental investment and sexual selection. Pp 136-179 in Sexual selection and the descent of man 1871-1971 (Campbell, B. ed.). Aldine. Chicago, Illinois.

Van Tyne, J. & Berger, A.J. 1959. Fundamentals of Ornithology. John Wiley & Sons inc. New York.

Vijayan, V.S. 1987. Keoladeo National Park ecology study. Annual Report. Bombay Natural History Society, Bombay.

Vogl, R.J. 1974. Effects of fire on grasslands. Pp 139-194 in Fire and ecosystems (T.T. Kozlowski & C.E. Ahlgren, eds.). Academic Press, New York.

Walters, M. The complete birds of the World. David & Charles, Newton Abbot.

Ward, S.A. 1987. Optimal habitat selection in time-limited dispersal. Am. Nat. 129: 568-579.

Warriner, J.S. Warriner, J.C., Page, G.W. & Stenzel, L.E. 1986. Mating success and reproductive success of a small population of polygamous Snowy Plovers. Wilson Bull. 98: 15-37.

Wells, M.S. 1988. Effects of body size and resource value on fighting behaviour in a jumping spider. Anim. Behav. 36 : 321-336.

White, D.M. 1985. A report on the captive breeding of Australian bustard (Ardeotis australis) at Serendip wildlife research station. Bustard Studies 3: 195-218.

Wiley, R.H. 1973. Territoriality and non-random mating in Sage Grouse Centrocercus urophasianus. Anim. Behav. Mongr. 6: 85-169.

Wittenberger, J.F. 1978. The evolution of mating systems in grouse. Condor 80: 126-137.

Wittenberger, J.F. 1979. The evolution of mating systems in birds and mammals. Pp 271-349 in Handbook of behavioural neurobiology Vol 3: Social behavior of communicating (Marler, P. & Vandenberg, J.G. eds.). Plenum Press, New York.

Young, H. 1956. Territorial activities of the American Robin Turdus migratorius. Ibis 98: 448-452.

Zwickell, F.C. & Bendell, J.F. 1967. Early mortality and the regulation of numbers in Blue Grouse. Can. J. Zool. 45: 817-851.

* = Not consulted in the original.

ACKNOWLEDGEMENTS

I would like to express my deep sense of gratitude to Mr J.C. Daniel, Curator of the Bombay Natural History Society, and the supervisor for my doctoral research; for his advice, guidance and constant encouragement. I can never sufficiently express my gratitude to him for giving me the opportunity to live and work with wildlife.

I would like to thank Dr A.R. Rahmani, Project Scientist of the Florican Project, under whose direct supervision I worked. His encouragement and guidance, particularly during the years of my field work, is something that I will always be grateful for.

My colleagues, some of whom were simultaneously involved with their own doctoral dissertations, never grudged me the often exorbitant demands that I made on their time. I would like to express my deep sense of gratitude to Goutam Narayan, Vibhu Prakash, Ajay Desai, Carl D'Silva, Lima Rosalind and Neelam Patil for the support, advice and help they gave so unstintingly.

At the BNHS I also wish to thank all my colleagues, in particular Mr S.A. Hussein, Dr R.B. Grubh, Isaac Kehimkar, and M.O George.

During the course of this dissertation, I have piled up debts of gratitude across the country. Most of the analysis for this dissertation was done at the BNHS research station at Bharatpur. I thank Dr V.S. Vijayan for giving me the opportunity to work in his field station, and for the useful discussions that I had with him. At Bharatpur, I am particularly indebted to Dr P.A. Azeez, with whom I discussed at length various aspects of my study. His guidance in the analytical aspects of this dissertation is deeply appreciated. I also wish to thank Dr Lalitha Vijayan and M.K. Ramachandran for the productive discussions that I had with them. The rest of my colleagues at Bharatpur, too, were generous with their time, and extremely helpful. My colleagues at Mudumalai, Dr Krishnamurti and N. Sivaganesan were equally helpful. So were Dr Y.N. Rao, R. Manakadan, S. Alagar Rajan and V. Natarajan at Point Calimere, who also edited early drafts of this manuscript.

