STATUS, DISTRIBUTION AND ECOLOGY OF THE GREY-HEADED BULBUL *PYCNONOTUS PRIOCEPHALUS* IN THE WESTERN GHATS, INDIA

Thesis submitted to the

BHARATHIAR UNIVERSITY, COIMBATORE

for the degree of

DOCTOR OF PHILOSOPHY

in

ZOOLOGY

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Certificate

This is to certify that the thesis, entitled "**Status, distribution and ecology of the Grey-headed Bulbul *Pycnonotus priocephalus* in the Western Ghats, India**" submitted to the Bharathiar University, in Partial fulfillment of the requirements for the award of the Degree of **Doctor of Philosophy** in **ZOOLOGY** is a record of original work done by **Mr. P. Balakrishnan** during the period February 2002–December 2007 of his study in the Department of Conservation Ecology at Sálim Ali Centre for Ornithology and Natural History, under my supervision and guidance and the thesis has not formed the basis for the award of any Degree/Diploma/ Associateship/Fellowship or other similar title to any candidate of any University.

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Declaration

I, **P. Balakrishnan** hereby declare that the thesis, entitled "**Status, distribution and ecology of the Grey-headed Bulbul *Pycnonotus priocephalus* in the Western Ghats, India**" submitted to the Bharathiar University, in partial fulfillment of the requirements for the award of the Degree of **Doctor of Philosophy** in **ZOOLOGY**, is a record of original and independent research work done by me during February 2002–December 2007 under the Supervision and guidance of **Dr. V.S. Vijayan,** Department of Conservation Ecology, Sálim Ali Centre for Ornithology and Natural History, Coimbatore and it has not formed the basis for the award of any Degree/Diploma/Associateship/Fellowship or other similar title to any candidate in any University.

P. BALAKRISHNAN

Signature of the Candidate

To my parents, Santhakumari & Gangadharan Nair and
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P. Balakrishnan

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Summary

The Western Ghats of peninsular India is one of the globally important ecoregions harbouring some of the finest rainforests of the world. This mountain ranges host more than 507 species of birds including several endemics and restricted-range species. Little is known, however, about the ecology and conservation status of many species. Habitat loss and fragmentation due to human activities are the major threats to the restricted-range birds of the Western Ghats. Their narrow habitat requirements, particularly during the breeding season, are yet another possible important factor causing their decline. Hence, evaluation of their basic ecological requirements, particularly their selectivity to microhabitats during breeding is of significant value while formulating conservation programme for these species.

The Grey-headed Bulbul *Pycnonotus priocephalus* is a poorly known endemic to the Western Ghats. This restricted range species has a very limited distribution in the heavy rainfall areas in the hills along the south-western side of India from Belgaum and Goa to Kanyakumari. Observations, including both sightings and collections of Grey-headed Bulbul are very few from 1869 to 2002. It was reported as “fairly common but rather local”. However, the recent surveys do not show them ‘common’ in any of the areas covered. This indicates a decline in population probably due to habitat loss and fragmentation.

In the above background a detailed study was carried out to assess the status and distribution of Grey-headed Bulbul in the Western Ghats with respect to altitude and habitat and, to explore the habitat selection, foraging ecology and breeding biology of the species to identify key factors affecting its long- term conservation.

Intensive field surveys were carried out between February 2002 and January 2004 at 24 sites across the Western Ghats to assess the status of the target species. The ecology of the species was studied in the relatively undisturbed tropical wet evergreen forests in the Silent Valley National Park (11° 00’ and 11° 15’ N, 76° 15’ and 76° 35’ E) and Muthikkulam Reserved Forest (10° 56’ and 10° 59’ N, 76° 41’ and 76° 45’ E) between September 2002 and May 2005.

The results of the status survey suggest that Grey-headed Bulbul is a rare species; with an average encounter rate of 0.19 birds/km. They were recorded from the evergreen, moist deciduous and scrub forests with significant abundance (0.33 birds/km) in the low-elevation evergreen forests. There were no records of the species from the plantations, *shola* forests and montane grasslands. Maximum number of Grey-headed Bulbul sightings was from the elevations between 700–1,100 m. Even though breeding Grey-headed Bulbul was restricted to the evergreen forests, they were also recorded from the moist deciduous and scrub forests during the nonbreeding season. The results of the univariate analysis show that habitat type, elevation and the vegetation structure have potential influence on the occurrence of Grey-headed Bulbul. The step-wise logistic regression analysis identified canopy cover, shrub cover, ground cover and presence of water as the major predictors of species occurrence during the breeding season; and canopy cover, sub-canopy cover and vegetation types as predictors of the non-breeding season. Grey-headed Bulbuls were not seen in the areas with wood cutting, mining and other anthropogenic pressures. Seasonal variations in the occurrence and abundance were recorded at Silent Valley and surrounding forests. These variations were due to the seasonal migration of the species which in turn associated with the scarcity in fruits and adverse climatic conditions.

The habitat selection process of Grey-headed Bulbul and the competitive interactions with co-existing Yellow-browed Bulbul were examined at Silent Valley National Park and surrounding areas. The univariate and multivariate analyses revealed the non-random habitat selection of Grey-headed Bulbul at all the spatial scales examined. Both meso-scale (0.04 ha) and micro-scale (0.008 ha) vegetation components were important factors influencing habitat selection of Grey-headed Bulbul. During the breeding season, Grey-headed bulbuls foraged in areas dominated by the sub-canopy trees bearing fruits. The high shrub densities in the reed or *Strobilanthes* patches were significant for nesting site selection. Despite the high resource overlap between Grey-headed and Yellow-browed Bulbuls, the ecological separation was clear in terms of the nest sites. Grey-headed Bulbul overrides the competition for the nesting resources with Yellow-browed Bulbul and indirect factors affecting the fitness by selecting two different microhabitats. This asserts the significance of habitat conservation especially the areas with reed patches for breeding, since nesting in the *Strobilanthes* patches are constrained by biotic factors.

The foraging behaviour, phenology of the food plants and morphological characteristics of the fruits devoured by Grey-headed bulbuls were examined by using standard methods. The foraging maneuvers and food handling techniques were adaptive and

based on the type of food resources. They used least energy expensive methods for food procurements and handling. Grey-headed Bulbuls showed significant variations in their foraging behaviour during different stages of breeding; presumably an adaptive behavioural mechanism to cope with their energetic constraints and predation risks. They actively participated in the mixed-hunting flocks during the non-breeding season. General fruiting phenology at Silent Valley shows a bimodal pattern which is typical to the evergreen forests of Southern Western Ghats. On the other hand, the fruiting pattern of 25 major fruit plants of bulbul has shown a uni-model pattern which coincides with the breeding season of the species. The lack of keystone species and strict seasonality of preferred fruit plants create resource scarcity for Grey-headed Bulbul. This lean period of food coupled with adverse climatic conditions leads to the local migration of the species. The number of fruits available for Grey-headed Bulbul is constrained by its specialization in fruit choice in terms of size, colour, seed size and other physical traits. They avoided green and yellow fruits and larger dry fruits. The patchy distribution of Grey-headed Bulbul was associated with the clumped distribution of food resources within the evergreen habitats. The local migratory behaviour of Grey-headed Bulbul has particular conservation concern because most of the existing protected areas in the Southern Western Ghats are in the mid or higher elevations, and the habitats in the lower elevations remain un-protected. Therefore, lower areas adjoining the existing National Parks and Wildlife Sanctuaries need to be protected for the effective conservation of Grey-headed Bulbul and other altitudinal migrant bird species; and other fauna of the low elevations.

Breeding seasonality, nesting site, nest structure and placement; clutch size, brood size, nesting chronology, nest success and parental care of Grey-headed Bulbul were documented by following standard methods during 2003 to 2005. Breeding season of Grey-headed Bulbul which is confined to the drier months was influenced by the fruit abundance and rainfall. The nest sites of Grey-headed Bulbuls were associated with the reed and *Strobilanthes* patches in the mid-elevation evergreen forests. High competition for nesting substrates with Yellow-browed Bulbul and other species belongs to the same nesting guild leads Grey-headed Bulbul to breed in these two different microhabitats. The architecture of the nests varied, apparently, based on the microhabitat. These architectural variations could be an adaptive phenotypic plasticity evolved to improve the fitness and may have arisen from

multiple interacting factors such as differential micro-habitat use to avoid inter-specific competition and predation pressure. The breeding phenology of the species was similar to the patterns recorded in other bulbuls. Nest survival in Grey-headed Bulbul is comparatively lower than that of several threatened species. Meso- and micro scale nest-site characteristics around the nest did not significantly affect nest survival rates. High predation rates could mostly be attributed to the high diversity and abundance of potential nest predators. Grey-headed Bulbul adopted differential parental investment strategies during the incubation and nestling period in response to the varying predation pressure.

The results show that the restricted range, patchiness in occurrence, low population density, local migratory behaviour as a response to the resource scarcity and adverse climatic conditions; nest site limitations due to interspecific competition, low nesting success, high predation pressure; and distinct ecological requirements during breeding and non-breeding seasons of Grey-headed Bulbul make it extremely vulnerable to the habitat loss and fragmentation. The study also highlights the importance of reed patches and the low- and mid-elevation evergreen forests for the long-term survival of Grey-headed Bulbul. And, most such habitats are outside the protected areas. Therefore, formulation of a sustainable reed extraction scheme and filling the gaps in the existing Protected Area network, especially the addition of low elevation forests is necessary for the effective conservation and management of Grey-headed Bulbul. Moreover, Grey-headed Bulbul may be included under the "Vulnerable" category of the IUCN owing to its patchiness in occurrence, low population density and habitat loss.

Chapter 1

General introduction

1.1. Prologue

Extinction is the presumed ultimate fate of all species, as earlier types are superseded by later ones in an evolutionary succession (Newton, 1998). A number of factors such as low abundance (Pimm et al., 1993; Newton, 1998), small range size (Manne et al., 1999), geographic location (Manne et al., 1999), habitat specialization, proximity to locations of high human density, certain life-history traits like low reproductive rate (Pimm, 1991; Purvis et al., 2000), large body size (Gaston and Blackburn, 1995; Owens and Bennett, 2000), and higher trophic level may predispose a species to high extinction risk (Manne and Pimm, 2001; see also Birdlife international, 2000, 2001). Recent human-induced extinction rates are 100-1,000 times the geological background rate and are predicted to increase another 10-fold (Pimm et al., 1995). The present task for conservation biologists is preventing species extinction and thus slowing the rates of global biodiversity loss (Balmford et al., 2005; Ricketts et al., 2005). At this context, studies on the status and ecological requirements of rare species are of prime significance in formulating long-term conservation (Collar et al., 1994; Bennett and Owens, 1997; Stattersfield et al., 1998; Birdlife international, 2000, 2001, 2004a).

1.2. Global challenges and approaches of avian conservation

A total of 9,956 bird species has been recognised so far from the world (BirdLife International, 2007; see also Sibley and Monroe, 1990; Rasmussen and Anderton, 2005). About 154 species may have been lost in the last 500 years, with 17 of them in the last quarter of the 20th century, and two species since 2000. Approximately 12.3% of all bird species have a real risk of becoming extinct in the next 100 years. In a recent assessment, about 2,033 species have been prioritised for urgent conservation action. They include 189 Critically Endangered, 356 Endangered, 672 Vulnerable and 812 Near-Threatened bird species (BirdLife International, 2007).

Birds are primarily threatened by habitat loss because of habitat destruction and habitat degradation from agricultural practices and water management, which affect over two-thirds of the threatened species (Balmford and Long, 1994; Collar et al., 1994; BirdLife International, 2000; Owens and Bennett, 2000; see Butchart et al., 2004 for a review). Of these about 74% are affected by the recent loss of tropical forests. The habitat fragmentation due to the deforestation and conversions to plantations is one of the major causes of endangerment in birds, especially in the tropics (see reviews in Simberloff, 1995; Turner, 1996; Fahrig, 2002; BirdLife International, 2000; Raman, 2001).

About one-third of the world's threatened bird species are at risk from direct mortality because of human persecution, including harvesting, poisoning, egg collecting, and capture for trade, and by predation from introduced predators which has been especially devastating the fauna and flora on island ecosystems (Pimm et al., 1993; Newton, 1998; Manne et al., 1999; Owens and Bennett, 2000). These factors directly reduce survival and/or reproduction, to result in population declines (Newton, 1998). The birds with large body size and long generation times have more extinction risks through human persecution and introduced predators. However, several frugivorous or nectarivorous birds that were small, had short generation times, and were habitat specialists are also highly threatened by habitat destruction (Owens and Bennett, 2000). Introduced predators, introduced competitors, hybridization, disease, and other unknown risk factors are also known to increase the extinction risk of birds (Collar et al., 1994; Newton, 1998).

Global concern of severe threat to the birds and in general to the biodiversity has resulted in a rigorous approach in the habitat or area conservation effort. This approach for slowing the biodiversity loss has resulted in the identification of biodiversity hotspots (Mittermeier et al., 1999, 2004; Myers et al., 2000; Myers, 2003), Endemic Bird Areas (Stattersfield et al., 1998), Important Bird Areas (BirdLife International, 2004b) and the establishment of many protected areas. On the other hand the species conservation approach is still in its infancy in most part of the world, especially in the Asian and African continents. However, long-term studies and recoveries of many endangered species such as Whooping Crane (Allen, 1954), Northern Spotted Owl (Lamberson et al., 1992), Mauritius Kestrel (Jones et al., 1995), and Kakerori (Robertson et al., 1994; see also Cade and Temple, 1995; Green, 1995; Derrickson et al., 1998) have laid the foundation for this approach.

1.3. Diversity and conservation challenges of Indian avifauna

The great diversity of habitats and variety of climates have resulted in an extremely rich avian and other biodiversity in the Indian Subcontinent which contains about 1,300 species or over 13% of the world's birds (Grimmett et al., 1998). The geographic ramification of Southeast Asia, the tangled patterns of mountain chains, river drainage systems and a long period of stable climate seem to have been ideal for the evolution of a wide array of bird species in India (Ali and Ripley, 1987). Recently, Rasmusen and Anderton (2005) have described 120 new taxa from the Indian Subcontinent; mostly subspecies were elevated to the species level. As elsewhere in the world, the forests in India are also being lost to clear felling and conversion to agriculture, infrastructure and other land uses, and degraded by timber extraction, livestock grazing, shifting cultivation and over-exploitation of non-timber forest products. Similarly, grasslands are being converted into agriculture and other land-uses; and degraded by over-grazing, over-harvesting of grass, and inappropriate fire management (BirdLife International, 2000, 2004b). There has been a loss of about 38% of wetland habitats through reclamation, infrastructure development, and over-exploitation of wetland resources from 1991-2001 (Vijayan et al., 2004). As a result of this more than 131 bird species of India are threatened with global extinction. According to recent assessments, India supports populations of 12 Critically Endangered, 10 Endangered, 56 Vulnerable and 53 Near-Threatened bird species (BirdLife International, 2004a, 2007).

As a result of the global commitment of habitat preservation for biodiversity conservation, Himalayas, Indo-Burma, and Western Ghats and Sri Lanka in the Indian Subcontinent have been identified as biodiversity hotspots (Mittermeier et al., 1999, 2004). India has a Protected Area network comprising about 96 National Parks with a total area of 38,029 km^2 and 510 Wildlife Sanctuaries with a total area of 118,641 km^2 (Anonymous, 2007). Of the 465 Important Bird Areas (IBA's) identified in India, 435 support globally threatened species and 208 have restricted-range species (Islam and Rahmani, 2004). However, about 199 IBA's are in unprotected areas. A recent study recommends the need for developing a National Wetland Conservation Area Network for the conservation of threatened waterfowl and other biodiversity (Vijayan et al., 2004).

Several threatened bird species belong to different groups such as vultures, hornbills, laughing thrushes, floricans, megapods, pheasants and cranes have received considerable research attention in recent years (see reviews in BirdLife International, 2001, 2004a). Of the 16 restricted-range species of the Western Ghats, the status and, or ecology of a few species such as Black-and-Orange Flycatcher *Ficedula nigrorufa* (Khan, 1977, 1979), Nilgiri Laughing Thrush *Garrulax cachinnans* (Islam, 1985, 1994; Ahmed, 2005), Grey-breasted Laughing Thrush *Garrulax jerdoni* (Islam, 1985), Malabar Grey Hornbill *Ocyceros griseus* (Mudappa and Kannan, 1997; Mudappa, 2000; Maheswaran, 2000; Raman and Mudappa, 2003), White-bellied Shortwing *Brachypteryx major* (Robin and Sukumar 2002), Nilgiri Wood Pigeon *Columba elphinstonii* (Somasundaram, 2006) and Nilgiri Pipit *Anthus nilghiriensis* (Vinod, 2007) have been documented. Hence the status and ecological requirements of several restricted range and rare species are largely unknown. The gaps in information on the distribution, population, ecological requirements, and threats of several species are major hindrance in formulating conservation strategies (see BirdLife International, 2000).

In the present study I document the status and ecology of yet another restricted range species of the Western Ghats, the Grey-headed Bulbul *Pycnonotus priocephalus*.

1.4. Systematics and distribution of bulbuls

The family Pycnonotidae is a large group of passerines of the Old World tropics, widespread in Southern Asia, Africa, Madagascar, islands of the Western Indian Ocean (Figure 1.1). Although, a few species are distributed in temperate areas of Southeast Asia, the Middle East, Southern Turkey, North Africa and Cape region of South Africa, they are absent from Europe (Fishpool and Tobias, 2005). Several species are found in the Philippines, but the family's distribution is severely truncated by Wallace's line; a single species (*Thapsinillas affinis*) is native to the Moluccas and some small islands off Sulawesi. Throughout Africa and Asia, a few species of bulbuls (especially the genus *Pycnonotus*) tend to be common garden birds, and so the family is generally familiar to local people (Moyle and Marks, 2006). Several species have also been introduced to areas outside their natural distribution and become well established as in Hawaii and Australia (see Fishpool and Tobias, 2005).

The taxonomic history of Pycnonotidae has shown many taxonomic uncertainties, concerning both generic attribution and species limits. Delacour (1943) provided a synopsis of previous work on familial limits and taxonomic relationships among pycnonotid genera, and synthesised the available data into his own hypothesis of bulbul relationships. Later studies dealing with bulbul taxonomy and systematics focused primarily on population level questions (Smith et al., 1997, 2005), species limits (Chappuis and Erard, 1993), and relationships within a genus (Roy, 1997; Gregory, 2000). Recent analyses of DNA sequence have provided new insights into the phylogenetic relationships (Cibois et al., 2001; Pasquet et al., 2001; Beresford et al., 2005; Moyle and Marks, 2006). However, many aspects of bulbul systematics remain unresolved. Although, this uncertainty on the positions of several bulbuls and related species has been resolved through morphological, ecological and molecular studies (Beresford et al., 2005; Moyle and Marks, 2006), some species such as Kinkimavo *Tylas eduardi* of Madagascar, Malia *Malia grata* of Sulawesi, and Blackcap Mountain-babbler *Lioptilus nigricapillus* remain problematic. Thus with several exclusions taken into account, the family Pycnonotidae comprises 138 species and 355 taxa. However, recent molecular analysis and other studies suggest many of these are probably not pycnonotids (Pasquet et al., 2001; Beresford et al., 2005; Fishpool and Tobias, 2005; Moyle and Marks, 2006).

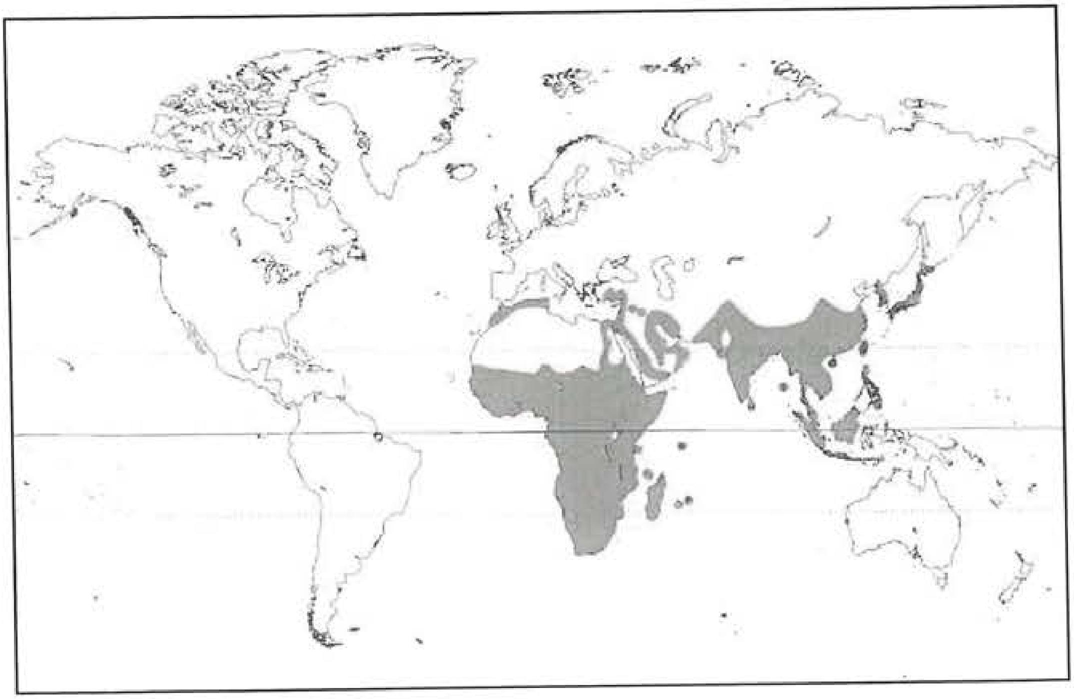

Figure 1.1. Distribution of bulbuls in the world (source: Fishpool and Tobias, 2005).

Of the 27 genera currently treated within the family, 11 are exclusively Asian and 14 are restricted to Africa and islands of the Western Indian Ocean. Remaining two genera occur in both the continents. The genus *Pycnonotus*, with 42 species, is by far the largest of the family. Recent phylogenetic studies using mitochondrial and nuclear DNA showed the possibility of separate radiations across both the continents, so broad was the genetic disjunction between African and Asian bulbuls (Moyle and Marks, 2006; see also Fishpool and Tobias, 2005). However, a few taxa embedded within the Asian clade suggest that the African *Pycnonotus* were recently derived from Asian ancestors, and likely arrived in Africa via the Middle East rather than long distance dispersal across the Indian Ocean (Moyle and Marks, 2006). Moreover, according to another recent study of passerine relationships (Barker et al., 2004), bulbuls are sister to a specious clade of babblers and Sylvioid warblers; a largely Asian radiation.

In the present study the nomenclature provided in Grimmett et al. (1998) has been followed for the bulbuls and other birds of Indian Subcontinent and Fishpool and Tobias (2005) for bulbuls restricted to other continents.

Thirteen species of bulbuls are considered as threatened which include one Critical, two Endangered, and ten Vulnerable species. Apart from these, another 14 pycnonotids are currently considered as Near-Threatened, which includes 10 Asian species (BirdLife International, 2000, 2004a). Of the 22 species of bulbuls recorded in India (Rasmussen and Anderton, 2005), eight were seen in the Southern or peninsular India (Table 1.1). Majority of these species are inhabitants of the clearings, edge habitats and scrubs.

1.5. Grey-headed Bulbul: species characteristics

The Grey-headed Bulbul *Pycnonotus priocephalus* -first described as *Brachypus priocephalus* by Jerdon in 1839- is one of the 16 restricted range bird species of the Western Ghats. It is a grey headed olive green bulbul, about 17-19 cm in length, with the rump barred black and yellow. *Above*, head grey with greenish forehead; back olive-green mottled with brown and grey on rump; upper tail coverts and centre of tail grey; outer retrices dark brown tinged with olive, broadly tipped with grey. *Below*, chin blackish, belly olive-green. Broad square tail characteristic and light coloured iris conspicuous. Sexes alike. They are arboreal, keeping chiefly to the foliage canopy of trees and tall vine-draped shrubs (Ali and Ripley, 1987; Fishpool and Tobias, 2005).

Grey-headed Bulbul has "a very limited range in the heavy rainfall area along the south-western side of India from Belgaum and Goa south through Kerala, and east to the Nilgiris and Palnis, western Mysore and Coorg; from the plains to c.1,000 m, rarely to 1,800 m; optimum zone between 600 m and 900 m" (Ali and Ripley, 1987).

Owing to the taxonomic uncertainties, Fishpool and Tobias (2005) suggested in-depth analysis of morphology, voice, behaviour and genetic studies to redefine its limits. This monotypic species may merit separation in resurrected genus *Brachypodius*, alongside *Pycnonotus atriceps* and *Pycnonotus fuscoflavenscens* (Fishpool and Tobias, 2005).

Table 1.1. List of bulbuls recorded in peninsular India (Classification followed Grimmett et al., 1998).

Common Name	Species and subspecies
Grey-headed Bulbul	*Pycnonotus priocephalus*
Black-crested Bulbul [1]	*Pycnonotus melanicterus gularis*[1]
Red-whiskered Bulbul	*Pycnonotus jocosus*
Red-vented Bulbul	*Pycnonotus cafer*
White-browed Bulbul	*Pycnonotus luteolus*
Yellow-throated Bulbul	*Pycnonotus xantholaemus*
Yellow-browed Bulbul	*Iole indica* [2]
Black Bulbul [3]	*Hypsipetes leucocephalus ganeesa* [3]

[1]In a recent taxonomic revision, these subspecies have been promoted and renamed as Flame-throated Bulbul *Pycnonotus gularis*, and [3]Square-tailed Black Bulbul *Hypsipetes ganeesa*; and [2]renamed as *Acritillas indica*; see Rasmussen and Anderton, 2005).

1.6. Previous field studies on bulbuls

Only a few widespread and the lowland Pycnonotids have been well studied in their native and other introduced ranges. There are detailed accounts of diet, vocalizations and behaviour, sex ratios, breeding biology, population expansion, hybridisation, diseases, body parasites and molting of Red-vented and Red-whiskered Bulbuls (e.g., Sibley and Short, 1959; Short, 1964; Vijayan, 1975, 1980; Walting, 1977, 1983; Balachandran et al., 1995; Kumar, 1999a; Kumar and Bhatt, 2000; Bhatt and Kumar, 2001)

In Africa, a few key studies have been conducted on the ecological and behavioural aspects of common species such as Cape Bulbul, Black-eyed Bulbul and Common Bulbul (e.g., Liversidge, 1970; Brossett, 1982; Keith, 1992; Lloyd et al., 1994, 1996, 1997, 1999; Craig et al., 1997; Lloyd and Palmer, 1998; Kruger, 2004).

The lowland species such as Red-vented Bulbul (Vijayan, 1975, 1980; Kumar, 1999a; Kumar and Bhatt, 2000; Bhatt and Kumar, 2001), White-browed Bulbul (Vijayan, 1975, 1980), Red-whiskered Bulbul (Balachandran et al., 1995), Yellow-vented Bulbul (Ward, 1969), and Styan's Bulbul (Hsu and Lin, 1997; Severinghaus, 1998) have been quite well studied in Asia. However, the ecological and behavioural aspects of several species, especially the mid and higher elevation bulbuls are restricted mostly to natural history notes (see reviews in Fishpool and Tobias, 2005).

1.7. Objectives

The goal of this research was to document the status and ecological requirements of the Grey-headed Bulbul. The specific objectives were to:

1. assess the status and distribution of the species along the geographical, altitudinal, and habitat gradients,
2. identify the primary foraging behaviour and explore the seasonal and annual variations,
3. describe the foraging and nesting habitat use at multiple spatial scales and identify the role of interspecific competition in habitat selection,
4. determine the phenological patterns and fruit characteristics of major food plants and examine the relationship of the same with the ecology of the species,
5. document the breeding biology of the species to describe the life history strategies, and
6. evaluate the major threats to the species and outline strategies for management and conservation.

1.8. Organization of the thesis

The thesis is divided into seven chapters. The first chapter provides a brief review of the global and Indian scenario of bird conservation and; previous field studies on bulbuls and restricted range bird species of the Western Ghats. Chapter 2 describes the study areas and the intensive study sites with descriptions of the climate, flora, fauna and management backgrounds. Chapter 3 presents the results of the surveys conducted to assess the present status and distribution of Grey-headed Bulbul in various geographic, elevation and habitat gradients. In Chapter 4, I describe the foraging and nesting habitat use of Grey-headed Bulbul at multiple spatial scales and role of interspecific competition in habitat selection process. Chapter 5 presents information on the foraging ecology of Grey-headed Bulbul and explores the fruit characteristics and phenological patterns of food plants. The breeding biology and parental care of the species are described in Chapter 6. Chapter 7 offers an overall discussion and concludes how the findings relate to the management and conservation of Grey-headed Bulbul and provides recommendations. Finally, a list of detailed bibliography was provided.

photo: Shiva Shankar

Grey-headed Bulbul *Pycnonotus priocephalus*, the study species.

Chapter 2

Study area

The first phase of this study was a status survey of the Grey-headed Bulbul, carried out in the Western Ghats covering four Southern Indian states, namely Kerala, Tamil Nadu, Karnataka and Goa (Figure 2.1). In the second phase, intensive ecological studies were carried out in the Silent Valley National Park and surrounding areas and, the Muthikkulam Reserved Forest, located in the Nilgiri Biosphere Reserve (Figure 2.2). In this chapter, I describe the key features of the Western Ghats as well as the intensive study areas.

2.1. The Western Ghats

2.1.1. Location, topography and climate

The Western Ghats is a chain of mountain range from almost the southern tip of India (8° N) up to the Tapti River (20° E), covering a distance of 1,600 km. It is almost parallel to the western coast with the distance from the sea ranging from 2 to 50 km and traverses through the states of Gujarat, Maharashtra, Goa, Karnataka, Kerala and Tamil Nadu. The Western Ghats is one of the ten biogeographic zones of India (Mani, 1974; Rodgers and Panwar, 1988; Rodgers et al., 2000, 2002). Tropical rainforests represent primary centers of species richness and endemism within the Western Ghats, and cover approximately 20,000 km^2. Dry, moist deciduous, and scrub forests cover another 20,000 km^2 (Collins et al., 1991). There are about 20 National Parks and 68 Wildlife Sanctuaries in the Western Ghats, covering about 15% of the Ghats (Rodgers et al., 2002).

The average height of the ghats is less than 1,500 m above sea level. The undulating hills in the Southern Western Ghats have many peaks such as Anaimudi (2,695m), Doddabetta (2,637m), Vandaravu (2,554m), and Agastyamalai (1,868m). These mountains mediate the rainfall regime of peninsular India by interrupting the monsoon storm systems. Along its entire length, this hill chain has a 30 km wide discontinuity -the Palghat Gap in Kerala- perhaps of tectonic origin through which a river could have flowed in ancient times. The Western Ghats are the main watershed in the peninsular India from which all the principal rivers, namely Godavari, Krishna and Cauveri originate and flow east to the Bay of

Bengal and, several small, perennial, torrential rivers originate from the ghats and flow west to join the Arabian Sea (Nair, 1991).

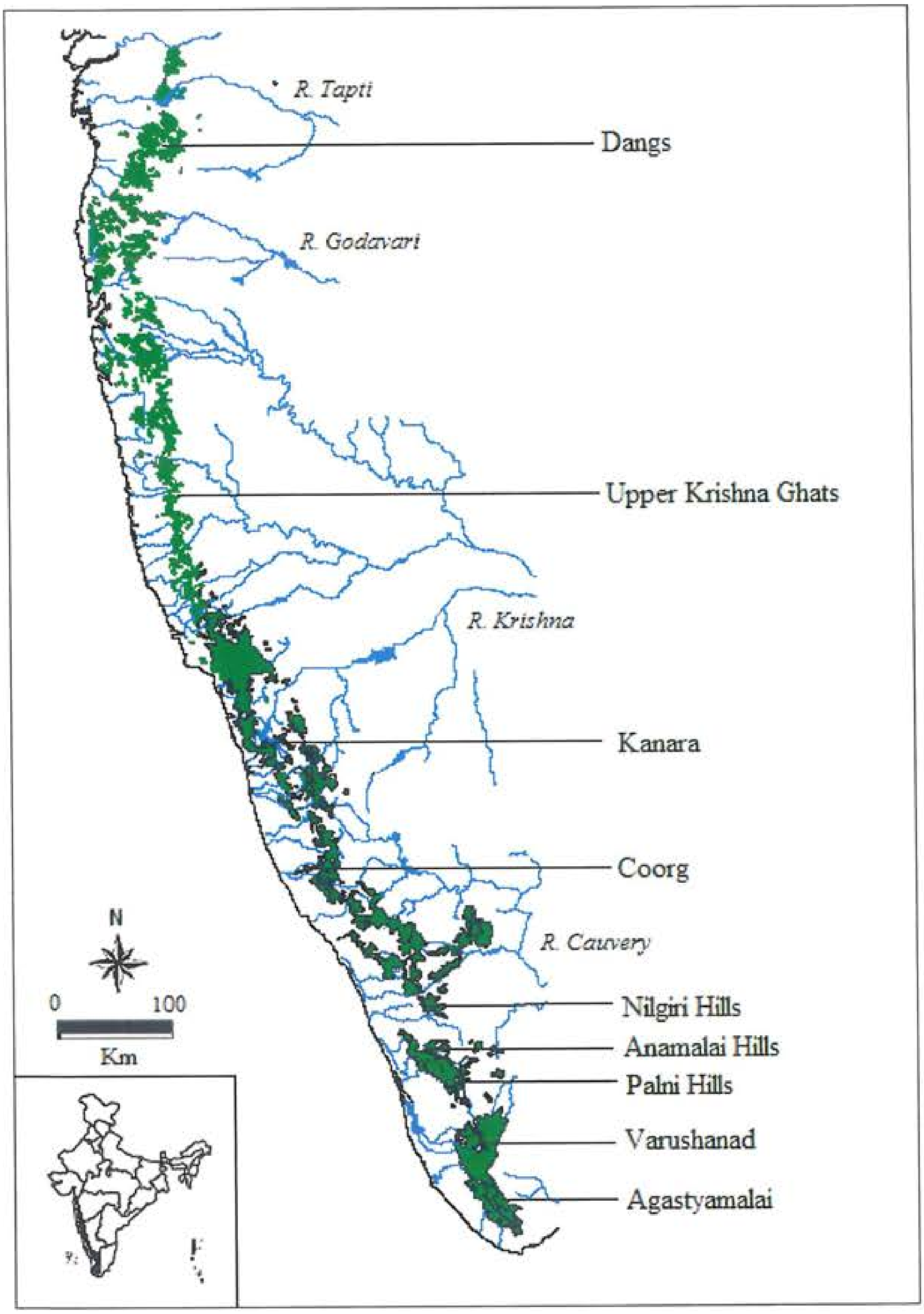

Figure 2.1. Map of the Western Ghats, South India.

Climatic conditions in the Western Ghats vary with the altitude and physical proximity to the Arabian Sea. Although the Western Ghats experiences a tropical climate, being warm and humid during most part of the year with mean temperature ranging from 20 °C in the south to 24 °C in the north the higher elevations experience subtropical climates and on occasions frost. The rainfall pattern shows pronounced variation from 500 mm in the rain-shadow areas to 7,500 mm in the western parts of the Ghats. The average rainfall in the evergreen forests ranges from 2,000 mm to 7,500 mm depending on the locality (Pascal, 1988).

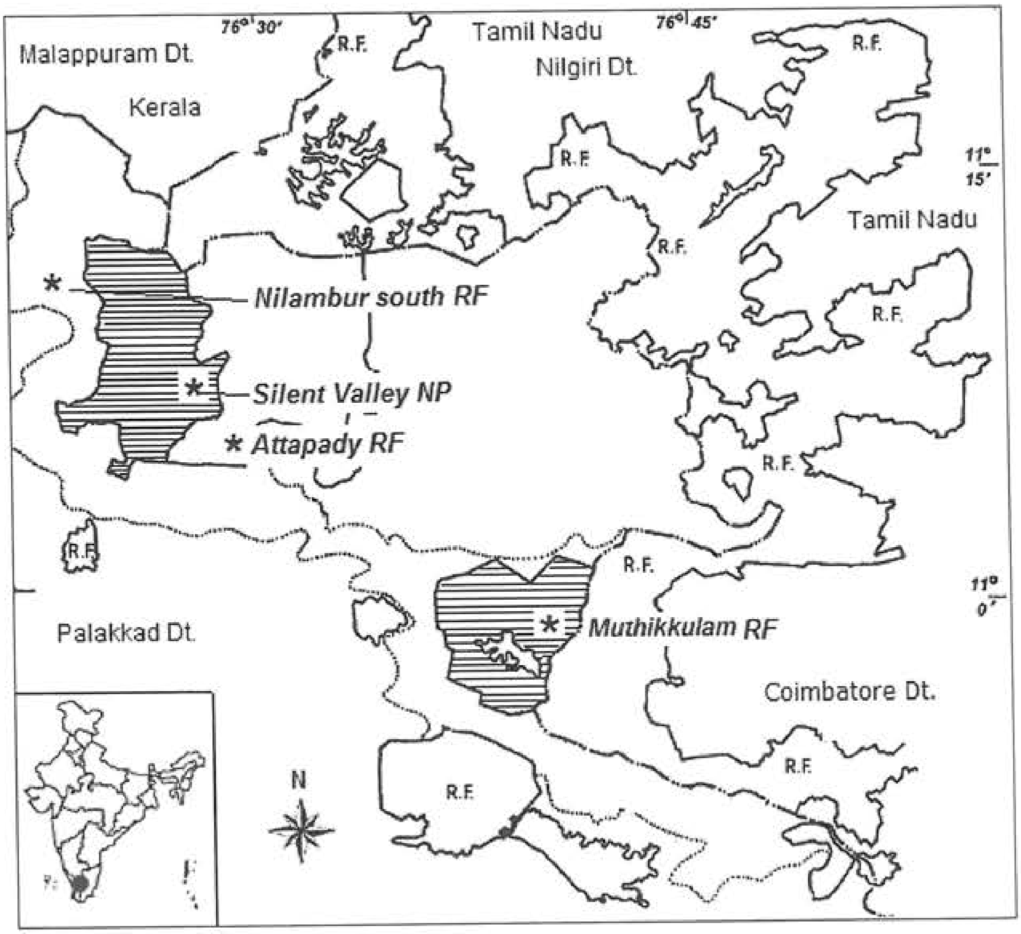

Figure 2.2. Map showing the intensive study sites: Silent Valley National Park and surrounding areas; and Muthikkulam Reserved Forest in the Nilgiri Biosphere Reserve, South India.

2.1.2. Flora

The variability in precipitation and topographic diversity generate a wide variety of vegetation types, ranging from wet evergreen and semi-evergreen forests on the western side and at high altitudes to dry deciduous forests and scrub vegetation on the eastern slopes and lowlands (Champion and Seth, 1968). Some of the tropical moist forests in the Southern Karnataka, Kerala and Tamil Nadu are among the best representative areas of Indo-Malayan rainforest formations (Nair, 1991). Pascal (1988) classified the tropical evergreen forests of the Western Ghats into low, medium and high-elevation types. Of the more than 16,000 species of flowering plants recorded from India, about 5,000 species belonging to nearly 2,200 genera and 217 families are found in the Western Ghats, including 1,700 endemic species. There are also 58 endemic plant genera, 49 of which are monotypic and some highly speciose. Of the 267 species of orchids (representing 72 genera), 130 are endemic. Amongst the lower plants, around 320 species of pteridophytes, 200 species of bryophytes, 300 species of algae, 800 species of lichens and, 600 species of fungi are known from the Western Ghats (Ramesh and Pascal, 1991; Kumar, et al., 1999, 2004).

2.1.3. Fauna

The tropical forests of the Western Ghats are characterised by high animal diversity and endemism. Of the 288 fish species recorded from the Western Ghats 118 are endemic to this region (Dahanukar et al., 2004). The highest rate of endemism is to be found among amphibians, with more than 78% endemics. The 126 species recorded so far apparently represent only 50% of the amphibian fauna of the Western Ghats, as it has been pointed out that specimens of at least another 115 species are lying with local biological collections, to be taxonomically described (Biju, 2001). About 199 species of reptiles are known from the Western Ghats with high endemism in families such as Uropeltidae, Gekkonidae, and Agamidae. The Western Ghats has been recognised as an Endemic Bird Area with 16 species of restricted-range birds (Stattersfield et al., 1998) and, it has more than 507 species of birds, including about 360 terrestrial species and more than 40 'disjuncts' (Ali and Ripley, 1987; Daniels, 1989; Zacharias and Gaston, 1999). According to a recent evaluation, the Western Ghats supports populations of two Critically Endangered, one Endangered, seven Vulnerable, and eight Near-Threatened bird species including a few wintering species (BirdLife

International, 2001; 2004a). Although the mammalian diversity is low, the Western Ghats is considered as one of the six high priority hotspots for the survival of the world's most endangered primates. Of the 400 species of Indian mammals (Menon, 2003), nearly 137 are known from the Western Ghats out of which 12 are endemic (Kumar et al., 1999, 2004). Even if knowledge of invertebrate diversity is poor (see, Daniels, 2003), levels of endemism within certain groups; for example, among the tiger beetles are very high (see Kumar et al., 2004). On the other hand, the number of butterfly species in this region is relatively low, with only 37 endemics of 330 (Kunte et al., 1999) in the Western Ghats.

2.1.4. Conservation problems

The Western Ghats faces severe threats from various anthropogenic activities such as deforestation, development activities, conversion of natural forests to plantations of tea, coffee, teak, *Eucalyptus*, and wattle; and habitat fragmentation (Nair, 1991). The lowland evergreen and semi evergreen forests below 500 m, probably once extended from the costal plain to the west of the ghats, have long been cleared and highly fragmented throughout their range (Rodgers and Panwar, 1988; Nair, 1991; Stattersfield et al., 1998; Mittermeier et al., 1999). Only 7.5 percent of the original forest cover still stands in a more or less pristine state (Myers et al., 2000). Prasad et al. (1998) have estimated 0.90% annual decline in the natural forest cover in Kerala for the period 1961–1988, while Menon and Bawa (1997) assessed the annual rate of deforestation in the Western Ghats to be 0.57% during the period 1920–1990. According to Jha et al. (2000) the loss of forest with a crown density up to 20% is about 2,729 km^2, *i.e.* 25.65% of the forest area over 22 years between 1973 and 1995 in the southern part of the Western Ghats. The Palakkad district of Kerala, where the intensive study areas are located is among the districts which faced the highest annual loss (2.1%: Jha et al., 2000). In all, approximately only 20% of the natural forest vegetation of the Western Ghats is thought to remain (Collins et al., 1991), but in a highly fragmented state, and the only tracts larger than 200 km^2 are found in the Agasthyamalai Hills, Cardamom Hills, Silent Valley-New Amarambalam Forests, and southern parts of the South Kannada District in Karnataka State. Considering the high degree of endemism and threats to the biodiversity, the Western Ghats have been recognised as one of the 34 biodiversity hotspots (Myers, 2003; Mittermeier et al., 2004).

2.2. Silent Valley National Park and surroundings

2.2.1. Location, topography and climate

The Silent Valley Forests (11° 00' and 11° 15' N, 76° 15' and 76° 35' E), locally known as 'Sairandhrivanam' is considered as one of the largest contiguous representative tracts of relatively undisturbed tropical evergreen forest in Southern India. It became the focus of India's perhaps most fierce and widely-publicised environmental debate in the late 1970's. This Valley is roughly a rectangular tableland extending over 8,952 hectares at the south-western corner of the Nilgiris. The Silent Valley National Park is surrounded on south and east, by the Mannarkkad and west by the Nilambur South Forest Divisions of Kerala and, on the north by the Mukurthi National Park of Tamil Nadu. The Attapady Reserved Forest of the Mannarkkad Division and Karuvarakundu Reserved Forest of the Nilambur South Division are ecologically contiguous with the Silent Valley National Park and formed a part of the present study area. The landscape of the National Park is highly undulating with high and continuous ridges along its north-eastern boundary. Along its entire length, the plateau slopes towards Kunthipuzha which originates at an altitude of about 2,400 m in the outer rim of the Nilgiris, descends rapidly to 1,150 m at the northern edge of the plateau and flows thereafter in the north-south direction through the Valley (Figure 2.3). The altitude ranges from 658 to 2,383 m with the highest peaks, Anginda (2,383 m), Sispara (2,206 m) and Kozhippara (1,904 m) on the northern boundary of the Valley.

The rainfall in the Silent Valley area shows a marked increase towards the northern and eastern parts. The mean annual rainfall is above 5,000 mm, with more than half of it occurring during the south-west monsoon (May-September). The rainfall in the region between Cheriya Walakkad and the upper slopes in the north of it at times is twice as heavier (> 8,000 mm) than in the southern extreme point at Neelikkal. This heavy rainfall area forms the major nesting habitat of Grey-headed Bulbul. The mean maximum and minimum temperatures at Walakkad during the study period were 25.78 °C and 19.83 °C respectively. January, February and March are comparatively drier months. From June to December the relative humidity is often high, around 95%.

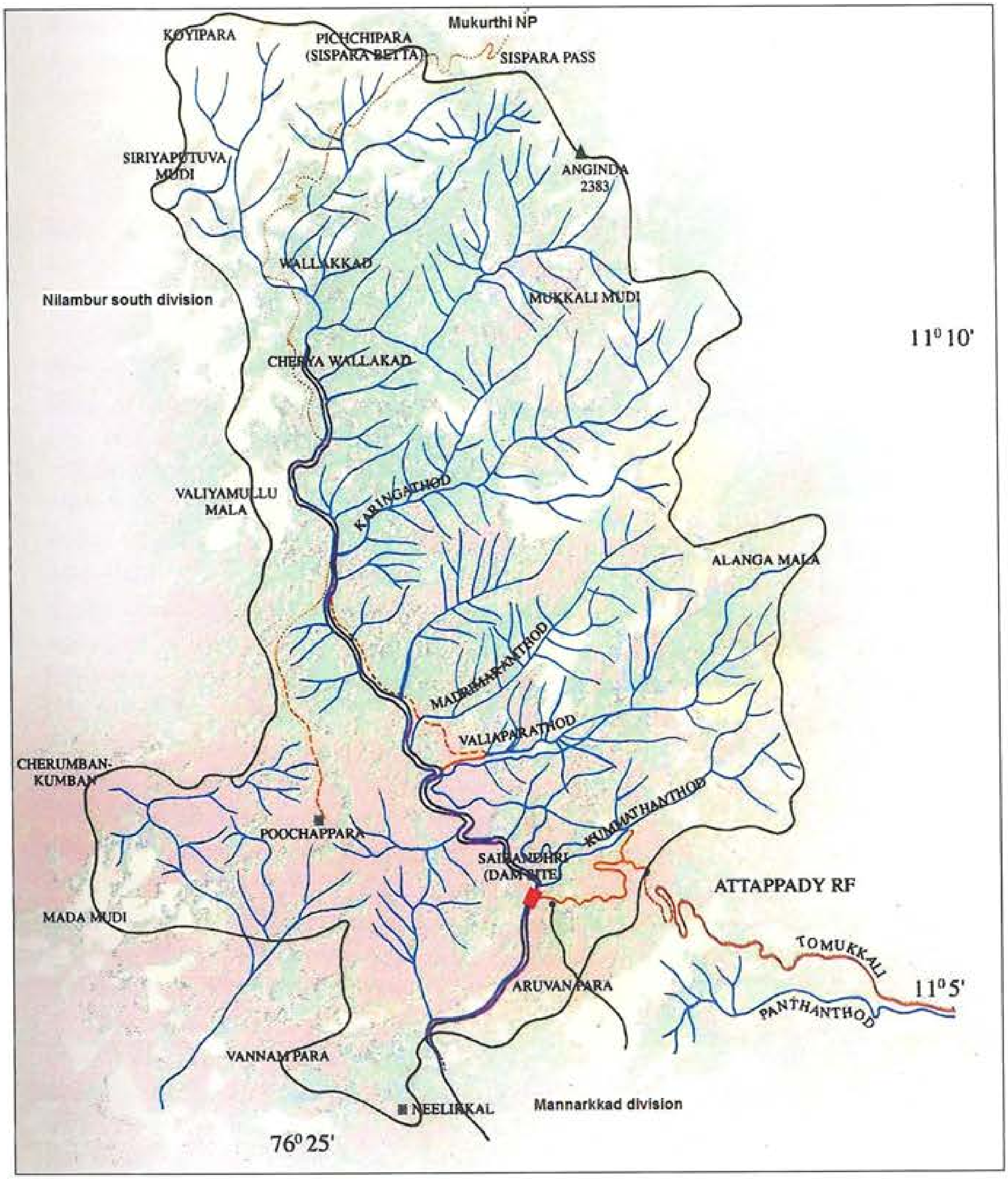

Figure 2.3. Silent Valley National Park with major hills and the tributaries of Kunthipuzha. (Source: Manoharan, et al., 1999).

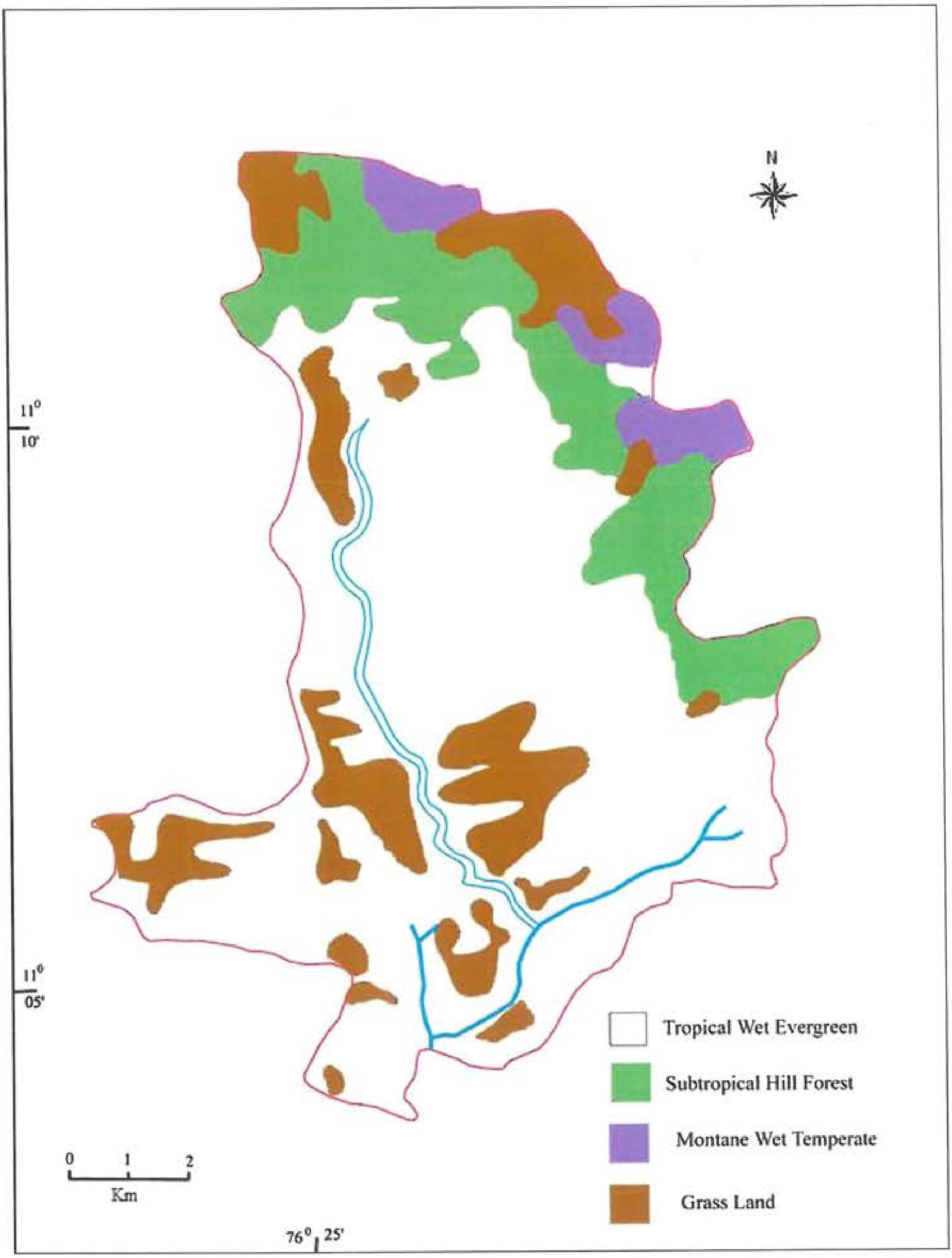

Figure 2.4. Vegetation cover types of the Silent Valley National Park. (Source: Premkumar, 2002)

2.2.2. Flora

The Silent Valley National Park has four main types of vegetation: a) west coast tropical evergreen forest forming extensive dense stands along hills and valleys between 900 and 1,300 m; b) southern subtropical broad leaved hill forest between 1,500 and 2,000 m; c) southern montane wet temperate forest, popularly referred to as 'sholas' and characterised by unrelated evergreen species with a dense closed canopy and; d) grasslands restricted to the narrow sector west of the Kunthipuzha and to the higher slopes and hill tops in the eastern sector (Ayyar, 1935; Champion and Seth, 1968; see Manoharan et al., 1999; Figure 2.4). West coast tropical evergreen forest is the climax vegetation and is characterised by six dominant associations, namely *Palaquium-Cullenia, Palaquium-Mesua, Mesua-Calophyllum, Calophyllum-Syzygium, Ochlandra-Poeciloneuron,* and *Ochlandra-Calophyllum.* The Silent Valley National Park harbours about 2,000 plant species including several rare and threatened plants. Intensive studies on the angiosperm flora reported more than 1,000 species from the Park (Manilal, 1988; Vajravelu, 1990). 107 species and one subspecies of orchids belonging to 54 genera have been reported in the Silent Valley National Park (Kumar, 1999b). Detailed descriptions of the vegetation of the area are reported elsewhere (Manilal, 1988; Vajravelu, 1990; Manoharan et al., 1999).