I would like to thank Dr A.J.T. Johnsingh, Dr R. Gadagkar, Dr Joshi and Dr Anil Gore, who helped me refine several aspects of my study. I would also like to thank Shahid Ali, Ajay Varadachary and Nitin Jamdar, whose comments and criticisms greatly improved this dissertation.

The Madhya Pradesh and Uttar Pradesh and Gujarat Forest Departments were of immense help in the field, and it was only their logistic support that made this study possible. In Madhya Pradesh, I would particularly like to thank Mr P.M. Lad, CCF (Wildlife), Mr B.M.S. Rathore, DFOs at Sailana, for their support. In Gujarat, Mr Dinesh Mishra, DFO, Mr N.D. Patel, ACF, and Mr Hemant Sutar, RFO, were most helpful at Dohad. In Uttar Pradesh, Mr R.P. Sharma and Mr V.S Bhadoria, CWWs, Mr R.P. Singh, Director, Dudwa National Park, former Directors Mr G.C. Mishra and Mr M. Singh and other officials of the Park provided help and facilities. At Dudwa, I would also like to thank Mr Arjan Singh, Mr and Mrs Balram Singh Dr S.P. Sinha and Qamar Qureshi for the help and hospitality they gave me while in the field.

I must record my appreciation to Mehboob Alam for his able and untiring assistance in the field, often under the most adverse conditions. I also would like to thank Kheema and Bheru, Florican Chowkidars par excellence, at Sailana. At Dudwa, Panna Lal 'Mahathiya' built excellent machans and Veepath accompanied me frequently into the forest. At Hornbill House, I wish to thank Uma Pratap Singh, who helped me in several ways.

I would like to thank my parents, brother and sister for things too numerous to mention.

APPENDIX

LIST OF SCIENTIFIC NAMES OF BIRDS REFERRED TO IN THE TEXT

(N.B. only scientific names of those species not mentioned in the text).

Blackwinged kite	Elanus caeruleus
Blyth's Baza	Aviceda jerdoni
Blackcrested Baza	Aviceda leuphotes
Crested Honey Buzzard	Pternis ptilorynchus
Pariah Kite	Milvus migrans
Brahminy Kite	Haliastur indus
Eastern Goshawk	Accipter gentilis
Shikra	Accipiter badius
Crested Goshawk	Accipiter trivirgatus
Sparrow Hawk	Accipiter nisus
Besra Sparrow Hawk	Accipiter virgatus
Long Legged Buzzard	Buteo rufinus
Buzzard	Buteo buteo
White Eyed Buzzard	Butastur teesa
Hodgson's Hawk-eagle	Spizaetus nipalensis
Changeable Hawk-eagle	Spizaetus (cirrhatus) limnaeetus
Crested Hawk-eagle	Spizaetus cirrhatus cirrhatus
Bonelli's Hawk-eagle	Hieraetus fasciatus
Booted Hawk-eagle	Hieraetus bennatus
Rufousbellied Hawk-eagle	Hieraetus kienerii
Imperial Eagle	Aquila heliaca
Tawny Eagle	Aquila rapax
Greater Spotted Eagle	Aquila clanga
Lesser Spotted Eagle	Aquila pomarina
Black Eagle	Ictinaetus malayensis
Ringtailed Fishing Eagle	Haliaeetus albicilla
Greyheaded Fishing Eagle	Ichtyophaga ichthyaetus
Himalayan Greyheaded F.E	Ichtyophaga nana
Hen Harrier	Circus cyaneus
Pale Harrier	Circus macrourus
Montagu's Harrier	Circus pygargus
Pied Harrier	Circus melanoleucos
Marsh Harrier	Circus aeruginosus
Short Toed Eagle	Circaetus gallicus
Crested Serpent Eagle	Spilornis cheela
Osprey	Pandion haliaetus
Laggar Falcon	Falco biarmicus
Peregrine Falcon	Falco peregrinus
Hobby	Falco subbuteo
Indian Hobby	Falco severus
Redheaded Merlin	Falco chiquera
Lesser Kestrel	Falco naumani
Kestrel	Falco tinnunculus