2.2.3. Fauna

Silent Valley National Park is a part of the Nilambur-Silent Valley-Coimbatore Elephant Reserve. It also holds one of the two viable populations of the lion-tailed macaque, an endemic endangered primate (Green and Minkowski, 1977). Thirty four species of mammals were reported from the valley (Balakrishnan, 1999; Premkumar, 2002). The large carnivores include the tiger *Panthera tigris*, leopard *Panthera pardus* and sloth bear *Melursus ursinus*. The Silent Valley and surrounding forest areas seem to harbour all the 17 species of small carnivores that are reported from the Western Ghats. Of these, the presence of ten species in the park is confirmed (Yoganad and Kumar, 1999). Of the 12 species of fishes recorded from the Kunthipuzha, three are new to science (see Easa and Shaji, 1999). The park harbours more than 60 species of reptiles (see Easa and Shaji, 1999; P. Balakrishnan and K.S.A. Das, *unpubl. data*). About 20 species of amphibians including two new species of frogs and one new species of caecilian were recorded from Silent Valley (see Easa and Shaji, 1999). More than 150 species of butterflies and 400 species of moths were known from the Park (Mathew, 1990; Das and Vijayan, 2004). The area remains still under-explored for the lower invertebrates, except for the studies of ZSI (1986), and Burton and Sivaramakrishnan (1993). The avifauna of Silent Valley is better documented than any other group of vertebrates (see reviews in Vijayan and Balakrishnan, 2005; Vijayan and Das, 2006). Totally, 211 species have been reported from the park (Sugathan, 1999). Of the 16 restricted-range bird species, 15 are recorded from the park. The globally endangered Nilgiri Laughing Thrush *Garrulax cachinnans* is a common resident in the shola forests of the upper reaches of Silent Valley between Sispara and Anginda peaks.

2.2.4. Land-use history and conservation issues

The anthropogenic degradation of the rainforests of the Silent Valley was started by the arrival of colonial planters during the middle of 19th century. 400 ha of forest were given on lease to the coffee planters between 1847 and 1873. However, after a futile attempt to cultivate coffee, the planters abandoned the area in 1889 (Nair et al., 1999). In 1888 the whole watershed of the Silent Valley was declared as reserved land under section 26 of Forest Act, as land at the disposal of the Government. The earliest attempts for timber extraction in the Silent Valley date back to 1901-02 with the selection felling of *Dysoxylum malabaricum*. Large scale selection felling of merchantable species such as *Mesua ferrea, Palaquium ellipticum, Hopea parviflora* and *Acrocarpus fraxinifolius* was started in 1928. Approximately, 48,000 cubic metre of timber is estimated to have been extracted through the selection fellings in the Silent Valley, mainly from its southern half (Nair et al., 1999). The vain attempts to construct roads to transport the merchantable tree species due to the steep terrain, loose soil, heavy cost of construction and the likelihood of landslides have prevented the tree extraction in the northern part of the valley (Premkumar, 2002).

The proposal of a dam across River Kunthi generated strong protests from the ecologists and environmentalists nationally and internationally, which ultimately resulted in abandoning the hydro-electric project and establishment of the Silent Valley National Park in 1984. There are no permanent human habitations within the Park; however, tribal villagers and lowland inhabitants periodically enter the valley to collect the minor forest products and for hunting and fishing (see reviews in Manoharan et al., 1999). The wildlife present in the areas closer to the Neelikal–Cherumban Koomban–Kozhippara–Sispara boundaries are more vulnerable.

2.3. Muthikkulam Reserved Forest

2.3.1. Location, topography and climate

The Muthikkulam Reserved Forest (10° 56' and 10° 59' N, 76° 41' and 76° 45' E) comes under the fairly undisturbed high elevation tropical forest stretch called Palamala–Elival hills, situated in the south-western corner of the Nilgiri Biosphere Reserve (Figure 2.5). This is an isolated block of 6,385.95 ha falling in the Agali range of Mannarkkad Forest Division in Kerala. Muthikkulam is surrounded by the Bolampatty Reserved Forest of Coimbatore in the east, Dhoni Hills of Palakkad Forest Division in the south, forested areas of Agali and Attapady ranges of Mannarkkad Forest Division and the private plantations in the north and west respectively. This reserve is a plateau with elevation varying from 610 m at the exit of Siruvani River to 2,065 m at the highest peak north west of Elival Hill. This is a high rainfall zone with ecological conditions rather similar to those of Silent Valley. The annual rainfall is above 4,500 mm and mean annual temperature below 27 ºC.

2.3.2. Flora

Porter (1887) quoted by Ayyar (1935) described Muthikkulam (Attappady Block VI) as a dense mass of evergreen forest with no deciduous forest and little grassland. The evergreen forests were mentioned as magnificent; with finer trees than he had seen either in Nilgiri or Anamalai sholas. This area represents two major vegetation types, tropical evergreen forest dominated by the *Cullenia exarillata-Palaquium ellipticum* association; and montane shola-grasslands (Champion and Seth, 1968; Nair and Balasubramanyan, 1985; Ramankutty, 2001). Nair and Balasubramanyan (1985) recorded 297 plant species belonging to 33 genera from this reserve. The common trees of this rainforest include species such as *Cullenia exarillata, Palaquium ellipticum, Dysoxylum malabaricum, Dysoxylum ficiforme, Holigarna arnottiana, Myristica dactyloides,* and *Syzygium arnottianum.* Muthikkulam is the home for the critically endangered *Vateria macrocarpa* (*Vellappine* in local language). So far it is recorded only from the type locality apart from a population located near Bolampatty range, Coimbatore in Tamil Nadu adjacent to Muthikkulam. Kumar (2000) recorded 60 species of microlichens from Muthikkulam. However, the floristic studies in Muthikkulam compared to those in Silent Valley are very poor.

2.3.3. Fauna

Although no comprehensive assessments have been made, the faunal species richness and endemism are also expected to be very high and typical of the Western Ghats. Muthikkulam supports good population of the Asian elephant *Elephas maximus* and endemic species such as the lion-tailed macaque *Macaca silenus*, Nilgiri langur *Trachypithecus johnii*, Nilgiri tahr *Hemitragus hylocrius*, and Nilgiri marten *Martes gwatkinsii* (Ramankutty, 2001; Balakrishnan, 2005, 2006). The herpetofauna represents 15 species of amphibians and 52 species of reptiles (Easa, 1998; Balakrishnan, 2006). 16 species of fishes also were recorded from this area (Easa and Basha, 1995).

Prasad et al. (1998) listed 121 species of birds, while during the present study 196 species were recorded of which 106 species were not recorded earlier, thus amounting to a total of 227 species (see Balakrishnan, 2006). Of the 16 restricted-range bird species seen in the Western Ghats, 14 are recorded during this study. Vulnerable species such as Nilgiri Wood Pigeon *Columba elphinstonii*, White-bellied Shortwing *Brachypteryx major,* Broad-tailed Grassbird *Schoenicola platyura,* Kashmir Flycatcher *Ficedula subrubra,* Wood Snipe *Gallinago nemoricola* and Yellow-throated Bulbul *Pycnonotus xantholaemus* were also recorded from Muthikkulam. There were only a few recent reports on the wintering sites of Kashmir Flycatcher and Wood Snipe (see BirdLife International, 2001, Islam and Rahmani, 2004; Zarri and Rahmani, 2004). However, Yellow-throated Bulbul was recorded from Bolampatty Reserved Forest contiguous to Muthikkulam (BirdLife International, 2001). Of the four restricted range bird species with Near-Threatened status, three, namely Black-and-Orange Flycatcher *Ficedula nigrorufa*, Nilgiri Flycatcher *Eumyias albicaudata* and, Nilgiri Pipit *Anthus nilghiriensis* were recorded from this site. Apart from these, three Near-Threatened species with wide distribution, namely Grey-headed Fish Eagle and, Malabar Pied and Great Hornbills were also present at Muthikkulam. There is no literature available on the invertebrate fauna. However, about 135 species of butterflies have been recorded during the present study (Balakrishnan, 2006). Conservation potential of Muthikkulam was mentioned in several studies (e.g., Nair, 1991; Ramankutty, 2001).

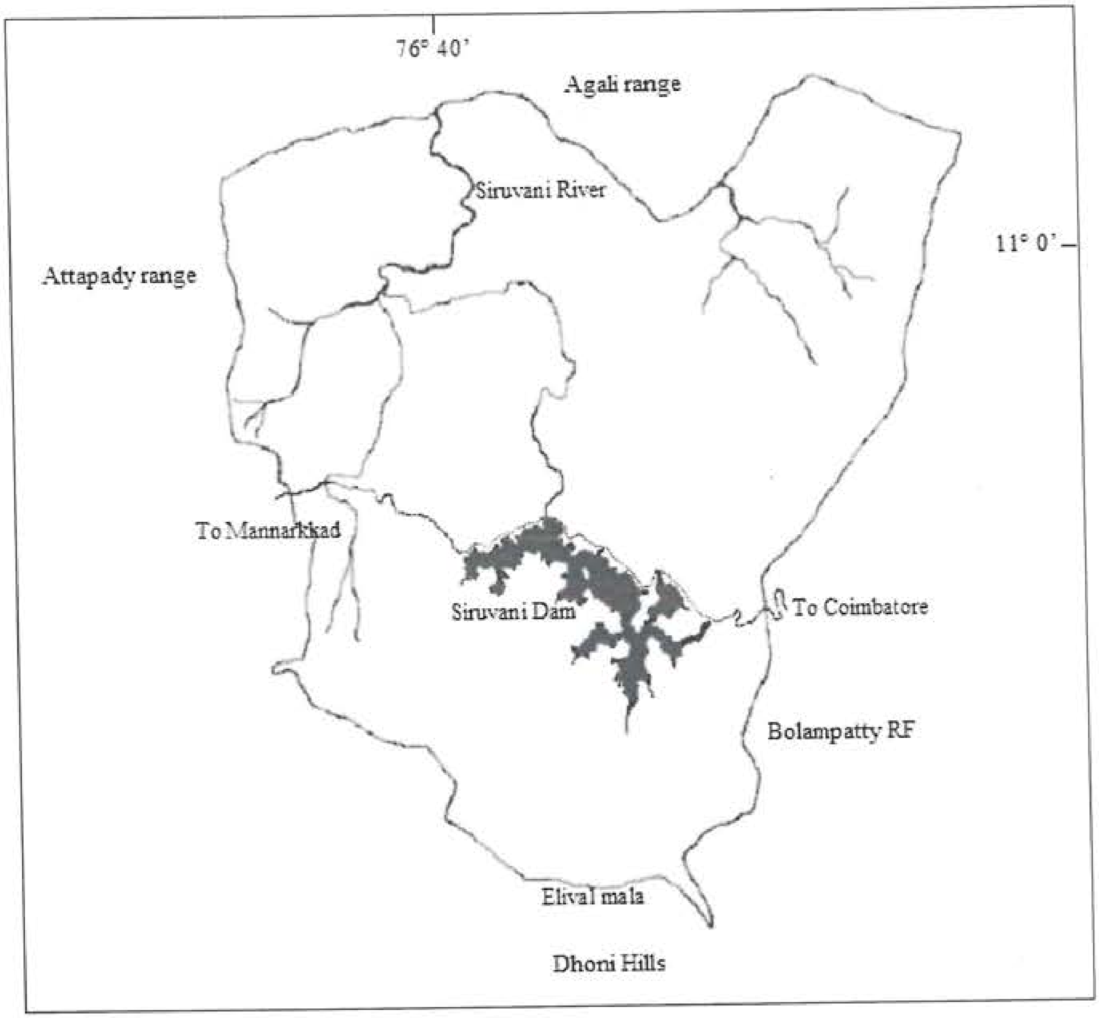

Figure 2.5. Muthikkulam Reserved Forest, Kerala.

2.3.4. Human activities and conservation issues

Muthikkulam Hills originally belonged to private parties and were acquired under the Land Acquisition Act, 1894. In 1912 this area was notified as a Reserved Forest in order to protect the catchments of Bhavani River and its tributaries. About 351 ha were under shifting cultivation in the past. Most of the mid-altitude evergreen forests in the Muthikkulam Hills were damaged due to the selection felling practised since 1920 for railway sleepers, Kolmarams, and plywood timber. Moreover, a large area of evergreen forests was destroyed for the construction of the Siruvani dam in the post independence period. The reeds and bamboos in these hills were uninterruptedly extracted till 1950-51. Later, the reed areas were divided into three coupes and the extraction is still continuing in a three year felling cycle. Most of the cane species (*Calamus spp.*) have become rare in these forests, because of the uncontrolled harvesting. In 1920, seedlings of several exotic species such as *Eucalyptus tereticornis* and *E. grandis* were planted around the Muthikkulam Bangalow and other grasslands. In addition, three plantations of Eucalyptus totaling an area of 81.02 ha were raised, but all were failed (Ramankutty, 2001).

At present there are about 25 families of tribal inhabitants at Singampara, rehabilitated from the old dam site. Although each family has been given land for agriculture, majority of them are depending on the forest products and on the construction works inside and outside the reserve. Agriculture is not pursued much mainly because of their lack of interest in it and also the occasional incidents of wildlife conflicts. There has been a significant disturbance of vegetation around the Siruvani dam, which forms the main source of drinking water for most part of Coimbatore District, but the other areas of the plateau have fairly undisturbed and pristine vegetation. One of the major threats to the biodiversity of Muthikkulam is the maintenance activities related to the dam and the road passing through the reserve. All the elephant trails to the water source were blocked by construction of side walls along the roadsides. This is forcing elephants to use the road and thus leading to conflicts. These threats were started during the early construction period of the dam. To quote Davidar in 1978 wrote, "Chaotic conditions prevail in the basin at the moment. Men and machines by the hundred are engaged in building a large dam to replace the old one, under a Tamil Nadu-Kerala water sharing agreement. …. It will be years before conditions return to normal, if ever". Hunting does not seem to be a major threat to the avifauna of this reserve. However, poaching of species such as Grey Junglefowl and Red Spurfowl, and egg collection of many other species are common in the fringes of reserve and areas near the settlements. Hunting of many larger vertebrates was registered by the forest department. It was noted that limited availability of arms and communication facilities to the forest department officials is a major hindrance in preventing poaching. Uncontrolled tourism inside the reserve is yet another factor resulting conflicts with wildlife. Increase of pilgrims and tourists to the religious enclaves in the Muthikkulam Shola and Vellingiri Hills in the Bolampatty Reserved Forest has a moderate impact on the biodiversity conservation.

Views of the study sites in the Silent Valley National Park, Kerala.

Views from the Muthikkulam Reserved Forest, Kerala.

Chapter 3

Status and distribution of Grey-headed Bulbul

3.1. Introduction

Species are often regarded as the fundamental independent building blocks of bio-diversity. Evaluation of the status of the concerned species is an important component of practical conservation. The most important data for avian conservation are population size and range (Thompson, 2002), and trends in one or other of these. In general, single-species management has become well established in the temperate zone, where knowledge and expertise on habitat management, monitoring techniques and avian ecology are relatively advanced (Allen, 1954; Bibby et al., 1998, 2000; Lamberson et al., 1992; Robertson et al., 1994; James et al., 1996; Greenwood, 2003). But in the tropics, where the great majority of threatened species occur (BirdLife International, 2001, 2004a), this approach is very poorly developed. Moreover, due to the lack of the baseline population data, measuring the trends also become impractical.

The Western Ghats of India has been recognised as one of the 34 biodiversity hotspots and an important Endemic Bird Area. However, this region has been poorly documented for the conservation status of the birds (Raman, 2001). About 507 bird species, predominantly terrestrial species (360), had been recorded from this hotspot (Ali and Ripley, 1987; Daniels, 1989). Although the ornithological studies in the Western Ghats date back to the colonial period, population studies are very few. Most of the surveys merely indicate the presence or absence of various species (e.g., Vijayan et al., 1999; Zacharias and Gaston, 1999) and, rarely included information on the population densities of the species except by Daniels (1989), Kannan (1994), Raman (2001), Robin and Sukumar (2002), Raman and Mudappa (2003), and Ahmed (2005). Furthermore, most of the surveys were limited to smaller spatial scales.

The Grey-headed Bulbul has been listed as Near-Threatened species (Collar et al., 1994; Stattersfield et al., 1998), and has a very limited range in the heavy rainfall areas from Belgaum along Goa to Kanyakumari. The observations, both sightings and the collections of Grey-headed Bulbul from 1869 to 2002 are very few (see Vijayan and Balakrishnan, 2005).

There are a few ringing reports of Grey-headed Bulbul from the Palni Hills (Hussain, 1991; S. Balachandran, *pers. comm.*). Ali and Ripley (1987) described the status of the species as 'fairly common but rather local'. However, none of the recent surveys record them as 'common' any where in its range (Prasad et al., 1998; Vijayan *et al.*, 1999; Zacharias and Gaston, 1999).

BirdLife International (2001, 2004a, 2007) classified Grey-headed Bulbul as a 'Least Concern' species, and estimated the species' global extent of occurrence within 20,000-50,000 km^2. This evaluation and estimates are based on the site records and descriptions of Ali and Ripley (1987) and Grimmett et al. (1998). The global population size of the species has not been quantified (BirdLife International, 2004a). This indicates a gap in the knowledge on the status and distribution of Grey-headed Bulbul, and actual extent of suitable habitat in its range.

3.2. Objectives

The main objectives of this study were to:

1). assess the status and distribution of the species along the geographical, elevational, and habitat gradients,

2). identify the correlates of the distribution of Grey-headed Bulbul with the broad-scale habitat features,

3). document the threats that the species faces across its range and,

4). provide guidelines for the conservation and management of the species.

3.3. Study area

The status survey was conducted in 24 areas in the Southern Western Ghats passing through the states of Kerala, Tamil Nadu, Karnataka and Goa between February 2002 and January 2004 (Figure 3.1). This covered six National Parks (Silent Valley, Eravikulam, Mukurthi, Indira Gandhi, Kudremukh and Molem); five Wildlife Sanctuaries (Chinnar, Parambikulam, Srivilliputhur, Cotigoa and Bondla); one Tiger Reserve (Kalakad-Mundanthurai) and twelve Reserved Forests (Wayanad South, Nilambur South, Attapady, Muthikkulam, Munnar, Bolampatty, Palni Hills, Dindigul, Kukkal Shola, Amarawathy, Anaikatty and Castle Rock). Although with variations, the climatic conditions, faunal and floral characteristics of these areas are more or less identical to the general features of the Western Ghats described in

Chapter 2. Seasonal and monthly variations in abundance and distribution of Grey-headed Bulbul were monitored at Silent Valley National Park, Attapady Reserved Forest, Karuvarakundu Reserved Forest (Kalikavu Range of Nilambur South Forest Division), and Muthikkulam Reserved Forest (see Chapter 2 for detailed descriptions).

3.4. Field methods and data analyses

3.4.1. Bird surveys

Surveys were conducted between February 2002 and January 2004 in various parts of the Western Ghats. Prior to the initiation of the systematic surveys, preliminary surveys were conducted in Muthikkulam Reserved Forest and Silent Valley National Park, after which the target species could be correctly identified from sight and aural cues. To improve the familiarity with calls and accuracy of identification, the bird was followed as much as possible whenever located. These field trials also helped to determine the best approach to conduct the bird census.

The open-width line transects (Bibby et al., 1998, 2000) were found appropriate for this study for the following reasons:

a) long continuous transects were more appropriate than restrictive point counts, to cover the largest areas of every habitat type, to make full use of limited time available and to record highest proportions of species (Thiollay, 2002),

b) the target species was highly mobile and occur at lower densities in certain evergreen patches (Ali and Ripley, 1987), which was found true in my preliminary observations and,

c) to cover more area and thus larger sample size to get reasonably precise estimates (Bibby et al., 1998; Buckland et al., 1999). Moreover, the distinct loud and frequent calls of the species could be heard from a distance of c. 50 m.

A thorough literature search was done before conducting the fieldwork and, all localities known to have records of Grey-headed Bulbul were categorised (Table 3.1, see Vijayan and Balakrishnan, 2005 for details) and state wise maps prepared. Based on the available literature and personal communications with various field biologists, areas with recent and frequent sightings of Grey-headed Bulbul were identified for the surveys. At each survey site, transects were set up that followed existing trek paths or animal trails. Each habitat was covered as much as possible given the constraints of impenetrability due to dense vegetation and inaccessibility due to steepness of terrain and other physical barriers.

Table 3.1. Summary of recent and past sightings of Grey-headed Bulbul in the Western Ghats.

Year	Sightings	Place	Source	Remarks
GOA				
1972-1968	8	Canacona, Molem	L. Vijayan, *in litt.**	Sightings and specimens
KARNATAKA				
1869-1998	22	Many locations	L. Vijayan, *in litt.**	Sightings and specimens
2002	?	Karkala	S. A. Hussain*	Sightings
KERALA				
1872-1998	44	Many locations	L. Vijayan, *in litt.**	Sightings and specimens
1975, 1978	?	Many locations	Vijayan, 1975,1978	Sightings
1998	?	Many locations	Prasad et al., 1998	Sightings
1999	9	Pooyankutty	Azeez et al., 1999	Sightings
1999	?	Many locations	Zacharias and Gaston, 1999	Sightings
2002	?	Aralam WS	T.N. Vijayakumar*	Sightings
TAMIL NADU				
1869-1998	17	Many locations	L. Vijayan, *in litt.**	Sightings and specimens
1978	?	Nilgiris	Khan, 1978	Sightings
1991	3	Palni Hills	Hussain, 1991	Ringing records
2001	?	Anamalai Hills	Raman, 2001	Sightings
2001	?	KMTR	Raman, 2001	Sightings
2002	?	Mully slopes	A.M.A. Nixon*	Sightings
2002	?	Bennai	B. Maheswaran*	Sightings
2002, 2003	?	Palni Hills	S. Balachandran*	Sightings and ringing
2002	?	Lower Nilgiris	K. Geetha Nayak*	Sightings

(*Personal communications 2002 and 2003).

The temporal fluctuations in the presence and abundance of Grey-headed Bulbul were monitored in 50 line transects of one km each established in Silent Valley National Park. Monthly censuses were conducted in these transects between January 2003 and December 2004 (except transects in the northern part of the Valley which were not censused during the months of heavy monsoon). Apart from this, seasonal surveys were conducted in Attapady (20 transects), Nilambur South (16 transects), and Muthikkulam Reserved Forests (50 transects) during February 2002 – December 2004.

All transects were censused between 06.30 and 11.30 hrs by walking at a slow uniform pace (approximately 1 km/h). No surveys were conducted during periods of rain, fog or high winds. Preliminary census data have not been used in the analyses.

3.4.2. Habitat sampling

Five habitat types were surveyed, namely tropical wet evergreen forest (evergreen forest), montane temperate forest (*shola* forest), tropical moist-deciduous forest, plantations (coffee, teak, *Eucalyptus*, wattle and abandoned *Cardamom* plantations in Kudremukh, Kalakkad Mundanthurai Tiger Reserve, Parambikulam, Palni Hills, Munnar, Dindigul, and Wayanad), or dry thorn forest (scrub forest), based on Champion and Seth (1968). For analyses, transects were divided along their length into fixed intervals of one km. In each kilometer of transect, the habitat type and altitude (by using an altimeter) were recorded. For each bird seen or heard, the altitude, dominant and co-dominant plant species, and GPS location were recorded, the last one whenever possible. Various estimates of the vegetation structure, topographic features and anthropogenic disturbances were recorded at every one km of transect as detailed in Table 3.2.

3.4.3. Data analyses

The encounter rate was calculated as the number of individuals per km surveyed. Advantages of using encounter rate, rather than the actual population density, as measure of population density are that the former is readily related to the probability of detection of a population and often is simple and inexpensive to obtain (Green and Young, 1993). Moreover, density calculations from the transect data and further extrapolation to a wider area may lead to biased estimates of abundance due to the patchy distribution of the species. More advanced density estimators (e.g., DISTANCE, see, Laake et al., 1994; Buckland et al., 1999) were not appropriate, because of small sample size. Altitude of sightings was grouped into three categories (<1,000 m, 1,000–1,500 m, and >1,500 m). Encounter rates were calculated for both vegetation and elevation categories in each site and, correlates of Grey-headed bulbul sighting and habitat characteristics were examined using standard non-parametric tests (Seigel and Castellan, 1988; Zar, 1999).

In order to determine important habitat attributes influencing the probability of a site being occupied by Grey-headed Bulbul, the data were analysed using both univariate and multivariate tests. For presence/absence surveys, logistic regression is the most commonly used statistical model (Osborne and Tigar, 1992; Hinsley et al., 1995; Augustin et al., 1996; Brito et al., 1996; Bustamante, 1997; Franco et al., 2000; Luck, 2002; Franco and Sutherland, 2004). The regression parameters were estimated by a multiple logistic regression analysis (Hosmer and Lemeshow, 2000), with a forward stepwise selection procedure (maximum likelihood method) to reduce the number of independent variables actually entered into the model. All possible combinations of habitat variables were entered into different models and the best combination was selected based on improvements in the fit and predictive power of the model (Henderson and Velleman, 1981; James and McCulloch, 1990).

Table 3.2. Descriptions of the independent habitat variables measured at every one km of the survey transect, in the Western Ghats during 2002–2004 (* Arcsine transformed).

Variable	Code	Description
Mean canopy height (m)	MNCHT	Mean height of the trees in the transect
Canopy cover *	CCV	Visual estimate of the percentage canopy cover in the transect
Sub-canopy cover *	SCCV	Percentage sub-canopy cover as above
Shrub cover *	SHCV	Percentage shrub cover as above
Ground cover *	GCV	Percentage ground cover as above
Elevation (m)	ELVN	Mean elevation of the transect, measured by an altimeter
Vegetation type	VEGT	Vegetation types (1 = wet evergreen / semi evergreen, 2 = shola, 3 = moist deciduous, 4 = plantations, 5 = scrub)
Livestock	LVSK	Presence (1) or absence (0) of livestock grazing
Cutting / mining / hunting	CMH	Presence (1) or absence (0) of cutting, mining or hunting
Dist. to water	DTWR	Distance to the nearest stream or dam (1 = <100 m, 2 = 100 – 500 m, 3 = >500 m)
Dist. to human settlements	DTHS	Distance to the nearest human settlements as above
Dist. to paved roads	DTPR	Distance to nearest paved road as above

3.5. Results

3.5.1. Geographical distribution

Altogether 69 sightings (140 individuals) of Grey-headed Bulbuls were made from 728.5 km surveyed across the four South Indian States with an average encounter rate of 0.19 birds/km (Tables 3.3 and 3.4). Most of the sightings (88.41%) were of paired individuals. Of the 24 areas surveyed, Grey-headed Bulbuls were present at 12 sites. The highest number (32) was recorded from Kudremukh National Park, Karnataka followed by Silent Valley National Park, Kerala (26), Cotigoa Wildlife Sanctuary, Goa (24) and Muthikkulam Reserved Forest, Kerala (22). The encounter rates varied highly among sites with higher rates in Cotigoa Wildlife Sanctuary, Silent Valley National Park and Muthikkulam Reserved Forest (1.5, 0.45, and 0.42 birds/km respectively). Area–wise distribution of sightings (Tables 3.3 and 3.4) shows that larger evergreen forests had higher number of sightings. However, at Kalakad-Mundanthurai Tiger Reserve, which encompasses a large forest area, only a single sighting comprising three individuals could be made. At Palni Hills, no Grey-headed Bulbuls were sighted during the survey. These results and further surveys at the Silent Valley National Park and Muthikkulam Reserved Forest revealed the seasonal local migratory behaviour of Grey-headed Bulbul. Thus to explore the distribution patterns of Grey-headed Bulbul along different elevational and vegetation gradients during the breeding and non-breeding seasons, survey data were categorised based on the seasons.

3.5.2. Distribution in different vegetation types

Grey-headed Bulbuls were recorded from the evergreen, moist deciduous and scrub forests. There was no record of the species from the plantations, *shola* forests and montane grasslands. In general, the encounter rate (0.33 birds/ km) in the lowland evergreen forests (< 1,000 m) was significantly higher than that in any other habitat type and elevation (Figure 3.2). All the sightings of Grey-headed Bulbul during the breeding season were from the evergreen forests (Table 3.5). 100 individuals were recorded from 281 km of evergreen forests surveyed during the breeding season. The low-elevation evergreen forests (n = 177 km) had marginally higher encounter rates than the mid-elevation evergreen forests (n = 99.5 km), although it was not statistically significant (Mann–Whitney *U*-test: $z = -1.262$; $p = 0.207$; Table 3.5). 72 individuals (36 sightings) of the species were recorded from 177 km of low elevation evergreen forest (< 1,500 m) surveyed during the breeding season.

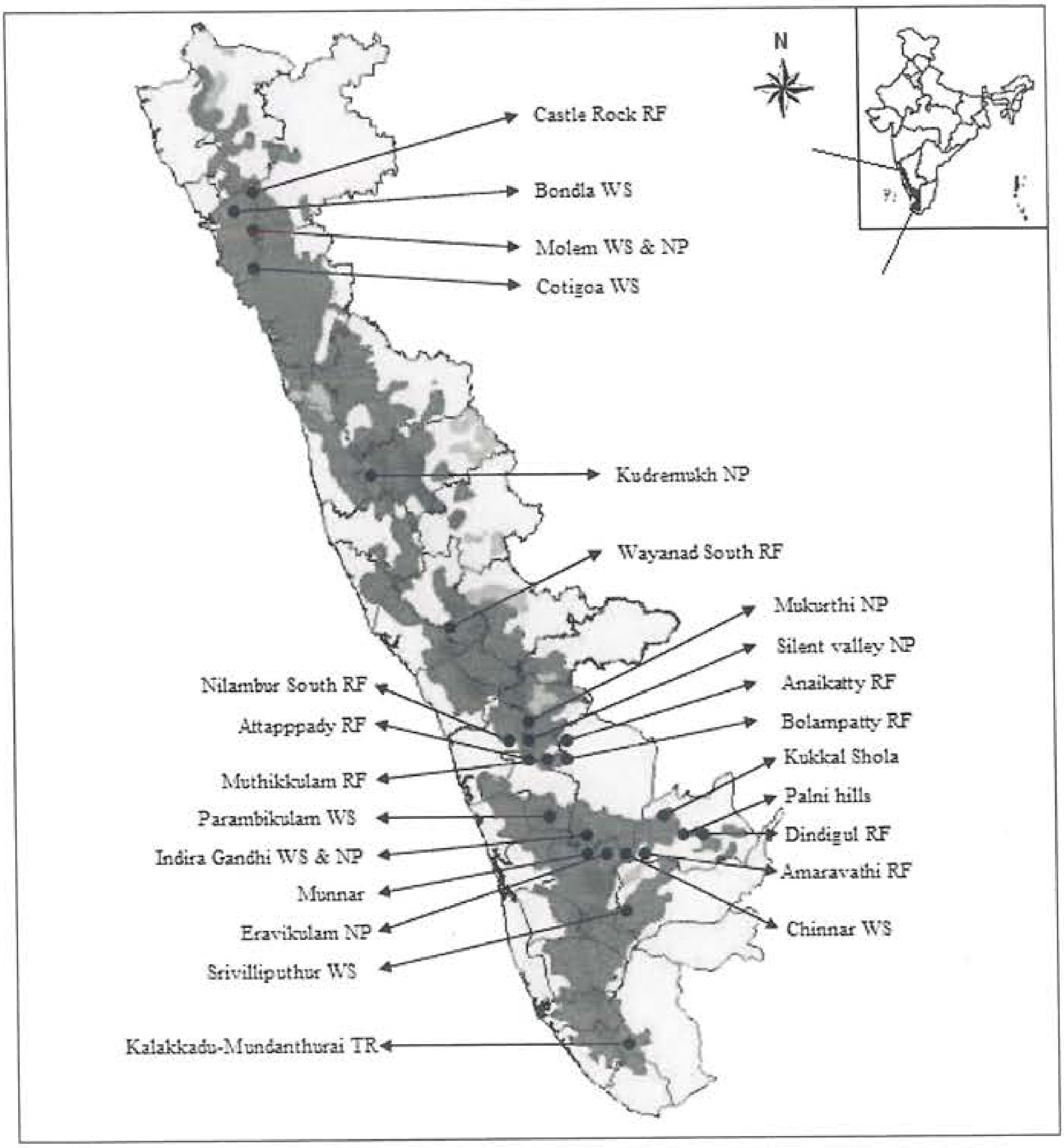

Figure 3.1. Areas surveyed across four South Indian States.

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Table 3.3. Area-wise sampling effort, sightings and encounter rates of Grey-headed Bulbul during the breeding season in the Western Ghats.

Areas surveyed	Geographical co-ordinates	Altitude	Annual rainfall (mm)	Survey month	SE (km)	NS	ER
Palni Hills	10° 07’ - 10° 20’ N & 77° 16’ - 77° 45’ E	700 - 2200	1000 - 4000	Apr-02	52.50	0	--
Dindigul RF	10° 17’ - 10° 28’ N & 77° 18’ - 77° 46’ E	300 - 2200	900 - 3000	Apr-02	34.00	0	--
Kudremukh N P	13° 01’ - 13° 29’ N & 75° 01’ - 75° 25’ E	100 - 1892	4000 - 7000	May-02	119.5.00	36	0.30
Nilambur South R F	11° 20’ - 11° 31’ N & 76° 06’ - 76° 16’ E	250 - 2064	2600 - 4000	Jan-03	16.00	8	0.50
Mukurthi N P	11° 15’ - 11° 30’ N & 76° 15’ - 76° 60’ E	300 - 2670	2010 - 6330	Feb-03	3.00	0	--
Silent Valley N P	11° 00’ - 11° 15’ N & 76° 15’ - 76° 35’ E	700 - 2383	2000 - 5000	Jan-03	57.50	26	0.45
Attappady R F	10° 55’ - 11° 14’ N & 76° 25’ - 76° 43’ E	162 - 2323	900 - 4000	Jan-03	22.00	4	0.18
Cotigoa WS	14° 53’ - 15° 47’ N & 73° 40’ - 74° 20’ E	100 - 850	1000 - 3000	Jan-03	16.00	24	1.50
Bondla WS	74° 07’ - 74° 07’ N & 15° 25’ - 15° 26’ E	50 - 300	1000 - 3000	Jan-04	4.00	0	--
Molem WS & NP	73° 40’ - 74° 20’ N & 14° 40’ - 15° 47’ E	50 - 850	3000 - 4000	Jan-04	25.00	0	--
Castle Rock RF	74° 19’ - 74° 20’ N & 15° 24’ - 15° 25’ E	100 - 850	3000 - 4000	Jan-04	4.00	2	0.50

SE: sampling effort in km, NS: number of individuals recorded and ER: encounter rate

Table 3.4. Area-wise sampling effort, sightings and encounter rates of Grey-headed Bulbul during the non-breeding season in the Western Ghats.

Areas surveyed	Geographical co-ordinates	Altitude	Annual rainfall (mm)	Survey month	SE (km)	NS	ER
Kalakad-Mundanthurai	08° 25’ - 08° 53’ N & 77° 10’ - 77° 35’ E	40 - 1826	3000 - 4000	Jul-02	118.50	3	0.03
Srivilliputhur WS	09° 21’ - 09° 48’ N & 77° 21’ - 77° 46’ E	200 - 2019	700 - 3000	Jul-02	16.00	0	--
Kukkal shola	10° 07’ - 10° 20’ N & 77° 16’ - 77° 45’ E	1500 - 1850	1000 - 4000	Jul-02	7.00	0	--
Amarawathy RF	10° 07’ - 10° 20’ N & 77° 16’ - 77° 45’ E	400 - 1600	1000 - 3000	Jul-02	16.00	5	0.31
Chinnar WS	10° 15’ - 10° 21’ N & 77° 15’ - 77° 17’ E	500 - 2400	1000 - 3000	Aug-02	87.00	7	0.08
Eravikulam N P	09° 40’ - 10° 45’ N & 76° 25’ - 77° 20’ E	900 - 2697	3000 - 5000	Aug-02	5.00	0	--
Munnar	09° 50’ - 10° 16’ N & 76° 39’ - 77° 18’ E	900 - 2637	2000 - 5000	Aug-02	2.00	0	--
Anaikatty RF	11° 05’ - 11° 31’ N & 76° 39’ - 76° 47’ E	610 - 750	2000 - 3000	Aug-02	5.00	1	0.20
Muthikkulam RF	10° 56’ - 10° 59’ N & 76° 41’ - 76° 45’ E	600 - 2025	3000 - 5000	Sep-02	52.50	22	0.42
Bolampatty RF	10° 50’ - 11° 22’ N & 76° 38’ - 76° 52’ E	364 - 1611	2000 - 3500	Nov-02	2.00	0	--
Indira Gandhi WS & NP	10° 24’ - 10° 54’ N & 76° 44’ - 77° 48’ E	340 - 2513	800 - 4500	Oct-02	47.00	2	0.04
Parambikulam WS	10° 20’ - 10° 32’ N & 76° 35’ - 76° 51’ E	500 - 1439	1000 - 2590	Oct-02	11.00	0	--
Wayanad South R F	11° 35’ - 11° 48’ N & 75° 48’ - 76° 13’ E	700 - 1308	1000 - 3000	Sep-03	6.00	0	--

SE: sampling effort in km, NS: number of individuals recorded and ER: encounter rate

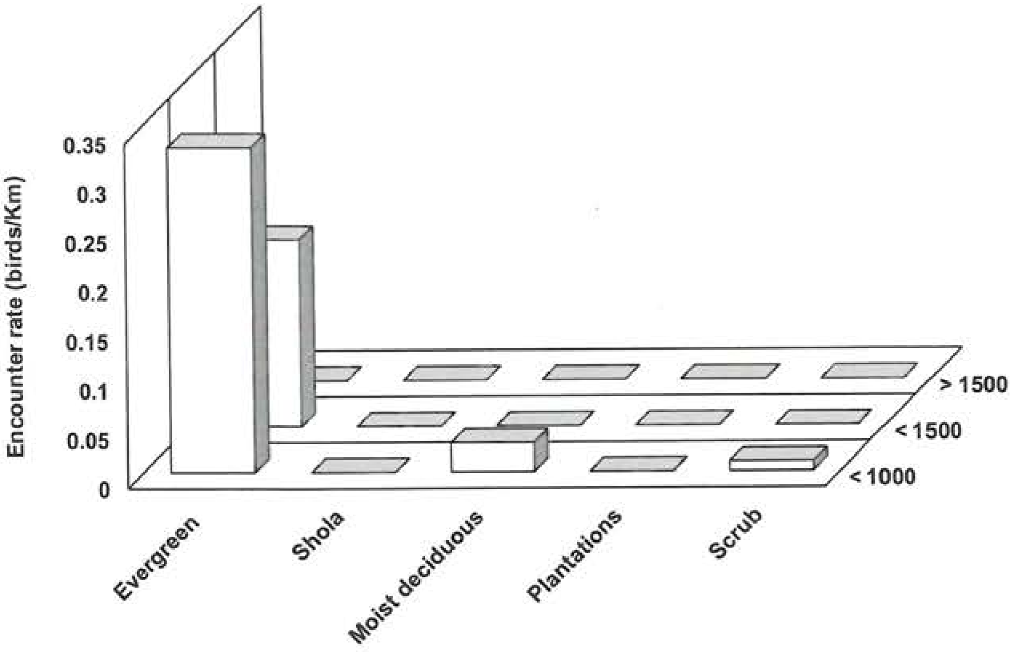

Figure 3.2. Encounter rates of Grey-headed Bulbul in different altitudes and vegetation types (Data for both breeding and non-breeding seasons were pooled).

Except for one sighting each from the moist-deciduous and scrub forests, all the non-breeding season records were from the evergreen forests (see Table 3.6). A total of 18 sightings of 36 individuals were obtained from 211.5 km of evergreen forests surveyed during the non-breeding season. Within the evergreen habitats, low-elevation forests had more sightings and encounter rates (Table 3.6). In the 82 km of mid-elevation evergreen forest surveyed during non-breeding season, only seven individuals could be recorded. However, these sightings were from two rain-shadow areas; Amarawathy Reserved Forest and Chinnar Wildlife Sanctuary. Furthermore, nomadic individuals were recorded regularly during the south-west monsoon at Anaikatty Reserved Forest, another rain-shadow area and offshoot of Western Ghats. This clearly indicates the influence of monsoon rains on the local migration of Grey-headed Bulbul.

Table 3.5. Sightings of Grey-headed Bulbul in different elevation zones and vegetation types during the breeding seasons 2002-2004 in Western Ghats.

Altitude in m	Vegetation types														
	Evergreen			Shola			Moist-deciduous			Plantations			Scrub		
	S E	N S	ER	S E	N S	ER	S E	N S	ER	S E	N S	ER	S E	N S	ER
< 1,000	177.00	72	0.41	0.00	0	0.00	8.00	0	0.00	17.00	0	0.00	11.00	0	0.00
1,000 – 1,500	99.50	28	0.28	8.00	0	0.00	0.00	0	0.00	2.00	0	0.00	0.00	0	0.00
>1,500	4.50	0	0.00	26.50	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00
Total	281.00	100	0.36	34.50	0	0.00	8.00	0	0.00	19.00	0	0.00	11.00	0	0.00

(SE: sampling effort in km, NS: number of individuals recorded and ER: encounter rate).

Table 3.6. Sightings of Grey-headed Bulbul in different elevation zones and vegetation types during the non-breeding seasons 2002-2004 in Western Ghats.

Altitude in m	Vegetation types														
	Evergreen			Shola			Moist-deciduous			Plantations			Scrub		
	S E	N S	ER	S E	N S	ER	S E	N S	ER	S E	N S	ER	S E	N S	ER
< 1,000	129.50	29	0.22	0.00	0	0.00	35.00	3	0.09	16.00	0	0.00	63.00	1	0.02
1,000 – 1,500	82.00	7	0.09	0.00	0	0.00	14.00	0	0.00	11.50	0	0.00	0.00	0	0.00
>1,500	0.00	0	0.00	19.00	0	0.00	0.00	0	0.00	5.00	0	0.00	0.00	0	0.00
Total	211.50	36	0.17	19.00	0	0.00	49.00	3	0.06	32.50	0	0.00	63.00	1	0.02

3.5.3. Distribution along the elevational gradient

Distribution pattern of Grey-headed Bulbul shows that the species is restricted to the low and mid-elevation forests during both breeding and non-breeding seasons (Tables 3.5, 3.6). Sightings at the lowest and highest elevation during the survey were at 60 and 1,210 m respectively. Maximum number of Grey-headed Bulbul sightings was from the elevations between 700–1,100 m (Figure 3.3 and 3.4). In Southern Western Ghats, Grey-headed Bulbuls were almost restricted to the mid-elevation evergreen forests. On the other hand, in the Goa part of the Western Ghats where there is not much forest above 900 m; the species was recorded in the low-altitude evergreen forests. However, the breeding status of the species in this part of the ghats is unknown. Even though, a few observations obtained from the mid-elevation forests are in the rain-shadow areas, more than 80% of the non-breeding season sightings were from the low-elevation forests.

3.5.4. Landscape scale and anthropogenic factors

The results of the univariate analysis show that vegetation type, elevation and all the vegetation variables have potential influence on the occurrence of Grey-headed Bulbul during the breeding season (Table 3.7). Most of the sightings were from areas dominated by *Strobilanthes* (39.13%, 27 sightings) and reeds (30.43%, 21 sightings) followed by *Lantana camara* (16%, 11 sightings). Breeding season sightings were restricted to the mid and low elevation evergreen forests. The locations of sightings were characterised with low canopy height, low canopy cover and high shrub cover. Although, the non-breeding sites had a similar vegetation structure, occurrence of the species was neither influenced by the canopy height nor altitude (Table 3.7). The presence of water was a key predictor of species occurrence with about 89.86%. Most of Grey-headed Bulbul sightings (89.86% or 62 detections) within 20 m of the wet streams ($\chi^2 = 154.942$; $df = 3$, $n = 69$; $p < 0.01$). Also its occurrence was influenced by different anthropogenic factors. The species was not seen in the areas with wood cutting, mining or high hunting pressure. No breeding pairs were recorded within 500 m of the human settlements. However, the impact of livestock grazing and paved roads on the occurrence of Grey-headed Bulbul was not clear (Table 3.7), as a few pairs were sighted in the areas with livestock grazing at Cotigoa Wildlife Sanctuary, Goa; and also in the Protected Areas where paved roads are present.

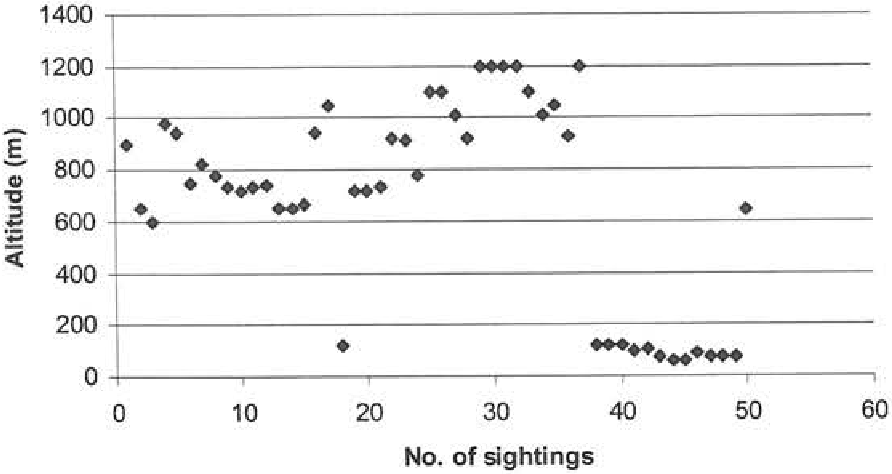

Figure 3.3. Sightings of Grey-headed Bulbul in different elevations during the breeding seasons 2002-2004 in the Western Ghats.

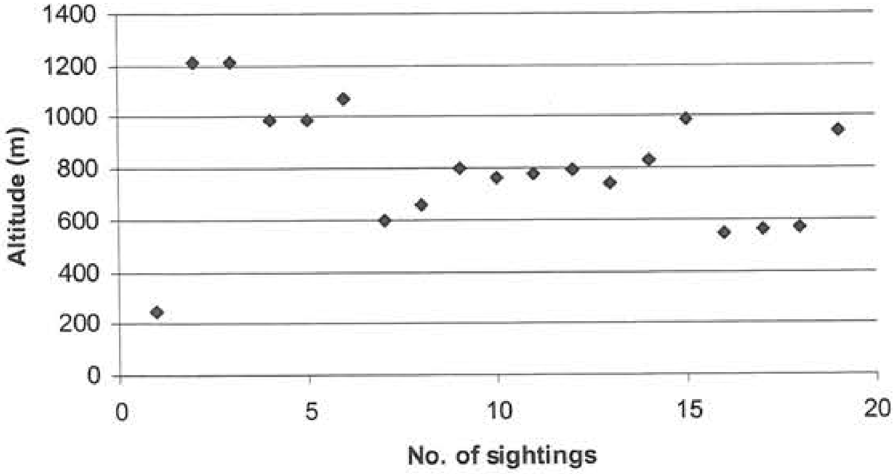

Figure 3.4. Sightings of Grey-headed Bulbul in different elevations during the non-breeding seasons 2002-2004 in the Western Ghats.

There were no significant correlations ($r_s < 0.7$) among the variables, thus all the 12 vegetation and anthropogenic variables were included in the logistic regression models (see Table 3.2 for variable description) in order to assess their relative importance in the probability of occurrence of the species.

The final model of breeding season distribution included four variables (Table 3.8) was highly significant ($\chi^2_4 = 264.87, p < 0.001$), classifying correctly 98.6% (Nagalkerke R^2) of the sites (99.3% of absences and 94% of presences). The final model was not significantly different from the statistically perfect model (Hosmer–Lemeshow goodness-of-fit $C_8 = 0.172$, $p > 0.05$). The canopy cover, shrub cover, ground cover and presence of water were the major predictors of species occurrence during the breeding season. Although Grey-headed Bulbul was seen in different vegetation types during the non-breeding season, its occurrence was not random in these habitats. The step-wise logistic regression analysis identified canopy cover, sub-canopy cover and vegetation types as predictors of the non-breeding season occurrence of Grey-headed Bulbul (Table 3.9). The final model, which included three variables was highly significant ($\chi^2_3 = 136.03, p < 0.001$), and classified 99.5% (Nagalkerke R^2) of transects (99.7% of absences and 94.7% of presences).

Table 3.7. Variation in the independent variables measured at transects with and without Grey-headed Bulbul during breeding and non-breeding seasons.

Variable	Breeding season		Non-breeding season	
	F	*p*	*F*	*p*
Mean canopy height (m)	13.228	0.001	3.472	0.063
Canopy cover	107.710	0.001	23.678	0.001
Sub-canopy cover	65.689	0.001	64.140	0.001
Shrub cover	63.973	0.001	44.710	0.001
Ground cover	67.514	0.001	46.630	0.001
Elevation (m)	10.471	0.001	0.381	0.538
Vegetation type	11.179	0.001	6.951	0.009
Livestock	2.678	0.103	1.471	0.226
Cutting / mining / hunting	2.678	0.005	4.708	0.031
Dist. to water	136.459	0.001	62.874	0.001
Dist. to human settlements	8.928	0.003	3.018	0.083
Dist. to paved roads	0.018	0.894	0.326	0.569

Table 3.8. Summary of the final model derived to predict the breeding season occurrence of Grey-headed Bulbul (see Table 3.2 for variable description).

Variables	Coefficients (*B*)	S.E.	Wald	*p*
CCV	-0.491	0.132	13.888	0.001
SHCV	0.230	0.084	7.449	0.006
GCV	0.190	0.069	7.480	0.006
DTWR	-17.115	5.554	9.495	0.002
Constant	18.891	7.082	7.115	0.008

Table 3.9. Summary of the final model derived to predict the non-breeding season occurrence of Grey-headed Bulbul (see Table 3.2 for variable description).

Variables	Coefficients (*B*)	S.E.	Wald	*p*
CCV	-1.010	0.373	7.330	0.007
SCCV	0.389	0.156	6.213	0.013
VEGT	-7.676	2.821	7.404	0.007
Constant	32.379	13.346	5.886	0.015

3.5.5. Monthly and seasonal variation in the distribution and abundance of Grey-headed Bulbul at Silent Valley and surrounding areas

There was no significant annual variation in the encounter rates of Grey-headed Bulbul at Silent Valley National Park during the two years of study ($z = -1.532$, $n = 12$, $p = 0.125$). The average encounter rate was 0.70±0.13 birds/km during 2003, while it was 0.73±0.19 birds/km during 2004. However, significant seasonal variation in the presence and abundance of the species was recorded. No Grey-headed Bulbul was recorded in the Silent Valley between June to December, except two vagrant pairs during June 2004 and one pair during July 2004 recorded from the fringes of the Park adjacent to the Attapady Reserved Forest (Figure 3.5). Of the many abiotic and biotic factors examined, the maximum temperature ($r_s = 0.\ 412$, $p < 0.05$), number of food plant species with fruits ($r_s = 0.827$, $p < 0.001$; Figure 3.6) and fruit abundance ($r_s = 0.\ 607$, $p < 0.01$; Figure 3.7) had high positive correlation with the abundance of Grey-headed Bulbul. During the heavy monsoon months the birds were almost absent at Silent Valley. However, the encounter rates were not statistically correlated with the monthly rainfall ($r_s = -0.\ 210$, $p = 0.324$; Figure 3.8) and number of rainy days per month ($r_s = -0.\ 175$, $p = 0.413$; Figure 3.9).

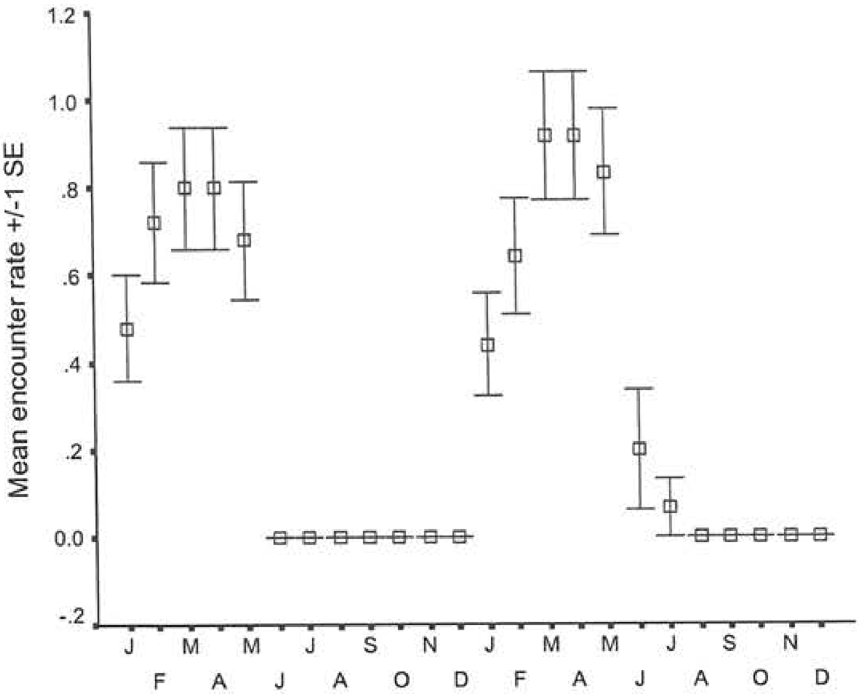

Figure 3.5. Mean (± SE) monthly encounter rate (birds/km) of Grey-headed Bulbul in the Silent Valley National Park during January 2003-December 2004.

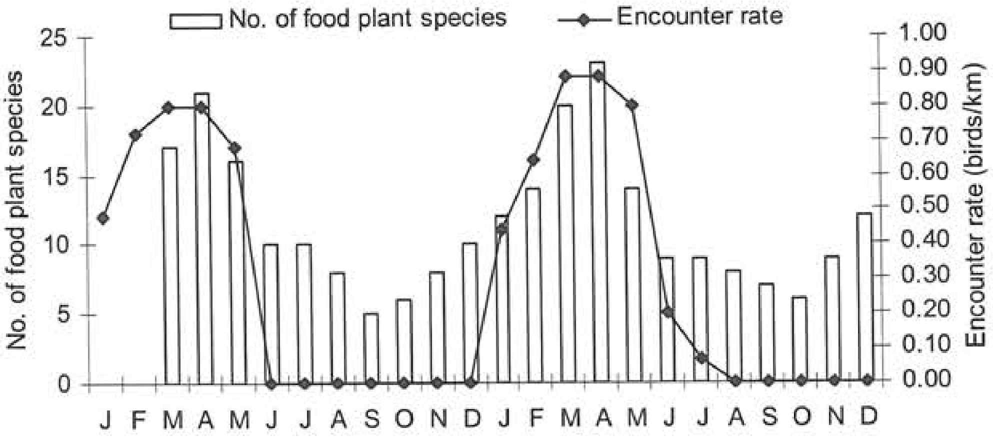

Figure 3.6. The correlation of number of food plants in fruit and encounter rate (birds/km) of Grey-headed Bulbul at the Silent Valley National Park, Kerala (January 2003-December 2004).

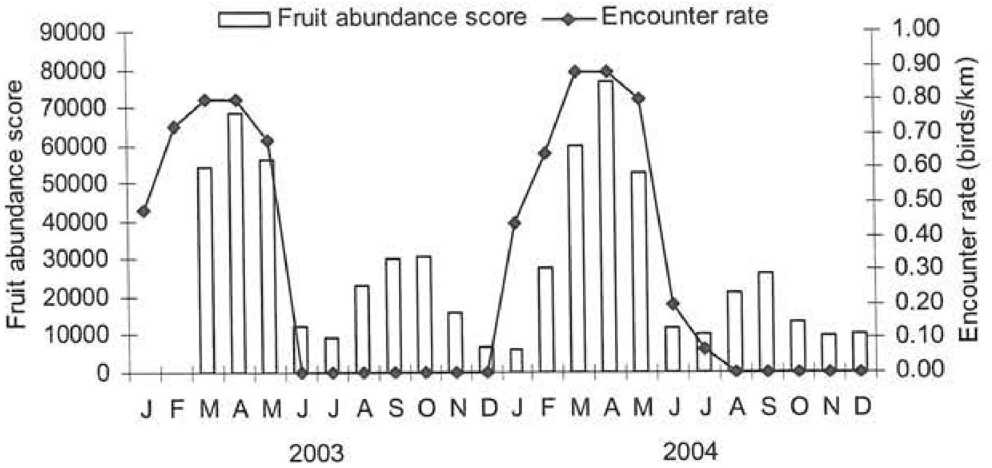

Figure 3.7. The correlation of fruit abundance and encounter rate (birds/km) of Grey-headed Bulbul at the Silent Valley National Park, Kerala (January 2003-December 2004).

Grey-headed Bulbuls bred in Kalikavu range of Nilambur South Forest Division contiguous to Silent Valley National Park, where the encounter rates were consistent during the breeding seasons of 2003 (0.63±0.11 birds/km) and 2004 (0.67±0.07 birds/km). However, there were no sightings during non-breeding seasons from this reserve, which receives high rainfall almost equal to that of the northern part of Silent Valley. Even though Grey-headed Bulbuls were recorded from Attapady Reserve Forest contiguous to Silent Valley during the breeding season, there is no breeding record from this reserve in spite of the intensive field search. Moreover, encounter rates of the species were also significantly lower compared to that of Silent Valley during breeding season (0.26±0.09 and 0.25±0.15 birds/km respectively for 2003 and 2004.

The results of the seasonal surveys in Muthikkulam Reserved Forest show an opposite pattern to that obtained from Silent Valley. Although, a few individuals were seen during the early breeding season, the encounter rate (0.08±0.13 birds/km) was significantly lower compared to that in the non-breeding season (0.50±0.13 birds/km). The correlates of these variations in the bird abundance with the abiotic and biotic factors were not explored in this study. However, the evergreen forests of Muthikkulam which lies in the south western corner of the Nilgiri Biosphere Reserve receives low rainfall compared to Silent Valley.

Moreover, although no quantitative studies were conducted, the general observations indicate significant variations in the phenological patterns in the food plants of Grey-headed Bulbul compared to those in Silent Valley.

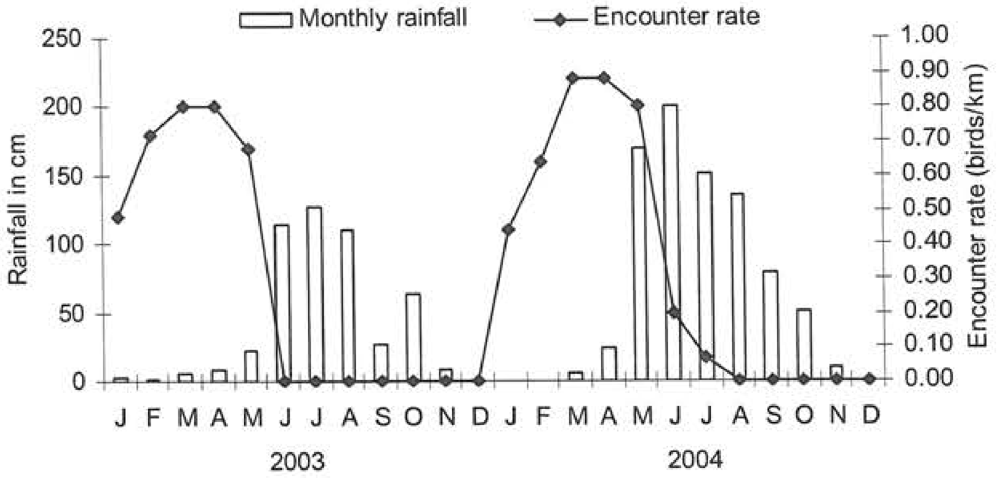

Figure 3.8. The correlation between the monthly rainfall and encounter rate (birds/km) of Grey-headed Bulbul at the Silent Valley National Park, Kerala (January 2003-December 2004).

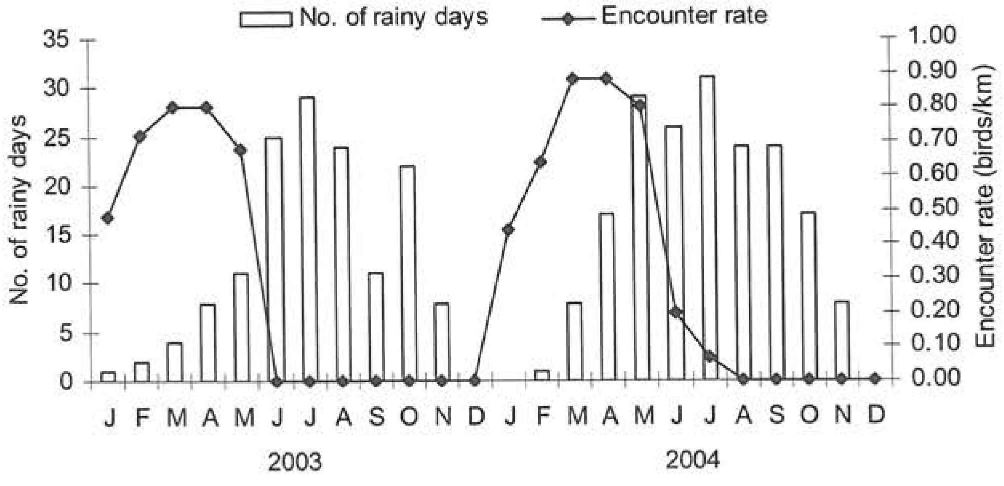

Figure 3.9. The correlation between the rainy days and encounter rate (birds/km) of Grey-headed Bulbul at the Silent Valley National Park, Kerala (January 2003-December 2004).

3.6. Discussion

The result of this study and the literature survey (Table 3.1; see also Islam and Rahmani, 2004) indicate that Grey-headed Bulbuls are present in about 33 sites. They were recorded from 12 of the 24 areas surveyed during the present study. Of these, six were in the unprotected areas with various levels of habitat disturbances. Protected Areas such as Silent Valley National Park and Kudremukh National park had larger breeding populations of Grey-headed Bulbul. Muthikkulam Reserved Forest form one of the major non-breeding habitats. However, this habitat is highly threatened with various anthropogenic pressures. During the non-breeding season, the species was recorded from the low-altitude habitats of Kalakad-Mundanthurai Tiger Reserve, Indira Gandhi Wildlife Sanctuary and National Park, and Chinnar Wildlife Sanctuary. However, their encounter rate was significantly lower in these protected areas. Ali and Ripley (1987) recorded the extent of occurrence of the species from Goa to Kanyakumari and reported it as 'fairly common' in the evergreen forests that receive heavy rainfall. But within these areas, they have a distinct patchy distribution. The occupancy pattern obtained during the survey of larger forests such as Kudremukh National Park, Silent Valley National Park and Muthikkulam Reserved Forest clearly indicates the patchiness in occurrence. Although the present survey provides a baseline distribution pattern, status of the species in areas that could not be surveyed during this study (Southern Kerala and Northern Karnataka of the Western Ghats), and the breeding status in the lower elevation evergreen forests remain unknown.

In spite of considerable sampling in all the vegetation types, Grey-headed Bulbuls were recorded only from the evergreen forests during the breeding season. This indicates that breeding of the species is restricted to the low and mid-elevation evergreen forests. On the other hand, a few pairs were also recorded from the moist-deciduous and scrub forests other than the evergreen forests in the rain shadow areas during the non-breeding season. However, there is no record of the species in the shola forests and plantations during both seasons. Although many Western Ghats' endemics such as Nilgiri Laughing Thrush, White-bellied Shortwing, Malabar Parakeet, Crimson-backed Sunbird, Rufous Babbler, Crimson-fronted Barbet, Malabar Whistling Thrush, White-bellied Blue Flycatcher and White-bellied Treepie were seen adapted to the areas of modified rainforests (Zacharias and Gaston, 1999; Raman, 2001; Robin and Sukumar, 2002; Ahmed, 2005), Grey-headed Bulbul's adaptability and survival in such areas have never been reported. The absence of the species in the plantations (all are modified rainforests) during this survey supports the view that Grey-headed Bulbul is a habitat specialist and is susceptible to habitat modification.

The altitudinal limit of Grey-headed Bulbul was generally considered as below 1,000 m and rarely up to 1,800 m (Ali and Ripley, 1987). Even though, the low elevation forests in the protected areas such as Cotigoa Wildlife Sanctuary support a good population of Grey-headed Bulbul, maximum number of sightings was in the evergreen forests lying between 800–1,200 m. It was not sighted above 1,500 m during this survey. However, Vijayan (1975) recorded the species twice inside the shola in Eravikulam at c.1,972 m altitude. Zarri and Rahmani (2005) have seen Grey-headed Bulbul at Taishola (2,200 m) in the upper Nilgiris. These may be considered as vagrants. The presence of Grey-headed Bulbul in the Cotigoa Wildlife Sanctuary and foothills of the Kudremukh National Park indicates that the species does prefer lowland rainforests also. Therefore, their absence in the lowland rainforests elsewhere, probably, indicates the amount of deforestation and other human activities that have been reported in these areas (Nair, 1991; Myers et al., 1999; Menon and Bawa, 1997; Jha et al., 2000). The lowland rainforests of the Southern Western Ghats in Kerala were cleared long ago and much of the lowland rainforests at 100 m elevation exist only in the South Canara, North Canara and Udupi Districts of Karnataka (Prasad et al., 1998; Krishnamani, 2002).

The results of univariate and logistic regression analysis of the broad-scale habitat variables show that locations of sightings were characterised with low canopy height; low canopy cover and high shrub cover. Sites in the larger evergreen forests (e.g., Kudremukh National Park, Silent Valley National Park, Muthikkulam Reserved Forest), with high densities of reed and *Strobilanthes*; and low canopy height and canopy cover had higher number of sightings. The presence of water was a key predictor of the species' occurrence during the breeding season. Although vegetation structure had a significant role in the distribution of Grey-headed Bulbul within the evergreen forests, food availability, rainfall and other factors influences their presence (see Chapter 4). Fluctuation in the food availability and high rainfall may be the reason for the absence of Grey-headed Bulbul in the mid-elevation evergreen forests of Palni Hills during the non-breeding season. Moreover, they were recorded during the same survey from the adjoining Amarawathy Reserved Forest which lies in the rain shadow area. It is interesting to note that in a bird community study along an elevational gradient at Kalakkad-Mundanthurai, Raman (2001) recorded Grey-headed Bulbul at a single site (558 m) only. Although the availability of the food and nesting resources are unknown, all the sites studied were characterised by high canopy cover and tall trees (Raman, 2001). This further supports the view that Grey-headed Bulbuls have distinct micro habitat preferences within evergreen forests, which in turn leads to the patchy distribution of the species (see Chapter 4).

Grey-headed Bulbul's occurrence was influenced by different anthropogenic factors. The species was not seen in the areas with felling, mining or other anthropogenic pressures. It was not sighted at Bhagwan Mahavir National Park (Molem, Goa), during the present study where the species was recorded as common in the earlier ornithological expeditions (Grubh and Ali, 1976; Lainer, 1999). Increasing degradation of the natural forest through 'government sponsored tourism' (Lainer, 1999) and uncontrolled movement of the vehicles carrying the mine products from Castle Rock may be the reasons for its absence. No breeding pairs were recorded within 500 m of the human settlements. However, the impact of livestock grazing on the distribution of Grey-headed Bulbul was not clear, as they were seen both in areas of grazing and non-grazing. Grey-headed Bulbul's susceptibility to the habitat alteration and disturbances were mentioned in the earlier studies also. Vijayan (1975) recorded the species at Kallarkutty east of Kothamangalam in Kerala (c. 455 m) in January 1974. It was not recorded later, since the habitat was completely burned up for agriculture (Vijayan, 1975).

The seasonal migratory behaviour of Grey-headed Bulbul was established by regularly monitoring them over two years at Silent Valley National Park and the seasonal surveys at Attapady, Muthikkulam and Karuvarakundu (in Kalikavu range of Nilambur South Forest Division) Reserved Forests. Silent Valley and the adjacent Karuvarakundu Reserved Forest support a healthy breeding population of Grey-headed Bulbul. Their breeding activities commenced in the first half of January and ended in May. The birds were absent in the Park and adjoining areas during the non-breeding season (June–December), except two vagrant pairs in the fringes during June 2004 and one pair during July 2004. Scarcity in the cumulative fruit availability of the 25 major food plants and the adverse climatic conditions (low temperature and high rainfall, see also Chapter, 5) during June to

December (Figure 3.7) could be the reason for its absence. On the other hand, the Muthikkulam Reserved Forest, which lies in the rain shadow area form a major non-breeding habitat for Grey-headed Bulbul. The rainfall pattern of this area is entirely different from that of Silent Valley. Although no quantitative assessments were made, the fruit abundance was quite high during the non-breeding season of Grey-headed Bulbul at Muthikkulam. Patterns of interspecific variation in fruiting phenologies and variation in climatic conditions such as temperature and rainfall have been inferred as the ecological basis behind the irregular to nomadic distribution patterns of many frugivores (Frankie et al., 1974; Wheelwright, 1983; Levey, 1988; Blake and Loiselle, 1991; Loiselle and Blake, 1991; Powell and Bjork, 1994; Bancroft et al., 2000; Strong and Johnson, 2001; Tellería and Pérez-Tris, 2003; Tellería et al., 2005; Oliveira et al., 2006; see also Chapter 5).

In conclusion, the low population density, patchiness in occurrence and the local migratory behaviour of Grey-headed Bulbul have significant conservation importance. The results highlight the importance of large evergreen forests with broad elevational gradient for the conservation of Grey-headed Bulbul. Although Protected Areas such as Silent Valley National Park, Kudremukh National Park, and Cotigao Wildlife Sanctuary support healthy breeding populations of Grey-headed Bulbul, several unprotected areas particularly those lies in the low-elevations are important for the long-term survival of the species. Thus, establishment of larger conservation complexes rather than the existing smaller fragmented Protected Areas could benefit the long-term survival of Grey-headed Bulbul and other nomadic species (see also Chapter 7).

3.7. Summary

- Status and distribution of Grey-headed Bulbul was assessed across four South Indian States, namely Kerala, Tamil Nadu, Karnataka and Goa followed by a regular monitoring in Silent Valley National Park and surrounding reserved forests.
- Sixty nine sightings were made in the 728.5 km transects surveyed with an average encounter rate of 0.19 birds/km.
- Large stretch of evergreen forests with an altitudinal range of 700–1,000 metre was the preferred habitat.

- The encounter rate (0.33 birds/ km) in the lowland evergreen forests (<1,000 m) was significantly higher than that in any other habitat type and elevation
- Although, breeding of the species was seen only in the mid-elevation evergreen forests, they were recorded from low-elevation evergreen, moist deciduous and scrub forests during the non-breeding season.
- The absence of Grey-headed Bulbul from the plantations, which are modified rainforests, indicates the species' susceptibility to habitat modifications.
- The sighting locations were characterised with low canopy height; low canopy cover, high shrub cover and presence of water.
- Grey-headed Bulbuls' occurrence was influenced by different anthropogenic factors; they shy off from areas with wood cutting and mining.
- Seasonal migration of Grey-headed Bulbul was associated with the variation in fruit abundance and adverse climatic conditions.
- The results highlight the gaps in the existing protected area system and the importance of the lowland rainforests for the conservation of Grey-headed Bulbul and other local migratory species.

Chapter 4

Habitat selection by Grey-headed Bulbul

4.1. Introduction

For centuries field observers are aware that each species of bird is attached to a certain kind of habitat, and an experienced field observer can predict the species of birds to be encountered in a particular habitat by just a quick glance. Habitat selection can be defined as a series of decisions made by an individual resulting in the use of one habitat in preference to other available habitats (Jones, 2001). Numerous studies have been conducted to identify and explain the relationship between birds and their environments (see Cody, 1985 for a review). The long history of the study of avian habitat selection started in the early catalogue era, followed by the qualitative natural history era and the well advanced recent quantitative mathematical ecology era (see Block and Brennan, 1993). The observations of White (1906) and the theories and ideas of Darwin (1897) form some of the earliest records of associations between individual species and particular types of vegetation. Further to this, a more ecological approach and the basic concept of niche were developed (Grinnell, 1917; Elton, 1927). The niche concept was further developed by Hutchinson (1957), who described it as an "n-dimensional hypervolume" of which each dimension defined the limits of a particular environmental condition. The application of the term 'habitat' has been used as a unifying, theoretical concept to explain the diversity of avian life history pattern (Rotenberry, 1981). Habitat has been defined variously. The more recent definition of a species' habitat is the resources and environmental conditions that support occupancy, survival and reproduction (Morrison et al., 1992). However, the concept of 'niche-gestalt' (James, 1971) is central to the traditional view of avian habitat selection. This concept explains that birds have a search image for a particular pattern of vegetation, which defines their ecological niche. The widespread acceptance of this concept can be seen in a number of studies demonstrating the bird associations with different aspects of the composition and structure of vegetation using multivariate analyses (Cody, 1985; Martin, 2001; Lawler and Edwards Jr., 2002, 2006; Luck, 2002; see Jones, 2001 for a review).

Birds are theorised to select habitat in a way that maximizes their fitness by increasing their ability to survive and reproduce (Hildén, 1965). The evolution of habitat preferences is determined by, and determines, the bird's morphological structure and behavioural functions, its ability to obtain food and shelter successfully in the habitat (Cody, 1985). The ultimate factors that influence avian survival and reproduction include habitat structure, floristics, weather, food availability, conspecifics, phylogenetic constraints, interspecific competition and predation (Hildén, 1965; James, 1971; Block and Brennan, 1993; Martin, 1993a, b, 2001; Luck, 2002; see Cody, 1985 for a review). These factors might operate independently, hierarchically as a system of sequential decisions or overrides, or synergistically in a complex manner since the birds have the ability to view their environment at a wider range of spatial scales (Orians and Wittenberger, 1991; Sedgwick and Knopf, 1992; Jones, 2001).

Although the distinction between the ultimate and proximate factors influencing habitat selection is not always clear, they are linked each other and have combined influence on the habitat selection process. The relationship between the structural features of vegetation and the presence of bird species are demonstrated in many earlier studies (see Cody 1985). MacArthur and MacArthur (1961) demonstrated that excellent predictions of bird abundance in a variety of temperate vegetations could be made strictly on the basis of knowledge of the vertical distribution of foliage in the vegetation. The architectural characteristics of branches and leaves may influence the selection of a particular tree or shrub for nesting. This will lead to the specificity for nest plants and thus influence the site selection and nest survival (see Martin 1992a, 1993a). The microclimatic conditions at the nest sites have been found to be influenced by the density and arrangement of vegetation surrounding them (Walsberg, 1985). The nest-patch choice is often influenced by risk of predation or parasitism of young (Martin and Roper, 1988; Martin, 1993a, b, 1998). Nests that are higher off the ground often receive less predation pressure than those closer to the ground (Li and Martin, 1991). Dense vegetation surrounding the nest site will provide more concealment to the nests and might reduce the predation rates. Again, distance to the habitat edges or openings are known to influence the breeding success and thus have significant influence in the nest site selection process. The *total foliage hypothesis* has been used to explain why increasing numbers of species can co-exist in habitats with more foliage and structural complexity (Martin, 1988a; Hansell, 2000).

Habitat structure affects foraging opportunities for birds by determining abundance and distribution of prey. It also influences the search and attack methods employed by birds to obtain the food. Moreover, the structure and complexity of the vegetation may provide an index of the food availability. The frugivorous birds might respond directly to the quantity and quality of the food resources and insectivorous birds rely on the composition and structure of the vegetation for proximate cues (Cody, 1981).

Although, ecologically similar species differ in their distribution, habitat or feeding ecology, or in more than one of these respects (Lack, 1947-48, 1971), many bird species share part of their food and other resources with other species. However, similar habitat preferences and limitations in the resources result inter-specific competition (Cody, 1985; Martin, 1993a; Newton, 1998). Similarities in microhabitat use infer fitness costs; hence, natural selection should work towards a divergence of habitat preferences between species (Martin, 1996a, 1998). Questions concerning species coexistence have been related to specialization in resource utilization (see Egas et al., 2004). Theoretically, differential habitat selection allows closely related species to coexist by minimizing competition over limited resources (Rosenzweig, 1981). Several biotic and abiotic interactions were used to explain differences in habitat use among coexisting species (see Rosenzweig, 1981; Cody, 1985; Martin, 1986, 1996a). However, in the case of inter specific competition birds are likely to respond to proximate cues obtained from the structure and composition of the vegetation (see Cody, 1985). Overlap in the habitat characteristics of nest patches among coexisting species can increase risk of nest predation and, thereby, favour differences in microhabitat use among them (Martin 1988a, b, 1996a, 2001).

Although the habitat selection process was influenced by a number of factors such as availability of nest material, physical factors, predators and predation rates (see Chapter 6); the distribution, abundance and breeding productivity of a species are influenced by the vegetation structure of its habitat. This fundamental configuration reflects environmental suitability in terms of song perches; foraging, roosting and nesting sites (Sedgwick and Knopf, 1992).

One of the most exciting and controversial areas of ecology in the 1990s was the influence of scale upon patterns of distribution and abundance in animals and plants (Wiens, 1989; Levins, 1992). Birds have been found to be associated with physical structures and patterns of vegetation at several different spatial scales (Sedgwick and Knopf, 1992; Saab, 1999; Lawler and Edwards Jr., 2006). Variation is apparent at all scales, from the global to the microscopic and this leads to different responses in different species, often at different stages in life cycles or activities (Addicott et al., 1987). Birds may select foraging or nesting sites at multiple-spatial scales in a hierarchical fashion, first selecting patterns at large-spatial scales and then continuing to make decisions at progressively smaller scales until a site is selected (Hildén, 1965; Hutto, 1985; Jones, 2001). It is important to consider multiple spatial scales because factors affecting species distributions may function at different scales (Wiens, 1989; Kristan, 2006), and these ecological processes are best understood when studies are conducted at multiple spatial and temporal scales (e.g., Wiens, 1989; Sedgwick and Knopf, 1992; Saab, 1999; Beck and George, 2000; Lawler and Edwards Jr., 2006).

Traditional methods to quantify the avian habitat selection have been conducted at small spatial scales incorporating only a small portion of the individual's territory (Cody, 1985). The 0.04 ha circular plot technique is perhaps the most frequently used, and a modification of this method has been recommended as a standard methodology for sampling avian habitats (Noon, 1981; see also James and Shugart, 1970; Sedgwick and Knopf, 1992; Martin et al., 1996; Sodhi et al., 1999; Beck and George, 2000). Its ecological validity stems from the fact that plot size (0.04 ha) is smaller than the average territory size for virtually all passerines and thus should include vegetation typical of the species in question without including areas outside the territory (Sedgwick and Knopf, 1992). And also, the 0.04 ha scale "should include an adequate sample of the vegetation" (James, 1971). Moreover, the vegetation patterns at these scales are generally accepted as the proximate cues that reflect ultimate factors such as predation risk, competition, the availability and predictability of food resources, and other stresses and constraints imposed by the physical environment (Hildén, 1965; Cody, 1985; Martin, 1988c). Recently, larger spatial scales are emphasised for bird-habitat research, especially the landscape scale (see reviews in Allen, 2001). However, studies at the larger spatial scales often conducted with the help of relatively expensive GIS and remote sensing techniques. Although the present study is restricted to the habitat selection at two spatial scales, Grey-headed Bulbul-habitat relationship at the landscape level was obtained from the surveys conducted in its entire range of distribution (see Chapter 3).

In both tropical and temperate habitats much work has been done on avian habitat selection; nesting and foraging site selection particularly have received considerable attention (e.g., Li and Martin, 1991; Sakai and Noon, 1991; Saab, 1999; Martin, 2001; Luck, 2002). Many bird species in tropical habitats are habitat specialists. Thus most times the problem of preferential habitat use is a crucially important factor that helps to frame conservation strategies (Araújo et al., 2002; Luck, 2002). The voluminous work on the birds of the Indian subcontinent by Ali and Ripley (1987) describes the broad-scale associations of birds with different vegetation types. Even though, several studies on the bird communities and on many single species were done, only a few studies addressed the habitat selection at smaller scales especially for the restricted range bird species of the Western Ghats (Ahmed, 2005).

In the present study, I examine the habitat relationships of Grey-headed Bulbul and co-existing Yellow-browed Bulbul at multiple spatial scales, specifically at the meso- (territory) and micro-scales (nest site). A landscape scale habitat relationship of the species was described in Chapter 3.

4.2. Objectives

In this chapter I explore the process of habitat selection by Grey-headed Bulbul and its interspecific competitor Yellow-browed Bulbul. The specific objectives were to:

1). understand the foraging and nesting habitat selection of Grey-headed Bulbul at different spatial scales and,

2). compare microhabitat use of these two species in order to test whether differing habitat preferences can account for resource partitioning and thus enable coexistence.

4.3. Study area

Data for this study were collected from the Silent Valley National Park and the surrounding Reserved Forests of Kerala (Karuvarakundu Reserved Forest of Nilambur South Forest Division and Attapady Reserved Forest of Mannarkkad Forest Division). Detailed descriptions of the study sites are given in chapter 2.

4.4. Methods

4.4.1. Foraging and nesting site selection

To document the habitat selection of Grey-headed Bulbul at multiple spatial scales, the habitat features were measured on three types of sampling plots: (1) nesting site, (2) foraging site, and (3) random site. Scales were defined as follows: (1) meso-scale covered an area of 0.04 ha surrounding nest, foraging and randomly selected points, and (2) micro-scale in which characteristics of the focal tree (nesting, foraging and random) and the surrounding vegetation were measured in an area of 0.008 ha (James and Shugart, 1970; Martin et al., 1996).

Nest searches were conducted throughout the breeding seasons of 2003, 2004 and 2005. Nests were located following specific adult behaviour and by searching individual plants within the territories as described by Martin and Geupel (1993, see also Martin et al., 1996). Vegetation features at nesting sites were measured in a sampling plot centered on the nest. All the measurements at the nesting sites were taken after the fledging of the nestlings in order to avoid disturbances. Although there was some broad-scale overlap in the nesting sites used in different years, they were well outside the areas of the micro- and meso-scales, and thus treated as independent data sets. The foraging sites were located by visually searching for foraging birds and flagging a foraging tree in a patch regularly used by the bird (see Beck and George, 2000). At the nesting and foraging sites a number of vegetation characteristics and other factors were measured as described in section 4.4.1. The probable habitat attributes which influence the site selection at different scales are devised based on the ecology of the species or derived/modified from a number of studies (e.g., Sedgwick and Knopf, 1992; Martin et al., 1996). Identical measurements were made at the random locations to differentiate the nesting and foraging habitat use from habitat availability. The random sites were selected at least 300 m from the nesting or foraging habitat sampling point at a non-random direction. Sample sizes for three sampling plots were 50 nesting sites, 50 foraging sites and 70 random sites.

4.4.1.1. Meso-scale variables

At the meso-plot scale, the vegetation structure and other habitat characteristics were measured within an 11.3 m radius circular plot (0.04 ha) around each nest, foraging and random sites. Number of all trees (≥10 cm GBH); canopy trees (>10 m height) and sub-canopy trees (≤10 m height) were counted. The number of food plant trees and shrubs or lianas used as food plant species was counted separately. Mean tree height, mean girth at breast height of all trees and maximum tree height in each plot was calculated. Visual estimates of canopy, sub-canopy, shrub, ground vegetation, epiphytes, rock and bare ground cover were recorded in each plot. Altogether 17 variables were measured or calculated to describe the habitats selected by Grey-headed Bulbul at the meso-scale (Table 4.1).

4.4.1.2. Micro-scale variables

The micro-scale habitat characteristics were measured within the meso-scale in a circle of 5 m radius (0.008 ha) from the center, at each of the three sampling-plot types (nesting, foraging, and random). At each plot, I recorded or measured the height and girth at breast height (GBH) of the focal plant (nesting, foraging or random trees); densities of saplings, shrubs, reeds, *Strobilanthes*, pteridophytes and, dominant and co-dominant plant species. The adjacent tree and shrub characteristics measured include the height, girth at breast height and distance from the focal plant. Distances to the water, trek path, and nearest animal trail from the focal plant were also measured at this scale. In total, at the micro-scale 19 variables were recorded to describe the micro-habitats selected by Grey-headed Bulbul (Table 4.2).

4.4.2. Interspecific comparison

Both the Grey-headed and Yellow-browed Bulbuls occupy similar patches in the evergreen forests for foraging and nesting. This poses questions regarding the resource partitioning and coexistence. To examine the variation in the habitat use, and interspecific competition for resources, I measured the nesting site characteristics of these two species at two spatial scales. The habitat sampling was based on the protocol described above and the vegetation features and other measures were made at the meso- and micro-plot scales.

Table 4.1. Descriptions of meso-scale (0.04 ha) habitat features measured or calculated at nesting and foraging sites of Grey-headed Bulbul, and random sites at Silent Valley National Park and surroundings (@ Arcsine transformed).

Code	Variables	Method of measurement/calculation
MNTHT	Mean tree height (m)	Mean height of all the tree species in the 0.04 ha plot.
MXTHT	Max tree height (m)	Height of the tallest tree in the 0.04 ha plot.
MNTGBH	Mean tree GBH (cm)	Mean GBH of all the tree species in the 0.04 ha plot.
TRDEN	Tree density (#/plot)	Number of trees (≥10 cm GBH) per 0.04 ha plot. Multi-stemmed trees were considered a single tree if stems diverged above the ground.
CTDEN	Canopy tree density (#/plot)	Number of trees (>10 m height) per 0.04 ha plot.
SBDEN	Sub-canopy density (#/plot)	Number of trees (≤10 m height) per 0.04 ha plot.
FTDEN	Food trees (#/plot)	Number of food trees per 0.04 ha plot.
FSLDEN	Food shrubs & liana (#/plot)	Number of shrubs and lianas used as food plants per plot
DDTDEN	Dead tree density (#/plot)	Number of dead trees (snags) per 0.04 ha plot.
DNTDEN	Downed tree density (#/plot)	Number of downed trees per 0.04 ha plot.
PBG	Percent bare ground@	Percentage of bare ground per 0.04 ha plot calculated by visual estimation.
PRC	Percent rock cover@	As above for rock cover.
PEPI	Percent epiphyte cover@	As above for all epiphytes
PCC	Percent canopy cover@	As above for all canopy trees
PSCC	Percent sub-canopy cover@	As above for all sub-canopy trees
PSC	Percent shrub cover@	As above for all shrubs
PGC	Percent ground cover@	As above for all ground vegetation

4.4.3. Statistical analyses

At two spatial scales, 36 variables (17 meso-plot variables and 19 micro-plot variables) were measured to describe and discriminate the variation of habitat structure among the nesting, foraging and random plots. Habitat variables that did not meet assumptions of normality were transformed (see Table 4.1), after being assessed by frequency distribution, normal probability plots and the Shaprio-Wilks test (Zar, 1999). To identify the variations in the habitat structure at foraging, nesting and random sites, data for each scale were analysed using both univariate and multivariate approaches. First, the means of continuous variables were compared by using One-way ANOVA with Bonferroni multiple comparison tests to determine differences among the site types. Principal component analysis (PCA) based on correlation matrices was conducted to reduce dimensionality of the data. The principal component factors that had eigenvalues > 1.0 were extracted to explain the maximum variation in the data set. The factor matrix was rotated by the Varimax method with Kaiser Normalization to assist in interpretation and display of the results (Norušis, 1998). The discriminant function analysis (DFA) was used to compare the vegetation characteristics surrounding foraging trees or nesting trees and randomly placed plots at meso- and micro-scales. The Wilks' Lambda F-statistic was used to test the equality of discriminant scores.

Table 4.2. Descriptions of micro-scale (0.008 ha) habitat features measured or calculated at nesting and foraging sites of Grey-headed Bulbul, and random sites at Silent Valley National Park and surroundings.

Code	Variables	Method of measurement/calculation
HTFP	Focal plant height (m)	Height of the focal plant species (nesting, foraging and random plant)
GBHFP	Focal plant GBH (cm)	GBH of the focal plant
SAPDEN	Sapling density (#/plot)	Number of saplings per 0.008 ha plot
SHBDEN	Shrub density (#/plot)	As above for all shrubs
DODEN	Dominant plant density (#/plot)	As above for the dominant species
CDDEN	Co-dominant plant density (#/plot)	As above for the co-dominant species
SBDEN	*Strobilanthes* density (#/plot)	As above for all *Strobilanthes*
REETDEN	Reed density (#/plot)	As above for all reeds
PTEDEN	Pteridophyte density (#/plot)	As above for all Pteridophytes
LNDEN	Liana density (#/plot)	As above for all lianas
DTWTR	Distance to water (m)	Distance to water from the focal plant
DTTKP	Distance to trek path (m)	Distance to trek path or road from the focal plant
DTANT	Distance to animal trail (m)	Distance to animal trail from the focal plant
DTNT	Distance to adjacent tree (m)	Distance to adjacent tree from the focal plant
HTNT	Height of adjacent tree (m)	Height of adjacent tree by visual estimation
GBHNT	GBH of adjacent tree (cm)	GBH of adjacent tree
DTNS	Distance to adjacent shrub (m)	Distance to adjacent shrub from the focal plant
HTNS	Height of adjacent shrub (m)	Height of adjacent shrub by visual estimation
GBHNS	GBH of adjacent shrub (cm)	GBH of adjacent shrub

The nest site characteristics of the Grey-headed and Yellow-browed Bulbuls were compared using one-way ANOVA to determine differences among population means. Further to this, a Principal component analysis was done to reduce the dimensionality of the data (see above). The Discriminant function analysis was performed to discriminate the nesting sites of Grey-headed (n = 50) and Yellow-browed Bulbuls (n = 81). Finally, a binary logistic regression (Hosmer and Lemeshow, 2000) was done to determine which measured or calculated variables contribute to ecological separation of the two species at different spatial scales. The regression parameters were estimated by a stepwise forward selection process (maximum likelihood method) to reduce the number of independent variables actually entered into the model. All possible combinations of habitat variables were entered into different models and the best combination was selected based on improvements in the fit and predictive power of the model (Henderson and Velleman, 1981; James and McCulloch, 1990). Nagelkerke's R^2 was interpreted as proportion of explained variance of the dependant variable (Nagelkerke, 1991; Norušis, 1998). The most parsimonious model was fitted by using significant changes in -2loglikelihood with the addition or deletion of variables based on the goodness-of-fit statistic (χ^2), the Hosmer-Lemeshow goodness-of-fit test and R^2 variance explained for each model (Tabachnick and Fidell, 1996; Hosmer and Lemeshow, 2000; Peng et al., 2002).

Prior to all the multivariate analysis, Pearson correlation coefficient analysis was performed to determine the multicollinearity between the independent habitat variables and, $r \geq 0.70$ was considered as criterion for either omitting or retaining a variable (see Tabachnick and Fidell, 1996; Luck, 2002). However, both biological and statistical aspects were considered for the omission or retention of variable in each analysis. All the statistical analyses were performed using the statistical package SPSS 10.0.1 for Windows (SPSS Inc., 1999). The data presented are means ± S.E. values and a probability level of ≤ 0.05 was considered statistically significant and ≤ 0.01 was considered highly significant.

4.5. Results

4.5.1. Foraging and nesting site selection

4.5.1.1. Meso-scale

At the meso-scale, 13 of the 17 measured or calculated habitat variables significantly differed between the foraging and random sites (One-way ANOVA, $p < 0.05$; Table 4.3). Univariate tests showed that Grey-headed Bulbuls selected patches with high densities of sub-canopy trees ($\leq$ 10 m height) for foraging. The foraging plots were characterised by small trees (MNTHT and MNTGBH), but high sub-canopy cover (PSCC) compared to the random plots (One-way ANOVA, $p < 0.001$).

Nine of 17 meso-scale habitat variables significantly differed between the nesting and random sites. Although there was no difference in the availability of food plant species (FTDEN and FSLDEN) among the nesting and random plots, the foraging plots are characterised by high food plant density. Total tree density (TRDEN) and densities at different strata (CTDEN and SBDEN) were significantly lower in nesting sites compared to those in the foraging and random sites ($p < 0.001$, Table 4.3). Vegetation cover (PCC, PSCC, PSC, PGC and PEPI) differed significantly among the site types ($p < 0.001$, Table 4.3). Both nesting and foraging plots are characterised by higher shrub cover (PSC) than the random sites. However, the canopy cover (PCC) was significantly lower in the nesting and foraging sites compared to the random sites. There was no difference in the densities of snags (DDTDEN) and fallen trees (DNTDEN) among the site types (Table 4.3).

Five factors were obtained from the principal component analysis accounting for 68.79% of the variability in habitat structure (Table 4.4). The first factor (PC1) was positively correlated with sub-canopy density, total tree density, food tree density and negatively correlated with tree heights. The second factor (PC2) is largely a measure of the canopy tree density and cover. The third factor (PC3) was negatively correlated with rock and bare ground cover and fourth factor (PC4) is a measure of the snags and downed trees. Finally, the fifth factor (PC5) correlated positively with the epiphyte density (Table 4.4).

Table 4.3. Meso-scale habitat characteristics (mean ± SE) at nesting, foraging and random sites of Grey-headed Bulbul at Silent Valley National Park and surrounding areas (see Table 4.1. for variable descriptions).

Variables	Nesting (N)	Foraging (F)	Random (R)	*F*	*p*	*Bonferroni*
MNTHT	10.62±0.41	8.49±0.34	10.92±0.29	14.271	0.001	F<N, F<R, N=R
MXTHT	21.60±0.75	17.84±0.63	21.84±0.66	10.070	0.001	F<N, F<R, N=R
MNTGBH	57.32±3.81	31.79±1.47	47.33±2.13	22.161	0.001	F<R<N
TRDEN	41.60±3.26	74.98±1.13	73.27±2.76	35.664	0.001	N<F, N<R, F=R
CTDEN	13.86±1.36	19.84±1.68	33.17±1.52	43.813	0.001	N<F<R
SBDEN	25.46±2.70	54.94±3.40	40.10±2.55	23.408	0.001	N<R<F
FTDEN	18.52±1.91	45.08±2.71	13.89±1.02	80.587	0.001	N<F, R<F, N=R
FSLDEN	22.66±5.17	51.12±3.80	11.29±1.22	36.498	0.001	N<F, R<F, N=R
DDTDEN	0.82±0.24	1.42±0.32	1.13±0.16	1.447	0.238	N=F=R
DNTDEN	1.36±0.24	0.82±0.28	0.76±0.12	2.451	0.089	N=F=R
PBG	5.32±1.28	6.32±1.08	2.67±0.58	4.275	0.015	R<F, N=F, N=R
PRC	11.88±2.45	3.60±1.21	2.17±0.46	12.896	0.001	R<N, F<N, R=F
PEPI	1.56±0.46	6.32±0.90	3.03±0.61	11.607	0.001	N<F, R<F, N=R
PCC	34.90±2.67	39.80±2.39	61.93±1.95	42.811	0.001	N<R, F<R, N=F
PSCC	54.60±2.87	68.70±1.38	44.71±2.32	27.567	0.001	R<N<F
PSC	74.60±1.81	62.80±1.46	27.59±2.96	109.749	0.001	R<F<N
PGC	70.50±2.70	62.60±1.83	28.33±2.47	93.054	0.001	R<F, R<N, N=F

Table 4.4. Factor loadings of individual variables derived by a principal component analysis of meso-scale habitat characteristics measured at the nest, foraging and random sites of Grey-headed Bulbul (see Table 4.1. for variable descriptions).

Variables	PC1	PC2	PC3	PC4	PC5
Eigenvalue	4.008	2.663	1.473	1.163	1.012
Variation (%)	26.72	17.76	9.82	7.75	6.75
Cumulative %	26.72	44.48	54.30	62.05	68.79
SBDEN	0.921	0.087	0.034	-0.004	0.097
MNTHT	-0.822	0.151	0.071	0.069	-0.012
TRDEN	0.802	0.505	0.126	0.060	0.112
FTDEN	0.754	-0.223	0.018	0.096	0.389
MXTHT	-0.677	0.270	0.048	0.252	0.067
PSCC	0.549	-0.377	0.270	0.232	0.002
CTDEN	-0.064	0.829	0.198	0.105	0.050
PCC	-0.038	0.807	0.170	0.125	0.085
PSC	0.150	-0.770	0.098	0.063	0.143
PBG	0.086	-0.188	-0.692	0.089	0.269
FSLDEN	0.238	-0.362	0.629	0.165	0.342
PRC	-0.014	-0.229	-0.625	0.290	-0.079
DDTDEN	0.067	0.164	0.023	0.700	-0.063
DNTDEN	-0.136	-0.050	-0.237	0.679	0.041
PEPI	0.129	0.059	-0.036	-0.061	0.901

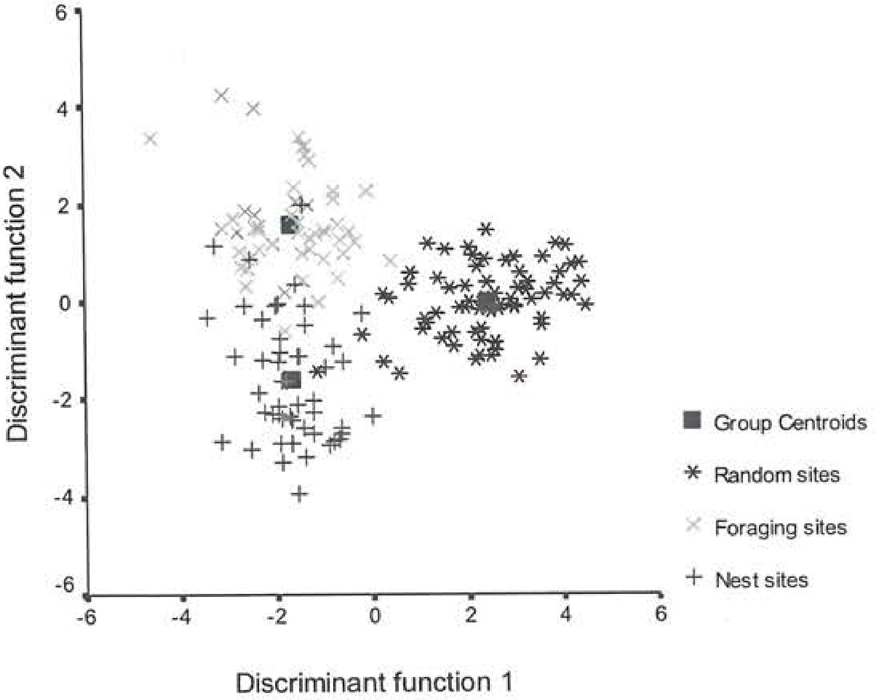

Figure 4.1. Ordination of discriminant scores of foraging, nesting and random plots of Grey-headed Bulbul on two axes derived from the analysis of meso-scale habitat characteristics.

Fifteen of the 17 meso-scale variables were included in the discriminant function analysis. Two discriminant functions were significant ($\chi^2 = 408.79, 148.52; p < 0.001$; Table 4.5). The first discriminant function accounted for 72.8% variability in the habitat data, and was positively correlated with canopy tree density ($r = 0.345$) and canopy cover ($r = 0.322$), and negatively correlated with shrub cover ($r = -0.537$) and food plant density ($r = -0.316$). The second function was positively correlated with the food plant density ($r = 0.604$), tree density ($r = 0.456$), sub-canopy density ($r = 0.428$) and food shrubs and liana density ($r = 0.353$). In the ordination plot, the nesting and foraging sites were situated to the left along DF1, indicates the correlations with shrub cover, canopy tree density and canopy cover. Foraging sites located in the top of DF2, being associated with the high densities of food trees, sub-canopy and total trees (Figure 4.1).

Table 4.5. Summary of the discriminant analysis of meso-scale habitat features at foraging, nesting and random sites of Grey-headed Bulbul at Silent Valley National Park (see Table 4.1. for variable description).

	DF1	DF2
Canonical correlation	0.896	0.778
Wilks' lambda	0.078	0.395
Eigen value	4.087	1.530
Significance (*p*)	0.001	0.001

Variables entered	Correlation with function	
PSC	-0.537	-0.188
CTDEN	0.345	0.157
PCC	0.322	0.079
PBG	-0.125	-0.009
FTDEN	-0.316	0.604
TRDEN	0.163	0.456
SBDEN	0.001	0.428
FSLDEN	-0.246	0.353
PEPI	-0.048	0.326
MNTHT	0.129	-0.259
PRC	-0.118	-0.252
PSCC	-0.227	0.245
MXTHT	0.100	-0.228
DDTDEN	-0.053	-0.108
DNTDEN	0.002	0.106

Table 4.6. Micro-scale habitat characteristics (mean ± SE) at nesting, foraging and random sites of Grey-headed Bulbul at Silent Valley National Park and surrounding areas (see Table 4.2. for variable descriptions).

Variables	Nesting (N)	Foraging (F)	Random (R)	*F*	*p*	*Bonferroni*
HTFP	2.72±0.22	6.27±0.32	11.10±0.54	99.556	0.001	N<F<R
GBHFP	4.76±0.25	29.08±2.15	48.03±3.69	59.086	0.001	N<F<R
SAPDEN	26.52±3.01	27.82±2.46	22.27±1.51	1.790	0.170	N=F=R
SHBDEN	184.56±14.78	78.82±4.94	28.31±3.14	93.537	0.001	R<F<N
DODEN	126.56±12.65	50.04±3.63	23.83±1.89	60.086	0.001	R<F<N
CDDEN	31.96±3.04	20.94±1.22	11.33±0.51	37.683	0.001	R<F<N
SBDEN	34.90±6.75	6.66±1.51	5.19±1.21	20.102	0.001	F<N, R<N, F=R
REETDEN	84.60±16.43	0.70±0.34	4.97±1.47	29.121	0.001	F<N, R<N, F=R
PTEDEN	4.60±0.70	3.96±0.84	2.51±0.40	3.114	0.047	N=F=R
LNDEN	17.90±4.95	26.26±1.92	7.81±0.88	11.606	0.001	R<N, R<F, N=F
DTWTR	9.57±1.28	139.48±25.33	124.03±21.32	11.573	0.001	N<F, N<R, F=R
DTTKP	28.41±5.83	106.04±43.03	117.81±25.90	2.720	0.069	N=F=R
DTANT	3.47±0.63	12.90±5.93	3.73±0.32	2.898	0.058	N=F=R
DTNT	2.45±0.20	1.52±0.12	1.39±0.08	18.238	0.001	F<N, R<N, F=R
HTNT	11.29±0.81	8.26±0.49	11.59±051	8.874	0.001	F<N, F<R, N=R
GBHNT	56.96±5.44	39.50±3.16	51.67±3.51	4.329	0.015	F<N, N=R, F=R
DTNS	0.77±0.62	1.08±0.07	1.19±0.10	1.284	0.280	N=F=R
HTNS	2.08±0.18	1.81±0.11	1.43±0.07	7.860	0.001	R<N, N=F, F=R
GBHNS	4.46±0.40	4.94±0.19	5.24±0.23	2.019	0.136	N=F=R

4.5.1.2. Micro-scale

Of the 19 measured or calculated habitat variables at the micro-scale, 13 differed among the site types (Table 4.6; $p < 0.01$). Eleven variables varied between nesting and random sites, while seven differed between the foraging and random sites. There was no difference ($p < 0.05$) among foraging, nesting and random sites in the densities of saplings (SAPDEN) and pteridophyes (PTEDEN), distances to the trek paths (DDTKP) and animal trails (DTANT), and the nearest shrub characteristics (DTNS and GBHNS). The nesting sites were characterised by high densities of shrubs (SHBDEN), dominant plant species (DODEN), co-dominant plant species (CDDEN), *Strobilanthes* (SBDEN), and reeds (REETDEN). The nesting sites were closer to the water sources (DTWTR) compared to the foraging or random sites (Table 4.6; $p < 0.01$).