Black Grouse	*Lyrurus tetrix*
Ruffed Grouse	*Bonasa umbellus*
Sage Grouse	*Centrocercus urophasianus*
Black Partridge	*Francolinus francolinus*
Grey Partridge	*Francolinus pondicerianus*
Francolin	*Francolinus* sp.
Quail	*Coturnix* sp.
Monal	*Lophophorus impejanus*
Khaleej	*Lophura lecomelana*
Red Jungle Fowl	*Gallus gallus*
Koklas	*Pucrasia macrolopha*
Chir	*Catreus wallichii*
Peafowl	*Pavo cristatus*
Pheasant	*Phasianus colchicus*
Great Bustard	*Otis tarda*
Kori Bustard	*Ardeotis kori*
Arabian Bustard	*A. arabs*
Great Indian Bustard	*A. nigriceps*
Australian Bustard	*A. australis*
Denham's Bustard	*Neotis denhami*
Black Bustard	*Eupodotis afra*
Buff Crested Bustard	*E. ruficrista*
Black Bellied Bustard	*E. melanogaster*
Bengal Florican	*Houbaropsis bengalensis*
Lesser Florican	*Sypheotides indica*
Little Bustard	*Tetrax tetrax*
Houbara Bustard	*Chlamydotis undulata*
Snipe	*Gallinago* sp.
Woodcock	*Scolopax rusticola*
Gulls	*Laridae*
Terns	*laridae*
Jungle Crow	*Corvus macrorynchos*
Indian Pied Hornbill	*Anthracoceros malabaricus*
Mistle Thrush	*Turdus viscivorus*
Reed Warbler	*Acrocephalus* sp.

SYNOPSIS

of

a thesis on

Some aspects of the breeding behaviour of the Lesser Florican *Sypheotides indica* (J.F. Miller) and the Bengal Florican *Houbaropsis bengalensis* (Gmelin).

Submitted to the University of Bombay for the degree of Doctor of philosophy in Zoology, by Mr. Ravi Sankaran, under the guidance of Mr. J. C. Daniel, Curator, Bombay Natural History Society, Bombay.

The family Otididae, commonly known as the bustards, is represented in the Indian subcontinent by three species namely the Lesser Florican *Sypheotides indica* (J.F. Miller), Bengal Florican *Houbaropsis bengalensis* (Gmelin) and the Great Indian Bustard *Ardeotis nigriceps* (Vigors). Having been popular game birds, considerable literature on the general habits, breeding behaviour and distribution are present for the Lesser and Bengal Florican (Jerdon 1864, Hume and Marshall 1879, Baker 1921, Dharmakumarsinhji 1950, Ali and Ripley 1969, Magrath *et al* 1985, Inskipp and Inskipp 1985, Ali *et al* 1985, Rahmani *et al* 1988, Narayan *et al* 1989). Excepting for the detailed studies on the Bengal Florican from the wetter part of its range, Assam, (Narayan and Rosalind 1988, Narayan *et al* 1989, Narayan 1990) the other studies were of either short durations or not detailed or both. As a result of habitat loss and excessive hunting pressures, both these species are now threatened by extinction (Goriup and Karpowicz 1981, Magrath *et al* 1983). As a part of a larger effort to conserve these species by the Bombay Natural History Society, intensive studies on the breeding behaviour with special emphasis on courtship displays were done.