The 17 micro-scale habitat variables included in the principal component analysis were summarised into seven principal components (PCs) with an eigenvalue larger than 1, and these accounted for 67.18% of total data variance (Table 4.7). The first PC expressed the shrub (SHBDEN), reed (REETDEN) and co-dominant plant densities (CDDEN). Second PC was largely a measure of the adjacent tree characteristics (HTNT and GBHNT), while third PC expressed the adjacent shrub features (GBHNS and HTNS). The fourth PC was associated with the distances to water and trek path. The fifth PC was negatively correlated with the *Strobilanthes* density, whereas the sixth PC was associated with the pteridophyte density and distance to the animal trail. Finally the seventh PC was correlated with the distance to the nearest shrub.

Two significant discriminant functions (DFs) were derived from the analysis of 17 micro-scale habitat characteristics ($\chi^2 = 312.56, 61.22$; $p < 0.001$; Table 4.8). The first discriminant function accounted for 89.1% variability in the habitat data, and was positively correlated with shrub density ($r = 0.537$) and co-dominant plant density ($r = 0.341$); and negatively correlated with the focal plant height ($r = -0.545$). The second function was positively correlated with the liana density ($r = 0.464$), distance to animal trail ($r = 0.271$) and distance to water ($r = 0.271$); and negatively correlated with reed density ($r = -0.377$), *Strobilanthes* density ($r = 0.252$) and height and GBH of the nearest tree ($r = -0.474, -0.312$). Nesting sites were situated in the right along DF1, having high values for shrub cover and co-dominant plant density. The positions of site types in the ordination plot along DF2 were influenced by various vegetation and distance variables (Figure 4.2).

Table 4.7. Factor loadings of individual variables derived by a principal component analysis of micro-scale habitat characteristics measured at the nesting, foraging and random sites of Grey-headed Bulbul (see Table 4.2. for variable descriptions).

Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Eigenvalue	3.000	2.190	1.567	1.371	1.154	1.095	1.043
Variation (%)	17.65	12.88	9.22	8.06	6.79	6.44	6.14
Cumulative %	17.65	30.53	39.75	47.81	54.60	61.04	67.18
SHBDEN	0.744	0.049	0.098	-0.177	-0.405	0.056	0.050
CDDEN	0.742	-0.087	0.067	-0.213	-0.006	0.120	-0.157
REETDEN	0.657	0.040	-0.004	-0.104	0.373	-0.104	0.271
DTNT	0.655	0.269	-0.043	0.291	-0.023	-0.099	-0.109
HTFP	-0.649	0.185	0.143	0.089	0.250	-0.072	-0.186
HTNT	0.055	0.928	0.006	-0.057	0.052	-0.038	-0.052
GBHNT	0.128	0.910	-0.083	-0.041	-0.026	-0.031	-0.046
LNDEN	0.151	-0.496	-0.098	-0.004	0.080	-0.018	-0.163
GBHNS	-0.098	-0.004	0.860	0.029	0.167	-0.126	-0.027
HTNS	0.219	0.003	0.645	-0.174	-0.051	0.204	0.337
DTTKP	0.009	-0.097	0.078	0.752	0.111	0.002	-0.093
DTWTR	-0.182	-0.013	-0.144	0.695	0.025	-0.036	0.120
SBDEN	0.226	0.025	-0.156	-0.166	-0.798	0.001	0.003
SAPDEN	0.167	-0.247	-0.411	-0.396	0.425	0.146	0.114
DTANT	-0.048	-0.081	0.111	0.053	0.149	0.787	-0.153
PTEDEN	0.097	0.040	-0.151	-0.111	-0.153	0.721	0.168
DTNS	0.029	0.054	0.096	0.025	0.028	-0.006	0.900

4.5.2. Interspecific comparison of nesting sites

4.5.2.1. Meso-scale

Of the 15 meso-scale habitat characteristics measured or calculated at the nesting sites of Grey-headed Bulbul and Yellow-browed Bulbul, six varied significantly ($p < 0.05$, Table 4.9). The Yellow-browed Bulbul nests were placed in stands with high canopy and sub-canopy tree density than those of Grey-headed Bulbul sites. However, Grey-headed Bulbul preferred sites with larger trees (MNTGBH) compared to those by Yellow-browed Bulbul. Accordingly the percentage canopy and sub-canopy cover varied significantly between the sites used by these two species (Table 4.9).

Table 4.8. Summary of the discriminant analysis of micro-scale habitat features at foraging, nesting and random sites of Grey-headed Bulbul at Silent Valley National Park (see Table 4.2. for variable description).

	DF1	DF2
Canonical correlation	0.891	0.565
Wilks' lambda	0.140	0.680
Eigen value	3.859	0.470
Significance (*p*)	0.001	0.001

Variables entered	Correlation with function	
HTFP	-0.545	-0.313
SHBDEN	0.537	-0.121
CDDEN	0.341	0.077
DTNT	0.228	-0.194
HTNS	0.153	0.094
PTEDEN	0.093	0.088
DTTKP	-0.088	0.073
GBHNS	-0.079	0.002
HTNT	-0.010	-0.475
LNDEN	0.099	0.464
REETDEN	0.270	-0.377
GBHNT	0.039	-0.312
DTANT	-0.005	0.271
DTWTR	-0.164	0.271
SBDEN	0.234	-0.252
SAPDEN	0.052	0.153
DTNS	0.055	-0.086

Table 4.9. Meso-scale nesting site characteristics of Grey-headed Bulbul (GHB) and Yellow-browed Bulbul (YBB) at Silent Valley National Park and surrounding areas (see Table 4.1. for variable descriptions).

Variables	GHB	YBB	*F*	*P*
MNTHT	10.62±0.41	10.94±0.27	0.447	0.505
MXTHT	21.60±0.75	21.78±0.59	0.035	0.852
MNTGBH	57.32±3.80	48.36±1.73	5.856	0.017
TRDEN	41.60±3.26	54.79±2.24	11.817	0.001
CTDEN	13.86±1.36	23.91±1.00	36.518	0.001
SBDEN	25.46±2.70	30.88±1.81	2.986	0.086
DDTDEN	0.82±0.24	0.68±0.13	0.306	0.581
DNTDEN	1.36±0.24	0.56±0.10	12.681	0.001
PBG	5.32±1.28	6.05±0.99	0.207	0.650
PRC	11.88±2.45	1.77±0.39	25.998	0.001
PEPI	1.56±0.46	2.49±0.36	2.545	0.113
PCC	34.90±2.67	54.32±1.72	41.142	0.001
PSCC	54.60±2.87	49.14±1.82	2.853	0.094
PSC	74.60±1.81	73.52±1.84	0.156	0.693
PGC	70.50±2.70	66.30±1.67	1.96	0.164

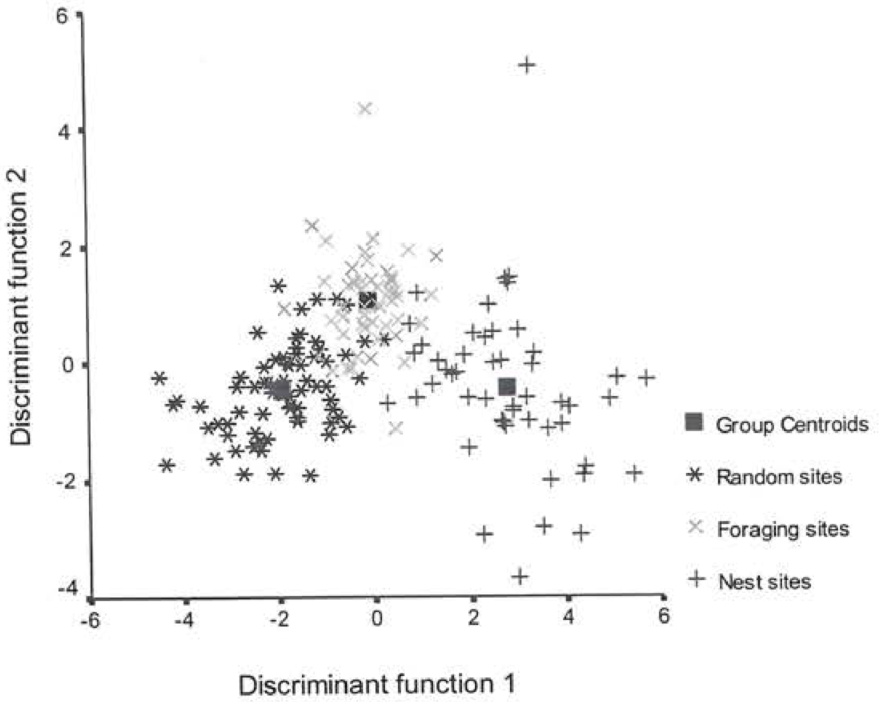

Figure 4.2. Ordination of discriminant scores of foraging, nesting and random plots of Grey-headed Bulbul on two axes derived from the analysis micro-scale habitat characteristics.

Table 4.10. Factor loadings of individual variables derived by a principal component analysis of meso-scale habitat characteristics measured at the nesting sites of Grey-headed and Yellow-browed Bulbuls (see Table 4.1. for variable descriptions).

Variables	PC1	PC2	PC3	PC4	PC5
Eigenvalue	3.058	2.483	1.505	1.347	1.032
Variation (%)	21.84	17.74	10.75	9.62	7.37
Cumulative %	21.84	39.58	50.33	59.95	67.32
SBDEN	0.895	0.163	0.031	-0.008	-0.022
MNTGBH	-0.833	0.131	0.070	0.009	-0.007
TRDEN	0.810	0.497	0.063	0.015	0.099
PSCC	0.641	-0.027	-0.157	0.042	-0.095
MXTHT	-0.568	0.566	-0.187	0.153	0.058
CTDEN	0.142	0.780	0.070	-0.013	0.248
PCC	0.109	0.747	0.110	-0.090	0.215
PBG	0.106	-0.588	-0.169	0.031	0.363
PGC	-0.076	0.035	0.872	0.120	0.049
PSC	-0.026	0.151	0.856	-0.121	-0.016
DNTDEN	0.052	0.237	0.094	0.722	-0.289
DDTDEN	-0.021	-0.248	-0.093	0.785	0.152
PEPI	-0.155	0.092	0.123	0.097	0.738
PRC	-0.071	-0.197	0.085	0.290	-0.536

Table 4.11. Summary of the discriminant function analysis of the meso- and micro-scale habitat features at the nesting sites of Grey-headed and Yellow-browed Bulbuls (see Tables 4.1 and 4.2. for variable description).

Meso-scale		Micro-scale	
	DF1		DF 1
Canonical correlation	0.795	Canonical correlation	0.828
Wilk's lambda	0.368	Wilk's lambda	0.315
Chi-square	121.105	Chi-square	137.075
Eigenvalue	1.721	Eigenvalue	2.180
Significance level	0.001	Significance level	0.001
Variables entered	Structure matrix	Variables entered	Structure matrix
PCC	-0.427	CDDEN	0.418
CTDEN	-0.402	REETDEN	0.364
PRC	0.341	NPDEN	0.355
DNTDEN	0.237	HTNS	0.321
TRDEN	-0.225	DTNT	0.267
MNTGBH	0.160	DTWTR	-0.253
PSCC	0.119	SHBDEN	0.232
SBDEN	-0.109	PTEDEN	0.228
PEPI	-0.106	DTANT	0.164
PGC	0.092	SAPDEN	-0.105
DDTDEN	0.045	DTNS	-0.093
PBG	-0.031	LNDEN	-0.059
PSC	0.022	GBHNS	-0.025
MXTHT	-0.005	DTTKP	-0.014
		NPHT	0.01
		SBDEN	-0.008
		HTNT	-0.004

Five principal components derived from the analysis of the uncorrelated meso-scale habitat features of nesting sites explained 67.32% variation in the data. PC1 explained 21.84% variation and was positively correlated to the shrub and tree densities, and percentage sub-canopy cover; and negatively correlated to the GBH and tree height. PC2 explained the canopy tree cover and density. PC3 is largely a measure of shrub and ground cover. PC4 explained the densities of snags and downed trees, while PC5 is associated with the epiphyte cover (Table 4.10). However, associations of these composite variables were difficult to interpret. Therefore, all the uncorrelated variables were included in further analyses.

DFA indicated successful discrimination of Grey-headed and Yellow-browed Bulbul nesting sites based on first component (Wilk's lambda = 0.368, χ^2 = 121.105; $p < 0.001$). This component was positively correlated with rock cover (r = 0.341) and fallen trees (r =

0.237); and negatively correlated with canopy cover (r = -0.427), canopy tree density (r = -0.402), and total tree density (r = -0.225; see Table 4.11).

Table 4.12. Summary of meso-scale variables included in logistic regression models describing the nesting site selection of Grey-headed and Yellow-browed Bulbuls at Silent Valley National Park and surrounding areas.

Variables	Coefficients (β)	S.E.	Wald$_{df}$	p
MNTGBH	-0.079	0.021	13.647_1	0.001
CTDEN	0.097	0.038	6.464_1	0.011
PRC	-0.167	0.052	10.402_1	0.001
PCC	0.061	0.020	9.302_1	0.002
PSCC	-0.081	0.023	12.227_1	0.001
Constant	4.910	1.772	7.673_1	0.006

Table 4.13. Micro-scale nesting site characteristics of Grey-headed Bulbul (GHB) and Yellow-browed Bulbul (YBB) at Silent Valley National Park and surrounding areas (HTNP = height, GBHNP = girth at breast height and, NPDEN = densities of the nesting plants; see Table 4.2. for other variable descriptions).

Variables	GHB	YBB	F	p
HTNP	2.72±0.22	2.64±0.22	0.053	0.818
GBHNP	4.76±0.25	14.07±1.75	17.324	0.001
NPDEN	86.46±15.04	12.60±2.84	35.859	0.001
SAPDEN	26.52±3.01	32.38±1.86	3.071	0.082
SHBDEN	184.56±14.78	125.00±8.08	14.578	0.001
DODEN	126.56±12.65	51.33±4.77	41.875	0.001
CDDEN	31.96±3.04	13.40±0.92	48.734	0.001
SBDEN	34.90±6.75	37.64±5.39	0.100	0.752
REETDEN	84.60±16.43	3.91±1.99	37.787	0.001
PTEDEN	4.60±0.70	1.84±0.35	15.204	0.001
LNDEN	17.90±4.95	23.37±2.01	1.383	0.242
DTWTR	9.57±1.28	117.85±20.29	17.501	0.001
DTTKP	28.41±5.83	30.79±9.79	0.032	0.858
DTANT	3.47±0.63	1.94±0.21	7.394	0.007
DTNT	2.45±0.20	1.58±0.09	20.126	0.001
HTNT	11.29±0.81	11.45±0.46	0.033	0.856
GBHNT	56.96±5.44	58.49±2.85	0.075	0.785
DTNS	0.77±0.08	0.94±0.08	2.116	0.148
HTNS	2.08±0.18	1.21±0.06	30.321	0.001
GBHNS	4.46±0.40	4.59±0.20	0.107	0.745

Fourteen meso-scale variables were analysed using logistic regression to determine the most parsimonious model. The final model which included five variables (Table 4.12) was highly significant ($\chi^2_5 = 90.27$, $p < 0.001$), classifying correctly 84.6% (Nagelkerke R^2) of the sites (76% of Grey-headed Bulbul and 90% of Yellow-browed Bulbul nesting sites). The final model was not significantly different from the statistically perfect model (Hosmer-

Lemeshow goodness-of-fit $C_8 = 10.59$. $p = 0.226$). Variations in the canopy (PCC), sub-canopy (PSCC) and rock covers (PRC), canopy tree density (CTDEN), and mean tree GBH in the regression analysis confirm the discrimination of the bulbul nesting sites at the meso-scale derived by the discriminant function analysis (see Table 4.12).

4.5.2.2. Micro-scale

The univariate analysis of the micro-scale nesting site variables of Grey-headed and Yellow-browed Bulbuls shows significant variations in 11 of the 20 measured or calculated variables (One-way ANOVA, $p < 0.05$). The nesting sites of Grey-headed Bulbul were characterised by high densities of nesting plants, shrubs, dominant and co-dominant plant species, reeds and pteridophytes (Table 4.13). Their nests were placed in patches closer to small streams compared to those of Yellow-browed Bulbul.

Table 4.14. Factor loadings of individual variables derived by a principal component analysis of micro-scale habitat characteristics measured at the nesting sites of Grey-headed and Yellow-browed Bulbuls (see Table 4.2. for variable descriptions).

Variables	PC1	PC2	PC3	PC4	PC5
Eigenvalue	3.094	2.676	1.613	1.455	1.115
Variation (%)	18.20	15.74	9.49	8.56	6.56
Cumulative %	18.20	33.94	43.43	51.99	58.55
HTNP	-0.754	0.337	0.037	0.162	-0.022
DTNS	-0.726	0.073	0.060	-0.009	0.148
DTWTR	-0.688	-0.069	-0.304	-0.036	0.066
SHBDEN	0.601	0.592	0.171	0.122	0.221
SBDEN	0.572	0.285	-0.312	-0.134	0.313
NPDEN	0.125	0.766	0.246	0.118	0.144
SAPDEN	0.285	-0.695	0.088	0.002	0.057
REETDEN	0.030	-0.049	0.770	0.157	-0.131
DTNT	-0.314	0.412	0.613	-0.068	-0.033
CDDEN	0.423	0.104	0.522	0.323	0.115
PTEDEN	0.237	0.081	0.486	-0.129	0.379
HTNS	-0.046	0.219	0.177	0.737	0.172
GBHNS	-0.254	-0.053	-0.145	0.683	0.241
DTANT	0.147	-0.025	0.100	0.672	-0.188
DTTKP	0.045	0.379	0.115	-0.144	-0.630
LNDEN	0.289	-0.134	-0.318	0.027	-0.483
HTNT	0.069	0.261	-0.060	0.087	0.446

Five principal components derived from the analysis of 17 micro-scale variables poorly explained the total variation in the data (58.5%, Table 4.14). Therefore, all the uncorrelated habitat variables were entered into the discriminant function analysis (DFA) and logistic regression. DFA of 17 micro-scale variables correctly discriminated the nesting sites of the Grey-headed and Yellow-browed Bulbuls (Wilk's lambda = 0.315, χ^2 = 137.075; $p <$ 0.001). Along the first canonical discriminant function of the DFA, both the species were well separated by the densities of reeds (r = 0.364), nesting plants (r = 0.355) and co-dominant plants (r = 0.418; Table 4.11).

Seventeen of the 20 micro-plot variables were included in the logistic regression analysis. Dominant plant density (DODEN) and GBH of nesting plant and nearest tree and (GBHNP, GBHNT) were correlated with other variables and were discarded. The final model which included five variables (Table 4.15) was highly significant (χ^2_6 = 138.34, $p < 0.001$), classifying correctly 96.1% (Nagelkerke R^2) of the sites (96% of Grey-headed Bulbul and 96.2% of Yellow-browed Bulbul nesting sites). The final model was not significantly different from the statistically perfect model (Hosmer-Lemeshow goodness-of-fit C_8 = 4.10; p = 0.848). The final model identified significant variations in the densities of nesting plants, shrubs, reeds and dominant plants; and characteristics of the nearest shrubs (Table 4.15).

Table 4.15. Summary of micro-scale variables included in logistic regression models describing the nesting site selection of Grey-headed and Yellow-browed Bulbuls at Silent Valley National Park and surrounding areas.

Variables	Coefficients (β)	S.E.	Wald$_{df}$	p
NPDEN	-0.075	0.020	13.608$_1$	0.001
SHBDEN	0.064	0.019	11.787$_1$	0.001
CDDEN	-0.361	0.098	13.671$_1$	0.001
REETDEN	-0.033	0.012	7.665$_1$	0.006
DTNS	3.486	1.204	8.381$_1$	0.004
HTNS	-4.919	1.420	11.995$_1$	0.001
Constant	7.141	2.050	12.140$_1$	0.001

The ecological separation in the nesting site between Grey-headed and Yellow-browed Bulbuls at both meso- and micro-scale are evident from the above analyses. However, a few nesting sites in the *Strobilanthes* patches were found overlapping. Furthermore, in these microhabitats the species were found to use the same plant species for nesting. To explore the level of this overlap, nesting sites (*vine nests*) of Grey-headed Bulbul in the *Strobilanthes* patches were compared with those of Yellow-browed Bulbul in the similar habitats.

The final model derived from the logistic regression analysis of 12 meso-scale variables was highly significant ($\chi^2_4 = 61.94$, $p < 0.001$), classifying correctly 87.9% (Nagelkerke R^2) of the sites (93.2% of Yellow-browed Bulbul and 87.9% of Grey-headed Bulbul nesting sites in the *Strobilanthes* patches). The final model included four variables, namely canopy tree density, rock cover, canopy cover and sub-canopy cover (Table 4.16).

The logistic regression analysis of 19 variables at the micro-scale also found significant differences in the nesting sites. The final model was highly significant ($\chi^2_5 = 84.51$, $p < 0.001$) and explained 95.6% (Nagelkerke R^2) variance in the data (98.3% of Yellow-browed Bulbul and 90.6% of Grey-headed Bulbul nesting sites in the *Strobilanthes* patches). The variables contributed these variations are the nest plant density, shrub density, co-dominant plant density, distance to the animal trail, and girth at breast height, and height of the nearest tree species (Table 4.17). This clearly shows that two species of bulbuls were ecologically well separated at both the scales of measurements. Although these two species share a few nesting plant species and other resources, they are ecologically segregated in terms of timing of breeding also (see chapter 6).

Table 4.16. Summary of meso-scale variables included in logistic regression models describing the nesting sites of Grey-headed and Yellow-browed Bulbuls in *Strobilanthes* patches.

Variables	Coefficients (β)	S.E.	Wald$_{df}$	p
CTDEN	-0.143	0.047	9.311_1	0.002
PRC	0.095	0.043	4.913_1	0.027
PCC	-0.081	0.027	8.905_1	0.003
PSCC	0.067	0.030	5.105_1	0.024
Constant	2.442	1.808	1.825_1	0.177

Table 4.17. Summary of micro-scale variables included in logistic regression models describing the nesting sites of Grey-headed and Yellow-browed Bulbuls in *Strobilanthes* patches.

Variables	Coefficients (β)	S.E.	Wald$_{df}$	p
NPDEN	0.053	0.015	12.901_1	0.001
SHBDEN	-0.053	0.015	13.338_1	0.001
CDDEN	0.29	0.085	11.729_1	0.001
GBHNT	-0.029	0.014	4.405_1	0.036
HTNS	4.154	1.289	10.392_1	0.001
Constant	-4.869	2.023	5.792_1	0.016

4.6. Discussion

4.6.1. Habitat selection of Grey-headed Bulbul

Grey-headed Bulbul is a resident species with a limited range in the heavy rainfall areas in the Southern Western Ghats from Belgaum and Goa to Kanyakumari. They are found in dense evergreen cane-brakes in swampy jungles and *Lantana* thickets in abandoned forest clearings - a biotope similar to that of Black-crested Bulbul, but preferentially more humid areas with denser growth (Ali and Ripley, 1987; Grimmett et al., 1998; Fishpool and Tobias, 2005). The present study revealed the occurrence of Grey-headed Bulbul in evergreen, semi evergreen, moist-deciduous and scrub forests (see Chapter 3). However, the most preferred habitat is evergreen forests in the low and mid-elevations. Grey-headed Bulbul occurs in a variety of habitats during non-breeding season; however, breeding of the species is almost restricted to the evergreen forests within an elevation of 900 to 1,400 m. This study examined the habitat selection of Grey-headed Bulbul in its breeding habitat only.

Grey-headed Bulbul exhibited varying degrees of selectivity and used different sets of selection criteria, at both the spatial scales examined, at Silent Valley National Park, as has been found for other bird species elsewhere (e.g., Bergin, 1991; Luck, 2002). Both the univariate tests and discriminant function analysis provided similar outcomes in describing the habitat selection of Grey-headed Bulbul. Within the evergreen forests, Grey-headed Bulbuls selected foraging sites based on the characteristics of trees at the meso-scale. Selectivity of well-defined microhabitats for foraging can be considered as a logical extension of the patch choice in foraging theory (Hutto, 1985). Grey-headed Bulbuls selected patches with smaller trees for foraging. Mean tree height (MNTHT), height of the tallest tree (MXTHT), and the mean tree girth at the breast height (MNTGBH) were significantly lower in the foraging sites compared to those in both random and nesting sites. This is further supported by a large set of data collected to assess the foraging heights and heights of trees used by the species. Grey-headed Bulbuls foraged at a height of 5.01 ± 2.60 m on trees averaged 6.41 ± 3.39 m during the breeding season (see Chapter 5 for details).

Although the tree densities were similar, high sub-canopy tree density at the meso-scale best characterised the foraging sites. This is further supported by high sub-canopy cover and shrub cover at these sites. The high foliage cover at the foraging sites may provide concealment from predators and more foraging opportunities to prey on invertebrates. The foraging sites are characterised by high densities of trees (FTDEN) and, the shrubs and lianas (FSLDEN) were used as food plants. These measures were highly correlated with the abundance of tree species such as *Syzygium cumini, Clerodendrum viscosum, Antidesma menasu, Oreocnide integrifolia, Callicarpa tomentosa,* and *Symplocos cochinchinensis*; and shrub species such as *Lantana camara, Leea indica, Maesa indica,* and *Chloranthus brachystachyus.* Most of these species are the major food plants of Grey-headed Bulbul during the breeding season. This suggests that their local distribution was determined by the presence and abundance of food resources.

The high densities of shrubs (SHBDEN), dominant plants (DODEN) and co-dominant plants (CDDEN) at the micro-scale characterised foraging sites of Grey-headed Bulbul. These variables were largely a measure of the abundance of food plant species such as *Lantana camara* and *Maesa indica.* The foraging trees were significantly smaller than the focal plant characteristics at the random sites. Another important feature of the foraging sites was the high abundance of lianas (LNDEN). The selection of vine draped areas provides a large number of invertebrate prey and protection from the predators. These preferences are related to the feeding habits and techniques used by the species. It may be noted that Grey-headed Bulbuls more often used the perch-gleaning (see Chapter 5) which is relatively simple and energetically inexpensive to obtain both fruits and invertebrate diet (Remsen and Robinson, 1990).

The non-random pattern of foraging site selection indicates that the food plant distribution is an important factor in the spatial distribution of Grey-headed Bulbul (see also Chapter 5). The environment in the tropical habitats is heterogeneous, i.e. patchy, at a number of different spatial scales (e.g., Wiens, 1976; Addicott et al., 1987; Kotliar and Wiens, 1990). Individual animals perceive and react to this patchiness at only particular levels of the hierarchy according to their biological characteristics (Kotliar and Wiens, 1990). Resource patches are regarded as the lowest level in this hierarchical ecological process (Ims, 1995). In the case of Grey-headed Bulbul, the optimal selection of the foraging sites is influenced by the patchiness in food plant resources within a larger landscape. Moreover, the influence of edges and the internal patchiness of the environment on the avian habitat selection are well known (see Morrison et al., 1990). Furthermore, patchy distribution of the food resources, restrict a species to only a portion of its potential habitat (Block and Brennan, 1993).

The vegetation structure at the nesting sites of Grey-headed Bulbul is substantially different at both meso- and micro-scales from the random and foraging sites. Sites with low tree density at canopy and sub-canopy (TRDEN, CTDEN and SBDEN1) levels were important in distinguishing the nesting habitat at the meso-scale. Although, shrub cover was high in the nesting sites, canopy and sub-canopy cover were low because of the low tree densities. Similarity in the density of food trees, lianas and shrubs in comparison to those in the random sites shows that the nesting site selection is independent of the distribution of food plants within the nesting patch. Furthermore, Grey-headed Bulbuls foraged in areas away from the nesting sites, probably to reduce the activities at the nesting sites and thereby prevent the nest loss by predation (see Chapter 6).

At the micro-scale, high densities of shrubs (SHBDEN), lianas (LNDEN), dominant (DODEN) and co-dominant plants (CODEN) were the major vegetation attributes distinguishing sites used for nesting from randomly chosen plots. This indicates that although the canopy and sub-canopy cover was moderate, the presence of dense and complex vegetation at the nest heights may impede the ability of mobile predators to locate the nests. The nesting sites were more homogenous with high abundance of reeds (REETDEN) or *Strobilanthes* (SBDEN). The high shrub density around the nest sites will provide high concealment to the nests and its content. However, there was no variation in the nest concealment between the successful and failed nest sites (see Chapter 6). Earlier also, several field and experimental studies failed to demonstrate a correlation between nest concealment and breeding success (e.g., Filliater et al., 1994; Howlett and Stuchburry, 1996). However, absence of positive effects of nest cover on nest survival does not automatically mean a lack of natural selection on higher nest concealment (Remes, 2005; see also Ghalambor and Martin, 2001). Almost all the nesting sites were in the close proximity of water. The higher densities of *Ochlandra* and *Strobilanthes* patches near the water may be the reason for the proximity of the nesting sites to the lower order streams.

Grey-headed Bulbuls place their nests in reed and *Strobilanthes* patches. The vegetation characteristics at both the meso- and micro-scale levels varied significantly between these two patches (see Chapter 6). The variation in the micro-habitat use within the same area pose difficulties to define the hierarchical ecological processes involved in the nesting site selection. These variations may be the result of the rarity and competition for the preferred niche-resources. The variation in the nest architecture attributes did, however, appears to be an adaptation to cope with the differential use of micro-habitats (see Chapter 6). Thus, it seems to be an adaptation to maximize the fitness of the species (see below).

Apart from the structure and composition of the vegetation, a number of factors are known to influence the avian nest site selection (Hansell, 2000; see also Chapter 6). Nest site choice can reduce nest predation (Ricklefs, 1969; Collias and Collias, 1984; Tarvin and Smith, 1995; Howlett and Stutchbury, 1996; Hansell, 2000) and unfavorable effects of microclimatic variables on eggs or nestlings (Martin, 2001). Nesting in patches with relatively high densities of nest plants reduces the risk of predation by increasing the number of potential nest sites in the surrounding area. The 'needle in a haystack' hypothesis (Filliater et al., 1994) or 'potential prey site' hypothesis (Martin, 1993a; Hansell, 2000) predicts that birds select nest sites in areas where there are many potential nest sites, thereby reducing the probability that a site containing a nest will be discovered by a predator. This hypothesis was tested by many researchers (e.g., Martin, 1988b, 1993a; Martin and Roper, 1988) and found that nest predation was reduced when the nest patch contained more potential nest sites and not just more vegetation cover. This is similar to the site selection processes of Crimson-backed Sunbird, a restricted range bird species of the Western Ghats (Balakrishnan, *unpubl. data*). Nests of Grey-headed Bulbul in the reed patches are placed exclusively on *Ochlandra travancorica*. Their site selection at the reed patches agrees with the 'potential prey site' hypothesis (Martin and Roper, 1988; Hansell, 2000), however, the vine nests placed on *Syzygium* saplings draped with lianas in the *Strobilanthes* patches were rare sites in the plot. The fitness consequences of selection of a rare plant in the plot was not clear since, nests on *Syzygium* had a lower success compared to those placed on common species (*Ochlandra*) (see also Filliater et al., 1994).

4.6.2. Habitat selection of Yellow-browed Bulbul

At the landscape scale, Yellow-browed Bulbuls were associated with the evergreen biotype chiefly in sholas, evergreen forest edges, secondary forest, coffee plantations, undergrowth and occasionally gardens in the humid areas (Ali and Ripley, 1987; Fishpool and Tobias, 2005). The nests were placed on isolated shrubs in interior forests with heterogeneous vegetation. However, nests placed in the shrub layers were covered with fresh green moss and thus camouflaged from the predators. On the other hand, most of the nests placed on the sub-canopy trees such as *Antidesma menasu, Olea dioica,* and *Glochidion* spp. with less foliage cover were devoid of the decorative layer of moss. Moreover in general, the foliage cover over the nests was comparatively less than that in the nest of Grey-headed Bulbul.

4.6.3. Interspecific habitat relationships

The Grey-headed and Yellow-browed Bulbuls are breeding residents confined to an optimum elevation zone of 900-1,500 m in the humid evergreen forests (Ali and Ripley, 1987). Both the species share similar foraging strategies, foraging substrates, and some of the nesting plants. Although, the information on predators is moderate, these two species could potentially have similar predators since they come into same nesting guild. Despite these high resource overlaps, the ecological isolation in nesting site selection is well established by the univariate and multivariate analyses. At the meso-scale, the discriminant function analysis discriminated the nesting sites of Grey-headed and Yellow-browed Bulbuls in terms of the canopy cover, rock cover, canopy tree density and total tree density in the plots. However, of the 15 variables measured at the meso-scale, only five differed in the univariate analyses. In the logistic regression analysis, only five variables were needed to correctly classify 76% of Grey-headed Bulbul sites, and 90% of Yellow-browed Bulbul sites. This is highly significant, as model robustness declines with the number of predictors involved. Harrell et al. (1996) suggest that this number should not exceed m/10, where m is the total number of observations.

At the micro-scale, the sites with high densities of shrubs, nest plant species, reeds, and co-dominant plants were important in distinguishing the nests sites of the Grey-headed and Yellow-browed Bulbuls. All the nest plants selected by Yellow-browed Bulbul were in rare sites in the plot. Moreover, their nesting sites had heterogeneous vegetation structure. On the other hand, the density of surrounding vegetation was high and homogenous even though Grey-headed Bulbuls selected rare nesting sites such as *Syzygium* saplings. The logistic regression analysis of the structural characteristics of the highly overlapping nesting sites occurring in the *Strobilanthes* patches also differentiated the habitat use by Grey-headed and

Yellow-browed Bulbuls. Even though, the statistical relationship is strong in separating the nesting sites at smaller scales; several vegetation parameters and nesting plants were similar between these species.

As a resident and early season breeder, Yellow-browed Bulbuls have the broadest range of nest sites available to them. They start breeding in the *Strobilanthes* patches well before the arrival of the local migratory Grey-headed Bulbul. In the early breeding season Grey-headed Bulbuls preferred reed patches while in the late season they did so in the *Strobilanthes* patches. Sharing of similar nesting guild by the co-existing species probably necessitated Grey-headed Bulbul's avoidance of *Strobilanthus* patches in the early season. Moreover, any overlap in habitat characteristics of nest patches among coexisting species can increase risk of nest predation and, thereby, favour differences in microhabitat use among coexisting species (Martin 1988a, b, 1996, Martin and Martin, 2001a, b). The temporal avoidance of patches occupied by Yellow-browed Bulbul further supported by the view that individuals may also use information on hetero-specifics (Cody, 1985; Martin and Martin, 2001a, b), either by their presence or abundance (i.e. hetero-specific attraction, Parejo et al., 2005) or by their reproductive performance (Martin and Martin, 2001a, b), as integrative indices of habitat suitability. Furthermore, habitat preferences are assumed to be adaptive, such that fitness is higher in preferred habitats (Jaenike and Holt, 1991).

It can be concluded that the presence of Yellow-browed Bulbul in *Strobilanthes* patches during the early breeding season influences Grey-headed Bulbuls to select alternative patch (reed patch) for nesting. However, once the former species complete their breeding, the latter starts nesting in *Strobilanthes* patches. Many of these patches were indistinguishable from the typical Yellow-browed nesting sites. This adaptive patch selection could be justified, because *Strobilanthes* patches usually have high food abundance and the intermittent rains during the late breeding could influence the thermal properties of the moss nests constructed in the reed patches. Moreover, undisturbed reed patches in the inaccessible terrains, which deter nest predation are rare even in the pristine habitats. This indicates that nest sites are important limiting resources for Grey-headed Bulbul as reported for many other open-cup nesting species (Martin and Roper, 1988; Martin, 1996b, 1998; Martin and Martin, 2001a).

4.7. Summary

Studies of habitat use of species are essential to formulate species conservation strategies. Past studies and theories of habitat selection have identified the association of birds with the patterns of vegetation at several different spatial scales as a hierarchically structured ecological process. The present study examined the habitat selection process of Grey-headed Bulbul and the competitive interactions with co-existing Yellow-browed Bulbul at Silent Valley National Park and surrounding areas.

- Grey-headed Bulbul displayed non-random habitat selection at all the spatial scales examined.
- The foraging patches were characterised by higher densities of small trees and lianas, and higher sub-canopy and shrub covers.
- The foraging site choice was determined by the presence and abundance of tree species such as *Syzygium cumini, Clerodendrum viscosum, Antidesma menasu, Oreocnide integrifolia, Callicarpa tomentosa,* and *Symplocos cochinchinensis*; and shrub species such as *Lantana camara, Leea indica, Maesa indica,* and *Chloranthus brachystachyus*.
- The nesting sites had low vegetation cover and densities at the canopy and sub-canopy layers.
- At smaller scales, higher densities of shrubs, lianas, dominant, and co-dominant plants were the strongest vegetation attributes distinguishing nesting sites.
- The nesting sites had a homogenous shrub layer with high abundance of either reeds or *Strobilanthes*.
- Although broad-scale overlaps occur, the nesting sites of Grey-headed and co-existing Yellow-browed Bulbuls were distinct in terms of the densities of canopy trees, nesting plants, and dominant plant species.
- Grey-headed Bulbul avoids the competition for the nesting resources with Yellow-browed Bulbul and indirect factors affecting the fitness by selecting two different microhabitats in the early (reed patches) and late stages (*Strobilanthes*) of breeding.
- Habitat conservation, especially the areas with reed and *Strobilanthes* patches are important for Grey-headed Bulbul.

Chapter 5

Foraging ecology of Grey–headed Bulbul

5.1. Introduction

Food is often considered the resource that most likely to limit bird populations (Newton, 1998; Sodhi, 2002) and it has been implicated as an important limiting resource for rare species (Gaston and Kunin, 1997). Food supply is known to influence a number of ecological patterns, including timing of annual cycles, territoriality, habitat selection and territory placement, diet, mating system, clutch size, reproductive success, population size, geographic distribution, community structure and interspecific competition (see Levey, 1988; Hutto, 1990; Powell and Bjork, 1994). Moreover, studies on foraging behaviour and food resources comprise part of an overall attempt by biologists to associate behaviour, distribution, and abundance of birds to their biotic and abiotic environments (see reviews in Morrison et al., 1990). Furthermore, the timing of breeding and moulting, bird diversity and abundance or density, ranging behaviour and flock size are also known to be influenced by food-supply (Perrins 1970; Sodhi, 2002).

Much of the early work in the area of foraging ecology are motivated by theories of the niche, optimal foraging, predator-prey theory, ecomorphology, comparative morphology, and phylogeny (see Morrison et al., 1990 for a review).

Knowledge of foraging behaviour has a special significance in explaining patterns in nature because survival and reproduction depend, ultimately, on an individual's success at acquiring and using energy from food resources (Hutto, 1990). It has been widely demonstrated that food abundance and distribution are the primary determinants of foraging behaviour (see Morrison et al., 1990 for a review). Optimal foraging behaviour, however, may encompass other conflicting activities such as antipredator behaviour that lead animals to trade food intake rate against other activities. Decision making based on trade-offs may be influenced by the internal state of the animal (Krebs and Kacelnik, 1991). Closely related birds nearly always show differences in the frequency of use of foraging maneuvers (Root 1967). Theory and empirical evaluation of adaptations dictate that morphological features designed to perform one type of movement are unlikely to be well designed for other types of movements (Moermond, 1990).

The way that food is handled is important, because (1) food-handling time must be considered in the cost-benefit ratio of any food type, (2) it is a factor in studies of adaptive morphology, and (3) it has important implications for the study of plant frugivore interactions (see reviews in Morrison et al., 1990).

Intraspecific variation in foraging behaviour between sexes or between seasons is well known. These variations associated with the stages of breeding cycle are pronounced (Brennan and Morrison, 1990; Sakai and Noon, 1990; Dobbs and Martin, 1998). Moreover, behavioural and morphological traits that affect foraging efficiency should be adapted in part to the diets available during the periods when food limits survival or reproduction (Martin and Karr, 1990). Thus, knowledge of partitioning of a species' foraging niche by sex or season is essential to increase our understanding of its life history.

Multi-species foraging flocks are a widespread phenomenon in both tropical and temperate forests. Two principal selective advantages thought to favour the evolution of mixed-species flocking behaviour are decreased predation and increased foraging efficiency (see Jullien and Thiollay, 1998; Chen and Hsieh, 2002). However it can also lead to increased intraspecific competition, particularly when food is limited (Milinski and Parker, 1991). Numerous studies on mixed-species flocks have been conducted in the tropics (see Jullien and Thiollay, 1998; Chen and Hsieh, 2002 for reviews). Many restricted range bird species of the Western Ghats are known to participate in the mixed-species flocks. However, no detailed information is available on the flock feeding strategies of these species.

Several studies have reported ecological and evolutionary aspects of the linkage between fruit consumption by vertebrate frugivores and seed dispersal of tropical forest trees (e.g., Wheelwright, 1985a; Terborgh, 1986; Levey, 1988; Loiselle and Blake, 1994; Ganesh, 1996; Corlett, 1998; Herrera, 1998). Plants bearing fleshy fruits designed for dispersal by birds are more conspicuous in tropical habitats than in temperate-zone habitats, mainly because the tropics contain more plant species. Specialization has made some plants and animals completely dependent on each other for long-term survival, and cases of co-extinction are unfortunately well known (Stork and Lyal, 1993). The ecological and evolutionary importance of interactions between fleshy-fruit producing plants and the frugivorous birds that disperse their seeds depends on the degree of spatio-temporal variability in the interaction and the degree of specialization of each species (Gautier-Hion et al., 1985).

Population reductions and extinctions of birds (Gaston et al., 2003) in the 21st century may disrupt ecosystem processes and services of potential importance to society (Chapin et al., 2000; Luck et al., 2003). Even though there has been little research on the economic importance of avian pollination and seed dispersal, a recent review of literature (Sekercioglu et al., 2004) reveals that bird pollination and dispersal of a number of economically or ecologically important species have been demonstrated in Indomalayan, Neotropical, and Palearctic regions (see also Sekercioglu, 2006). Moreover, the avian seed dispersal is important in reducing the cost of restoring degraded lands (e.g., Robinson and Handel, 1993). Although animal-plant mutualisms are less specialised in the tropics, they may be easily disrupted by population declines of one or another component of the interaction, for example due to habitat alteration (Alcantara et al., 1997). In addition, studies on these mutualistic interactions suggested for the conservation of frugivores to preserve the structure and diversity of plant communities in the context of global habitat alteration (see Tellería et al., 2005). However, the societal importance of ecosystem services is often appreciated only during their loss (Sekercioglu et al., 2004).

Tropical rainforests, once thought to provide relatively constant environmental conditions year-round, have mostly been found to be seasonal environments (Wikelski, et al., 2000). All tropical forests studied to date show pronounced phenological variation between seasons and/or between years. Moreover, significant seasonal variations in the abundance of shrub understorey arthropods and fruits are well documented in the tropics and neotropics (e.g., Blake and Loiselle, 1991; Poulin et al., 1992; Loiselle and Blake, 1991; van Schaik et al., 1993). The phenological variations are deemed as adaptations to abiotic factors that include rainfall, day length, irradiance and temperature. The biotic factors *inter alia* encompass mode of seed dispersal, activities of pollinators and seed dispersers, variation in germination conditions, life history traits, canopy position and the relative abundance of trees themselves (see reviews in Wheelwright, 1985a; van Schaik et al., 1993; Chapman et al., 1999, 2005). There has been a pronounced variation in the environmental factors along north-south, east-west, and altitudinal gradients in the Western Ghats (Pascal, 1988). These variations resulted by climatic and topographical disparities may affect different biological processes including the fruit abundance which in turn restrict the breeding season and other activities of several species of birds.

Seasonal changes in biotic interactions such as seasonal migrations in the tropics are well studied (see Wikelski et al., 2000 for a review). It has long been recognised that food availability probably plays a significant, if not dominant, role in the evolution of migratory behaviour and in the regulation of the distribution and dynamics of migrant populations (see reviews in Morrison et al., 1990). Although several species of frugivores are depending on some 'keystone species' during the periods of fruit scarcity (Kannan and James, 1999; Maheswaran, 2002), a number of Western Ghats' species are seasonal local migrants.

Patterns of distribution, abundance and patchiness of resources are factors influencing the spatial distribution of many animal species. Their occurrence may be limited to the patches suitable for their requirements. Thus, knowledge about the spatial distribution and abundance of resources is important to understand the spatial distribution pattern of the species and its correlates. To understand the connection between foraging behaviour and resource use, one needs to know the type of food that the birds use and the factors which influence their selection. Optimal foraging theory has shown that birds often select food based on energy, time, and effort (see reviews in Morrison et al., 1990). Some species are generalists, foraging in a variety of microhabitats, whereas other species are more specialised in foraging and nesting (see Ali and Ripley, 1987).

Birds must be able to discriminate between food items on the basis of their energetic and nutritional rewards to meet efficiently their energy and nutrient requirements (Bosque and Calchi, 2003). Also, the fruit traits may influence the accessibility and foraging preference of frugivores, consequently different plant seeds are dispersed by different animals (Herrera, 1987, 1998; Kitamura et al., 2002; Thompson, 2002a). The characteristics of fruits that influence the food choice of birds include the colour, size, protection, and phenology of fruits along with size and number of seeds, and the nutritional aspects of the fruit pulp (Herrera, 1987, 1998, 2002; Wheelwright, 1985b; Willson and Whelan, 1990; Whelan and Willson, 1994; Chen et al., 2004). Many previous studies have shown the correlation of gape width and fruit selection by birds (see Wheelwright, 1985b). The relationships between the colour and the nutritional aspects were unknown (Izhaki, 1992). However, the colour preferences may be correlated with the availability. For instance, black fruits dominate the bird dispersed fruits in all the tropical and sub-tropical regions (Willson et al., 1990, Herrera, 2002; Balasubramanian and Maheswaran, 2003; Chen et al., 2004), whereas the European bird-dispersed fruits are more likely to be red (Willson et al., 1990, Herrera, 2002). Fruit preferences were best explained by interspecific differences in the nutritional composition of fruit pulp, specifically lipid and carbohydrate content, and their interaction (Fuentes, 1994; Herrera, 1998). Recent studies have also emphasised the importance of digestive characteristics as determinants of fruit choice by frugivorous birds (e.g., Fuentes, 1994; Herrera, 1998).

Arthropods were considered as a major food resource for the breeding passerines (Vijayan, 1975; Levey, 1988; Loiselle and Blake, 1991; Poulin et al., 1992). The effective quantification of invertebrate prey availability is complicated by perceptual differences between investigator and subject; it is difficult to determine which prey are truly available to foragers, let alone what foragers prefer (Hutto 1990; Poulin and Lefebvre, 1997). Yet, information on the invertebrate abundance in the breeding habitats may provide insights to the distribution, abundance, and habitat selection processes.

Studies of the foraging ecology and the role of bulbuls in ecosystem functioning are limited (Vijayan, 1975; Ali and Ripley, 1987; Bhatt and Kumar, 2001; see Fishpool and Tobias, 2005 for a review). Most species of bulbuls are frugivorous and known as key pollinators and seed dispersers (see Kitamura et al., 2002). No previous studies have documented the foraging behaviour, dietary choices and availability of food resources of the Grey-headed Bulbul.

5.2. Objectives

The foraging ecology of Grey-headed Bulbul was studied with the following specific objectives:

1). document the primary foraging behaviour and assess the seasonal and annual variations among them.

2). examine the foraging behaviour of the species in different stages of breeding and in the mixed-species flocks.

3). explore the fruiting phenology and fruit characteristics of the food plant species.

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4). identify and record the abundance and spatial distribution of Grey-headed Bulbul food plant species and invertebrates.

5.3. Study area

I investigated the foraging behaviour of Grey-headed Bulbul along with its seasonal and annual variations at Silent Valley National Park and Muthikkulam Reserved Forest from September 2002 to May 2005. The mixed-species hunting behaviour of the species was studied at Muthikkulam Reserved Forest. The phenological studies were carried out in Silent Valley National Park. Phenological transects laid were in an elevation of 1020-1300 m; this altitude forms the major breeding habitat of Grey-headed Bulbul. The density and distribution of food plants and abundance of invertebrates were also studied at Silent Valley.

5.4. Field methods and data analyses

5.4.1. Foraging behaviour

The foraging behaviour of Grey-headed Bulbuls were documented by following Remsen and Robinson (1990). I recorded the foraging maneuvers of each bird sighted by walking slowly through the existing trek paths or animal trails. For each foraging observation, foraging maneuvre, substrate (twig, leaf, flower and air), height of the foraging location, species and height of the foraging tree; horizontal position of the bird in the canopy (nine categories: three vertical and three horizontal), and foliage density at the foraging site (calculated in percentage cover within a one-meter radius around the bird). The relative height was calculated as the activity height of the bird relative to the total height of the plant (Remsen and Robinson, 1990). Foraging maneuvers and food handling techniques were categorised based on Remsen and Robinson (1990).

Annual and seasonal variations in the foraging behaviour, feeding techniques and foraging locations were tested using Chi-square tests, Mann-Whitney *U*-tests and One-way ANOVA (Zar, 1999).

5.4.2. Foraging heterogeneity within the breeding cycle

Foraging birds in the individual breeding territory were followed (Altmann, 1974; Remsen and Robinson, 1990) to identify the heterogeneity in foraging behaviour within the breeding cycle. For each foraging individual, data were collected as described under section 5.4.1

(foraging behaviour). Data collected during the breeding seasons (mid January to mid May) during 2003 to 2005 were categorised based on the stage of breeding cycle (pre-incubation, incubation, brooding and post-brooding). Heterogeneity in the foraging behaviour and resource use during different stages of breeding were tested using One-way ANOVA with Bonferroni multiple comparison tests (Zar, 1999).

5.4.3. Foraging in the mixed-species flocks

Mixed-species flocks are defined after Stotz (1993) as associations between two or more species moving in the same direction for at least 5 min. Grey-headed Bulbuls participated in the mixed-hunting flocks only during the non-breeding season. Thus all the data were collected from non-breeding study site (Muthikkulam Reserved Forest) only.

Once a flock containing Grey-headed Bulbul was located, it was followed for up to 1 hr or until it disappeared from sight. For each flock, I recorded the number of species, species identity and number of individuals. To minimize duplication of observations, I excluded multiple flocks encountered in the same area. To describe the foraging diversity of the major participants of the mixed-hunting, I recorded a single foraging event for each bird in the flock. Foraging maneuvers and food handling techniques were categorised based on Remsen and Robinson (1990). For each foraging individual, data were collected on the behaviour, foraging positions, substrate and food plants as given in section 5.4.1.

The foraging niche-breadth was calculated by following Levin (1968) as

$$\beta = 1 / \Sigma P_i^2$$

and, the foraging niche-overlap (Pianka, 1973) between Grey-headed Bulbul and other flock participants was calculated as

$$\o_{ij} = \Sigma P_{ij} P_{ik} \; / \; \sqrt{\Sigma P^2_{ij} \, P^2_{ik}}$$

Where $\o_{ij}$ = Pianka's measure of niche overlap between species j and species k

P_{ij} = proportion resource i is of the total resource used by species j

P_{ik} = proportion resource i is of the total resource used by species k.

5.4.4. Fruiting phenology and abundance

The fruiting phenology was monitored in two transects established in an elevation of 1,020-1,300 m at Silent Valley National Park from March 2003 to May 2005. Each transect was 2000 x 20 m, providing a total area of 4 ha each. 25 five major food plant species including eight canopy trees, seven sub-canopy trees, six shrubs, three lianas and one epiphyte were monitored. Apart from this, phenological patterns of 37 non-food species were monitored for comparison. Thus, a total of 62 species were monitored for the fruiting phenology by methods modified from Blake et al. (1990), and Chapman et al. (1994).

Twenty individuals each of all the common food and non-food species and all individuals (8–16 individuals) of six less common or rare species in the plots were monitored. Phenological records were made during middle of each month. The fruit abundance on each individual was ranked on relative scores as: 0 for none, 5 for less than 10 fruits, 55 for 11 to 100 fruits, 550 for over 100 fruits (each score corresponding to the mid-point of those class intervals; see Mudappa, 2001, see also Wallace and Painter, 2002).

Influence of environmental factors on the phenological patterns was tested using Spearman rank correlation. Temporal variation in the environmental factors, phenology of food plants and general fruiting were tested using Wilcoxon matched pairs signed rank test.

5.4.5. Fruit characteristics

Fruit characteristics of the food plants and variations from other species were studied by comparing 29 most commonly used species with 41 un-used fruit species. The fruit characteristics were recorded from samples varying 20–30 fruits of each species. Fruit plant species were categorised as different growth forms (canopy trees, sub-canopy trees, shrubs, lianas and epiphytes) based on Manilal (1988). The fruit traits considered were fruit type (*berry*: a pulpy, indehiscent fruit with several carpels, each with one or more seeds; *drupe*: a fleshy, indehiscent fruit with seed enclosed by a stony endocarp; and *capsule*: a dry, dehiscent fruit with more than one carpel); fruit colour (*black, red/brown, yellow, green, purple* and others); fruit size (*small*: $\leq$ 10 mm, *medium*: 11–20 mm, and *large*: > 20 mm); fruit protection (*fleshy* and *dry*); pulp thickness (*thick, moderate, thin* and *absent*); water content (*dry*: <25%, *moderate*: 25 - 50% and *watery*: > 50%); seed size (*small*: $\leq$ 5 mm, *medium*: 6–10 mm, and *large*: > 10 mm); number of seeds per fruit (*single* or *multi*-seeded) and, seed protection (*thick, thin* and *absent*). The differences in the characteristics of used and un-used fruits were assessed by χ^2 contingency tests (Siegal and Castellen, 1988; Zar, 1999).

5.4.6. Density and distribution of food plants

The density and distribution of the food plants of Grey-headed Bulbul were estimated by using the belt transects and circular plots. Four belt transects, two each in the forest edges and forest interior were laid at Silent Valley. Each transect was 2,000 x 20 m, providing a total area of 4 ha each. The density of all Grey-headed Bulbul food plants was estimated by total counts in these transects. Since the belt transects do not detain the spatial distribution of plants, densities of 15 major food plant species were estimated from 171 circular plots (0.04 ha) spread throughout the study area. These plots were located in the nesting (n = 51), foraging (n = 50) and random sites (n = 70). Variations in the abundance of each food plant species in these plots were tested using One-way ANOVA with Bonferroni multiple comparison tests (Zar, 1999).

5.4.7. Invertebrate abundance

Ten representative bulbul territories and ten non-territories were chosen and sampled during January to May 2005. Considering the foraging habits of bulbuls, two different methods, namely sweeping and beating (Southwood, 1978; Cooper and Whitmore, 1990) were applied to assess prey availability for the birds as follows:

1). Sweeping: Invertebrates were sampled from the vegetation using an insect net; they were released after counting and taking measurement. In the territories of the Grey-headed Bulbul, 3 m by 3 m plots were laid and divided into nine sub-plots. Sweeps were made once per each sub-plot using a circular net with a mouth width of 30 cm radius and 1.5 m long handle.

2). Beating/shaking: The invertebrates on under-storey vegetation were sampled by shaking or beating shrubs and small trees and the insects thus dislodged were collected on a 1 m by 1 m tray of white woolen sheet laid below the plants prior to beating. Three such samples were made from each territory. Invertebrates falling on the tray were counted and measured.

The null hypothesis of homogeneity of invertebrate abundance between territories and non-territories and among nest types was tested using the chi-square tests (Zar, 1999).

5.5. Results

5.5.1. Foraging behaviour and feeding technique

A total of 1,827 observations were made on the feeding habits of Grey-headed Bulbul. They forage in pairs or rarely in groups. The food comprises fruits (65.57%) and arthropods (34.26%). The foraging behaviour of Grey-headed Bulbul was grouped into the following two categories based on the classification of Remsen and Robinson (1990):

a). *near-perch maneuvers,* and

b). *ariel maneuvers.*

The major near-perch maneuvers identified were

1). *glean*: pick food items from a nearby substrate, including the ground that can be reached without full extension of legs or neck, no acrobatic movements are involved.

2). *reach*: extend completely the legs or neck upwards, outwards, or downwards to reach food.

3). *hang*: use legs and toes to suspend the body below the feet to reach food that cannot be reached from any other perched position, and

4). *lunge*: those maneuvers in which the food item is beyond the range of "reach," but rapid leg movements rather than flight are used to approach and capture the prey.

The aerial maneuvers were:

1). *sally*: to fly from a perch to attack a food item (and then return to a perch), and

2). *leap*: launch into the air to reach a food item too far for a "reach" but too close for a "sally." This differs from "sally" in that the upward thrust seems to come mostly from leg movements rather than wing movements.

Gleaning was the most preferred foraging maneuver (70.17%) followed by reach (14.01%), hang (9.30%) and sally (5.58%). Of the different tactics used to catch the insects, gleaning was the most used maneuver (chi-square test for goodness of fit, $\chi^2 = 482.23$; $df = 4$, $n = 626$; $p < 0.001$).

The major food handling techniques used by Grey-headed Bulbul are the following:

1). *gulp*: swallow upon capture without any noticeable manipulation other than being held briefly by the bill. Smaller fruits and lepidopteron larvae were handled by this method.

2). *engulf*: capture and swallow in one continuous motion, without being held by the bill. Most of the smaller arthropods were handled by engulfing and, 3). *bite*: bite off pieces of food items. Larger fruits of *Persea macrantha, Leea indica, Litsea floribunda, Syzigium* spp., and *Symplocose racemosa*; and larger insects were handled by this method.

5.5.2. Foraging location: horizontal and vertical

The mean foraging height was 4.49 ± 2.52 m (range: 1–20 m) and the mean height of trees used for foraging was 5.78 ± 3.30 m (range: 1–22 m). The birds foraged more in the upper (36.20%) and middle edges (23.44%) of the canopy. Foraging in the edges is significantly higher than that in the inner areas of the canopy (chi-square test for goodness of fit, $\chi^2 = 1162.46$; $df = 5$, $n = 1826$; $p < 0.01$). The average foliage density at the point of observations was 33.76 ± 18.37 % (range: 2–80 %).

5.5.3. Variation in foraging: breeding *vs.* non-breeding

In general, there were no marked changes in the food categories of Grey-headed Bulbul during the breeding and non-breeding seasons. Fruits were the most preferred food during breeding (66.09%) and non-breeding seasons (63.95%) followed by arthropods (33.69% and 36.05% respectively). However the fruit species varied significantly between the seasons (see below). Foraging maneuvers and food handling techniques were consistent during the breeding and non-breeding seasons (Figures 5.1 and 5.2).

A significant difference was found in the mean height of trees used for foraging (6.41 ± 3.39 and 3.81 ± 1.98, Mann–Whitney *U*-test: $n_{\text{breeding}} = 1386$, $n_{\text{non-breeding}} = 441$; $z = -16.36$; $p < 0.001$) and the mean foraging height (5.01 ± 2.60 and 2.88 ± 1.29, Mann–Whitney *U*-test: $n_{breeding} = 1386$, $n_{\text{non-breeding}} = 441$; $z = -18.01$; $p < 0.001$) during the breeding and non-breeding seasons (Figure 5.3). During the breeding season, the birds forage more in the upper canopy of taller trees, while during non-breeding season they do so in under storey shrubs. But there was no difference in the relative foraging heights between the seasons ($z = -0.777$; $p < 0.437$, Figure 5.4). In both seasons, the birds foraged in the upper parts of the trees (Figure 5.5).

Foraging at the edges is significantly higher than that at the inner areas of the canopy during both breeding (chi-square test for goodness of fit, $\chi^2 = 955.94$; $df = 2$, $n = 1384$; $p <$

0.01) and non-breeding seasons (chi-square test for goodness of fit, $\chi^2 = 203.08$; $df = 2$, $n = 440$; $p < 0.01$; Figure 5.6).

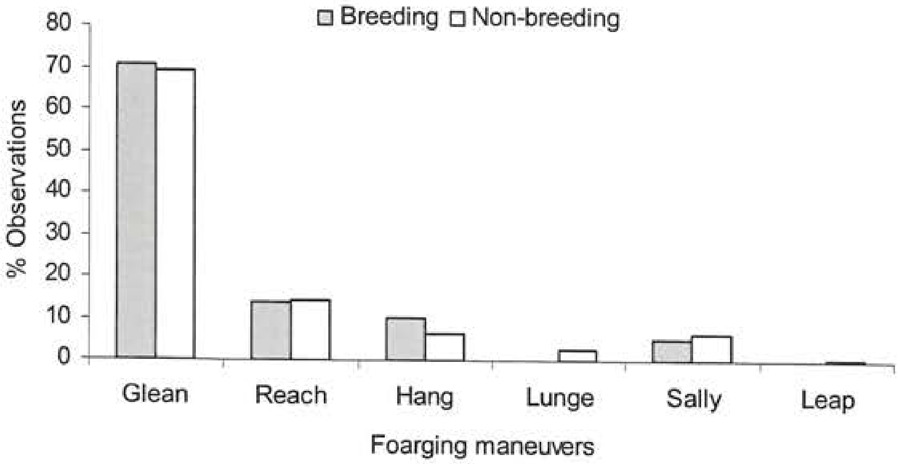


Figure 5.1. Comparison of the foraging methods of Grey-headed Bulbul during breeding (n = 1,386) and non-breeding seasons (n = 441).

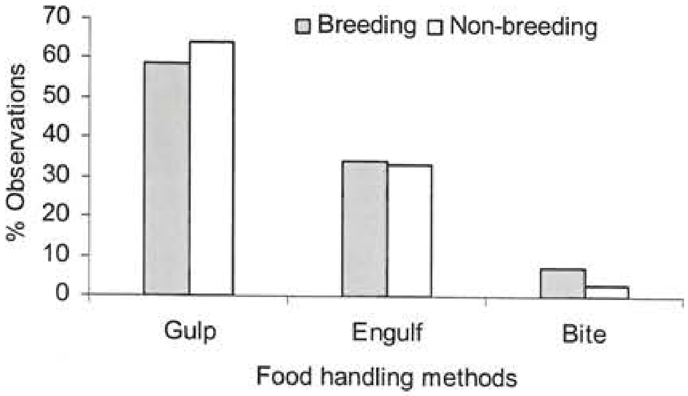


Figure 5.2. Comparison of the food handling methods of Grey-headed Bulbul during breeding (n = 1,386) and non-breeding seasons (n = 441).

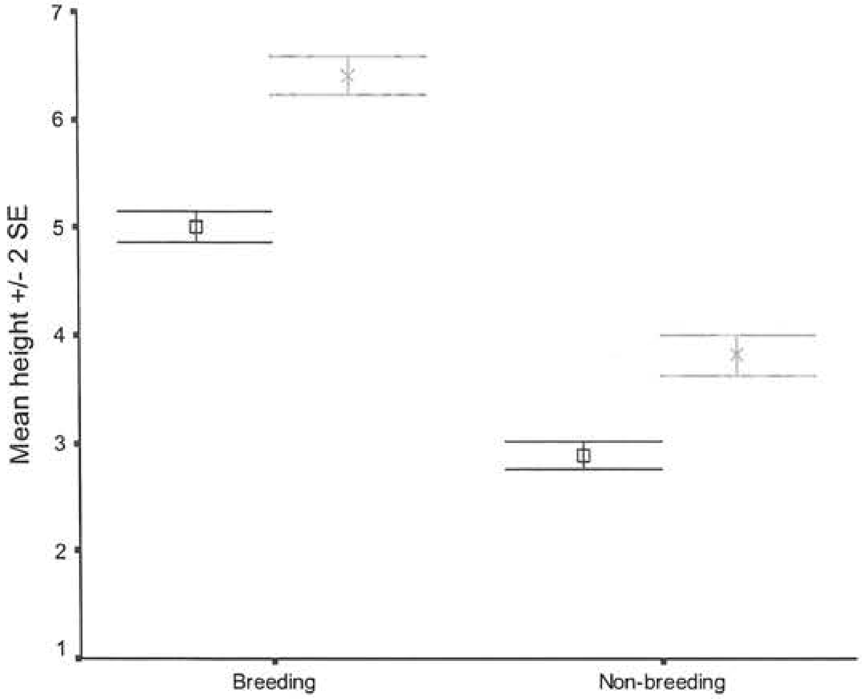


Figure 5.3. Variation in the foraging height (□) and height of the foraging trees (X) between breeding and non-breeding seasons.

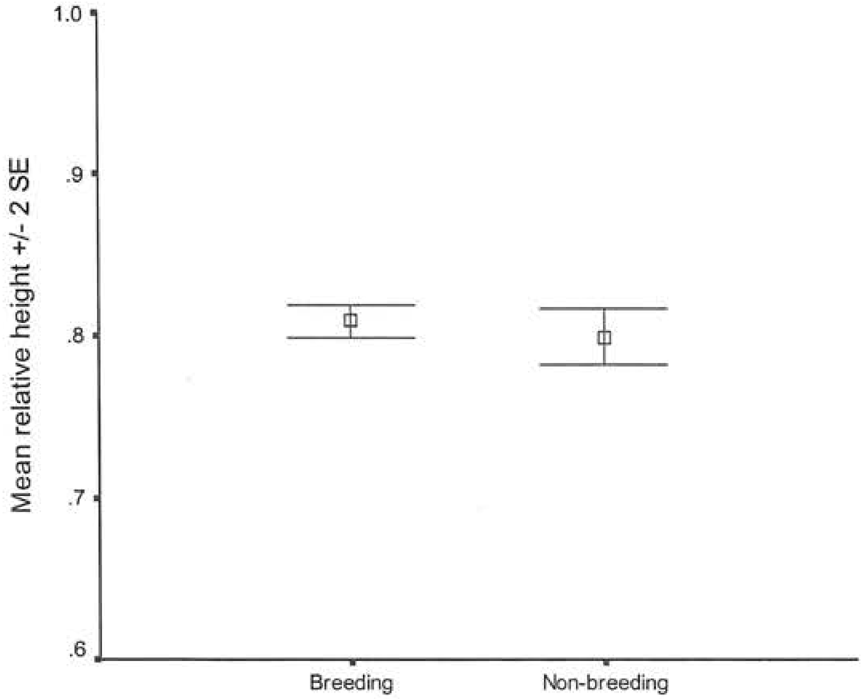


Figure 5.4. Variation in the relative foraging heights between breeding and non-breeding seasons.

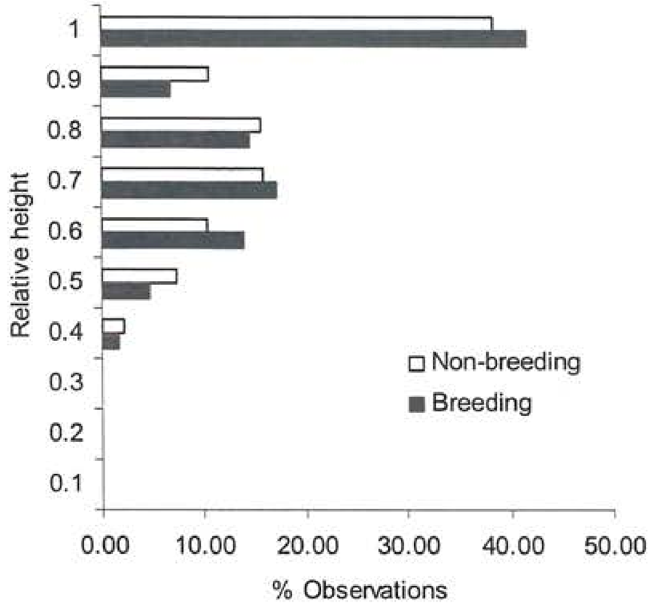
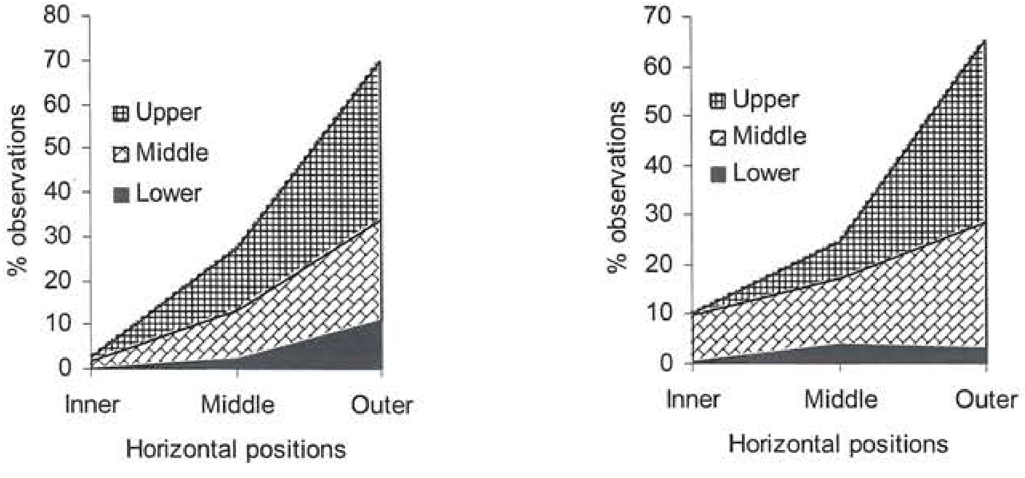


Figure 5.5. Proportion of the relative foraging heights during the breeding and non-breeding seasons.



(a) (b)

Figure 5.6. Horizontal height use by Grey-headed Bulbul during breeding (a) and non-breeding seasons (b).

5.5.4. Annual variation in foraging

Although there was no significant variation in the foraging height use (One-way ANOVA: $F = 2.783$, $p = 0.062$), the height of foraging trees ($F = 21.004$, $p < 0.001$) and the relative foraging heights ($F = 86.900$, $p = 0.001$) varied between years during the breeding seasons (Figures 5.7, 5.8; Table 5.1). However, yearly variations in the foraging height ($F = 17.525$, $p < 0.001$), height of the foraging trees ($F = 29.236$, $p < 0.001$) and relative foraging height ($F = 35.093$, $p < 0.001$) were prominent during non-breeding seasons of different years (Figure 5.9, 5.10; Table 5.1). However, the biological significance of these variations is not clear, since all the fruit bearing plants have shown significant intraspecific variations in the heights.

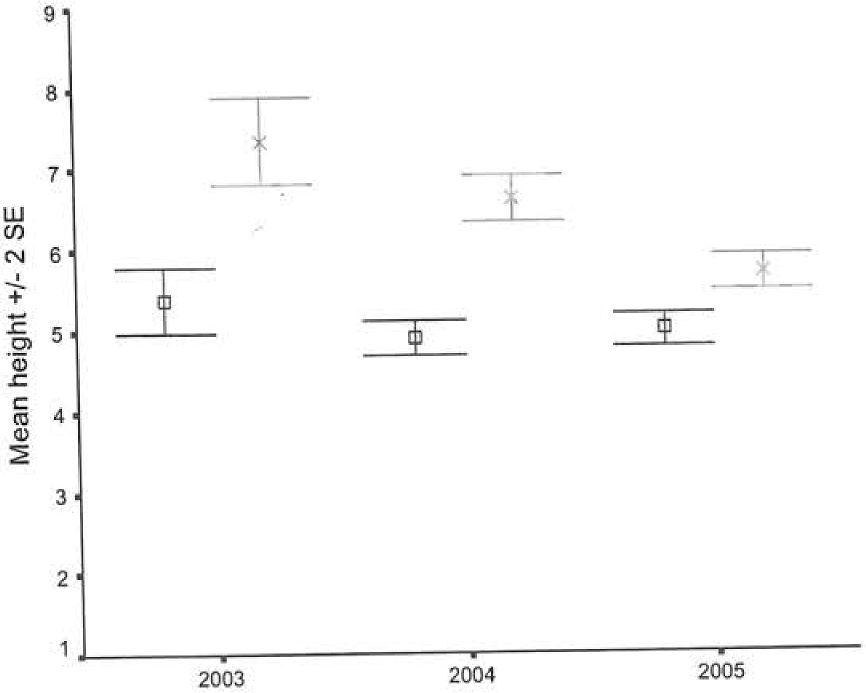


Figure 5.7. Annual variation in the foraging height (□) and height of the foraging trees (X) during breeding seasons of Grey-headed Bulbul.

Table 5.1. Comparisons of annual variations in the foraging height, height of the foraging tree and relative foraging height during the breeding and non-breeding seasons of Grey-headed Bulbul. Variable expressed as mean ± SE and *p* values after Bonferroni correction.

	Breeding seasons				
Variable	2003	2004	2005	*F*	*p*
Foraging height (m)	5.39±2.86	4.90±2.77	4.99±2.20	2.783	0.062
Height of foraging tree (m)	7.36±3.95	6.63±3.68	5.69±2.42	21.004	0.001
Relative foraging height	0.76±0.18	0.76±0.18	0.89±0.17	86.900	0.001

	Non-breeding seasons				
Variable	2002	2003	2004	*F*	*p*
Foraging height (m)	2.62±0.97	3.49±1.62	2.77±1.24	17.525	0.001
Height of foraging tree (m)	3.66±1.61	4.96±2.63	3.18±1.46	29.236	0.001
Relative foraging height	0.76±0.18	0.74±0.18	0.90±1.70	35.093	0.001

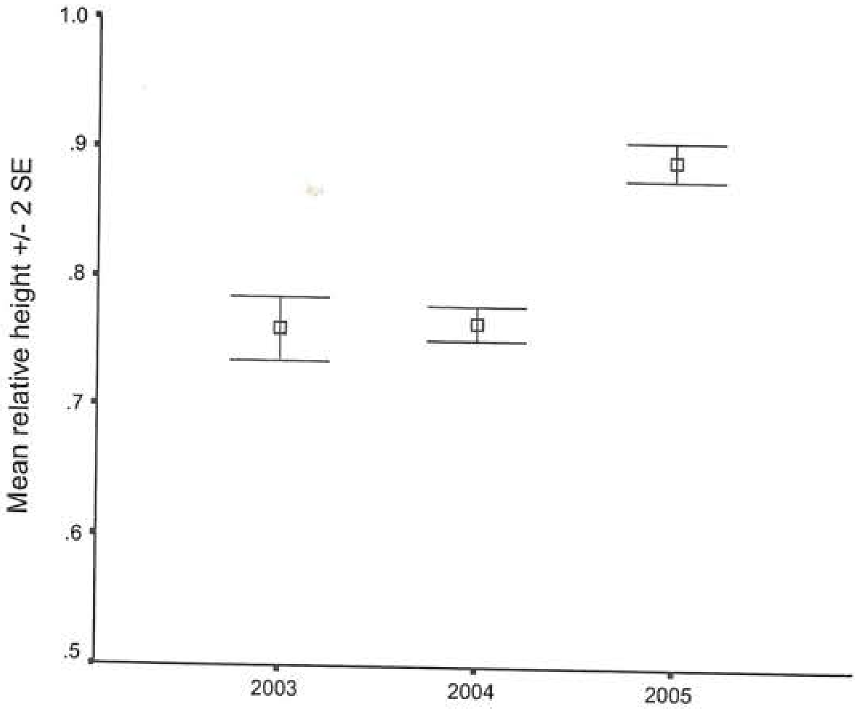


Figure 5.8. Annual variation in the relative foraging heights during the breeding seasons of Grey-headed Bulbul.

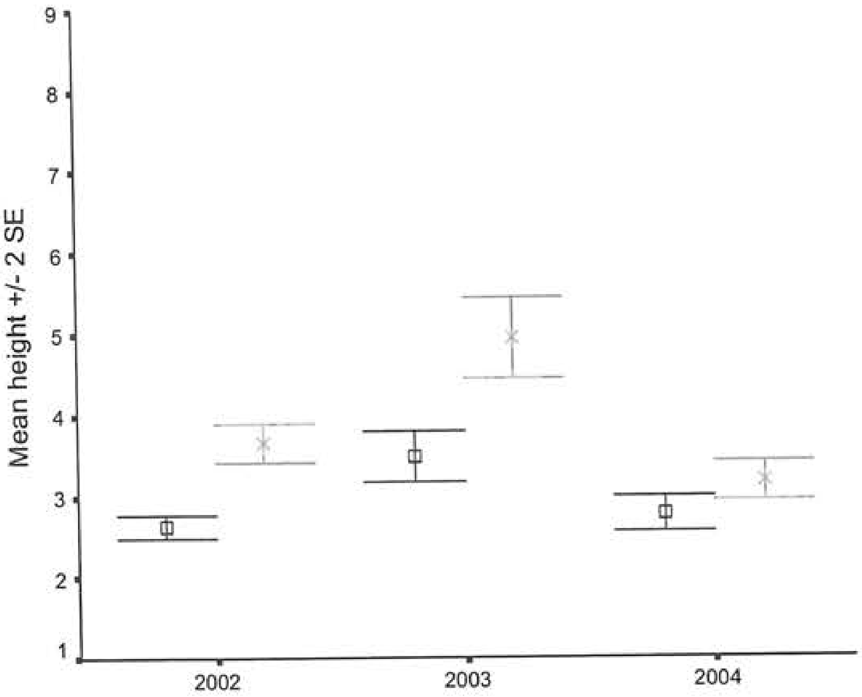


Figure 5.9. Annual variation in the foraging height (□) and height of the foraging trees (X) during non-breeding seasons of Grey-headed Bulbul.

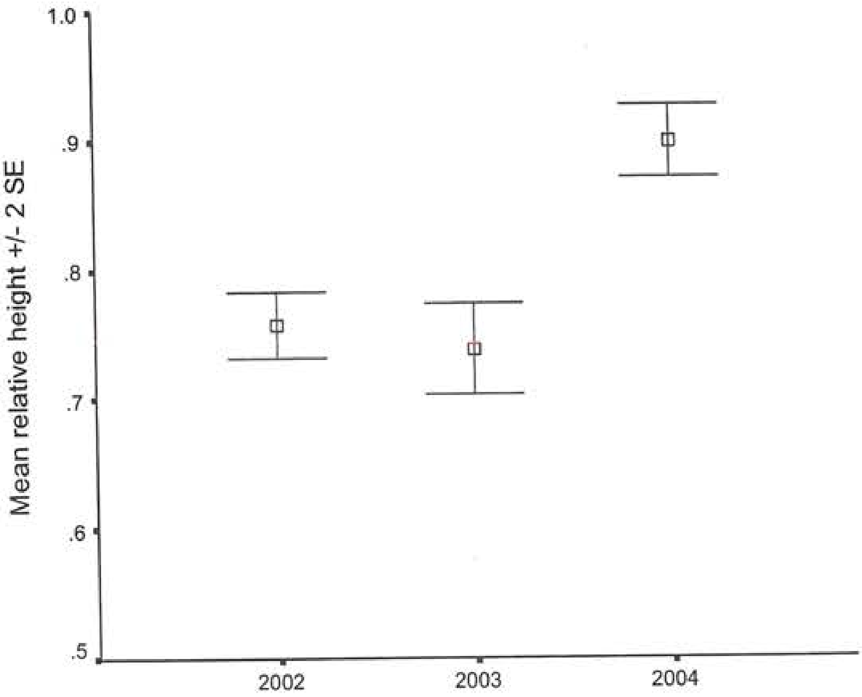


Figure 5.10. Annual variation in the relative foraging heights during the non-breeding seasons.

5.5.5. Heterogeneity of foraging behaviour within the breeding cycle

Grey-headed Bulbuls showed significant plasticity in the foraging behaviour during different reproductive stages. Although the prey-attack and aerial behaviour varied between the reproductive stages, gleaning was the dominant method in all the stages (Figure 5.11). There was a significant difference in the mean height of trees used for foraging and the mean foraging height (ANOVA with Bonferroni correction, $p < 0.001$) during different stages of reproduction (Table 5.2, Figure 5.12). During the incubation and brooding stages bulbuls foraged on taller trees. However, the relative foraging height was lower in these stages ($p < 0.001$, Table 5.2; Figure 5.13). Furthermore, the birds foraged in areas with high foliage cover during incubation and brooding periods compared to other stages of reproduction (ANOVA with Bonferroni correction, $F = 7.261$; $p < 0.001$). Bulbuls consumed fruits based on availability in different stages of breeding. The proportion of invertebrate consumption was comparatively higher during the final stages of reproduction.

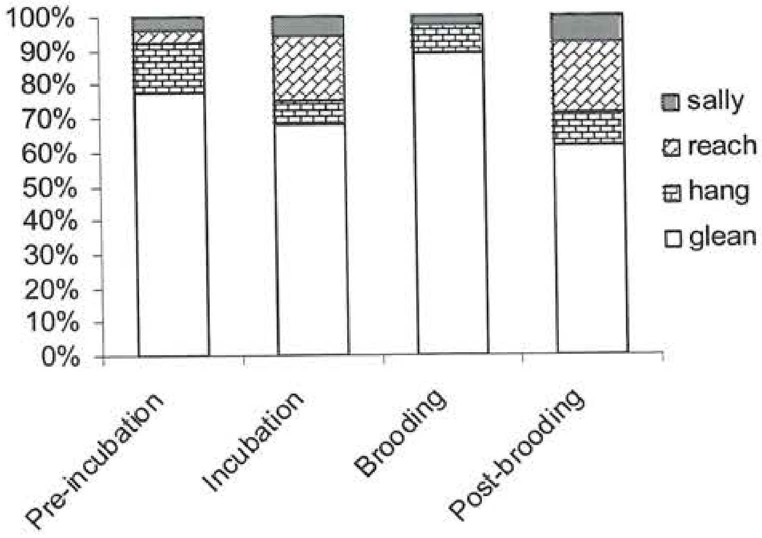


Figure 5.11. Comparison of the foraging methods of Grey-headed Bulbul during different stages of reproduction ($n = 324$).

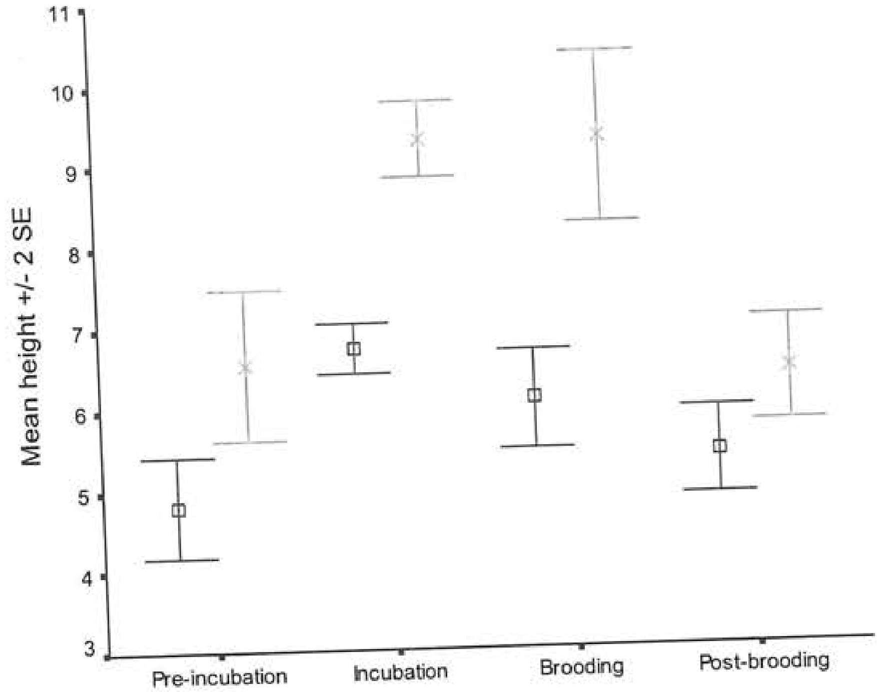


Figure 5.12. Variation in the foraging height (□) and height of the foraging trees (X) during reproductive stages of Grey-headed Bulbul.

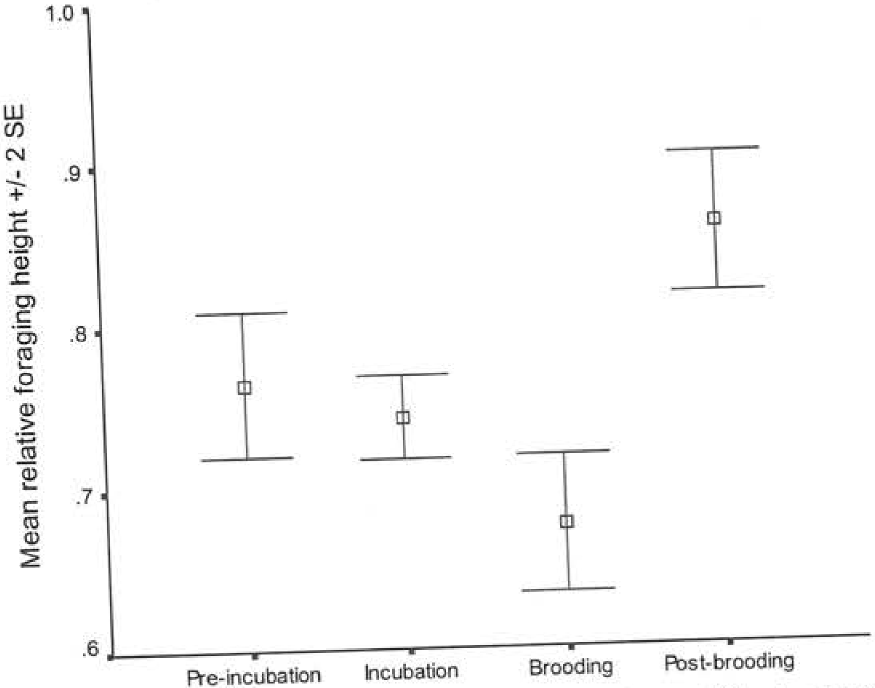


Figure 5.13. Variation in the relative foraging height during reproductive stages of Grey-headed Bulbul.

Table 5.2. Variations in the foraging height, height of the foraging tree and relative foraging height of Grey-headed Bulbul during different stages of reproduction. Variable expressed as mean ± SE and *p* values after Bonferroni correction.

Variable	Pre incubation	Incubation	Brooding	Post brooding	*F*	*p*
Foraging height (m)	4.79±2.29	6.73±2.03	6.08±1.84	5.40±2.14	14.811	0.001
Height of foraging tree (m)	6.55±3.40	9.31±2.99	9.31±3.16	6.40±2.54	22.404	0.001
Relative foraging height	0.76±0.16	0.74±0.17	0.68±0.13	0.86±0.17	11.447	0.001

5.5.6. Foraging in mixed-species flocks

Grey-headed Bulbuls were recorded in 54 mixed-species flocks during the non-breeding seasons. Mixed-hunting flocks observed comprised of 6.46±2.03 species at an average (range: 3–11 species). Mean number of individuals in a flock was 21.94±8.90 birds (range: 8–53 birds). Grey-headed Bulbuls participated in mixed-species flocks led by several species and in some flocks it was difficult to identify the leader species. Altogether 27 species were recorded in the mixed-hunting flocks with Grey-headed Bulbul as a member (Table 5.3).

Foraging niche breadths of ten common species involved in the mixed-hunting flocks were calculated from data on foraging manoeuvre, foraging height, foraging tree height, horizontal position of the foraging bird on the tree and food items (Table 5.4). Species such as the White-bellied Blue Flycatcher, Asian Paradise-Flycatcher, Common Iora, Grey-headed Canary Flycatcher and Yellow-browed Bulbul had larger niche breadths compared to that of Grey-headed Bulbul. Even though Grey-headed Bulbuls are having generalised foraging manoeuvres, food, and use of horizontal positions in the canopy during flock participation; they are specialists in terms of the selection of foraging trees and use of foraging heights.

Although foraging niche overlap with Grey-headed Bulbul was high for some of the foraging attributes, most species exhibited relatively low foraging niche-overlap (Table 5.5). However, most of the species along with Grey-headed Bulbul devoured insects during the mixed-species hunting and, thus showed high overlap (ø > 90) for food. Although species such as Yellow-browed Bulbul and Common Iora showed high overlap in the foraging height with Grey–headed Bulbul, the horizontal positions of foraging in the canopy varied significantly between these species.

5.5.7. Phenology and fruit characteristics of food plants

5.5.7.1. Food plants

Fruits of about 36 species were devoured by Grey-headed Bulbul during the breeding and non-breeding seasons. This consists of many canopy and sub-canopy trees, shrubs, lianas, and epiphytes (Figure 5.14). Of these, 12 species were used frequently and accounted for more than 80% of the total observations. *Symplocos cochinchinensis, Antidesma menasu, Clerodendrum viscosum, Syzygium cumini*, and *Litsea floribunda* were the most preferred fruits during the breeding season, while the fruits of *Maesa indica, Callicarpa tomentosa, Leea indica* and *Lantana camara* were preferred during the non-breeding season.

Table 5.3. Frequency of occurrence and flock characteristics of mixed-species flocks participated by Grey-headed Bulbul in Muthikkulam Reserved Forest.

Sl. No.	Bird species	No. of flocks	Frequency of occurrence	Mean no./flock	SE	Min. no./flock	Max. no./flock
1	Grey-headed Bulbul	54	100.00	1.87	0.39	1	3
2	Indian Scimitar Babbler	27	50.00	4.81	1.39	2	7
3	Grey-headed Canary Flycatcher	24	44.44	10.17	5.80	4	24
4	Yellow-browed Bulbul	19	35.19	2.21	0.92	1	4
5	White-bellied Blue Flycatcher	18	33.33	1.78	0.43	1	2
6	White-bellied Treepie	17	31.48	5.53	1.55	2	9
7	Asian Paradise-Flycatcher	17	31.48	1.94	0.43	1	3
8	Common Iora	14	25.93	1.86	0.36	1	2
9	Dark-fronted Babbler	13	24.07	8.08	2.56	5	12
10	Oriental White-eye	13	24.07	7.00	2.83	3	13
11	Black-lored Tit	12	22.22	1.83	0.58	1	3
12	Black Drongo	12	22.22	1.83	0.39	1	2
13	Scarlet Minivet	11	20.37	2.00	0.00	2	2
14	Greater Racket-tailed Drongo	11	20.37	1.91	0.30	1	2
15	Common Flameback	11	20.37	1.82	0.40	1	2
16	Red-whiskered Bulbul	9	16.67	3.22	3.03	1	11
17	Black Bulbul	8	14.81	5.88	3.04	2	12
18	Brown-cheeked Fulvetta	8	14.81	2.13	0.35	2	3
19	Rufous Treepie	7	12.96	1.71	0.49	1	2
20	White-cheeked Barbet	8	14.81	1.75	0.46	1	2
21	Velvet-fronted Nuthatch	7	12.96	1.86	0.38	1	2
22	Heart-spotted Woodpecker	7	12.96	1.57	0.53	1	2
23	Black-hooded Oriole	6	11.11	1.67	0.52	1	2
24	Asian Fairy Bluebird	5	9.26	2.00	0.00	2	2
25	Small Minivet	5	9.26	1.80	0.45	1	2
26	Black-naped Monarch	4	7.41	1.25	0.50	1	2
27	Crimson-fronted Barbet	2	3.70	1.50	0.71	1	2

Table 5.4. Foraging niche-breadths of the common bird species recorded in the mixed-species flocks with Grey-headed Bulbul.

Species	Niche breadth					
	Manoeuvre	Foraging height	Foraging tree height	Horizontal position	Food	Overall
Grey-headed Bulbul	4.25	2.87	2.91	3.65	1.56	3.05
Indian Scimitar Babbler	2.08	2.11	2.08	1.95	1.42	1.93
Grey-headed Canary Flycatcher	4.38	4.33	4.92	2.40	1.12	3.43
Yellow-browed Bulbul	2.53	4.74	4.61	3.57	1.69	3.43
White-bellied Blue Flycatcher	3.76	4.38	4.59	5.83	1.10	3.93
White-bellied Treepie	2.87	2.17	3.66	3.90	1.41	2.80
Asian Paradise-Flycatcher	4.15	5.38	4.46	3.85	1.06	3.78
Common Iora	4.03	3.74	2.60	5.33	1.53	3.45
Dark-fronted Babbler	2.34	3.06	2.99	3.84	1.05	2.66
Oriental White-eye	1.34	4.26	3.31	4.27	1.87	3.01

Table 5.5. Foraging niche overlap of Grey-headed Bulbul with the common species recorded in the mixed-species flocks.

Species	Niche overlap					
	Manoeuvre	Foraging height	Foraging tree height	Horizontal position	Food	Overall
Indian Scimitar Babbler	0.60	0.04	0.15	0.03	0.99	0.36
Grey-headed Canary Flycatcher	0.88	0.74	0.79	0.02	0.96	0.68
Yellow-browed Bulbul	0.88	0.89	0.78	0.02	0.54	0.62
White-bellied Blue Flycatcher	0.80	0.37	0.49	0.06	0.96	0.54
White-bellied Treepie	0.69	0.02	0.15	0.03	0.97	0.37
Asian Paradise-Flycatcher	0.79	0.49	0.73	0.20	0.96	0.63
Common Iora	0.89	0.86	0.91	0.03	0.99	0.74
Dark-fronted Babbler	0.86	0.52	0.99	0.28	0.96	0.72
Oriental White-eye	0.74	0.74	0.94	0.03	0.32	0.55

5.5.7.2. Phenology of food plants

The highest number of food species with fruits was observed between March and May in 2003 and between February and May in 2004. In both the years, maximum number of food plant species bearing fruits was recorded in April. Minimum fruiting was recorded in September and October during 2003 and 2004 respectively. The fruiting phenology of food plants was inversely correlated with rainfall (r_s = -0.440, n = 24, $p < 0.05$), while positively with the maximum temperature (r_s = 0.509, n = 24, $p < 0.05$). Even though, no significant associations were obtained between the number of rainy days (r_s = -0.371, n = 24, $p > 0.05$)

or minimum temperature and the phenological patterns ($r_s = -0.251$, $n = 24$, $p > 0.05$: Figure 5.15), maximum number of species fruited in months with a few rainy days. Maximum number of individual food plants was in fruit between February and May in all the years (Figure 5.16). Furthermore, fruit abundance of the food plant species was higher between February and May with a peak abundance in April (Figure 5.17).

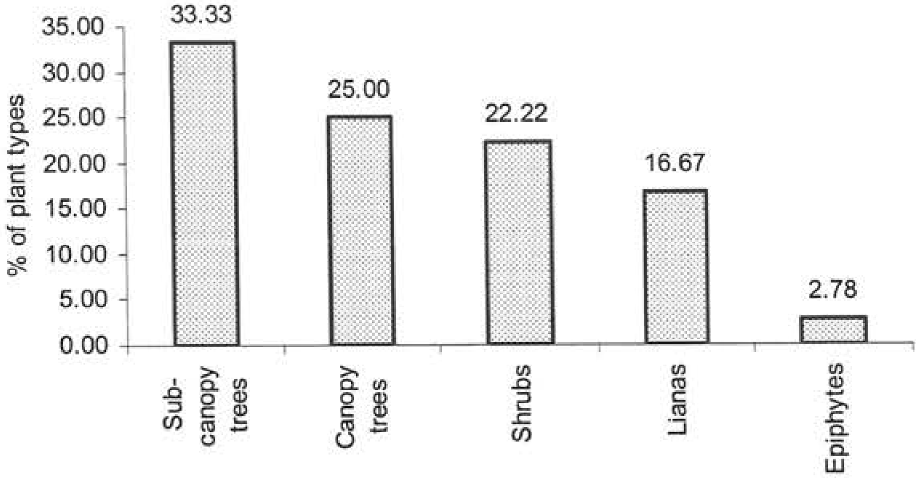


Figure. 5.14. Percentage of food plant types in the diet of Grey-headed Bulbul.

Of the ten major food plants of Grey-headed Bulbul, all the species except three had seasonality in fruiting. Fruiting season and fruit abundance of species such as *Antidesma menasu* (Figure 5.18), *Syzygium cumini* (Figure 5.19), *Syzygium sp* (Figure 5.20), *Viburnum corriatum* (Figure 5.21), *Symplocos cochinchinensis* (Figure 5.22), *Symplocos racemosa* (5.23), and *Litsea floribunda* (Figure 5.24) were during the dry months and coincide with the breeding season of Grey-headed Bulbul. *Maesa indica* (Figure 5.25), *Callicarpa tomentosa* (Figure 5.26), and *Clerodendrum viscosum* (Figure 5.27) were in fruit throughout the year at Silent Valley. However, the fruit abundance was high for first two and lower for *Clerodendrum viscosum* during the non-breeding season. There was not much annual variation in the fruit abundance for all the species monitored, except for *Callicarpa tomentosa* which had fewer fruits during the non-breeding season of 2004.

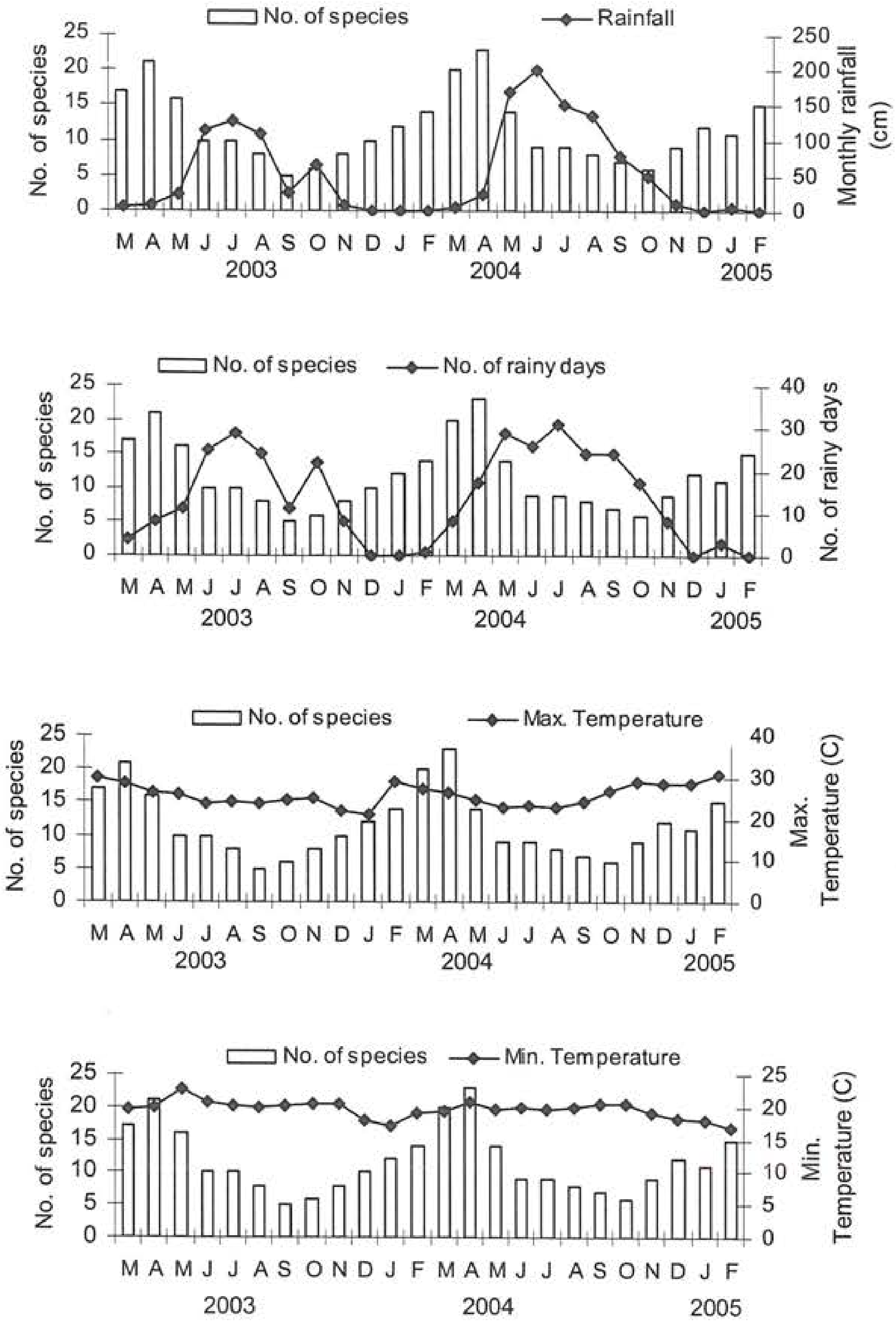


Figure 5.15. The correlation of monthly rainfall, number of rainy days, maximum and minimum temperatures and, fruiting phenology of the food plants of Grey-headed Bulbul in the Silent Valley National Park, Kerala (March 2003-February 2005). Meteorological data source: Forest Department, Walakkad Section, Silent Valley National Park.

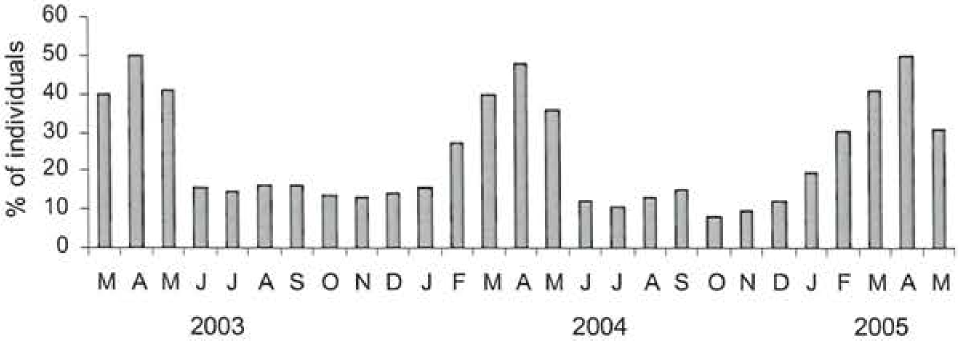


Figure 5.16. Fruiting pattern of the 25 food plants of Grey-headed Bulbul in different months at Silent Valley National Park.

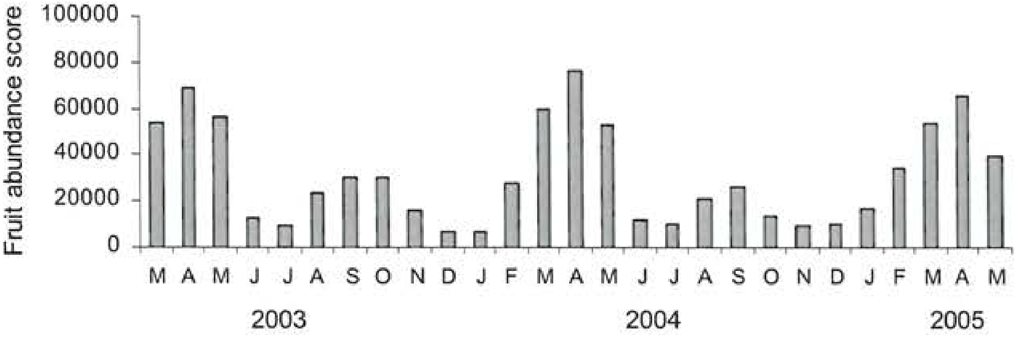


Figure 5.17. Total fruit abundance of the 25 food plants of Grey-headed Bulbul in different months at Silent Valley National Park.