The Lesser Florican was studied at the Sailana Kharmor Sanctuary, Ratlam district in Madhya Pradesh (23°31' N 75°01' E) and at the Rampura/Movalia/Kalitalai grasslands near Dohad, Panchmahal district in Gujarat (22°53' N 74°19' E). Studies on the Bengal Florican were from the driest part of its breeding range and were conducted at the Dudwa National Park, Lakhimpur Kheri district in Uttar Pradesh (between 28°24' N & 28°40' N and 80°34' E & 80°50' E). Behavioural observations were carried out following the focal animal sampling method (Altmann 1974). Other parameters included temperature, weather, cloud cover and intensity of rainfall. Grass heights were measured and insect abundance were assessed by the sweep count method once a week. The location and movement patterns of the birds within the territories were mapped intensively. The data on the breeding behaviour presented in this thesis was collected between June 1987 and October 1989. However, where ever necessary, data collected in both 1985 and 1986 are used. Analysis of data were done with the help of computer packages. Lotus and Systat were used to do statistical analysis and Seas was used to map territories and movement patterns of the individuals studied.

The Lesser Florican breeds in Western India during the south-west monsoon and the Bengal Florican breeds in the sub Himalayan alluvial grasslands in the summer. The environmental factors influencing the breeding habitat of both species were examined. It was found that as a result of great inter-year variability of the south-west monsoons, the breeding habitat of the Lesser Florican showed variation between years. Distribution rather than quantum of rainfall was found to have a greater influence on grass growth. Strong correlation was obtained between grass growth and insect abundance, with insect population increasing with grass height. The Lesser Florican movements were similarly linked to the distribution of rainfall rather than the quantum. The breeding habitat of the Bengal Florican was found to be relatively more stable and the reasons for this are discussed.

The territorial behaviour of both species are described in detail, and the distribution of agonistic interactions in the breeding season was analysed. The agonistic interactions in the Lesser Florican are mainly seen in the early part of the breeding season while in the Bengal Florican it is distributed more evenly throughout the breeding season. Thorough mapping of the study areas were made and territories of males identified. The inter-year variation in the location and spacing of territories are discussed. The home range and movement patterns of the Bengal Florican within its territories were also plotted. The area occupied by three male Bengal Floricans studied ranged between 18 and 28 hectares. Inter-male distances in the Lesser Florican was on average 366 metres with a maximum of 525 metres and a minimum of 275 metres. These distances were much greater in the Bengal Florican and ranged from a minimum of 350 metres to a maximum of 2.25 km. The territorial aspects of the Lesser and Bengal Florican breeding behaviour are discussed.

The different types of courtship behaviour in these species are described in detail. The rates of displays under different weather conditions were analysed. The Lesser Florican displays at the highest rates under overcast and cloudy conditions and least so in sunny weather. Males displayed during slight drizzles, but did not do so during heavy rains. There was no variation in the display rates under different wind speeds. The variation from no-site fidelity to spot specificity in display of the Lesser Florican are analysed and discussed. Choice of display sites and the grass heights at and around the display sites are shown. The Bengal Florican was seen to display at equal rates in all weather conditions. They however did not display during strong rains. Performance of 75 % of displays was temporally localised to within an hour of sunrise and sunset. The influence of stimulus and triggers on the Bengal Florican displays is analysed and discussed. Location of display sites of the Bengal Florican and the variation in the sizes of these sites is analysed and discussed. The pre-copulatory behaviour of both species is described. The distribution of encounters between males and females in the breeding season is analysed. Description of nests and nesting sites and some observations on the nesting behaviour of the Lesser Florican are given.

The breeding behaviour of the Lesser Florican and the Bengal Florican are compared. Absence of breeding area fidelity in the Lesser Florican and its presence in the Bengal Florican are explained by the stability or instability in those factors that determine the breeding environment of each species. The divergence of displays in these closely related species is shown and the similarities in the displays are pointed out. An attempt is made to explain the presence of reversed sexual dimorphism in size in both species. The dispersed lek breeding system that the Lesser and the Bengal Florican follow is discussed in relation to other polygynous species.