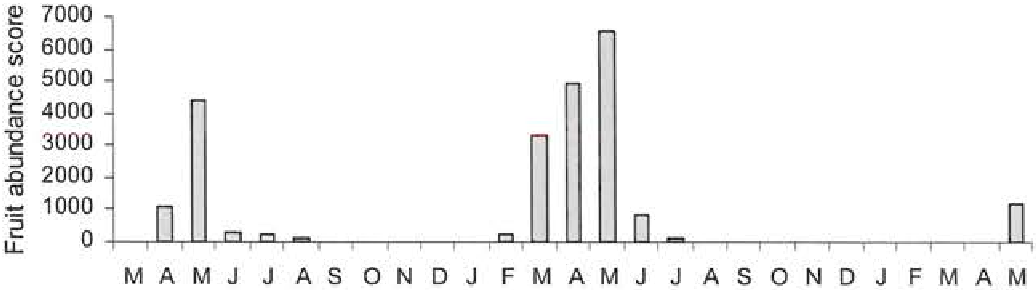


Figure 5.18. Monthly fruit abundance of *Antidesma menasu*, March 2003–May 2005.

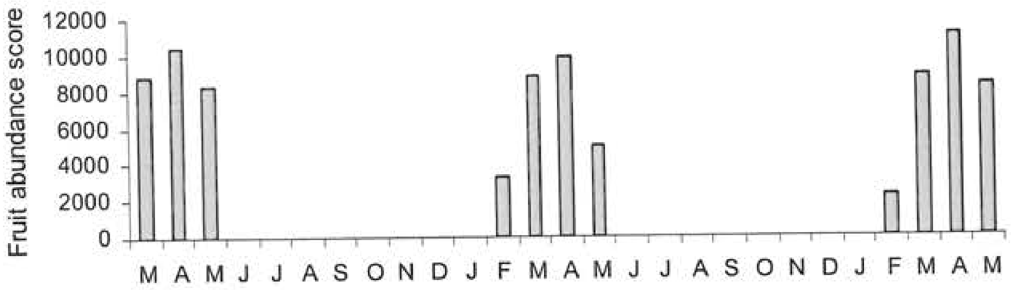


Figure 5.19. Monthly fruit abundance of *Syzygium cumini*, March 2003–May 2005.

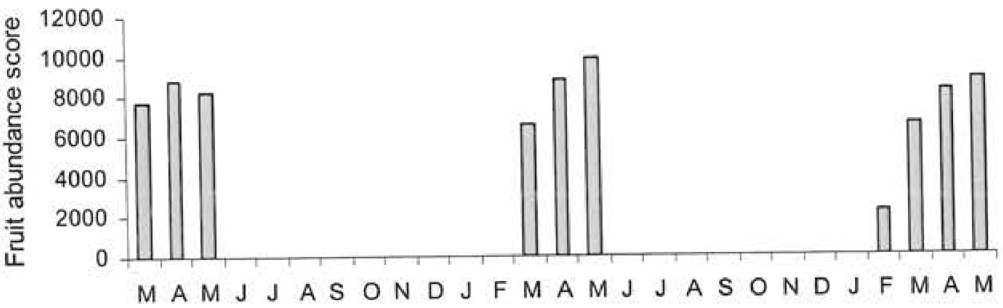


Figure 5.20. Monthly fruit abundance of *Syzygium* sps, March 2003–May 2005.

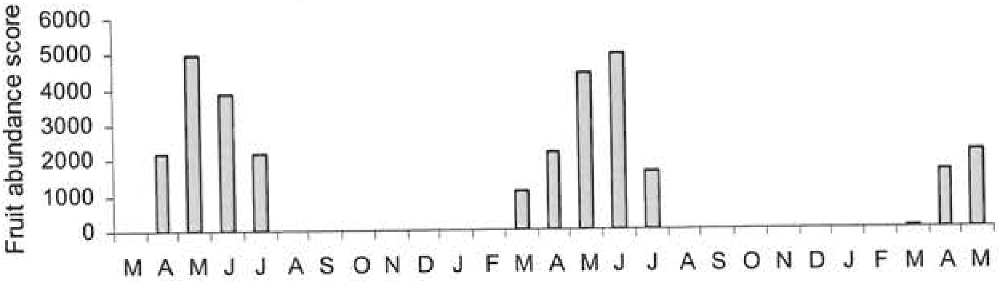


Figure 5.21. Monthly fruit abundance of *Viburnum corriatum*, March 2003–May 2005.

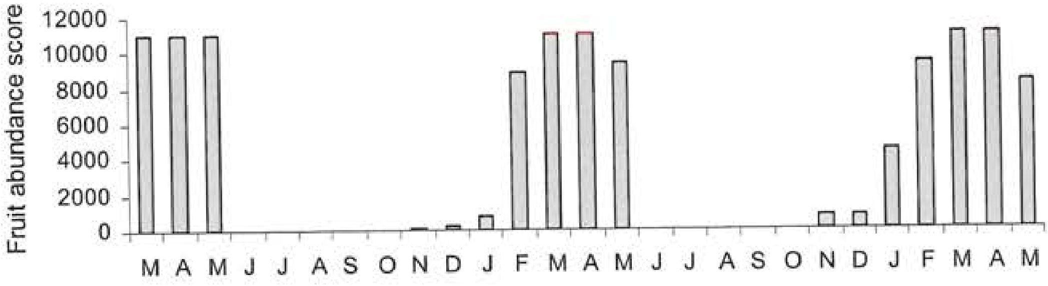


Figure 5.22. Monthly fruit abundance of *Symplocos cochinchinensis*, March 2003–May 2005.

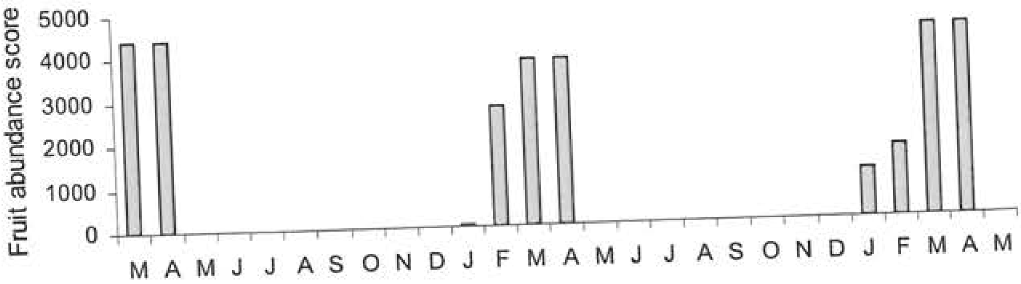


Figure 5.23. Monthly fruit abundance of *Symplocos racemosa*, March 2003–May 2005.

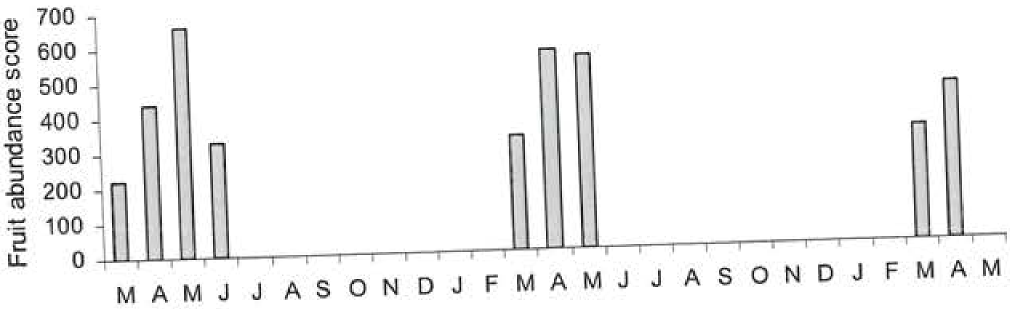


Figure 5.24. Monthly fruit abundance of *Litsea floribunda*, March 2003–May.

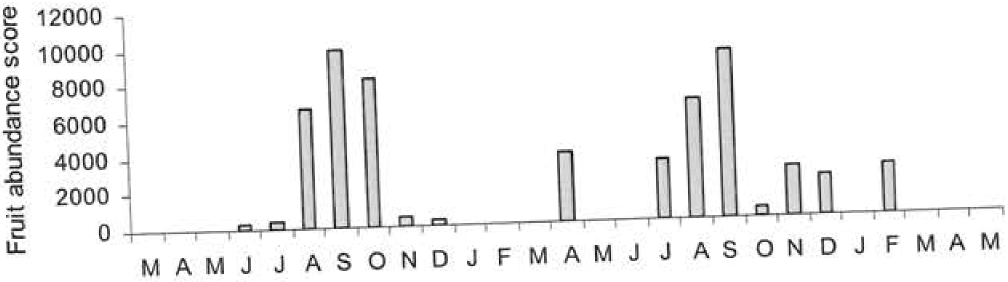


Figure 5.25. Monthly fruit abundance of *Maesa indica*, March 2003–May 2005.

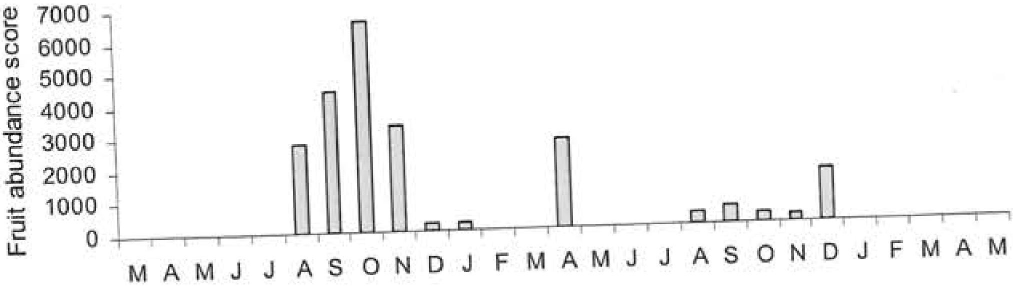


Figure 5.26. Monthly abundance of *Callicarpa tomentosa*, March 2003–May 2005.

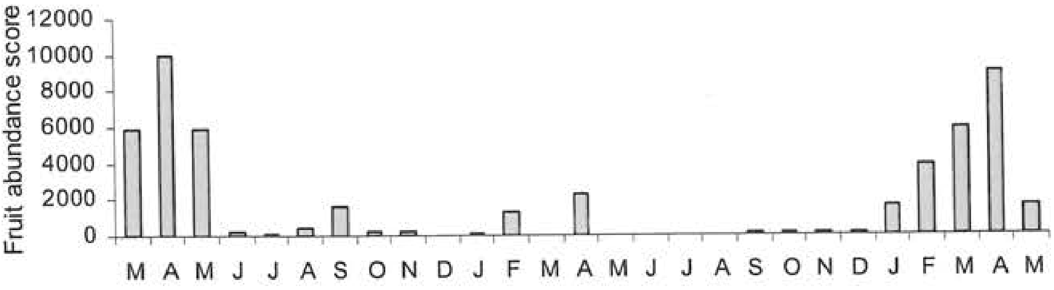


Figure 5.27. Monthly abundance of *Clerodendrum viscosum*, March 2003–May 2005.

5.5.7.3. General phenological pattern and correlates at Silent Valley

Sixty two plant species, including 25 species of food plants, were monitored at Silent Valley National Park. There was a marked seasonal pattern of fruit production. The number of species producing ripe fruits was high between March and June with peak fruiting in April. A second peak was observed in November and December. Although the general fruiting pattern shows a higher peak during the late summer-early south-west monsoon (March–May) and a smaller peak in the early north-west monsoon (November-December), food plant species of Grey-headed showed a single peak which coincides with the first peak of general fruiting and breeding season of the species (Figure 5.28). This clearly indicates a significant variation in the phenological patterns of food plant species and general fruiting pattern ($z = -4.288$, $p < 0.001$).

Although the monthly variations in rainfall ($r_s = 0.875$, $p < 0.001$) and rainy days ($r_s = 0.896$, $p = 0.001$) had significant correlation between the two years, the maximum ($r_s = 0.130$, $p = 0.688$) and minimum temperatures ($r_s = 0.517$, $p = 0.085$; $n = 12$) in different months varied between years. Moreover, there was no significant variation in the number of rainy days and, maximum and minimum temperatures between the years ($z = -1.78, -0.55, -1.22$ respectively, $n = 12$, $p > 0.05$), but the rainfall varied significantly between years ($z = -2.223$, $n = 12$, $p = 0.02$). The monthly or yearly variations in the environmental factors appeared to have not directly affected the fruiting phenology. The number of species in fruit in different months had no correlation with rainfall ($r_s = -0.016$, $p = 0.942$), number of rainy days ($r_s = 0.036$, $p = 0.869$); and maximum ($r_s = 0.248$, $p = 0.242$) and minimum temperatures ($r_s = 0.212$, $p = 0.319$).

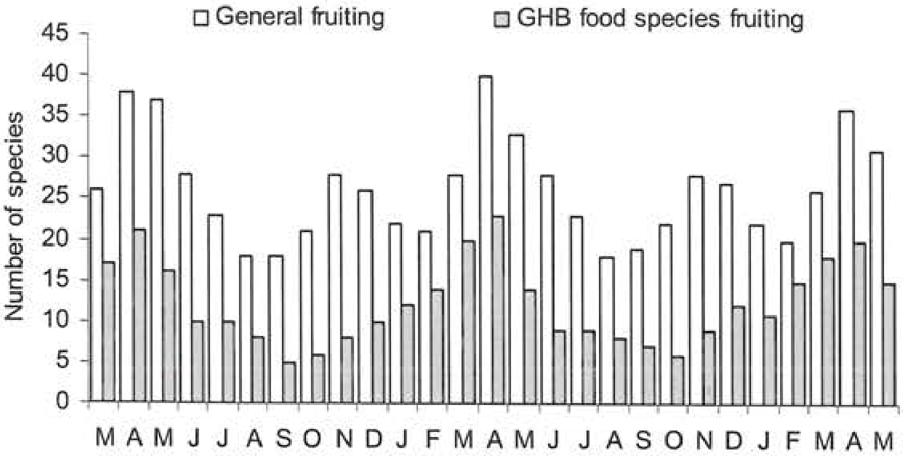


Figure 5.28. A comparison of the general fruiting phenology and Grey-headed Bulbul (GHB) food-species fruiting at the Silent Valley National Park, March 2003-May 2005.

5.5.7.4. Density and distribution of food plants

Nearly 70% (25 species) of all the food plant species of Grey-headed Bulbul was recorded from the belt transects and circular plots. *Antidesma menasu, Clerodendrum viscosum, Litsea spp., Oreocnide integrifolia* and *Syzygium* spp. were the most abundant food plants in the belt transects. Although variations exist within the forest edge and interior transects, the abundance of food plants was significantly higher in the edges except for some forest interior species such as *Syzygium* spp. and *Litsea stocksii* (Table 5.6). Abundance of all the lianas and shrubs used as food plants was significantly higher in the edges. However, the epiphytic *Scurrolla parasitica* was abundant in the interior habitats than in the edges.

All the 15 food tree species monitored for the phenological patterns occurred in the circular plots. However, the abundance of these species varied significantly among the plot types. It was significantly higher in the foraging plots than in the nesting and random plots (Table 5.7). *Symplocos cochinchinensis, Syzygium* spp., *Clerodendrum viscosum* and *Litsea* spp. were the most abundant species in the plots. Similarity in the abundance of a few species among the nest and random plots indicates a random distribution of these species (e.g., *Persea macrantha*). However, most species have a clumped distribution and these sites formed the foraging sites of Grey-headed Bulbul. This pattern is similar for the abundance of shrubs, lianas and epiphytes used as food species by Grey-headed Bulbul (see section 4.5.1).

Table 5.6. Density (total counts) of the food plants of Grey-headed Bulbul in forest edge and interior habitats at Silent Valley National Park.

Species	Edge habitat		Interior habitat	
	Plot 1	Plot 2	Plot 1	plot 2
Trees				
Antidesma menasu	360	295	81	113
Callicarpa tomentosa	13	3	2	0
Clerodendrum viscosum	480	320	27	18
Allophyllus cobe	95	53	0	11
Litsea floribunda	99	40	82	36
Litsea stocksii	22	21	34	28
Olea dioica	131	79	22	19
Oreocnide integrifolia	151	185	32	61
Persea macrantha	57	75	42	30
Symplocos cochinchinensis	0	22	8	4
Symplocos racemosa	2	6	4	18
Syzygium cumini	33	7	63	37
Syzygium sp.	0	1	27	49
Viburnum corriatum	70	5	23	12
Ziziphus rugosa	32	53	6	0
Shrubs, lianas and epiphytes				
Chloranthus brachystachyus	680	1880	261	426
Lantana camara	792	1870	17	0
Leea indica	192	105	96	38
Maesa indica	542	285	12	2
Psychotria nigra	196	245	78	64
Polygonam chinensis	126	115	104	67
Rubia cordifolia	62	70	12	14
Rubus ellipticus	16	3	10	7
Smilax sp.	412	71	57	82
Scurrolla parasitica	66	90	106	156

5.5.7.5. Fruit characteristics

Grey-headed Bulbuls preferred black fruits (37.04%) followed by red (29.63%) and purple fruits (25.93%). They avoided green and yellow fruits and larger dry fruits (Table 5.8). Of the 25 fruit species used by Grey-headed Bulbul, 83.33% were berries followed by drupes (13.33%). Although the availability of different sized fruits varied significantly, bulbuls devoured smaller fleshy fruits averaging 10.06±4.04 mm in size (range: 4 – 20 mm). The seeds of the fruits used averaged 6.21±4.40 mm in size. Most of the fruits were devoid of thick epicarp and thick seed coat, but were watery and contained thick pulp. Selection of the fruits did not appear to be based on the shape and number of seeds, and growth forms. However, it was associated with the fruit type, colour, size, protection, pulp thickness, water content and, seed size (see Table 5.8).

Table 5.7. Density and distribution of major food plant species of Grey-headed Bulbul in the nesting, foraging and random plots (0.04 ha) at Silent Valley National Park.

Species	Nest	Foraging	Random	F	p
Antidesma menasu	1.68±2.43	1.68±2.17	0.77±1.33	3.943	0.021
Callicarpa tomentosa	0.04±0.19	0.14±0.45	0.20±0.50	2.205	0.113
Clerodendrum viscosum	0.57±1.47	7.82±12.79	2.71±4.32	12.548	0.001
Allophyllus cobe	0.17±0.80	0.68±1.39	0.54±1.05	2.874	0.059
Litsea floribunda	2.08±2.78	2.76±2.48	1.06±1.28	9.363	0.001
Litsea stocksii	1.64±2.17	2.82±2.15	1.14±1.28	12.007	0.001
Olea dioica	0.04±0.19	0.68±1.48	0.27±0.61	6.654	0.002
Oreocnide integrifolia	0.81±2.42	3.18±3.78	1.24±1.59	11.531	0.001
Persea macrantha	0.42±1.05	0.38±0.75	0.36±0.76	0.112	0.895
Symplocos cochinchinensis	2.55±4.36	6.32±7.68	0.33±0.88	22.472	0.001
Symplocos racemosa	0.17±0.55	0.66±1.26	0.39±0.82	3.584	0.030
Syzygium cumini	1.38±1.89	5.74±4.69	1.47±1.55	38.289	0.001
Syzygium sp.	5.13±6.43	5.82±5.28	1.76±2.43	13.214	0.001
Viburnum corriatum	0.42±0.91	0.76±1.79	0.29±1.07	2.012	0.137
Ziziphus rugosa	0.04±0.19	0.10±0.71	0.09±0.37	0.244	0.784

5.5.8. Invertebrate abundance

Invertebrates form more than 30% of the food of Grey-headed Bulbul during both breeding and non-breeding seasons. The nestlings were also fed with arthropods. The exact type of invertebrate consumed could not be identified in the field, because of the poor visibility in the evergreen forests. Mean abundance of different invertebrate groups varied significantly between the territories and non-territories in both sweeping ($\chi^2 = 6.793$, $p < 0.01$; Figure 5.29) and beating methods ($\chi^2 = 7.223$, $p < 0.01$; Figure 5.30). Diptera, Hymenoptera, Coleoptera and spiders were the abundant groups in the sweep samples, whereas Hymenoptera, Coleoptera and spiders were abundant in beating samples. This shows that if the abundance of invertebrates in the study area gives an indication, the prey availability could be in the order of Hymenoptera, Diptera, Orthoptera, Coleoptera and spiders.

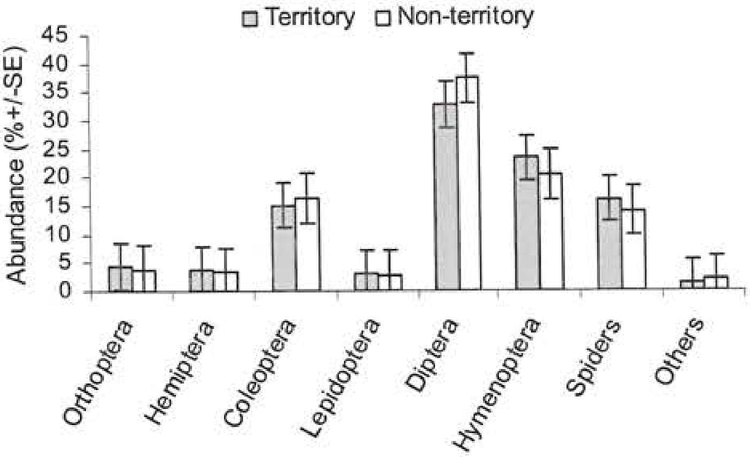


Figure 5.29. Abundance of invertebrates sampled by sweeping in Grey-headed Bulbul territories and non-territories at Silent Valley National Park.

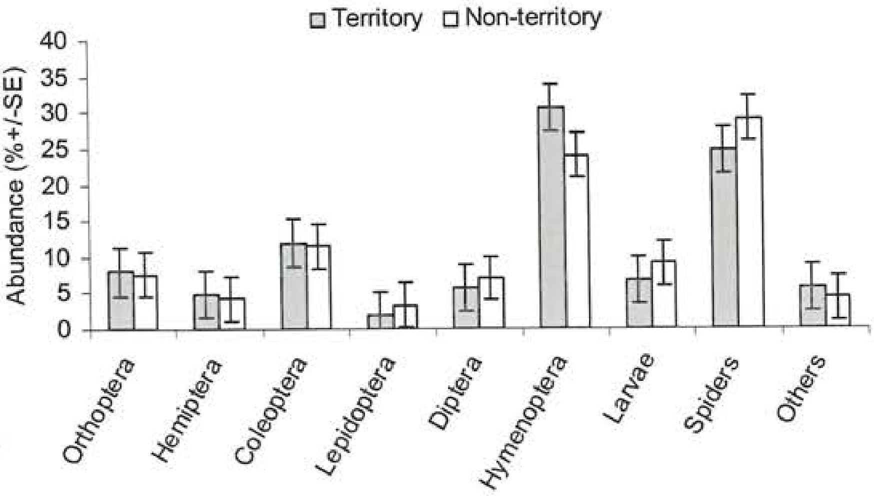


Figure 5.30. Abundance of invertebrates sampled by beating in Grey-headed Bulbul territories and non-territories at Silent Valley National Park.

Table 5.8. Comparison of Grey-headed Bulbul food species and non-food species fruit characteristics.

Parameter		% of species						χ^2	p
Growth form		Canopy trees	Sub-canopy trees	Lianas	Shrubs	Epiphytes			
	Bulbul food	25.00	33.33	16.67	22.22	2.78		6.31	NS
	Others	51.22	21.95	12.20	14.63	0.00			
Fruit type		Berry	Drupe	Others					
	Bulbul food	83.33	13.33	3.33				18.57	<0.001
	Others	31.71	56.10	12.20					
Fruit colour		Black	Red/brown	Yellow	Green	Purple	Others		
	Bulbul food	37.04	29.63	0.00	0.00	25.93	7.40	28.24	<0.001
	Others	7.32	24.39	19.51	39.02	7.32	2.44		
Fruit size		Small	Medium	Large					
	Bulbul food	64.00	32.00	4.00				16.66	<0.01
	Others	19.51	39.02	41.46					
Fruit protection		Fleshy	Dry						
	Bulbul food	96.55	3.45					12.64	<0.001
	Others	56.10	43.90						
Pulp thickness		Thick	Moderate	Thin	Absent				
	Bulbul food	75.86	20.69	0.00	3.45			30.76	<0.001
	Others	19.51	12.20	36.59	31.71				
Water content		Watery	Moderate	Dry					
	Bulbul food	79.31	17.24	3.45				26.44	<0.001
	Others	19.51	34.15	46.34					
Seed size		Small	Medium	Large					
	Bulbul food	52.00	32.00	16.00				9.44	<0.01
	Others	21.95	26.83	51.22					
No. of seeds		Single	Multi-seeded						
	Bulbul food	56.67	43.33					0.02	NS
	Others	58.54	41.46						
Seed protection		Thick	Thin	Absent					
	Bulbul food	37.04	48.15	14.81				1.03	NS
	Others	48.78	41.46	9.76					

5.6. Discussion

5.6.1. Foraging behaviour and variations

Grey-headed Bulbuls use varying foraging maneuvers and food handling techniques. *Gleaning* was the most frequently used method to obtain both fruits and invertebrates. *Gleaning* may be an energetically less expensive foraging technique, since it involves only simple pick of the food items from a nearby substrate without full extension of legs, neck or any acrobatic movements. Other maneuvers such as *reach*, *hang* and *sally* were used only when a fruit or an insect cannot be taken from a perch. The food handling techniques used by Grey-headed Bulbuls were *engulf*, *gulp* and *bite*. The uses of these techniques were based on the food items (see section 5.5.1).

Bulbuls are reported to use a variety of foraging behaviour based on food resources. Ali (1932) reported that Red-vented bulbuls nipped open mature buds of mistleotoes (Loranthaceae) and probed into the exposed corolla tubes for nectar. In Africa, species such as *Criniger barbatus* and *Andropadus tephrolaemus* took all their fruits from a perch while another species *Andropadus latirostris* frequently used its wings, to pick a fruit, with a flutter or while flying (Moremond, 1990). Gleaning of the fruits with flutter or while flying was also recorded in the Black Bulbul in South India (P. Balakrishnan, unpubl. data). Grey-headed Bulbuls used the aerial maneuvers while hunting insects among foliage. The differential strategies used by Grey-headed Bulbul for obtaining fruits and insects indicate their flexibility in the use of foraging techniques based on the type and size of resources.

Fruits were the most preferred food of Grey-headed Bulbul, followed by insects. This is similar to the patterns seen in majority of pycnonotids, which are essentially frugivores augmenting their diet with a certain amount of arthropod food (Vijayan, 1975, 1980; Ali and Ripley, 1987; Corlett, 1998; Bhatt and Kumar, 2001; Fishpool and Tobias, 2005). However, a significant number of species, mostly in Africa and Madagascar, are insectivorous, some with quite specialised niches (Fishpool and Tobias, 2005). Many of the open country species are skilled opportunists and extreme generalists. The Yellow-vented Bulbul, for example, has one of the broadest foraging niches yet measured among non-forest passerines (see Fishpool and Tobias, 2005). There was no significant variation in the food preferences of Grey-headed Bulbul during different seasons.

Although Grey-headed Bulbuls use similar general foraging strategies for the breeding and non-breeding seasons, there are differences in their foraging height and foraging tree use. During the breeding season, birds foraged at an average height of 5 m, while it was below 2 m during the non-breeding season. Similarly the height of the trees selected for foraging was also considerably lower during the non-breeding season (3.81m) compared to that in the breeding season (6.41m; see section 5.5.3). These variations could be mainly because of the differences in the vegetation structure of the breeding and non-breeding habitats. Grey-headed Bulbuls were restricted to the evergreen forests during the breeding season, while they were seen in the lowland evergreen forests, moist deciduous forests and thorny scrubs during the non-breeding season. However, relative foraging heights (in relation to the foraging tree height) remain the same during both the seasons. This indicates that Grey-headed Bulbul has a specialised forging niche, presumably due to competition with congeners and species having similar resource use (see also section 5.5.6).

Annual variations in the foraging heights and heights of the foraging trees were also observed. However, the reason for these variations is not clear since the birds foraged on the same type of food plants within the seasons of all years. Yet, the intra-species variation in the heights of the fruit bearing trees could be a plausible reason for the same.

5.6.2. Behavioural plasticity within the breeding seasons

Birds have to resolve many constraints during incubation and brooding compared to the other stages of life cycle. Changes in foraging behaviour during different nesting stages have received limited attention, but energy expenditure and acquisition during differing stages of breeding are critical elements for understanding life history strategies (Martin 1987, 1992b). Grey-headed Bulbuls showed significant variations in their foraging behaviour during different stages of breeding. These variations could be considered as the responses of birds to the varying time or energy constraints or changing prey availability and distribution (Root, 1967). However, the temporal change in prey availability not seems to have an influence on the foraging behaviour, since the birds at different breeding stages were observed on the same time. During all the stages of breeding, bulbuls foraged away from the nest sites, obviously to reduce the parental activity at the nest sites, which in turn reduce the egg and chick loss by predation (Slagvold, 1982; Martin and Ghalambor, 1999; Conway and Martin, 2000b; Martin et al., 2000a, b; see also Chapter 6). Foraging in areas with high foliage density during the incubation and brooding stages could reduce the predation risks. Although gleaning was the most used foraging maneuver during all the stages, energetically expensive maneuvers such as sallying were higher at the end of the nestling stages. Feeding rates were significantly higher during the incubation and brooding periods, as reported in many previous studies (see, Lovette and Holmes, 1995). The similar and rapid foraging rates during incubation and nestling periods compared to those during egg-laying suggest that incubation also may place time constraints on females, requiring them to forage speedily to be able to return to the nest quickly (Sakai and Noon, 1990; Dobbs and Martin, 1998). The trade off between the thermal needs of the eggs and the energy needs of the adult could be overcome by this increased feeding rate. Therefore, it is clear that the breeding birds use different behavioural mechanisms to cope with their energetic constraints and predation risks.

5.6.3. Mixed-hunting and its significance in non-breeding season

Grey-headed Bulbuls participated in mixed-hunting flocks led by different nucleus species during the non-breeding season. The most numerous participants in mixed-species flocks were permanent residents and most of them being insectivores. The mean size of these flocks was 6.46±2.03 species and 21.94±8.90 individuals. However, the flock size was quite larger in the general mixed-species flocks. Preference of arthropod food by Grey-headed Bulbul during mixed-species flocking resulted high food niche overlap with most of the flock members. Grey-headed Bulbuls exploited the arthropods in the middle or outer canopy areas by using several foraging maneuvers. They seemed to be avoiding the upper canopy where the highly overlapping and generalist species such as Yellow-browed Bulbul and Common Iora were abundant. Although Grey-headed Bulbuls participated the flocks containing Black and Red-whiskered Bulbuls at Muthikkulam, the number of observations were not enough to calculate the niche overlaps. In the lower altitude non-breeding habitats (scrub forests); Grey-headed Bulbuls occur along with other species of bulbuls also.

Many species of insectivorous birds in both the temperate and tropical latitudes are known to gather in mixed-hunting flocks during the non-breeding season (see Jullien and Thiollay, 1998; Chen and Hsieg, 2002). There could be several advantages for a species to be associated with the mixed-hunting flocks. An individual may increase its rate of food capture by associating with other individuals. For example, among the insect-eating birds flocking may be advantageous because prey may be flushed by the activities of other individuals. Another advantage of flocking behaviour is the reduction of predation rates. Moreover, grouping may have an antipredator function by the mobbing responses of several species (see Jullien and Thiollay, 1998; Chen and Hsieg, 2002).

Previous studies have provided evidence for the foraging efficiency and antipredator hypotheses (see Jullien and Thiollay, 1998; Chen and Hsieh, 2002) for mixed-species flocking. My observations clearly suggest that while foraging in mixed-species flocks the species almost exclusively feed on invertebrates. Although they are restricted to certain vertical heights, apparently due to the presence of other species which occupy similar niches, Grey-headed Bulbuls showed much generalised foraging maneuvers and use of horizontal positions in the canopy during flock participation.

Although identification of the nucleus species in many mixed-species flocks was difficult, species such as White-bellied Treepie and Common Flameback appeared as leader species in several flocks, where Grey-headed Bulbul was a participant. The alertness of the nucleus species and its propensity to give alarm calls could be the greatest incentive for attendant species to join the flock and exploit them further (Sullivan, 1984). Several species appeared as sentinel species were also recorded giving alarm calls by the approach of predators. Species such as Common Flameback, Indian Scimitar Babbler, Dark-fronted Babbler, and Brown-cheeked Fulvetta gave alarm calls continuously as the predators approached. In Peru, Munn (1986) reported that the flock members rely mainly on the alarm calls of the sentinel species in the understorey as well as canopy flocks. A similar alertness of both nucleus and sentinel species by the approach of predators were common in the flocks observed. These observations are supporting the foraging efficiency and anti-predator hypotheses and justify the participation of Grey-headed Bulbul during non-breeding season.

5.6.4. Plant phenology and correlates

The general fruiting phenology in the Silent Valley National Park showed two clear peaks. A higher peak during the late summer-early south-west monsoon (March–May) and a smaller one in the early north-west monsoon (November–December). Marked seasonal and annual variations in the abundance of fruits within or between habitats were recorded in the Western

Ghats (Pascal, 1988; Ganesh, 1996; Kannan and James, 1999; Mudappa, 2001; Maheswaran, 2002). The fruiting and flowering phenology in the northern part of the ghats shows a uni-model pattern (Pascal, 1988; Bhat and Murali, 2001; Krishnamani, 2002), whereas the rainforests of Southern Western Ghats exhibit a bi-model fruiting pattern (Pascal, 1988; Mudappa, 2001). Several studies in the tropical forests have shown that the areas with a bimodal pattern of rainfall exhibit a bi-model fruiting pattern (Terborgh, 1986; Mudappa, 2001; see van Schaik et al., 1993 for a review).

Fruiting patterns did not correlate with any of the environmental variables considered (monthly rainfall, rainy days, and maximum and minimum temperature). Although rainfall does not seem to have a direct influence on the phenological patterns, particularly in determining flowering seasonality, water availability sets limits on the time of fruit development and maturation (Herrera, 2002; see also van Schaik et al., 1993). Moreover, this shows that seasonal variations in other abiotic factors such as photoperiod, cloud cover, humidity and solar radiation may also have to be considered when interpreting phenological patterns, and hence production (see van Schaik et al., 1993; Chapman et al., 2005). Selection from dispersers also lead to either clumped or staggered fruiting seasons of locally coexisting plants (Herrera, 2002). Thus, long-term studies are required to uncover these complex interactions, considering the exceptionally high diversity of plants and their fruit dispersers in the wet evergreen forests in the habitats of Grey-headed Bulbul.

The timing of avian reproduction generally coincides with seasonal peaks in food supply (Lack, 1968). The fruiting pattern of 25 food plant species of Grey-headed Bulbul have shown strict seasonality which coincided with the breeding season of the species. However, this seasonality generates a resource bottleneck for this restricted range species. The fruit abundance on the food plants was peaked during the late summer-early south-west monsoon (March–May). The local migration of Grey-headed Bulbul was highly correlated with the lean periods of fruit availability and abundance in the mid-elevation evergreen forests. Seasonal migration and habitat shift are the two most generalised responses of frugivores to fluctuations in fruit availability. The nomadic behaviour of many tropical frugivores is a further behavioural mechanism that allows them to discover and exploit unpredictable patches of locally abundant fruits (Herrera, 2002). During all the three years of study, the birds began migrating to the lower altitudes by the end of May, immediately after the end of breeding. This time was marked by a dip in the fruit abundance as well as the onset of monsoon. The strict seasonal local migratory behaviour may be an adaptive response to cope with the temporal variability of food abundance with the adverse climatic conditions as reported for several avian frugivores and nectarivores (e.g., Wheelwright 1983, Levey, 1988; Blake and Loiselle, 1991; Loiselle and Blake, 1991; van Schaik et al., 1993; Powell and Bjork, 1994; Strong and Johnson, 2001; Tellería and Pérez-Tris, 2003; Tellería et al., 2005; Oliveira et al., 2006). For example, the Australian fruit pigeons regularly undertake migrations across lowland forests in response to the variations in fruit abundance (Crome, 1975). Resplendent Quetzals *Pharomacrus moccino* of the Costa Rican cloud forests move across different habitats tracking the abundance of their highly preferred lauraceous fruits (Wheelwright, 1983). Several species of hornbills wander over quite large areas while closely following broad-scale geographical variations in fruit availability (Kinnaird et al., 1996). The overwintering populations of Blackcap Warblers *Sylvia atricapilla* in Southern Spain are another species which closely track large-scale mosaics of fruit abundance (Rey, 1995). Although erratic local movements in response to fruiting or budding of preferred trees and cold weather cause population fluctuation of Nilgiri Wood Pigeon, another restricted range bird species of the Western Ghats (see BirdLife International, 2001), total disappearance of the species was not recorded from the breeding habitat (Somasundaram, 2006).

Most species of Pycnonotids are sedentary birds. However, species such as Black-and –White Bulbul, Common Bulbul, African Red-eyed Bulbul and Yellow-vented Bulbul are locally nomadic (Fishpool and Tobias, 2005). Altitudinal migration in response to the climatic variations and food availability has been observed in Himalayan Black Bulbul in north India and Black Bulbul in Western Ghats (Ali and Ripley, 1987; Raman, 1999). However, the higher level of frugivory and generalization in the diet allows species such as Yellow-browed Bulbul to be sedentary in the mid-elevation evergreen forests (Fishpool and Tobias, 2005).

Several species of avian frugivores and other vertebrates depend on a number of keystone resources during the scarcity of food and thereby maintain their population. It has been suggested that the year-round fruiting patterns of figs make them key resources in the habitats they occupy because frugivore communities rely on these 'keystone species' (Terborgh, 1986; Lambert and Marshall, 1991) during the fruit resource bottlenecks

(Terborgh, 1986; Lambert and Marshal, 1991; Kinnaird et al., 1996; O'Brien et al., 1998; Korine et al., 2000). In Southern India, figs form a major diet of several avian frugivores (Kannan and James, 1999; Maheswaran, 2002), and higher vertebrates (Krishnamani, 2002; but see Borges, 1993). Although five fig species (*Ficus amplissima, F. exasperate, F. hispida, F. laevis and F. tsjakela*) were recorded from Silent Valley, most of these species occur in low densities and have shown seasonality in fruiting (see Manilal, 1988). Rarity or seasonality of fig species in the rainforests with similar elevations and rainfall was recorded in previous studies in Kakachi (Ganesh, 1996) and Makut (Patel, 1997). Moreover, the role of figs as key resources is likely to differ among forests, and it depends on factors such as diversity of fruiting pattern among fig species, fig tree density and territoriality of frugivores (Patel, 1997; see also Borges, 1993).

The local migratory behaviour of Grey-headed Bulbul has particular conservation concern. The breeding of the species is almost entirely restricted to the undisturbed mid-elevation rainforests, while during the non-breeding season it confines to the lower elevation forests including the scrublands. Thus, the species requires two distinct habitats for its survival. However, most of the existing protected areas in the Southern Western Ghats lie in the mid or higher elevations, and the habitats on the lower elevations remain un-protected. Therefore, lower areas adjoining the existing National Parks and Wildlife Sanctuaries need to be protected for the effective conservation of altitudinal migrant bird species and other fauna of the low elevations (see also Chapter, 3 and 6).

5.6.5. Diet choice and availability

Apart from the abundance, diet choice is known to be influenced by a number of structural, visual and nutritional traits of the food resources, which interact with morphological capabilities of birds to determine the bounds of their diet (Herrera, 1987, 2002; Hutto, 1990). The taxonomic heterogeneity of the tropical plant communities leads to substantial interspecific variations in the fruit characteristics. The structural traits of the vertebrate-dispersed fruits that occur in the Western Ghats display high variability (Balasubramanian and Maheswaran, 2003; see also Mudappa, 2001). Majority of the fleshy fruits selected by Grey-headed Bulbuls were berries and drupes. Berries are the predominant fruits followed by drupes available for the frugivores in the Western Ghats (Manilal, 1988; Ganesh 1996;

Balasubramanian and Maheswaran, 2003). High abundance of the fleshy fruits may be associated with the availability and abundance of large number of seed dispersers.

Size is an important attribute of fruits, because it sets limits to ingestion by relatively small sized dispersers that swallow them whole, like the birds (Wheelwright, 1985b; Herrera, 2002). This is particularly true for species that swallow fruits whole; obviously, birds that can bite off pieces of fruits are less limited by fruit size (Blake et al., 1990). The interspecific differences in the fruit size of bird-dispersed plants explain differences in the species composition of dispersers and, the mean size of ingested fruits tends to be correlated with gape width among frugivorous birds (Wheelwright, 1985b). Fruit choice, the handling mode and the foraging efficiency of frugivorous birds is strongly influenced by fruit size (see Herrera, 1987). The size-based fruit selection of frugivores results in differential seed-dispersal success; and thus acts as a proximate mechanism for natural selection on fruit size (Wheelwright, 1983; see also Kitamura et al., 2002). Grey-headed Bulbuls preferred small sized fruits. This may be related to the morphological constraints of the species, since many previous studies have shown the correlation of gape width and fruit selection by birds (see Wheelwright, 1985b). Moreover majority of the fruits available for avian frugivores in the South Indian forests fall below 20 mm in size (Balasubramanian and Maheswaran, 2003).

Frugivorous birds generally discriminate fruits on the basis of colour and often exhibit consistent colour preferences. Grey-headed Bulbuls preferred black fruits followed by red fruits. Little is known of the fruit colour preferences of bulbuls. However, the available evidence suggests that the preference may be based on the availability. For example, Vijayan (1975) reported that Red-vented and White-browed Bulbuls, at Point Calimere in South India, preferred red and yellow fruits and it is correlated with the abundance of red fruits (see Balasubramanian, 1990). However, black fruits predominate among bird-dispersed plants in both tropical and subtropical regions (Herrera, 2002; Chen et al., 2004), whereas they are more likely to be red in European bird-dispersed fruits (Willson et al., 1990, Herrera, 2002). In frugivore diets in those neo-tropical forests examined, species with black fruits out number those with red and, in Panama, South Africa, Costa Rica and Peru, the proportion of species with fruits of one or both of these colours is some 62–66%. However, in French Guiana, birds prefer purple-black fruits (see reviews in Chen et al., 2004; Herrera, 2002). The colour preference of frugivores was similar in the South Indian forests also. For example, in a compilation of the 219 bird dispersed fruits, black and red fruits accounted for 70% of species (Balasubramanian and Maheswaran, 2003). Black and red fruits accounted for 86% of all the species used by Nilgiri Wood Pigeon (Somasundaram, 2006). However, of the 27 fruit species used by Malabar Grey-hornbill at Mudumalai Wildlife Sanctuary, purple and yellow fruits together accounted for 81% of the species (Maheswaran, 2002).

The fruit pulp, which is characterised by high water and carbohydrate content, and low protein and lipid content is the reward offered by the plants to dispersers (see Herrera, 1987). The interspecific variability in the nutrient content is a distinctive feature of the pulp as a food resource to birds (see Herrera, 2002). The nutritional aspects of the fruit species used by Grey-headed Bulbuls were not explored in this study. However, the relationships between the colour preferences and the nutritional aspects were unknown (Izhaki, 1992; see also Herrera, 1987; Whelan and Willson, 1994). Moreover, the frugivores generally may not discriminate fruits on the basis of nutritional quality (Whelan and Willson, 1994). Furthermore, in most part of the tropics, the colour preferences are correlated with the availability. Grey-headed Bulbuls used both single and multi-seeded fruits without any discrimination. Moreover, the fruit selection did not appear to be affected by the seed protection. Yet, they have shown a preference to fruits with small or medium sized seeds. Although several larger species with wider gape width such as hornbills and pigeons were known to ingest and disperse seeds of larger fruits (e.g., *Myristica*; see Kannan and James, 1999), smaller birds are constraint by relatively small gapes to handle these fruits. Nonetheless, the birds were found obtaining the pulp of a few larger fleshy fruits (e.g., *Persea macrantha, Litsea stocksii*) by biting maneuver.

Even though Grey-headed Bulbul's preferences for the invertebrate food remain unknown, if the availability forms a measure of the potential prey items, this could be in the order of Diptera, Orthoptera, Coleoptera and spiders. Although Hymenoptera was the dominant group in the sweeping and beating samples, high estimate was due to the abundance of several ant species, which may not form a prey for Grey-headed Bulbul. The pattern of insect abundance obtained during this study is similar to that reported by Mathew et al. (1998) where dominant insect orders with respect to number of individuals were Diptera and Lepidoptera followed by Coleoptera and Hymenoptera.

5.6.6. Patchiness of food resources and distribution of Grey-headed Bulbul

Understanding the distribution patterns and scale of patchiness of key resources, and the spatial and temporal stability of these patterns can provide valuable information on species' ecological requirements. In most habitats, plant communities determine the physical structure of the environment, and therefore, have a considerable influence on the distributions and interactions of animal species (see reviews in McCoy and Bell, 1991). Patchiness and distribution of food resources are known to affect the habitat use and distribution pattern of birds (e.g., Cody, 1985; Kotliar and Wiens, 1990).

The wet evergreen forests of Silent Valley National Park are well known for its diverse flora (Manilal, 1988; Vajravelu, 1990). Many of the plants in this area produce fleshy fruit and are dispersed by several frugivorous species. Despite the abundance of fruit bearing plants, Grey-headed Bulbul as a specialist in fruit selection, appears to face several constraints in finding its food. The temporal patterns of fruit abundance had a significant influence on the local migratory behaviour of Grey-headed Bulbul (see section 5.5.7.3; and Chapter 3). Again, the spatial distribution of food plants seems to have an influence in the patchy distribution of this bulbul. Most of the tropical plant species (particularly trees) are randomly distributed on large landscape scales, while they appear clumped locally (Richards, 1996). Most food plant species of Grey-headed Bulbul had a more clumped distribution in edges of the localized patches than in the continuous large evergreen patches. This non-random distribution pattern of the food plants was further evident from the comparisons of the density of food plants in the circular plots centered on the nesting, foraging and random plots. The foraging sites, located in the edges of the patches had higher densities of the food plants. On the other hand, the nesting and the random sites had fewer food plants since they are located mostly in the interior forest patches. A similar distribution pattern of food plant species of brown palm civet was reported by Mudappa (2001) at Kalakad-Mundanthurai Tiger Reserve in the Southern Western Ghats.

Although the abundance of invertebrates in an environment does not necessarily correspond to the amount of food available for a foraging bird, comparison of the general invertebrate availability in the territories and non-territories of Grey-headed Bulbul revealed a non-random distribution pattern. If the general invertebrate availability is considered as a measure of the potential prey items, Grey-headed Bulbul territories had higher invertebrate availability than the non-territories. Thus, the patchy distribution of Grey-headed Bulbul could be explained by the clumped distribution of food resources together with the availability of suitable nesting microhabitats within the evergreen forests (see also Chapters 4 and 6).

5.7. Summary

Information of the relationship between foraging ecology and several ecological patterns, including timing of annual cycles, territoriality, habitat selection, reproductive performance, population size, geographic distribution and migration are essential for the conservation and management of rare species. The present study examined the foraging behaviour and their variation in different circumstances, spatial and temporal availability and abundance of food resources of Grey-headed Bulbul at Silent Valley National Park and Muthikkulam Reserved Forest.

- The foraging maneuvers and food handling techniques used by Grey-headed Bulbul was based on the type of food resources.
- They used energetically less expensive methods (glean and gulp) for food procurements and handling.
- Foraging behaviour and tree use varied during different stages of breeding to cope with their energy requirements and predation risks.
- Grey-headed Bulbuls actively participated in the mixed-hunting flocks during the non-breeding season.
- Predation risk and competition by the congeneric and co-occuring species were more during the non-breeding season, when they migrate to lower elevation forests.
- General fruiting phenology at Silent Valley shows a bimodal pattern which is typical to the evergreen forests of Southern Western Ghats.
- However, the fruiting pattern of 25 major fruit plants of bulbul has shown a uni-model pattern which coincides with the breeding season of the species.
- The lack of keystone species and strict seasonality of preferred fruit plants create a resource bottleneck to Grey-headed Bulbul.

- The number of fruits available for Grey-headed Bulbul is constrained by their specialization in fruit choice in terms of size, colour, seed size and other physical traits.
- Grey-headed Bulbul preferred black fruits and avoided green and yellow and, larger dry fruits.
- The patchy distribution of Grey-headed Bulbul was associated with the clumped distribution of food resources within the evergreen habitats.
- They migrate to the lower elevations during the lean period of food and adverse climatic conditions in the mid-elevation breeding habitats.
- The local migratory behaviour of Grey-headed Bulbul has particular conservation concern because most of the existing protected areas in the Southern Western Ghats are in the mid or higher elevations.
- The lower elevation forests adjoining the existing National Parks and Wildlife Sanctuaries need to be protected for the effective conservation of Grey-headed Bulbul and other altitudinal migrant bird species and, other fauna of the low elevations.

Symplocos cochinchinesis

Syzygium cumini

Antidesma menasu

Clerodendrum viscosum

Major fruits devoured by Grey-headed Bulbul during breeding season

Maesa indica

Leea indica

Callicarpa tomentosa

Lantana camara

Major fruits devoured by Grey-headed Bulbul during non-breeding season.

Chapter 6

Breeding biology of Grey-headed Bulbul

6.1. Introduction

Challenges common to all birds are surviving and growing to maturity, reproducing and living from one breeding season to the next. The balance between these energetically conflicting demands is referred to as 'life-history' (Bennett and Owens, 2002). Understanding the population limitations and life-history traits and, their evolution are crucial factors in developing conservation and management of any rare avifauna (Newton, 1998; BirdLife International, 2000). Nevertheless, there have been very few studies of the life-history strategies of the rare tropical rainforest birds of the Western Ghats (Khan, 1977; Islam, 1985; Kannan, 1994; Maheswaran, 2002; Ahmed, 2005; Somasundaram, 2006; Vinod, 2007).

The temporal organization of life-history events depends on the seasonal changes in an environment (Wikelski et al., 2000). Both year-round and seasonal breeding patterns are common among tropical birds (Moreau, 1950; Skutch, 1950; Ward, 1969; Ali and Ripley, 1987; Pramod and Yom-tov, 1999; see Wikelski et al., 2000 for a review). Many bulbuls breed at varying times of the year. Open-country and low altitude species breed in all months but most of the high and middle altitude and rainforest bulbuls are seasonal breeders (Ali and Ripley, 1987; Fishpool and Tobias, 2005).

Although seasonal reproduction occurs in many tropical organisms, it remains largely unclear how the seasonal timing is achieved. The degree of environmental predictability has important consequences for the reproductive physiology of organisms (Wikelski et al., 2000). Environmental variables such as temperature and rainfall have been reported to affect the timing of breeding in birds. Increase in temperature may directly promote egg formation and laying, thus favouring the occurrence of hatching close to the peak of food availability (Lack, 1968; McCleery and Perrins, 1998). Rainfall directly or indirectly affects the breeding phenology by controlling the food availability and ambient temperature. Since, the productivity of most plants and invertebrates depends on rainfall, early rains may be a prerequisite for successful breeding. Food availability at the time when offspring have to be fed constitutes a significant factor for reproduction in birds (Lack, 1968; Perrins, 1970). Both temperate and tropical birds are known to fine-tune breeding to local food abundances (Vijayan, 1975; Ali and Ripley, 1987; Scheuerlein and Gwinner, 2002; Vijayan and Balakrishnan, 2005).

Unlike mammals, reptiles, and fish containing both oviparous and viviparous species, all birds lay eggs and deposit them in purpose-built sites called nests. An avian nest is a special construction forming a receptacle in which eggs and young develop (Soler et al., 1998). A nest acts as an insulator from the adverse environmental conditions, keeping the eggs or nestlings warm and protect from other physical factors (Kern, 1984; Kern and Riper, 1984; Collias and Collias, 1984; Soler et al., 1998) and, protect the offspring as well as the parents from being discovered and preyed (Campbell and Lack, 1985; Hansell, 2000). Nest building behaviour is a feature of the biology of birds since their origin and it has a key role in shaping the relationship in bird reproduction between parents and offspring (Hansell, 2000). The structural and functional architecture of the nest is a crucial factor affecting the nesting success and survival of the species. Nests have been described for a number of species (Ali and Ripley, 1987), but detailed descriptions of nest site characteristics and nest architecture are wanting for most of the restricted range species of the Western Ghats.

Altitudinal and geographical variations in the placement and architecture of nests were recorded for many bird species. These variations may be phenotypic expressions of genetic differences in the behaviour of individual birds or populations (Kern and van Riper, 1984), often believed to be adaptive to varying vegetation structure, in minimizing adverse climatic effects or reducing predation (Collias, 1964; Schaefer, 1976; Hansell, 2000). Although adaptive radiation among species in their nests between a geographical or altitudinal paradigm has been discussed (e.g., Schaefer, 1976; Kern and van Riper, 1984), the reasons for such variations within the same elevational and geographic limits are not explored. Within-species variation in nest design may be an adaptation to the varying vegetation structure, nest material availability, predation pressure, clutch size or a result of differences in experience (Slagsvold, 1989; Kulesza, 1990; Hansell, 2000). Several studies provide direct or indirect evidence of a relationship between clutch size and nest design (see Hansell, 2000).

Nest placement and design of arboreal and woven nests have frequently been suggested to reflect the resolution of trade-offs between a range of selective pressures (Møller, 1987, 1990; Götmark et al., 1995). Adaptations of nest construction, that reduce the rate of heat loss from eggs and young, and that reduce thermoregulatory costs of incubating females are likely to influence reproductive performance in many species (Williams, 1993). Nest orientation preference or avoidance must be linked to environmental cues that allow discrimination among directions. These cues may include large scale factors such as the earth's magnetic field and solar azimuth, local scale factors such as local water bodies, topographic features and habitat structure (Hildén, 1965) or nest-site scale factors such as tree structure, floristics or microclimate (Bergin, 1991).

It has long been recognised that tropical birds differ fundamentally from temperate zone birds in their life-histories (Stutchbury and Morton, 2001). Tropical birds have high nest predation, high adult survival and small clutch sizes (Lack, 1947-48, 1968; Ricklefs, 1969). More recent studies, however, have questioned the validity of these differences in tropical birds (Martin, 1996b; Geffen and Yom-tov, 2000). An important challenge in the study of life-histories is unraveling the factors that influence the enormous interspecific variation in life-history traits (Roff, 1992; Stearns, 1992). Many factors have been suggested to influence the life-history traits. The early investigators focused on clutch-size variation and described not only broad patterns of worldwide variation in clutch sizes, but also outlined several hypotheses to explain that variation, including food limitation, nest predation, and adult mortality (Lack, 1947-48; Skutch, 1949; see Godfray et al., 1991 for a review). However, all these hypotheses were based on studies from the north-temperate systems and thus cannot by themselves explain broad geographical life-history variations (see Martin, 2004 for a review). Several studies suggested that the clutch size and number of broods are correlated with body weight (Bennett and Owens, 2002), and the degree of nest predation which itself is influenced by nest type and nest location (Lack, 1968; Ricklefs, 1969; Slagvold, 1982; Møller, 1991; Martin and Li, 1992; Martin, 1995, 1996b; Owens and Bennett, 1995; Martin et al., 2000a, b; Doligez et al., 2003). Species that suffer higher nest predation tend to have smaller clutches, more broods and higher annual fecundity than species with low nest predation (Martin, 1995). However, many of these correlates remain untested for the birds of the Indian Subcontinent due to lack of information on these traits. In the present study, I attempt to document clutch size variation in the Grey-headed Bulbul and the factors controlling the evolution of clutch size variation.

Understanding nest survival is critical for bird conservation since the low survival rates have been noted in many globally declining species. The chief determinant of reproductive success in birds is the rate of nest failure (Ricklefs, 1969; Møller, 1991). Nest predation and brood parasitism are often primary constraints on reproductive success in passerine birds (Lack, 1954; Ricklefs, 1969; Martin and Roper, 1988; Martin, 1992b), and can thereby exert strong selection on phenotypic traits (Martin, 1996b; Martin and Ghalambor, 1999; Robert and Sorci, 1999). Thus predation pressure has undoubtedly influenced the evolution of avian morphology, physiology and behaviour (Martin et al., 2000b). The rate of nest depredation likely varies with nest age and date, but information on these aspects is very scanty for the restricted range bird species of the Western Ghats.

Many aspects of nesting behaviour and life-history strategies [e.g., parental defense (Cresswell, 1997), nest density (Martin, 1988b), and clutch size (Skutch, 1949; Martin et al., 2000a)] of birds appear to be adaptations to minimize predation risks (Filliater et al., 1994) and, thereby maximize their fitness by increasing their ability to survive and reproduce. The abundance and diversity of predators could affect rates of depredation (Chalfoun et al., 2002; Estrada et al., 2002); some predators actively hunt for nests using visual or olfactory cues (Martin, 1993a), whereas others incidentally stumble upon nests when foraging for other food items (Schmidt et al., 2001). Two main types of anti-predation strategies are favoured. First, if prey cannot defend itself against predators, selection favours predator avoidance adaptations. Second, if prey can reduce the impact of predators through communal antipredator attacks or through dilution of predators' effects, selection favours higher local prey density and hence, colonial pattern of distribution (Picman, 1988). The height and density of vegetation are two major determinants of predation risk. According to the "nest height" hypothesis nests placed high or low relative to the frequency distribution of nest heights in the population will be more successful than those close to the mean nest height (Li and Martin, 1991). The "nest concealment" hypothesis predicts that nests that are concealed regardless of the particular plant structure will be more successful than those that are not so concealed because of reduced auditory, olfactory, and visual cues to potential predators (Martin, 1993a). Many birds hide their nests or build them in inaccessible sites (Collias and

Collias, 1984). The predictions of the 'needle in a haystack' hypothesis (Filliater et al. 1994) or 'potential prey site' hypothesis (Martin and Roper, 1988), and the 'rare site hypothesis' (Filliater et al., 1994) suggest that the nest plant selection is also an important factor determining the fate the nest (Martin, 1988c; Hansell, 2000). The nest success in different species varies with the human disturbance or presence. The exposure of nest to predation may also influence the amount of effort that is devoted to nest building. If the probability of predation is high, selection may favour a small nest to minimize the problem of attracting the attention of nest predators. The duration of incubation and nestling periods are also positively related to the risk of nest predation (Bosque and Bosque, 1995; Martin and Ghalambor, 1999; Conway and Martin, 2000a, 2000b; Ghalambor and Martin, 2000).

Trivers (1972) introduced the term 'parental investment', which he defined as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." In birds, bi-parental care is the most common pattern (Lack, 1968; Krebs and Davis, 1993), although uni-parental care by either the male or female exists (Clutton-Brock, 1991; Wesolowski, 1994). Theory predicts that differences in parental care patterns among species arise from interspecific differences in the benefits for offspring survival versus parental costs, such as reduced parental survival, fecundity and mating opportunities (e.g., Clutton-Brock, 1991). Thus, an understanding of the parental care strategies in altricial species' provides important insights to the constraints and costs related to these traits.

Avian eggs, to hatch successfully, must be maintained at a temperature that allows embryonic development. The optimal temperature range for development is thought to be about 36–38 °C (Drent, 1975) and, as there are few environments in which ambient temperature remains constantly at this level, incubation by the parents is required to prevent embryos from chilling or overheating. In species where only one parent incubates, that parent must divide its time between the mutually exclusive activities of incubating to control clutch temperature and foraging to meet its own energy requirements. Furthermore, in species with uniparental incubation, absences from the nest during foraging bouts can negatively affect egg temperatures and subsequent embryo development, as well as the ability to protect eggs against predators (Williams, 1996; Conway and Martin, 2000a, 2000b). Incubation feeding is common in many species to overcome this constraint, but it increases the male parental visits at the nests. Thus, parents incubating eggs must resolve a number of conflicting demands in response to changing environmental conditions (reviewed in Williams, 1996). Consequently, factors that influence reproductive effort during incubation can affect the evolution of other life-history traits (e.g., clutch size, number of broods, and probability of renesting). The frequency with which females alternate incubation with other activities varies greatly among passerines. These variations are resulted by a combination of several proximate and ultimate ecological factors such as variation in body mass, frequency of mate feeding, food availability/foraging success, ambient temperature during incubation, and/or nest predation (Martin and Ghalambor, 1999; Conway and Martin, 2000a, 2000b; Ghalambor and Martin, 2000).

A large number of studies examined the reproductive costs associated with the nestling period (e.g., Lack, 1954, 1968; Williams, 1996). The rate at which parents deliver food to dependent offspring is critical for understanding a wide range of questions about behaviour, ecology, and life-history strategies (Lack, 1954; Davies et al., 1992). Therefore, an understanding of the parental care strategies from the nest building through the nestling stages is an important part in the avian life-history studies.

The current `extinction crisis' is largely a result of human disturbance of natural environments (see Newton, 1998; BirdLife International, 2001, 2004a). Thus, the possibility of extinction risk would be randomly distributed among bird species -any species that is unfortunate enough to get in the way of human disturbance will be threatened by extinction, irrespective of the peculiarities of its biology (Bennett and Owens, 1997). However, in a comparative analysis of threatened species, they found that taxa differ in the extent to which they are prone to extinction and these differences are apparently influenced by the biology of the species concerned (Bennett and Owens, 1997). For example, increases in extinction risk are associated with decreases in fecundity as low-fecundity populations take longer to recover when they are reduced to a small size than do high-fecundity populations (Pimm et al., 1988). The low-fecundity populations are more likely to be wiped out by catastrophic or stochastic events and are simply unable to recover if an external force, such as human disturbance or catastrophic change, unbalances the natural system (Bennett and Owens, 1997). These views emphasize the need for information on a broader range of life-history and ecological variables (see Bennett and Owens, 1997, 2002; Owens and Bennett, 2000;

BirdLife International, 2001, 2004a) from the natural and disturbed habitats for the effective management and conservation of rare avifauna.

6.2. Objectives

The aim of the present study was to document the breeding biology of Grey-headed Bulbul. The specific objectives were to:

1). examine the factors influencing breeding seasonality,

2). document the structural and functional architecture of the nest, and identify correlates of within-species variation in the nest architecture,

3). explore the breeding phenology and factors influencing the nest success and,

4). document the patterns of parental care.

6.3. Methods

6.3.1. Study area

The breeding biology of Grey-headed Bulbul was studied at Silent Valley National Park and the surrounding reserved forests (Karuvarakundu Reserved Forest in the Kalikavu range of Nilambur South Forest Division) of Kerala. Detailed descriptions of the study sites are given in chapter 2.

6.3.2. Field methods and data analyses

6.3.2.1. Breeding population

The breeding population of Grey-headed Bulbul was estimated by different methods. Monthly counts of the species were conducted in 50 line transects of one km each (Bibby, 1998, 2000) in the Silent Valley National Park. Results of these surveys are presented in Chapter 3. Apart from the transect counts, a total mapping method (Verner, 1985; Bibby, 1998, 2000) was employed during the breeding season. Results of these methods were combined to determine the total number of breeding pairs. The breeding seasonality was determined from the nesting records of each month during three years (2003, 2004 and 2005). The influence of rainfall, temperature, and availability and abundance of fruits (see section 5.4.4. for detailed methodology) on the breeding season was tested using Spearman rank correlation (Siegel and Castellan, 1988).

The area used by each breeding pair was mapped during the incubation and nestling periods to find out the approximate territory size. Maximum distance of each individual from the nest was recorded and it was used to calculate the average home range used by the species (see Bibby et al., 2000; Marshall and Cooper, 2004). The mapping of the territories was done in the morning hours; a time period coincides with the maximum activity of the species. Individual birds could not be colour marked because of the lack of requisite permits and thus precise estimates of territory size were not possible. The territories were proved to be non-overlapping due to the sparse distribution of the species and majority of the pairs had no immediate neighbours.

6.3.2.2. Nest search and monitoring

Nest searches were conducted throughout the breeding seasons of 2003, 2004 and 2005. Nests were located following specific adult behaviour and by searching individual plants within the territories as described by Martin and Geupel (1993) and Martin et al. (1996). Since the species is extremely shy and finding nests from the large stretch of *Strobilanthes* and reed patches were extremely difficult, most of the nests were located by observing the adult behaviour. The breeding status including the dates of nest construction, egg laying, incubation and nestlings was recorded every 2-3 days. Nests that fledged at least one young were considered successful. Observations of fledgling in or near the nest, or parents feeding new fledglings in the general area of the nest were taken as evidence of a successful nest. Depredation was assumed when eggs or nestlings disappeared.

6.3.2.3. Nest architecture and variation

Various aspects of nest morphometry were measured in the field, immediately after the fledging. Nest size parameters measured were diameter and the depth of the outer and inner wall and the thickness of the nest wall as described in Figure 6.1. The presence or absence of decorative materials such as spider cocoon was also recorded. Eight nests were collected from the field after the completion of the breeding during 2003-2005. These nests were weighed and examined to determine functional architecture and material composition (see Hansell, 2000). The animal and plant materials were separated and identified up to the species level whenever possible.

I estimated nest cup volume and nest volume as a fraction of an ellipsoid using the equation

$$\text{Volume} = 4/3 * p * r_1 * r_2 * r_3 * x$$

where r_1 and r_2 are the radii of the nests, r_3 is the depth of the nest, and x is a fraction of an ellipsoid (see Møller, 1982, 2006; Soler et al., 1998). Variation in the nest morphometry in different treatments was compared by one way ANOVA.

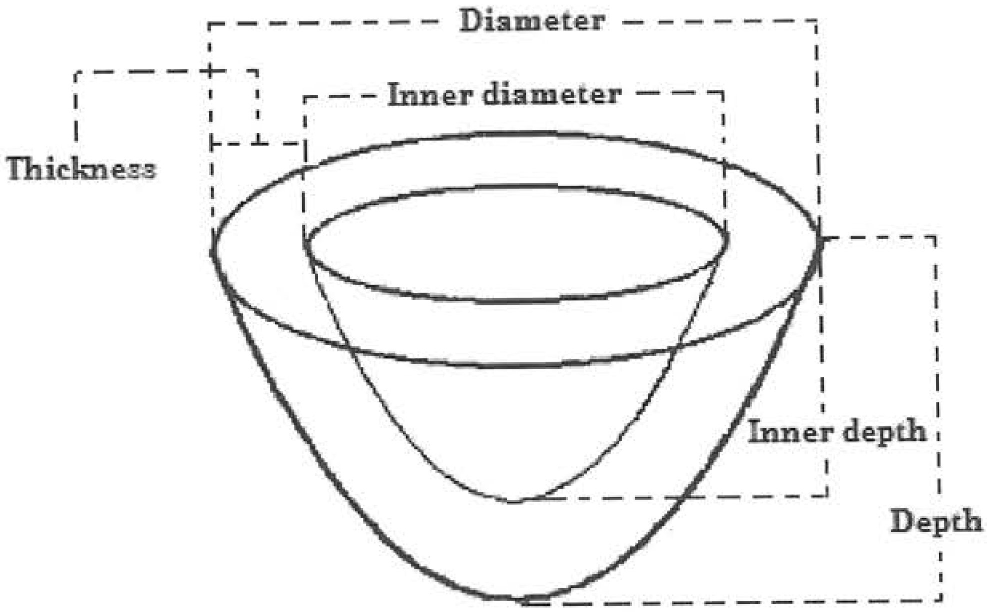


Figure 6.1. Definitions of nest measurements of Grey-headed Bulbul (modified from Soler et al., 1998; Hansell, 2000).

6.3.2.4. Correlates of nest architecture variation

To address the evolution of within-species variation in the nest architecture, several possible factors such as nest placement and concealment, microhabitat structure, food and nest material availability, predation pressure and competition were studied. Nest concealment was indexed by estimating percent foliage cover in a 1 m circle centered on the nest from 1 m from the side of each cardinal directions and above and below the nest (10% = 1, 20% = 2, ...; 100% = 10). These indices were then summed up to give an overall estimate of the degree of nest concealment (see Martin and Roper, 1988; Picman, 1988; Howlett and Stutchburry, 1996). The vegetation structure around the nest was measured at two spatial scales, namely meso and micro plots. A 0.04 ha circular plot was used to measure the habitat characteristics at the meso-plot scale. Micro-plot variables were measured in a 5 m circular plot which centers the nest tree (see chapter 4). For the two scales, I measured or calculated 40 variables (17 meso-plot variables and 23 micro-plot variables; see Tables 4.1.and 4.2 for variable descriptions) to describe and discriminate the variation of habitat structure among the nest types. Habitat variables that did not meet assumptions of normality were transformed after being assessed by frequency distribution, normal probability plots and the Shaprio-Wilks test. To identify the correlates of habitat structure and nest architecture, data for each scale were analysed using three approaches. First, I compared the means of continuous variables by using one-way ANOVA with Bonferroni multiple comparison tests. Second, I conducted a principal component analysis (PCA) based on correlation matrices to reduce dimensionality of the data. The principal component factors that had eigenvalues > 1.0 were extracted to explain the maximum variation in the data set. The factor matrix was rotated by the verimax method to assist in interpretation and display of the results (Norušis, 1998). Prior to multivariate analyses, Pearson correlation coefficient analysis was performed to determine the multicollinearity between the independent habitat variables and r 0.70 was considered as criterion for either omitting or retaining a variable (see Tabachnick and Fidell, 1996; Luck, 2002). However, both biological and statistical aspects were considered for the variable retention in each analysis. Fist two principal component scores are used for constructing biplots to separate the nest sites. Finally, canonical discriminant function analysis (SPSS Inc., 1999) was performed for each scale of measurement to discriminate the moss and vine nest sites (see Chapter 4 for detailed procedures).

To evaluate the influence of food on the evolution of nest design -which require differential energy and time requirements- the food availability was measured in terms of the abundance of food plants and invertebrates. The number and abundance of the food plants were estimated from the nest plots. Variation in the arthropod abundance was measured in five territories each in moss and vine nest plots. Details of the sampling procedures are described in section 5.4.7.

To examine the role of competition on the evolution of the life-history traits of Grey-headed Bulbul, resource utilization patterns of species belong to the same nesting guilds were explored in the field. All the bird species sharing the resources in terms of nest patches, nesting plants and nest materials were identified. The availability and abundance of nesting plants and nest materials were quantified at Silent Valley (see above). The breeding seasonality and inter-species nest distances of similar species were examined in the breeding seasons of 2003 to 2005.

Several methods such as infra-red cameras are available for the direct identification of the nest predators; however, I couldn't employ these methods due to logistical reasons. Therefore, I estimated the predation pressure at the nest sites based on direct sightings and indirect evidences of the presence of potential predators. The list of potential predators of Grey-headed Bulbul nests was prepared based on the previous observations on similar species (Vijayan, 1975, 1980; Ali and Ripley, 1987). All the potential avian predators were quantified through a series of area-search censuses (Bibby et al., 2000) at 33 live nest sites. The censuses were limited to 30 min and an area of 1 ha surrounding the nest (see Patten and Bolger, 2003; Stuart-Smith and Hayes, 2003). These counts were repeated up to five times during different stages of nesting. Occurrence of reptiles; and direct and indirect evidences on the presence of small mammals were also quantified during these counts. The correlates of mean predator abundance and daily mortality rates were calculated by Spearman rank correlations. The mean predator abundance among different treatments was compared by analysis of variance tests.

6.3.2.5. Nest orientation

Orientation of the nest relative to the main stem was recorded for 48 nests of Grey-headed Bulbul. I recorded all compass bearings to the nearest degree using a Suunto MCA-D compass. The summary statistics for circular data are presented as mean vector ($\mu \pm SE^{\circ}$) and the length of the mean vector (r). The null hypothesis of uniform distribution of nest orientation in all directions was tested by using Rao's spacing test and Rayleigh test (Batschelet, 1981; Zar, 1999). Rao's spacing test has distinct advantages in the analysis of nest orientation and other circular data over other commonly used goodness-of-fit and also accounts for many of the statistical implications when analyzing nest orientation data

(Bergin, 1991). Circular statistics were computed using the statistical package Oriana Version 2.01c (Kovach Computing Services, 2004).

6.3.2.6. Nest survival and correlative relationships

Reproductive success of Grey-headed Bulbul was estimated from 47 intensively monitored nests from the Silent Valley National Park and surrounding reserved forests during the breeding seasons of 2002 to 2005. Although annual reproductive success (young produced per female per year) is considered as a more desirable metric for examining population dynamics (Thompson et al., 2001), nest survival is a more sensitive indicator of the effects of habitat and annual differences (Armstrong et al., 2002). Early attempts to estimate nest survival rates included a simple calculation of the number of successful nests divided by the total number of nests found and commonly referred to as 'apparent nest success' (Jehle et al., 2004). However, this method provides a biased estimate of nest success because successful nests have a higher probability of being detected than failed nests (Mayfield, 1961, 1975). The only way to ensure an unbiased estimate using apparent nest success is to locate every nest at initiation (Klett and Johnson, 1982), which is not possible for an elusive rainforest species like Grey-headed Bulbul. Yet, the apparent nest success was calculated for the purpose of comparison with previous studies on other species of bulbuls and restricted range species. Many researchers calculated the reproductive success as an index of the chick fledged versus eggs laid (e.g., Vijayan, 1975; Khan, 1977; Islam, 1985; Ahmed, 2005; see Jehle et al., 2004 for a review). This method was also followed in this study to calculate the nesting success, hatching success and fledging success.

However, to obtain a more reliable estimate of the nest survival of Grey-headed Bulbul, I used the Mayfield estimator (Mayfield, 1961, 1975; modified by Johnson, 1979; and Hensler and Nichols, 1981). This method eliminates the need to monitor every nest beginning at initiation and provides a vast improvement over apparent nest success estimates. The Mayfield method for calculating survival rates incorporates the period of time a nest was under observation and vulnerable to loss. I calculated a daily mortality rate (m) by dividing the number of clutches that failed to survive by the total number of days all nests were under observation and exposed to loss. The daily survival rates (DSR) was calculated as:

$$\text{DSR} = 1 - \text{number of failed nests/number of exposure days.}$$

Here, 'exposure days' is the total number of days that active nests were monitored.

Finally, to obtain an estimate of nest survival over the entire nesting period, the daily survival rate is raised to the power equivalent to the average number of days (*d*) in the nesting period as:

$$\text{Nest survival} = (\text{DSR})^{d}.$$

Nest survival for the entire nesting period (d = 25) and for incubation (d = 13) and nestling periods (d = 12) were calculated separately. The variance (*v*) and standard error (SE) are approximated for the estimator of daily survival probabilities by following Johnson (1979) and Hensler (1985). These parameters were used to make statistical comparisons between the populations varied in clutch size and nest design, and between incubation and nestling stages of the nesting cycle.

Initiation dates, design, placement, and concealment of the nests; habitat structure, competition and predation pressure were quantified to examine the influence on nest success. Detailed descriptions of the methods and statistical methods followed were given in section 6.3.2.4.

6.3.2.7. Parental care

Although several methods (e.g., light-sensitive photo-resistors, electronic balances, thermocouples, video cameras, and temperature probes and data loggers) are available to study the parental behaviour (see, Joyce et al., 2001), use of traditional method which involves hourly or day-long watches at nests is still prevalent in behavioural studies (e.g., Norment, 1995). Twenty seven nests of Grey-headed Bulbul were studied to understand the parental care patterns during the incubation and nestling periods. All the observations were made during 06.00–18.00 hrs from a hide placed 15–20 m from the nest. The total observation period was 1,224 hrs (range: 3–72 hrs/nest), which include 672 hrs during the incubation stage and remaining (552 hrs) during nestling stage. To describe the incubation patterns, the following parameters were used.

1. mean on-bout duration: mean incubation duration/hour
2. mean off-bout duration: mean time spent away between two incubation visits/hour

3. nest attentiveness (percentage of total daylight hours spent on the nest; see Kendeigh, 1952; Conway and Martin, 2000b) as [mean on-bout duration / (mean on-bout duration + mean off-bout duration)]
4. nest trips/hour: 2[60 / (mean on-bout duration + mean off-bout duration)] or the number of times the female went to or from the nest per hour.

The parameters used for characterizing the parental care patterns during the nestling stage were:

1. nest attentiveness: percentage of total daylight hours spent on the nest
2. mean on-bout duration: mean brooding duration/hour
3. mean off-bout duration: mean time spent away between two feeding visits/hour
4. feeding rate: number of feeding visits/hour

For statistical reasons, parameter estimates were averaged across different stages of the nesting cycle (incubation and nestling stages), daylight hours, nest types and clutch variations. Variation in the parental care patterns in terms of nest attentiveness, on and off-bout durations and incubation or feeding bouts/hr among the nesting phases (incubation and nestling) and different clutches (single and double eggs), were tested for different daylight hours (06.00-09.00, 09.00-12.00, 12.00-15.00 and 15.00-18.00) and days in the nesting cycle using repeated-measures ANOVA (General Linear Model procedure, SPSS Inc., 1999; Quinn and Keogh, 2002). Whenever, the data did not meet the sphericity criterion (Mauchly's test of sphericity), the *F* statistics for the within-subject factor and interactions were corrected using the Greenhouse-Geisser adjustment (Beal and Khamis, 1990; von Ende, 1993; Norušis, 1998).

All the statistical analyses were carried out using the statistical package SPSS 10.0.1 for Windows (SPSS Inc., 1999). Variables expressed as percentages were transformed using the arcsine square root transformation (Zar, 1999) prior to analyses. Parametric tests were used whenever the quality of measurement met the criteria. Otherwise non-parametric tests were used (Siegal and Castellan, 1988; Zar, 1999). The data presented are means±S.E. values and a probability level of ≤ 0.05 was considered statistically significant and ≤ 0.01 was considered highly significant.

6.4. Results

6.4.1. Breeding population

The breeding population of Grey-headed Bulbul in the Silent Valley National Park and surrounding areas was almost consistent during the study period. 20 pairs were recorded from the intensive study area during the breeding season of 2003, while it was 23 and 25 pairs during 2004 and 2005 respectively (see also Chapter 3). All the parent and juvenile birds dispersed to the lower altitudes by the onset of monsoon and they were back in the study area by the end of December. From the observations of 20 breeding pairs, it is found that the birds used approximately 2 to 7.5 ha area surrounding the nest. The birds nesting in the reed patches which had lesser number of fruit plants had larger home ranges compared to those nesting in *Strobilanthes* patches.

6.4.2. Breeding seasonality

Fifty four nests of Grey-headed Bulbul were recorded from four different areas; 16, 18 and 20 nests during the breeding seasons of 2003, 2004 and 2005 respectively. Maximum number of nests were recorded from the Silent Valley National Park (46), followed by Karuvarakundu Reserved Forest of Nilambur South Division (6) of Kerala; and one each from Muthikkulam Reserved Forest of Mannarkkad Division, Kerala; and Cotigoa Wildlife Sanctuary, Goa. The breeding activities in all the three study years commenced in the first half of January and ended in May, by the onset of monsoon. Peak breeding was observed in April during 2004 and 2005 while it was in March during 2003 (Figure 6.2)

The breeding seasonality of Grey-headed Bulbul was positively correlated with the maximum temperature ($r_s = 0.660$, $n = 29$, $p < 0.01$) but inversely correlated with the monthly rainfall ($r_s = -0.373$, $n = 29$, $p < 0.05$) and the number of rainy days per month ($r_s = -0.350$, $n = 29$, $p < 0.05$). However, number of nests per month was not associated with the minimum temperature ($r_s = -0.316$, $n = 29$, $p > 0.05$; Figure 6.3). The breeding seasonality of bulbul shows a positive correlation with the fruiting phenology ($r_s = 0.895$, $n = 29$, $p < 0.01$), fruit abundance of food plants ($r_s = 0.867$, $n = 29$, $p < 0.01$), and percentage of plants with fruits ($r_s = 0.761$, $n = 29$, $p < 0.01$; Figures 6.4 and 6.5).

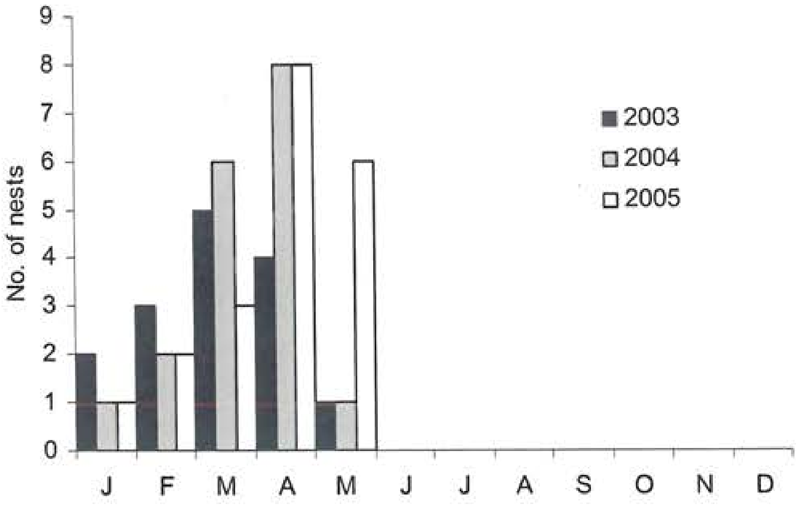


Figure 6.2. Breeding seasonality of Grey-headed Bulbul during 2003-2005.

6.4.3. Structural and functional architecture of the nest

All the Grey-headed Bulbul nests were cup shaped. Nest architecture varied, apparently, based on the microhabitat. The dominant (66.04%, $n = 35$) typical bulbul nests were made mainly of vines and grasses and seen mostly in *Strobilanthes* patches (hereafter referred to as *vine nests*). Second type of nests (hereafter referred to as *moss nests*) constructed mainly with *Ochlandra* leaves (33.96%, $n = 18$) were located mostly in reed patches. A single, third type of nest made of green leaves was also recorded (hereafter referred to as *leaf nest*).

The mass and morphology varied significantly between the two types of nests. Mean dry weight of the vine nests was 14.86±3.23 gm ($n = 8$), appreciably lighter than the moss nests which weigh 23.00±0.82 gm ($n = 4$). The mass of the vine nests varied depending on the clutch size; 12.00±0.82 gm for the nests with one egg ($n = 4$) and 17.75±1.26 gm for the nests with two eggs ($n = 4$). The external dimensions, material volume and cup volume of the nests varied significantly between the moss and vine nests (One way ANOVA, $p < 0.01$; Table 6.1).

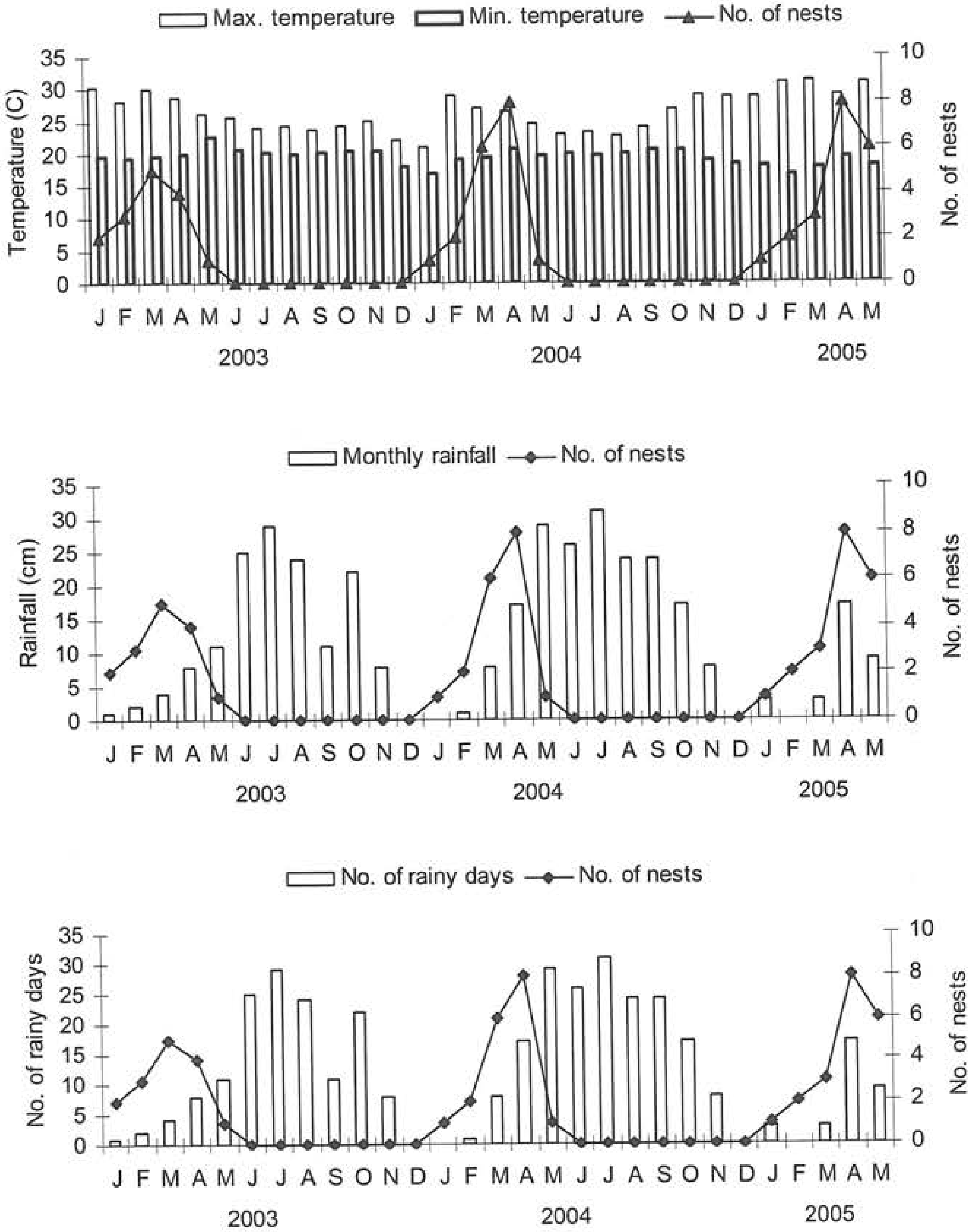


Figure 6.3. Correlation of the breeding seasonality of Grey-headed Bulbul with maximum and minimum temperatures, monthly rainfall and number of rainy days at Silent Valley National Park, Kerala.

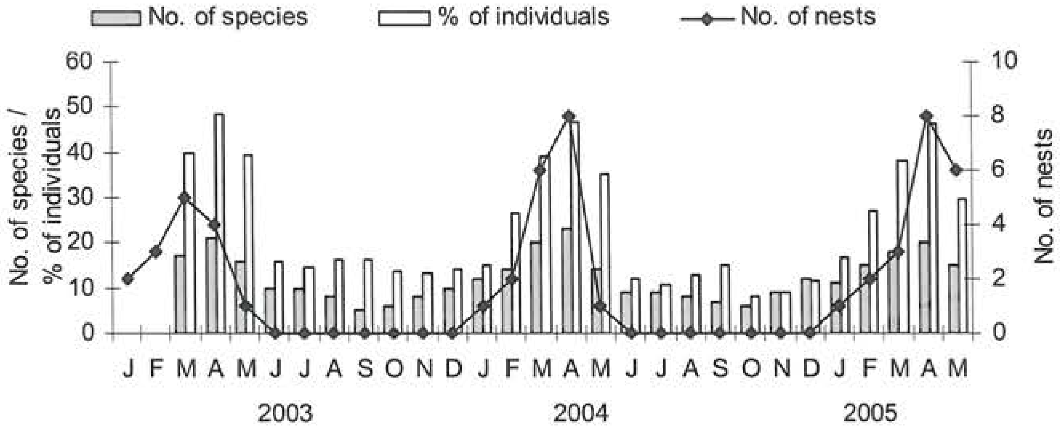


Figure 6.4. Correlation of the breeding seasonality of Grey-headed Bulbul with the fruiting phenology of 25 food plants at Silent Valley National Park, Kerala.

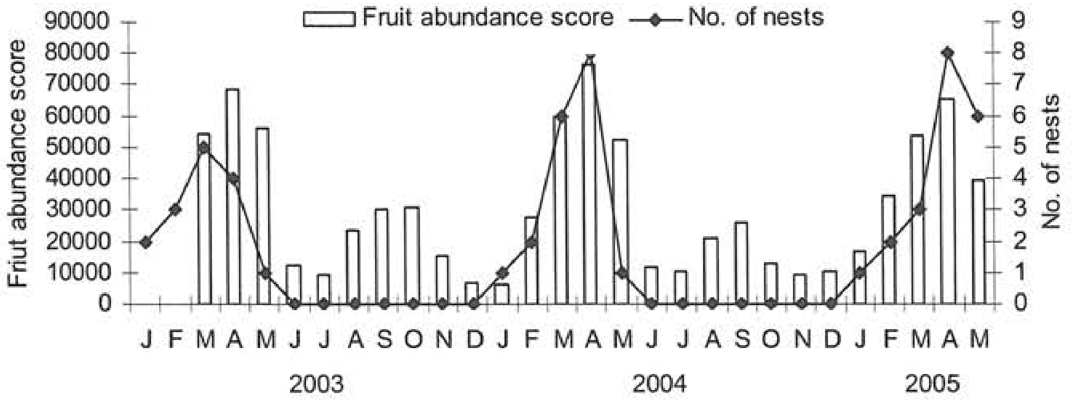


Figure 6.5. Correlation of the breeding seasonality of Grey-headed Bulbul with the fruit abundance of 25 food plants at Silent Valley National Park, Kerala.

Table 6.1. Variation in the morphometry of moss and vine nest of Grey-headed Bulbul.

Nest size Variables	Moss nest ($n = 11$)	Vine nest ($n = 24$)	F	p
Outer diameter (cm)	8.19±0.56	6.93±0.97	16.193	0.0001
Inner diameter (cm)	6.21±0.54	5.51±0.62	10.363	0.003
Outer depth (cm)	7.10±0.57	5.28±0.81	44.656	0.0001
Inner depth (cm)	4.65±0.28	3.24±0.74	36.481	0.0001
Thickness (cm)	1.98±0.15	1.41±0.42	18.493	0.0001
Cup volume (cm^3)	376.83±68.54	216.05±90.60	27.292	0.0001
Material volume (cm^3)	620.97±95.39	341.03±147.08	33.144	0.0001

The 'moss nests' have three structurally distinct zones. First one is the *structural layer*, which gives integrity to the nest shape constituted mostly by dry leaves and leaf sheaths of *Ochlandra travancorica*. The second structural component is the innermost zone which is considered as the *lining layer*. This layer, which is in direct contact with the eggs and the chick, was made with soft material such as *coma* and *papus hairs* of plants, fibre roots of pteridophytes and rarely small pieces of spider cocoon. The third nest zone, the *decorative layer* seen outside the structural layer, is made of fresh moss and rarely wood pieces and spider cocoons. The moss layer appears as a concealment mechanism making the nest less visible to visually hunting predators in green background where the nests were placed.

The 'leaf nest' which is placed close to the leaves of *Calamus pseudo-tenuis* had two distinct zones. The major portion of the *structural layer* constituted of fresh leaves of *Antidesma menasu*, and *Strobilanthes* spp. and a few dry leaves and long grass blades inside the rim. The inner *lining layer* was made with the fibre roots of pteridophytes and a few plant hairs. There was no moss layer on this nest. Apparently, the nest was highly concealed from the visually hunting predators because of the presence of fresh leaves on the outer structural layer and placed in a green background.

Most of the 'vine nests' were smaller and contained relatively less nest materials. However, two distinct nest layers were identified. The *structural layer* was constituted by vine tendrils, dry narrow grass blades, grass culms, dry inflorescence of *Antidesma menasu,* dry leaves of *Oreocnide integrifolia,* stems and leaf blades of pteridophytes and dry leaves and stems of *Chumnianthus* sp. The *inner lining layer* was nominal in smaller vine nests, but the nests with two eggs had a good amount of lining layer and were made with fibre roots of pteridophytes and, *coma* and *papus hairs* of plants. The outer decorative layer was totally absent in vine nests. The nests made with dry materials are camouflaged with the pale background of the stems in the under story.

Of the different material identified from the nests of Grey-headed Bulbul, one was of animal origin and the remaining were of plant origin. Plant species such as *Ochlandra travancorica, Antidesma menasu*, *Oreocnide integrifolia, Chumnianthus* sp., *Strobilanthes* spp.; and several species of grasses formed essential components of the structural layer of the nests of Grey-headed Bulbul. *Selaginella spp., Lindsaea ensifolia, Christella parasitica, Dryopteris cochleata, Odontosoria chinensis, Nepholepis auriculata, Pteridium aquilinum,* and *Blechnum orientale* are the pteridophytes used as nesting material.

6.4.4. Correlates of within-species variation in nest architecture

6.4.4.1. Microhabitat structure

There was a significant difference in the vegetation structure and other habitat attributes between the moss and vine nest plots. Of the 17 measured or calculated descriptors of habitat at the meso-scale, seven differed between the two nest types ($p < 0.05$; Table 6.2). All the vegetation cover variables except the sub-canopy cover (PSCC) were higher in the vine nest sites. The total tree density (TRDEN), food tree density (FTDEN), and sub-canopy tree density (SBDEN) were significantly higher in the vine nest plots (see Table 6.2).

Table 6.2. Mean values (±SE) for the habitat characteristics at moss and vine nests of Grey-headed Bulbul measured at the meso-scale.

Variables	Code	Moss nests ($n = 17$)	Vine nests ($n = 32$)	F	p
Mean tree height (m)	MNTHT	11.52±0.76	10.21±0.48	2.294	0.137
Max tree height (m)	MXTHT	22.53±1.42	21.22±0.89	0.672	0.416
Mean tree GBH (cm)	MNTGBH	72.83±8.87	49.32±2.82	9.847	0.003
Tree density (#/plot)	TRDEN	26.76±3.90	49.66±4.03	13.505	0.001
Canopy tree density (#/plot)	CTDEN	11.71±1.84	15.28±1.86	1.537	0.221
Sub-canopy density (#/plot)	SBDEN	13.24±2.58	31.78±3.51	12.825	0.001
Food trees (#/plot)	FTDEN	8.47±1.77	23.72±2.35	19.146	0.001
Food shrubs & liana (#/plot)	FSLDEN	9.12±4.42	29.59±7.48	3.599	0.064
Dead tree density (#/plot)	DDTDEN	0.53±0.19	1.00±0.36	0.824	0.369
Downed tree density (#/plot)	DNTDEN	1.47±0.39	1.34±0.31	0.061	0.806
Percent bare ground	PBG	5.24±2.26	5.53±1.61	0.012	0.915
Percent rock cover	PRC	17.82±5.07	9.09±2.60	2.897	0.095
Percent epiphyte cover	PEPI	0.35±0.17	2.19±0.69	3.699	0.061
Percent canopy cover	PCC	25.29±4.28	40.94±2.98	9.256	0.004
Percent sub-canopy cover	PSCC	48.82±6.22	57.81±2.98	2.182	0.146
Percent shrub cover	PSC	68.24±3.12	77.81±2.08	6.892	0.012
Percent ground cover	PGC	62.06±5.86	74.69±2.58	5.217	0.027

Based on the results of the Pearson correlation coefficient analysis, seven of the 17 habitat variables were selected for inclusion in the principal component analysis. Variable retention was based on both statistical and biological considerations. Two principal components were derived from this analysis that had an eigenvalue > 1.0 and explained 74.99% of cumulative variance in the data (Table 6.3). Total tree density (TRDEN), sub-canopy density (SBDEN), and food trees (FTDEN) had high factor loadings with the first principal component (0.963, 0.914 and 0.861, respectively). This component was interpreted as a measure of high densities of food plants, sub-canopy and total trees in the vine nest sites. The variables, ground cover (PGC) and shrub cover (PSC) had high factor loadings with the second principal component (0.890 and 0.853, respectively). This component was interpreted as a measure of high shrub and ground vegetation cover at the vine nest sites (Figure 6.6).

Table 6.3. Results of the principal components analysis of the meso-scale habitat structure.

Variables	PC1	PC2
Eigenvalue	3.684	1.565
Variation explained (%)	52.63	22.36
Cumulative %	52.63	74.99
TRDEN	0.963	0.027
SBDEN	0.914	0.056
FTDEN	0.861	0.277
MNTGBH	-0.778	0.144
PCC	0.662	0.257
PGC	0.024	0.890
PSC	0.116	0.853

Table 6.4. Summary of the discriminant function analysis of habitat features at moss and vine nest sites.

Meso-scale		Micro-scale	
	DF1		DF 1
Canonical correlation	0.772	Canonical correlation	0.871
Wilk's lambda	0.405	Wilk's lambda	0.241
Chi-square	36.654	Chi-square	56.288
Eigenvalue	1.472	Eigenvalue	3.158
Significance level	0.0001	Significance level	0.0001
Variables entered	Structure matrix	Variables entered	Structure matrix
FTDEN	0.526	NPHT	0.572
TRDEN	0.442	REETDEN	0.327
SBDEN	0.431	NPDEN	0.319
PCC	0.379	DTTKP	0.296
MNTGBH	-0.377	DTNT	0.292
PSC	0.327	SAPDEN	-0.245
PEPI	0.281	SBDEN	-0.218
PGC	0.250	SHBDEN	0.176
FSLDEN	0.228	HTNS	0.172
PRC	-0.207	HTNT	0.157
MNTHT	-0.182	LNDEN	-0.122
PSCC	0.179	DTANT	0.079
PBG	-0.003	DTWTR	-0.074
		DTNS	-0.061
		PTEDEN	0.037

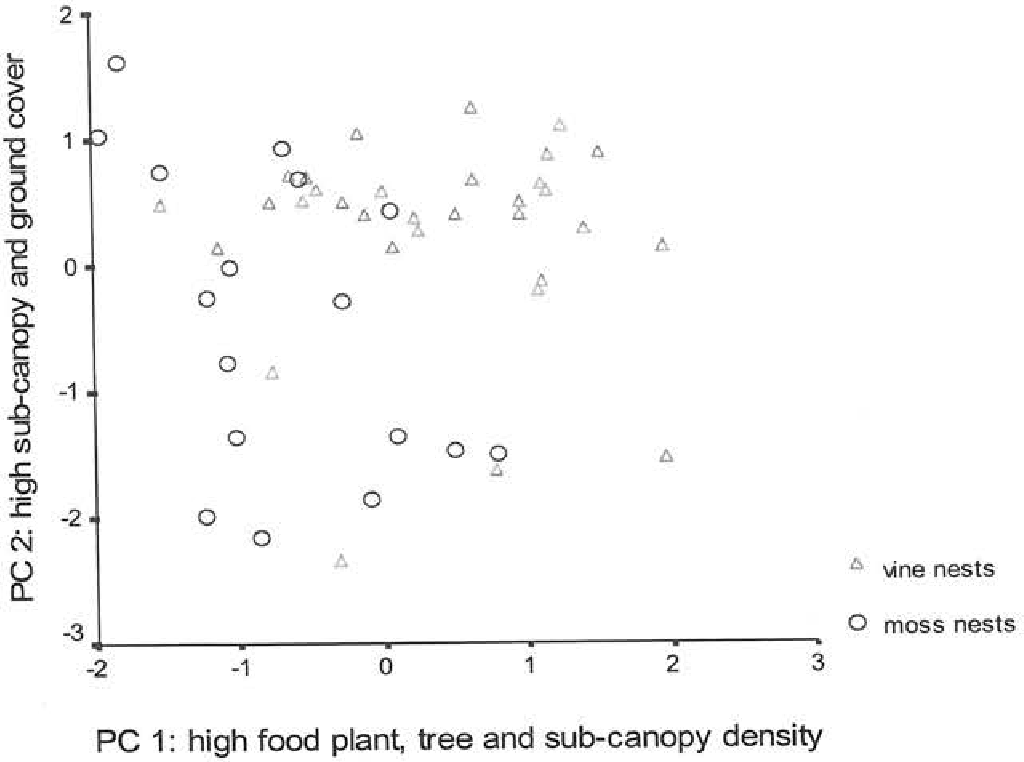


Figure 6.6. Plots of factor loadings of principal component analysis of the habitat characteristics of moss and vine nest plots at the meso-scale.

Thirteen variables were analysed using canonical discriminant function analysis to determine the variation in the habitat structure at the meso-scale among the nest types. A single discriminant function (DF1) was significant (Wilk's Lambda = 0.405, $\chi^2 = 36.654$, $p < 0.001$). This function was highly correlated with densities of food trees (FTDEN; $r = 0.526$), total trees (TRDEN, $r = 0.442$) and sub-canopy trees (SBDEN, $r = 0.431$). The variables entered and the resulted structure matrix is given in Table 6.4.

At the micro-scale, I found significant broad differences between the mean values of habitat variables among the moss and vine nest sites. Of the 23 measured or calculated descriptors of habitat, 12 differed between the two nest types ($p < 0.05$; Table 6.5). All the nest plant characteristics and densities of saplings and shrubs were significantly varied among the nest sites. In general, the moss nests were located in reed patches while the vine nests in patches dominated by *Strobilanthes*.

Table 6.5. Mean values (±SE) for the habitat characteristics at moss and vine nests of Grey-headed Bulbul measured at the micro-scale.

Variables	Code	Moss nests ($n = 17$)	Vine nests ($n = 32$)	F	p
Nest plant height (m)	HTNP	4.18±0.35	1.95±0.15	48.530	0.001
Nest plant GBH (cm)	GBHNP	6.18±0.44	4.00±0.22	22.583	0.001
Nest plant species density (#/plot)	NPDEN	159.65±26.39	49.97±15.07	15.130	0.001
Sapling density (#/plot)	SAPDEN	14.88±4.09	32.72±3.77	8.902	0.005
Shrub density (#/plot)	SHBDEN	228.41±28.23	162.91±16.43	4.621	0.037
Dominant plant density (#/plot)	DODEN	167.82±24.32	105.47±13.73	5.832	0.200
Co-dominant plant density (#/plot)	CDDEN	28.47±4.08	34.47±4.18	0.859	0.359
Strobilanthes density (#/plot)	SBDEN	10.41±3.91	45.88±9.49	7.022	0.011
Reed density (#/plot)	REETDEN	166.00±30.25	44.00±15.56	15.883	0.001
Live reed density (#/plot)	REELDEN	126.29±22.53	29.28±10.25	20.264	0.001
Dead reed density (#/plot)	REEDDDEN	39.71±8.64	14.72±6.35	5.404	0.024
Pteridophyte density (#/plot)	PTEDEN	4.88±0.96	4.22±0.94	0.203	0.654
Liana density (#/plot)	LNDEN	8.00±1.76	23.59±7.53	2.220	0.143
Litter depth (cm)	LTRDPT	4.79±0.33	4.67±0.23	0.095	0.759
Distance to water (m)	DTWTR	7.94±2.37	10.42±1.56	0.820	0.370
Distance to trek path (m)	DTTKP	54.82±15.12	14.58±1.74	12.968	0.001
Distance to animal trail (m)	DTANT	4.35±1.68	3.05±0.43	0.921	0.342
Distance to adjacent tree (m)	DTNT	3.36±0.39	2.00±0.18	12.627	0.001
Height of adjacent tree (m)	HTNT	13.24±1.63	10.05±0.86	3.642	0.062
GBH of adjacent tree (cm)	GBHNT	69.24±9.68	48.28±6.12	3.656	0.062
Distance to adjacent shrub (m)	DTNS	1.19±0.81	0.56±0.36	14.023	0.001
Height of adjacent shrub (m)	HTNS	2.57±0.40	1.80±0.16	4.405	0.041
GBH of adjacent shrub (cm)	GBHNS	4.93±0.83	4.25±0.45	0.644	0.426

Principal component analysis on nine habitat variables yielded four principal components that had an eigenvalue > 1.0 and explained 64.92% of cumulative variance in the data (Table 6.6). The first PC was positively correlated with densities of reeds (REETDEN) and nesting plants (NPDEN). While PC2 was negatively correlated with distance to animal trail. The third and fourth components were positively correlated to density of pteridophytes and distance to adjacent shrub respectively (Table 6.6). The ordination plots constructed based on the first and second PCA scores separated the nest types based on the nest plant and reed densities (Figure 6.7). Canonical discriminant function analysis resulted in marked differentiation between nest types at the micro-scale. A single discriminant function explained significant variation among the nest types (Wilk's Lambda = 0.241, $\chi^2 = 56.288$, $p < 0.001$). The height and density of nest plants and density of reeds were the most important habitat variables separating the nest types (Table 6.4).

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Table 6.6. Results of the principal components analysis of the micro-scale habitat structure.

Variables	PC1	PC2	PC3	PC4
Eigenvalue	2.093	1.447	1.245	1.058
Variation explained (%)	21.73	14.67	14.48	14.04
Cumulative %	21.73	36.4	50.88	64.92
REETDEN	0.812	0.015	-0.087	-0.052
NPDEN	0.803	0.103	0.041	0.368
SBDEN	-0.604	0.063	-0.120	0.259
DTANT	0.025	-0.851	-0.113	-0.120
DTTKP	0.384	0.442	-0.122	-0.387
PTEDEN	-0.042	0.114	0.818	0.119
DTWTR	-0.042	0.540	-0.645	0.097
DTNT	0.367	0.252	0.407	-0.376
DTNS	0.031	0.132	0.044	0.854

6.4.4.2. Food availability

Nearly 70% (25 species) of all the food plant species of Grey-headed Bulbul was recorded from 50 nest plots. Food plant species richness in the nest plots ranged from 3 to 11 with a mean of 6.56 species (SE = 2.27). Out of 2,083 trees encountered during the sampling of 50 nest plots, 931 (44.70%) trees belonged to food species of Grey-headed Bulbul. Besides this, a total of 1,124 (11.20%) shrubs and lianas of the food species also recorded from the plots. Food plant species richness, density and relative abundance varied significantly in the moss and vine nest plots (One-Way ANOVA: $p < 0.01$, Table 6.7). There was no significant difference in the density of shrubs and lianas –which contribute a smaller portion of the food during breeding season– between the moss and vine nest plots (One-Way ANOVA: $F = 3.628, p = 0.063$).

There was a marginal variation in the invertebrate abundance between the moss and vine nest plots. Abundance of all the invertebrate groups sampled by sweeping, except Coleoptera and Hymenoptera, was higher in the vine nest plots ($\chi^2 = 6.077, p < 0.014$; Figure 6.8). Almost similar pattern was observed in the abundance of invertebrates sampled by beating method ($\chi^2 = 6.345, p < 0.012$), except Hymenoptera which was abundant in the vine nest sites (Figure 6.9). Furthermore, the total number of invertebrates from both the methods was significantly higher in the vine nest sites.

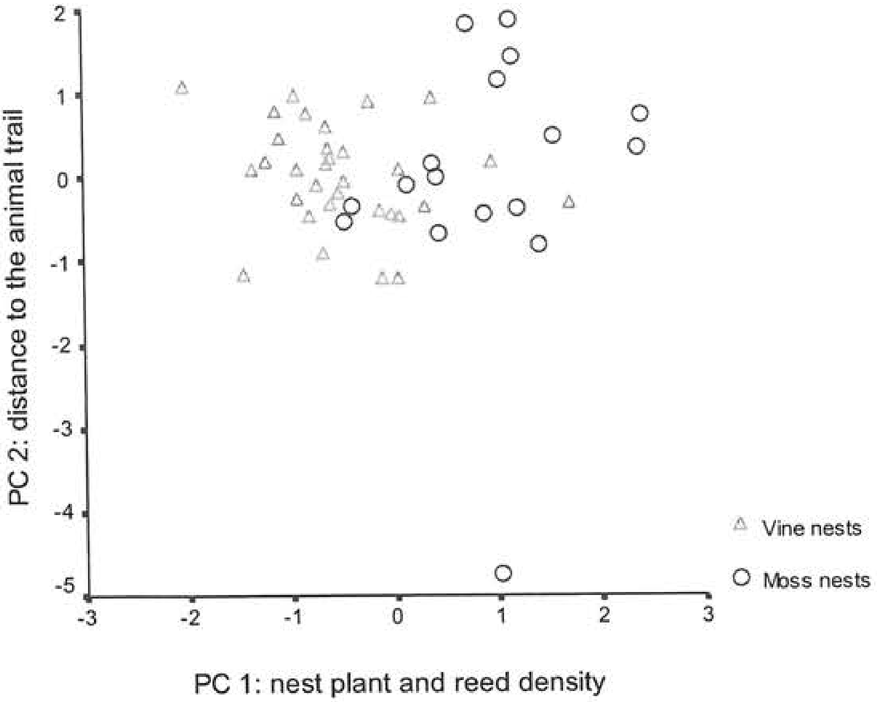

Figure 6.7. Plots of factor loadings of principal component analysis of the habitat characteristics of moss and vine nest plots at the micro scale.

Table 6.7. Comparison of the distribution and abundance of food plant species in moss and vine nest plots.

Food plant variables	Moss nest ($n = 17$)	Vine nest ($n = 33$)	F	p
No. of food plant species	5.41±2.00	7.15±2.20	7.465	0.009
Density of all food plants	17.59±20.05	53.18±47.77	8.589	0.005
Relative density of all food plants	0.08±0.08	0.26±0.18	15.219	0.001
Density of food trees	8.47±7.30	23.85±13.11	20.042	0.001
Relative abundance of food trees	0.33±0.19	0.48±0.18	8.238	0.006
Density of food shrubs and lianas	9.18±18.22	29.36±41.66	3.628	0.063
Relative abundance of shrubs and lianas	0.05±0.08	0.19±0.19	8.829	0.005

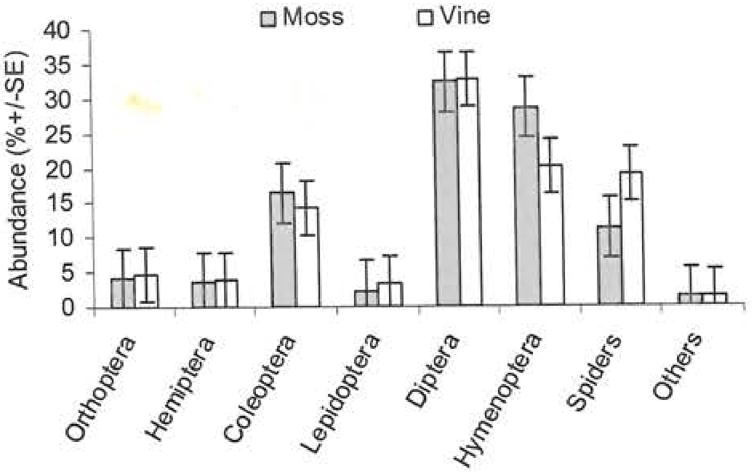

Figure 6.8. Abundance of different invertebrate groups sampled by sweeping at the moss and vine nest sites of Grey-headed Bulbul.

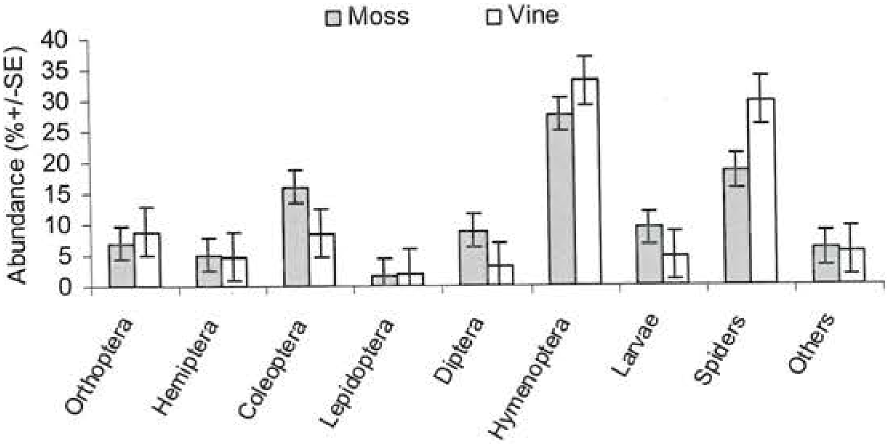

Figure 6.9. Abundance of different invertebrate groups sampled by beating at the moss and vine nest sites of Grey-headed Bulbul.

6.4.4.3. Nest architecture and clutch size

There was a significant increase in all the nest size variables with the increase in clutch from one egg to two (One-way ANOVA, $p < 0.0001$; Table 6.8). The nest cup volume is increased by an increase in the inner diameter and depth which in turn improved the chances of holding more nestlings. However, it is very difficult to make a conclusion on the influence of clutch on the nest size since the variation in both clutch and nest sizes were influenced by a number of interrelated factors and thus require experimental studies.

Table 6.8. Variation in the morphometry of Grey-headed Bulbul nests based on the clutch sizes.

Nest size variables	Moss nests (two eggs) ($n = 10$)	Vine nests (two eggs) ($n = 11$)	Vine nests (one egg) ($n = 14$)	F	p
Outer diameter (cm)	8.25±0.55	8.02±0.32	6.24±0.38	87.496	0.001
Inner diameter (cm)	6.28±0.51	6.08±0.38	5.13±0.38	26.800	0.001
Outer depth (cm)	7.11±0.60	6.15±0.57	4.81±0.56	50.047	0.001
Inner depth (cm)	4.61±0.27	4.18±0.48	2.73±0.27	105.817	0.001
Thickness (cm)	1.97±0.15	1.94±0.14	1.11±0.13	155.706	0.001
Cup volume (cm^3)	383.12±68.83	322.28±35.56	151.77±29.49	88.127	0.001
Material volume (cm^3)	629.82±95.66	507.44±86.98	242.83±56.38	80.821	0.001

6.4.4.4. Predation pressure

Predation on the Grey-headed Bulbul eggs or nestlings was rarely sighted. However, in one case the Jungle Striped Squirrel *Funambulus tristriatus* was found in the nest, feeding on eggs. Although the direct sightings or indirect evidences of the presence of species such as Small Indian Civet *Viverricula indica,* Common Palm Civet *Paradoxurus hermaphroditus,* Brown Palm Civet *Paradoxurus jerdoni,* Common Indian Grey Mongoose *Herpestes edwardsi,* the Brown Mongoose *Herpestes fuscus* and the Striped-necked Mongoose *Herpestes vitticollis* and Nilgiri Marten *Martes gwatkinsii* were obtained from the breeding habitats of Grey-headed Bulbul, these observations are not included in the analyses due to small sample sizes. The potential avian nest predators at the study site include White-bellied Treepie *Dendrocitta leucogastra*, Rufous Treepie *Dendrocitta vagabunda*, Greater Coucal *Centropus sinensis*, and Asian Koel *Eudynamys scolopacea.*

Although there is no direct observation of egg or nestling predation by snakes during this study, Common Vine Snake *Ahaetulla nasuta* was found swallowing the eggs of Yellow-browed Bulbul and Red-whiskered Bulbul. The same species was found swallowing an adult Red-vented Bulbul at Anaikatty Reserved Forest and similar instances were reported from other areas. Birds moved away from the nest sites in the presence of potential predators and were never seen mobbing or chasing the predators.

Predator abundance varied significantly between the moss and vine nest types. The number of predators in the moss nest sites (1.20±0.66/count, $n = 10$) were significantly lower than those in the vine nest sites (3.03±1.41/count, $n = 23$; $t = -3.898$, $p < 0.001$). Furthermore the nest sites with smaller clutches (3.27±1.50/count, $n = 17$) had higher predator abundance than those with two eggs (1.62±92/count, $n = 16$; $t = 3.789$, $p < 0.001$).

6.4.4.5. Competition for nest sites and nest material

Of the 12 plant species used by Grey-headed Bulbul for nesting (see section 6.4.8 for details), all the species, except an un-identified sapling, were used by several other species of birds as nest substrates at the study areas (Figure 6.10). Two species, namely Yellow-browed Bulbul and Brown-cheeked Fulvetta, which breed in the similar micro habitats as that of Grey-headed Bulbul shared nine and seven plant species respectively, as nest substrate with Grey-headed Bulbul. Most of these plant species were used by Grey-headed Bulbul as substrates for the vine nests.

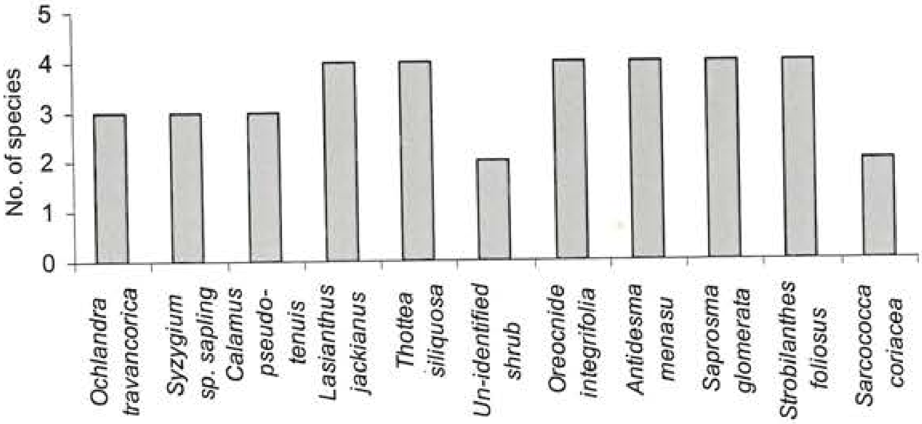

Figure 6.10. Number of bird species shared nesting plants with Grey-headed Bulbul at Silent Valley National Park and surroundings 2003-2005.

Although Grey-headed Bulbul shared breeding season with Yellow-browed Bulbul and Brown-cheeked Fulvetta (Figure 6.11), peak breeding differed from them ($r_s = 0.268$, $p = 0.168$; $r_s = 0.181$, $p = 0.347$). Peak breeding of Yellow-browed Bulbul and Brown-cheeked Fulvetta was during January-February, whereas it was March-May in the case of Grey-headed Bulbul. During the early breeding season, Grey-headed Bulbuls selected reed patches for nesting and almost all the nests were placed on *Ochlandra travancorica*. Most of the vine nests placed on substrates other than *Ochlandra* were recorded in the late breeding season. This clearly indicates that Grey-headed Bulbuls avoided competition for nest sites by breeding in two different microhabitats that in turn resulted in the variations in nest architecture.

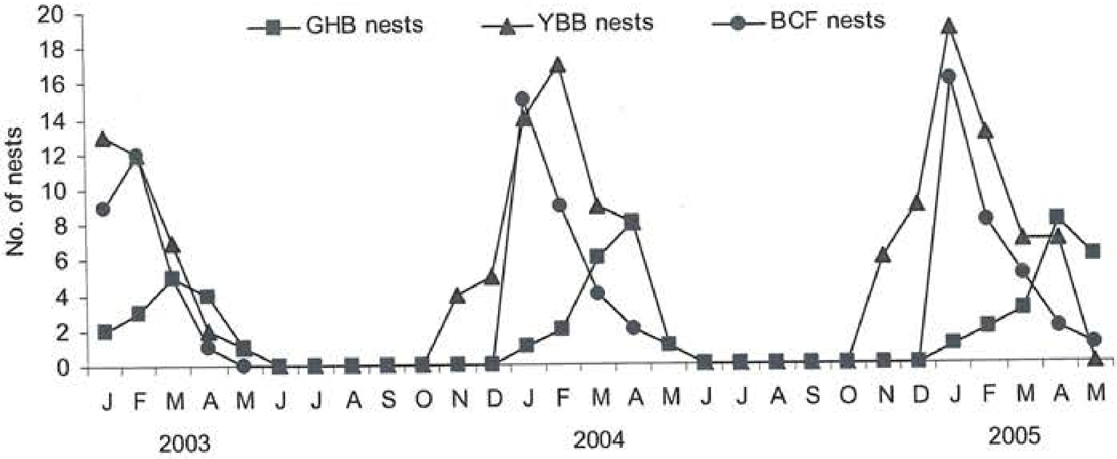

Figure 6.11. Comparison of the breeding seasonality of Grey-headed Bulbul (GHB), Yellow-browed Bulbul (YBB) and Brown-cheeked Fulvetta (BCF) at Silent Valley National Park, 2003-2005.

The nest material availability did not appear as a constraint to Grey-headed Bulbul. In general, birds use material available in the immediate surroundings of the nest sites. This may apparently contribute much in the variation of nest architecture in different microhabitats. The nest sites of Grey-headed Bulbuls are associated with the reed and *Strobilanthes* patches in the mid-elevation evergreen forests. The nests inside the reed patches are made mainly of the dry leaves and leaf sheath of *Ochlandra* as structural layer and are decorated with the fresh moss and thus well camouflaged with the background. On the other hand nests in the paler backgrounds (lower heights) or on the dry stem of the *Ochlandra* are made with vines and are devoid of the moss cover. Most of the nests in the *Strobilanthes* patches are made with vines, dried grasses, leaves of *Chumanianthus*, and dry inflorescence of *Antidesma menasu*. Except one nest which had high foliage cover, all these nests were devoid of moss layer (see section 6.4.3).

Grass and vine tendrils are common nest material used by several species of birds (see Ali and Ripley, 1987). In the habitats of Grey-headed Bulbul, other species of bulbuls and Brown-cheeked Fulvetta are the major species that used these materials. Dark-fronted Babbler *Rhopocichla atriceps* which commonly breeds in the reed patches used the dry leaves of *Ochlandra* as nest material. Moss is a major component in the structural and decorative layers in the nests of many forest species such as Yellow-browed Bulbul, Black Bulbul, Malabar Whistlingthrush, Nilgiri Laughingthrush, Grey-breasted Laughingthrush, Wynaad Laughingthrush, Crimson-backed Sunbird and, Brown-cheeked Fulvetta (Khan, 1977; Islam, 1985; Ali and Ripley, 1987; Ahmed, 2005; P. Balakrishnan, unpubl. data). Competition for moss as a nest material was not considered because of its abundance. Pteridophytes such as *Selaginella sp., Lindsaea ensifolia, Christella parasitica, Dryopteris cochleata, Odontosoria chinensis, Nepholepis auriculata, and Pteridium aquilinum* are the most used plants as nest substrate and nesting material. However, all these species are very common in the study site and other wet evergreen habitats of the Western Ghats (Manickam and Irudayaraj, 1992). In conclusion, nest material does not appear to be a constraint to Grey-headed Bulbul since the entire material is abundant at the local scale. However, competition for the nest substrates in the *Strobilanthes* patches during the early breeding season could be a reason for the differential micro habitat selection which in turn influences the nest design (see section 6.4.4.1).

6.4.5. Nest construction

The elusive nature of the species and the thick undergrowth in the nest sites made it extremely difficult to locate most of the nests during the early period of construction. Yet, I managed to collect some data on early stages of nest-building. Birds carrying nest material in the bill, which probably represented the beginning of nest-building, were noted from mid January through late April in all the breeding seasons. The degree of participation of male and female in nest construction could not be made clear from this study. However, it was noted that one of the sexes, probably the female, was more active in the construction. The other bird participated in construction by occasionally carrying the nest material to the nest and accompanying the female during the material gathering trips. The birds never approached the nest site directly with the material; instead they perched away from the location and then hopped towards the nest location.

The construction time varied significantly between the nest types. The average construction time for vine nests was 3–5 days ($n = 4$) and for moss nests 6–8 days ($n = 2$). These estimates could be considered as minimum, because the placement of the first nest material was not known. Little information on the effects of weather disturbances on nest building behavior was obtained. In one occasion, however, sudden rainfall temporarily halted building activity.

6.4.6. Nest placement

Generally, Grey-headed Bulbuls place the nests in the junctions of multiple branches in the shrubs and saplings camouflaging well with the plant substrates. The nests were 1.52±0.80 m (range: 0.52–4.8 m) above the ground (Figure 6.12), and at a mean relative height (nest height/tree height) of 0.61±0.20 (range: 0.18–1.00). All the nests were placed closer to the central stem except for those located on *Oreocnide integrifolia* and *Sarcococca coriacea.*

In general, there was no significant difference in the nest height (Kruskal-Wallis H, $\chi^2 = 1.178$, $p = 0.555$), nesting plant height (Kruskal-Wallis H, $\chi^2 = 1.855$, $p = 0.396$), and relative nest height (Kruskal-Wallis H, $\chi^2 = 1.753$, $p = 0.416$) between the breeding seasons (Figures 6.13, 6.14).

Nest placement attributes significantly varied between the moss and vine nests. The moss nests had higher nest heights (2.29±0.20 m *vs.* 1.08±0.05 m, $n = 18, 32$; Mann–Whitney U-test: $z = -5.254$; $p < 0.001$) and taller nesting plants than those in vine nests (4.17±0.33 m *vs.* 1.90±0.15 m, $n = 18, 32$; $z = -4.906$; $p < 0.001$; Figure 6.15). However, there was no difference in the relative nest heights between the moss and vine nests (0.59±0.05 *vs.* 0.63±0.03, $n = 18, 32$; $z = -1.001$; $p < 0.317$).

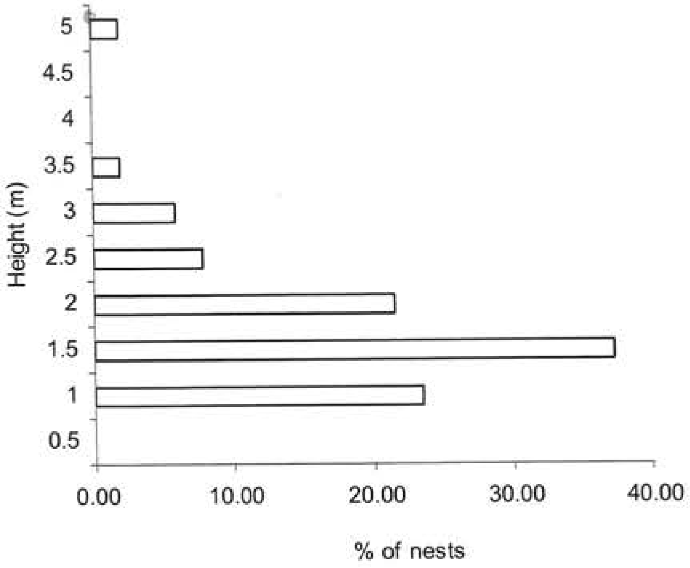

Figure 6.12. Vertical distribution of the nests of Grey-headed Bulbul during 2003–2005 ($n = 51$).

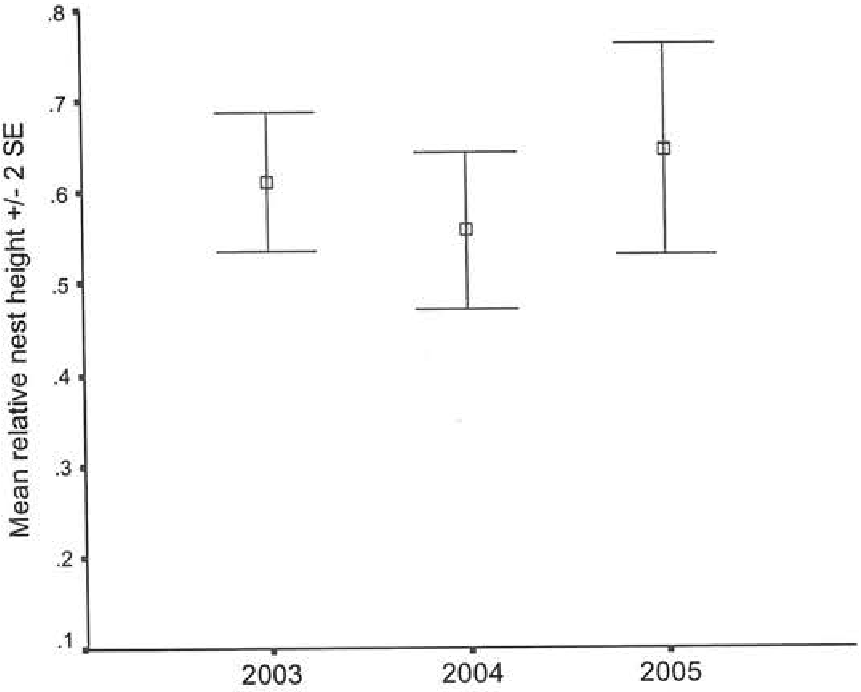

Figure 6.13. Comparison of the relative nest heights of Grey-headed Bulbul during 2003–2005.

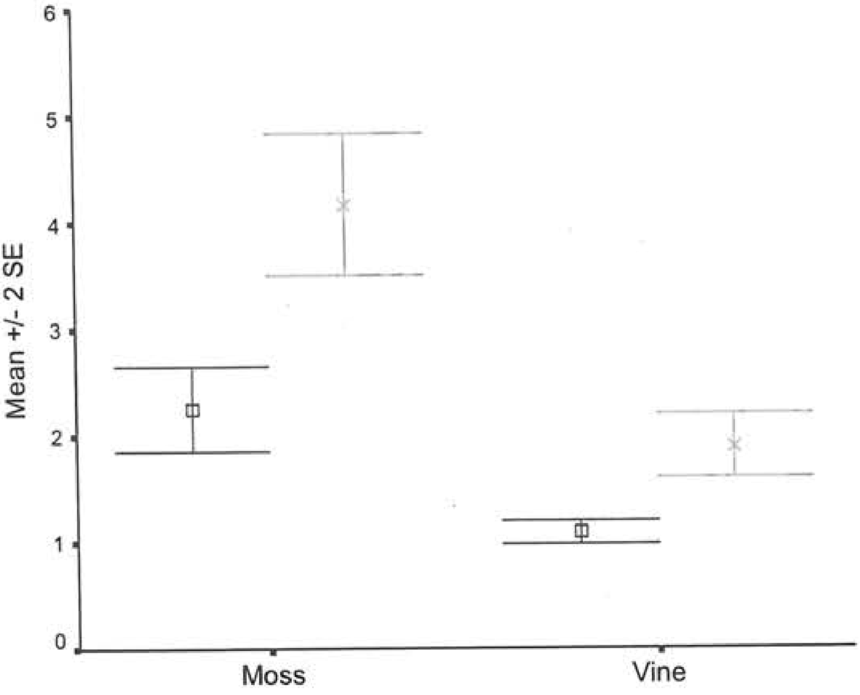

Figure 6.14. Comparison of the nest and nesting plant heights of the moss and vine nests of Grey-headed Bulbul.

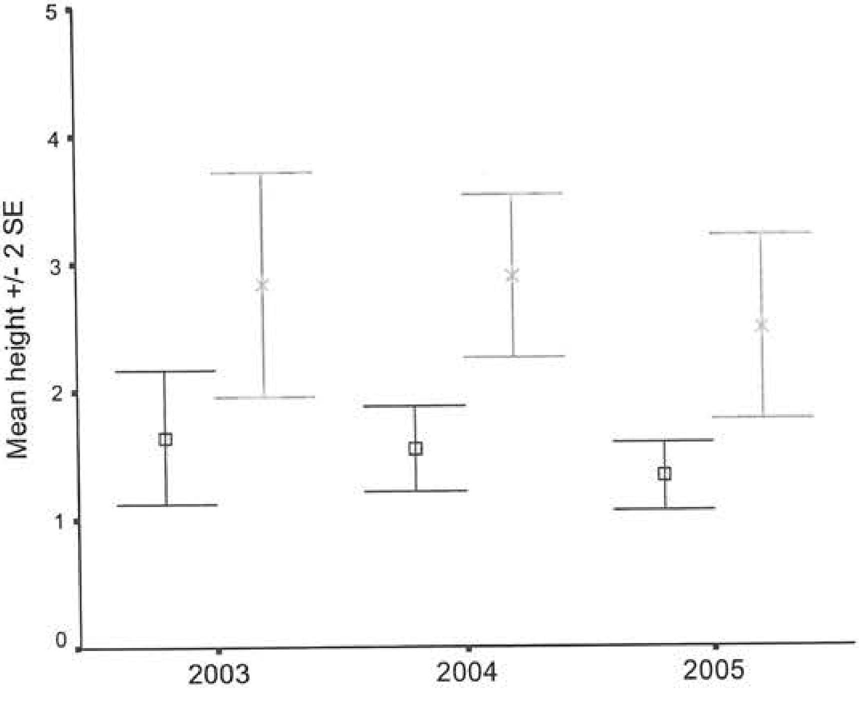

Figure 6.15. Comparison of the nest and nesting plant heights of Grey-headed Bulbul during 2003–2005.

6.4.7. Nest orientation

Nests were uniformly oriented around the nesting plants (Figure 6.16), with a mean vector of orientation equaling 160.45° (Rayleigh Test, $Z = 15.75$; Rao's Spacing Test, $U = 227.5$, $p < 0.01$). There was no significant difference in the nest orientation within and between the moss (Mean Vector (μ) =190.88°, Rayleigh Test, $Z = 6.199$, $p < 0.01$; Rao's Spacing Test, $U = 180$, $p < 0.05$; Figure 6.17) and vine nests (Mean Vector (μ) = 147.01°, Rayleigh Test, $Z = 11.085$; Rao's Spacing Test, $U = 207.5$, $p < 0.01$; Figure 6.18). Although similar pattern of orientation was existed for the failed nests (Mean Vector (μ) = 164.13°, Rayleigh Test, $Z = 13.867$; Rao's Spacing Test, $U = 220.5$, $p < 0.01$; Figure 6.19), successful nests had a more south-east orientation (Mean Vector (μ) = 141.26°, Rayleigh Test, $Z = 2.291$, $p < 0.099$; Rao's Spacing Test, $U = 130$, $p < 0.10$; Figure 6.20). In general the nests were placed in the leeward side of the nesting plants.

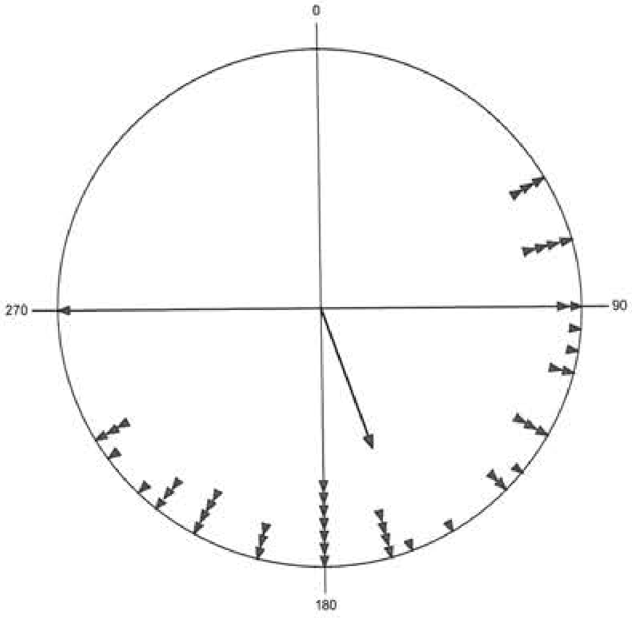

Figure 6.16. Orientation of Grey-headed Bulbul nests on plants used for nesting.

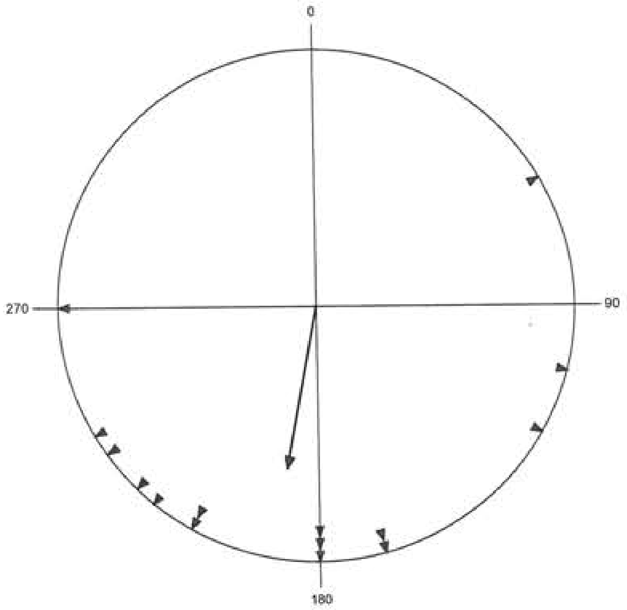

Figure 6.17. Orientation of the moss nests on plants used for nesting.

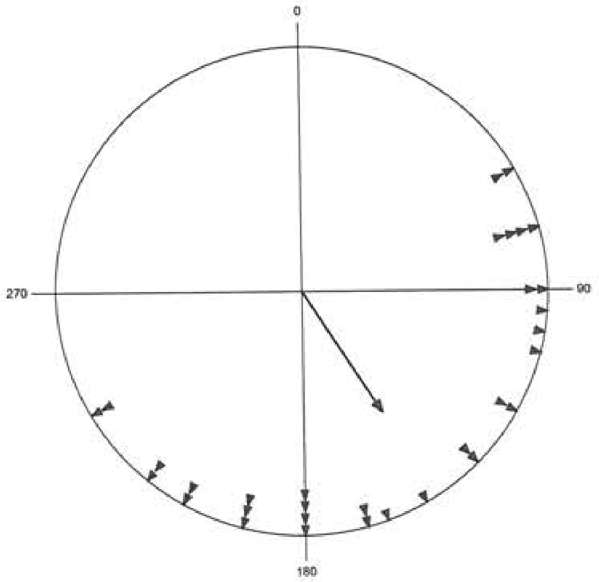

Figure 6.18. Orientation of the vine nests on plants used for nesting.

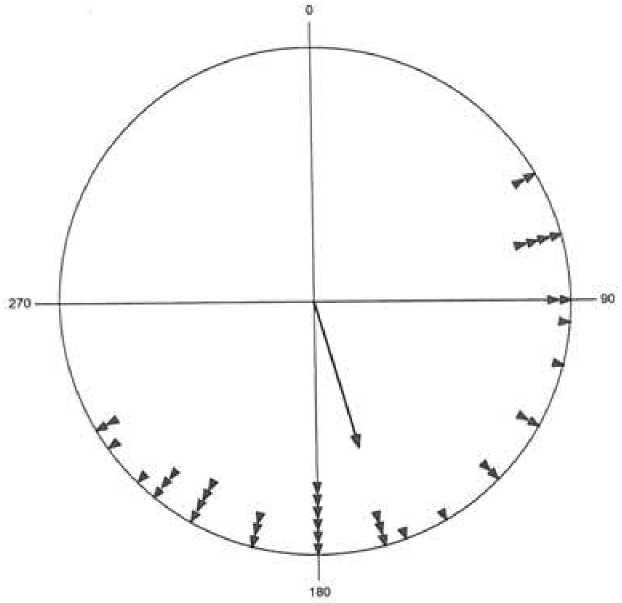

Figure 6.19. Orientation of the failed nests on plants used for nesting.

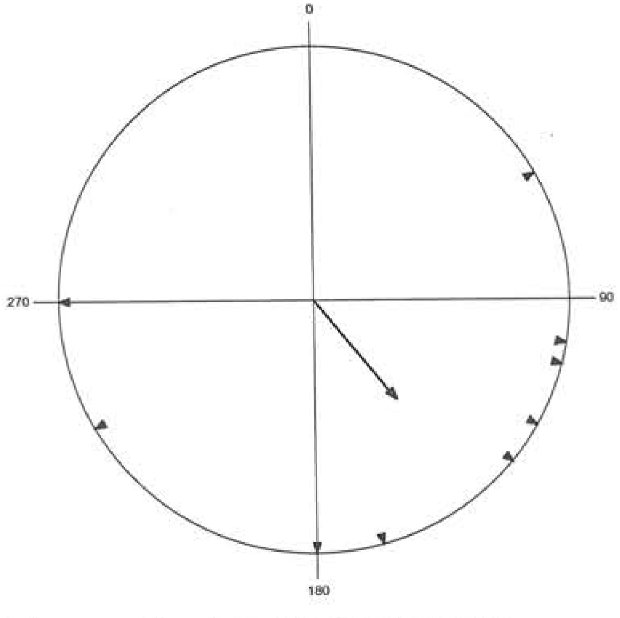

Figure 6.20. Orientation of the successful nests on plants used for nesting.

6.4.8. Nesting plants

Grey-headed Bulbuls nested in *Strobilanthes* and reed breaks. Nests were not distributed uniformly across all the similar habitats within the intensive study areas. Most of the nests located were on live plants, except a few which were on the dead branches of *Ochlandra travancorica, Strobilanthes foliosus* and sapling of *Syzygium sp.* Twelve species of plants were used by Grey-headed Bulbul for nesting. *Ochlandra travancorica* (38.89%) and *saplings* of *Syzygium sp.* (33.33%) were the most used plant species. (Table 6.9)

Table 6.9. Plant species used by Grey-headed Bulbul for nesting during 2002-2005 with their frequency and success rate.

Sl. No.	Plant species	No. of nests (%)	Successful (%)	Fledged/nest	Fledged/succ. nests
1	*Ochlandra travancorica*	21 (38.89)	19.05	0.33	1.75
2	*Syzygium sp. sapling*	18 (33.33)	5.56	0.06	1.00
3	*Calamus pseudo-tenuis*	3 (5.56)	66.67	1.33	2.00
4	*Laseanthus jackianus*	2 (3.70)	0.00	0.00	0.00
5	*Thottea siliquosa*	2 (3.70)	0.00	0.00	0.00
6	*Un-identified shrub*	2 (3.70)	50.00	0.50	1.00
7	*Oreocnide integrifolia*	1 (1.85)	100.00	2.00	2.00
8	*Antidesma menasu*	1 (1.85)	0.00	0.00	0.00
9	*Saprosma glomerata*	1 (1.85)	0.00	0.00	0.00
10	*Strobilanthes foliosus*	1 (1.85)	0.00	0.00	0.00
11	*Sarcococca coriacea*	1 (1.85)	0.00	0.00	0.00
12	*Un-identified sapling*	1 (1.85)	0.00	0.00	0.00

6.4.8.1. Determinants of nesting plant selection

Of the 12 plant species used for nesting, two (*Ochlandra travancorica* and saplings of *Syzygium* sp.) together bear 72.22% of nests. All the moss nests were on *Ochlandra travancorica,* except one recorded on *Strobilanthes foliosus.* Of the 35 vine type nests, 18 were on the saplings of *Syzygium* sp. The branching pattern of both the species appeared to be supportive for the nest of Grey-headed Bulbul, as the nests attached to the plant on 'multiple sides'. In general, the foliage cover of *Ochlandra* is considerably higher and thus provides greater concealment and a camouflaging background to the moss nests. On the other hand, most of the *Syzygium* saplings had less foliage cover. However, these plants were surrounded by several stems (saplings, shrubs and lianas) which provide a pale camouflaging background to the vine nests. A few vine nests found on *Ochlandra* were placed in a pale background surrounded by dry stems. Although the strategies are different for both the nest types, they support the hypothesis of 'background matching'.

All the *Ochlandra travancorica* nest sites were dominated by the same plant species (189.80±22.46 stems/0.008 ha) except in one case. This might reduce the probability of being discovered by the predator. Moreover, the abundance of sub-canopy trees was very low in the *Ochlandra* nest sites (13.35±2.21/0.04 ha) compared to those on *Syzygium* sites (37.06±5.09/0.04 ha; $F = 48.153$, $p < 0.001$). This may reduce the perching sites and movement of squirrels and avian predators searching for eggs and nestlings in *Ochlandra* sites. On the other hand the saplings of *Syzigium* were 'rare' nest sites in such patches. However, success of the nests placed on the *Syzygium* saplings were considerably lower than those placed on *Ochlandra travancorica* (see Table 6.9).

Of the three nests placed on *Calamus pseudo-tenuis* two were successful and are highly camouflaged with the surroundings. One of the successful nest made with fresh leaves had high foliage cover at the nest height and the second one was surrounded by liana draped stems, which provide a pale camouflaging background. However, the factors favoured the selection of these plants may be more complex than these observations.

6.4.9. Copulation and egg laying

Birds were highly secretive during the early phase of breeding. Only one instance of copulation behaviour could be observed. During this, birds were perched on a *Litsea floribunda* tree at a height of about 10 meters and the mounting lasted for five seconds. A single event of allopreening also observed. One egg was laid per day, and incubation started with the last egg. Vocalization was very limited during the construction and egg laying periods, especially at the immediate vicinity of the nests. During incubation period, both the birds foraged away from the immediate vicinity of the nests. No mate feeding was recorded during breeding. Calls from a perch, away from the nest were commonly heard during incubation. These calls appear to be contact calls and the frequency of the same increased during nest stages in which eggs or nestlings were present.

6.4.10. Clutch and brood sizes

The average clutch size of Grey-headed Bulbul was 1.53±0.50 eggs (range: 1–2, $n = 47$), with 53% of clutches with two and the remaining (47%) with one egg. There was a marked difference in the clutch size between the moss and vine nests. Of the 31 vine nests monitored 71% of clutches were with one egg and 29% with two eggs. All the moss nests monitored ($n = 15$) produced two eggs each. There was a significant reduction in the clutch size by the advance of the breeding season ($r_s = -457$, $n = 46$; $p < 0.01$; Figure 6.21). Egg size attributes were not measured considering the vulnerability due to predation. However, a single egg was measured when it fell down from the nest due to large animal movement. The length of this egg was 2.2 cm and breadth 1.5 cm.

Since the study population was not colour marked, the estimation of the brood size was quite difficult. Most species of bulbuls raise more than one brood per year. Available data suggest that Grey-headed Bulbul is a single-brooding passerine, although, possibility of a replacement brood cannot be ignored. Moreover, in spite of the extensive search in all territories, the number of nests recorded were fewer than the total number of pairs recorded in all the breeding seasons. The birds never reused the nests and no new nests were recorded in a territory where the predation occurred.

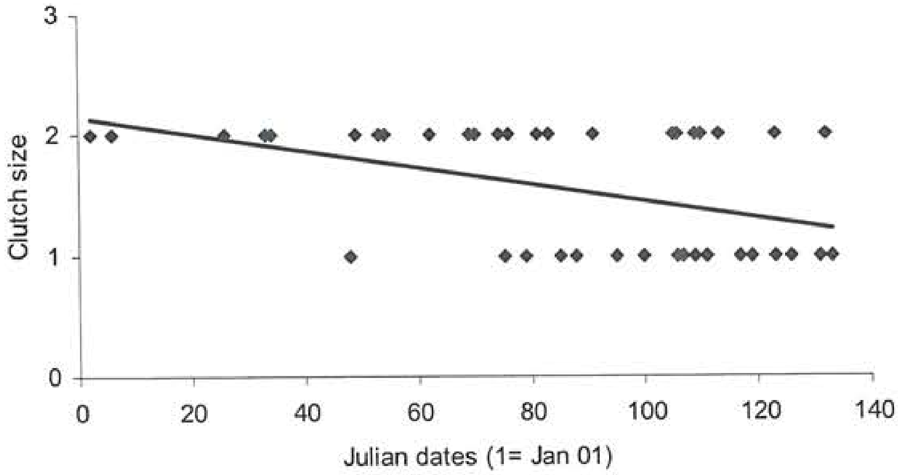

Figure 6.21. Relationship between the clutch initiation date and clutch size, combining all data for the three years (2003-2005).

6.4.11. Incubation and nestling period

The mean incubation period for all the nests for which a complete record is available from the clutch completion to hatching was 13.00±0.87 days (range = 12-14 days, n = 9 nests). Nestlings spent an average of 12±0.50 days (range = 11-13 days, n = 9 nests) in the nest. The nesting period from the start of incubation to fledgling lasted for 25±0.89 days (range: 24-26 days, n = 6 nests).

6.4.12. Nesting success

6.4.12.1. Apparent nest success

Forty-seven active bulbul nests with eggs or fledglings were found and monitored at Silent Valley and the surrounding areas during 2003–2005. Most of the nests were located during the egg laying and incubation stages. Seven nests with unknown fates were excluded from the analysis. Nine out of 47 nests were successful. Out of these, six nests produced two chicks each and the remaining one each. Apparent nest success declined each year (2003: 42.86%, n = 14; 2004: 13.33%, n =15; 2005: 5.56% n =18).

Table 6.10. Annual variation in the breeding performance of Grey-headed Bulbul in Silent Valley National Park and surrounding areas, 2003-2005. (*calculated as an index of chick fledged versus eggs laid).

Nesting parameters	2003		2004		2005		Pooled	
	No.	%	No.	%	No.	%	No.	%
Total nests	14		15		18		47	
Moss nests	6	42.86	4	26.67	5	27.78	15	31.91
Vine nests	7	50.00	11	73.33	13	72.22	31	65.96
Leaf nests	1	7.14	0	0	0	0	1	2.13
Nest with two eggs	8	57.14	6	40.00	11	61.11	25	53.19
Nest with one egg	6	42.86	9	60.00	7	38.89	22	46.81
Total eggs laid	22		21		29		72	
Egg predation/destruction	9	40.91	16	76.19	23	79.31	48	66.67
Chick hatched	13	59.09	5	23.81	6	20.69	24	33.33
Chick predation	2	15.38	2	40.00	5	66.67	9	37.50
Chick fledged	11	84.62	3	60.00	1	16.67	15	62.50
*Overall nesting success**		50.00		14.29		3.45		20.83

The overall nesting success was 20.83% when the number of young versus the eggs laid is considered as an index of success (15 chicks were fledged from 72 eggs of 47 nests, Table 6.10). Egg mortality was quite heavy (66.67%) due to high predation and it varied significantly between breeding seasons. Out of 72 eggs laid, only 24 (33.33%) were hatched. Nine chicks disappeared from the nests because of predation (Table 6.10).

Table 6.11. Mayfield estimates of nest survival for different reproductive stages of Grey-headed Bulbul. (*n is the number of nests monitored and number of successful nests in each stage).

Reproductive period	Nest exposure Days	Daily mortality rate	Daily survival rate	Nest survival variance	Confidence interval (95%)	Mayfield nest success (%)
Incubation (*n* = 47,14)*	326	0.101	0.899±0.017	2.791×10^{-4}	(0.866, 0.932)	24.97
Nestling (*n* = 14, 9)*	120	0.042	0.958±0.018	3.328×10^{-4}	(0.923, 0.994)	60.01
Overall nesting (*n* = 47, 9)*	446	0.085	0.915±0.013	1.748×10^{-4}	(0.889, 0.941)	10.79

Table 6.12. Mayfield estimates of nest survival of Grey-headed Bulbul in the different years. (**n* = number of nests monitored, number of successful nests in each year).

Year	Nest exposure Days	Daily mortality Rate	Daily survival rate	Nest survival variance	Confidence interval (95%)	Mayfield nest success (%)
2003 (*n* = 14,6)*	180	0.044	0.956±0.015	2.359×10^{-4}	(0.925, 0.987)	32.00
2004 (*n* = 15,2)*	102	0.108	0.892±0.028	8.050×10^{-4}	(0.836, 0.947)	5.69
2005 (*n* = 18,1)*	155	0.116	0.884±0.027	7.047×10^{-4}	(0.832, 0.936)	4.53

6.4.12.2. Mayfield estimator

The mortality rate for the incubation period was 0.101 failures per nest-day (33 failures/326 nest-days), and the survival rate for this 13-day period was 0.25 [$= (1 - 0.101)^{13}$]. The mortality rate for the nestling period was 0.042 failures per nest-day (5 failures/120 nest-days), and the survival rate for this period (= 12 days) was 0.60. The overall success rate was

10.79% (Table 6.11). There was no significant difference in the daily survival rates among years (range: 0.884–0.956). However, nesting success significantly varied among years (2003: 32%, 2004: 5.69%, 2005: 4.53%; Table 6.12).

6.4.13. Correlates of success

6.4.13.1. Nest success in relation to initiation date

The first nest of each season started in mid January and ended in mid May. The temporal distribution of nests monitored in the three breeding seasons had similar means (Kruskal-Wallis *H*, $\chi^2 = 0.023$, $p = 0.989$). The probability of nest survival decreased with the advance in the nesting season ($r_s = 0.475$, $n = 46$, $p < 0.001$). The late season nests had high mortality rate compared to those in early nests (Mann–Whitney *U*-test: $z = -3.055$, $p < 0.001$; Figure 6.22).

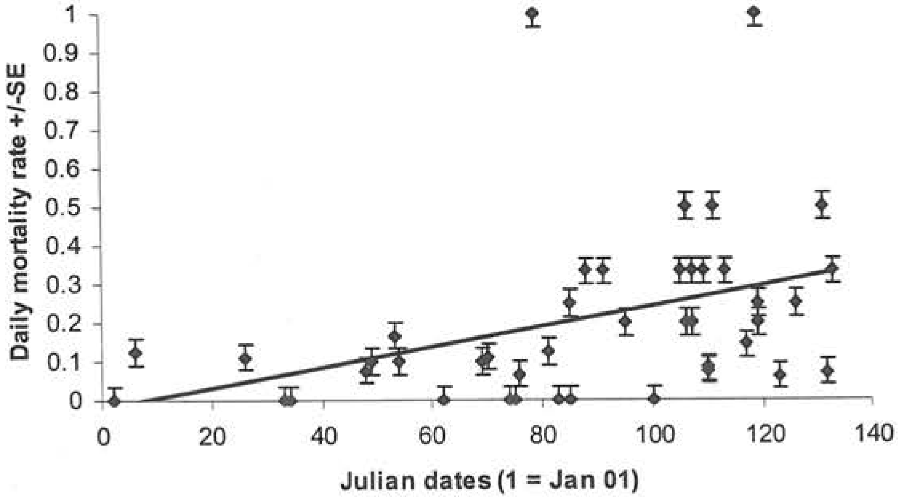

Figure 6.22. Relationship between nest initiation date and daily mortality rate, combining all data for the three years (2003-2005).

6.4.13.2. Nest types and success

Applying Mayfield's method, there was no significant variation in the egg survival among the moss (25.42%) and vine nests (22.33%). However, chicks of moss nests had a significantly better chance of surviving the nestling period (100%) than those of vine nests (34.55%). Consequently, overall nesting success of moss nests (16.66%) was significantly higher than the vine nests (6.52%, Table: 6.13). Apparent nesting success varied between the moss nests (26.67% of 15 nests) and vine nests (12.9% of 31 nests). Of the five moss nests recorded in 2003, four successfully fledged two chicks each, while none of the moss nests produced fledgling during the successive years. The leaf nest recorded in 2003 successfully fledged two chicks. Although the nest success varied significantly among the nest types, there was no significant variation in the nest morphometry between successful and failed nests (One way ANOVA, $p > 0.05$; Table 6.14).

Table 6.13. Daily survival probabilities (mean±SE) of eggs and nestlings and, percentage success for the incubation, nestling and overall nesting (incubation + nestling) periods estimated using Mayfield's method for the moss and vine nests of Grey-headed Bulbul in the Silent Valley National Park and surrounding areas.

Reproductive period	Estimated parameter	Moss nest ($n = 15$)	Vine nest ($n = 31$)
Incubation	Daily survival rate	0.900±0.029	0.891±0.022
	Egg survival variance	8.182 x 10^{-4}	4.804 x 10^{-4}
	95% confidence interval	(0.844, 0.956)	(0.848, 0.934)
	Percent success	25.42	22.33
Nestling	Daily survival rate	1.000±0.000	0.915±0.036
	Chick survival variance	0.000	1.315 x 10^{-3}
	95% confidence interval	(1.000, 1.000)	(0.844, 0.986)
	Percent success	100	34.55
Overall nesting	Daily survival rate	0.931±0.020	0.897±0.019
	Nest survival variance	4.050 x 10^{-4}	3.554 x 10^{-4}
	95% confidence interval	(0.891, 0.970)	(0.860, 0.933)
	Percent success	16.66	6.52

Table 6.14. Comparison of the morphometry of the successful and unsuccessful Grey-headed Bulbul nests.

Nest size variables	Successful nests ($n = 9$)	Failed nests ($n = 27$)	F	p
Outer diameter (cm)	7.70±1.19	7.29±1.08	0.934	0.341
Inner diameter (cm)	6.06±0.79	5.69±0.69	1.768	0.192
Outer depth (cm)	6.41±1.30	5.76±1.14	2.093	0.157
Inner depth (cm)	3.99±1.03	3.63±0.90	0.987	0.328
Thickness (cm)	1.64±0.47	1.60±0.46	0.062	0.804
Cup volume (cm^3)	232.57±151.14	259.94±112.45	1.817	0.187
Material volume (cm^3)	532.95±273.95	418.79±187.53	1.975	0.169

6.4.13.3. Nest placement, concealment and success

The vertical placement seems to be an important factor determining the fate of the nest. The mean nest height of successful nests (2.04±1.24 m) was higher than that of failed nests (1.39±0.62 m; One-Way ANOVA: F = 5.378, p < 0.05). Similarly, the nest plants of successful nests (3.81±1.91 m) were significantly taller than those of failed nests (2.53±1.34 m; One-Way ANOVA: F = 5.666, p = 0.05, Figure 6.23). However, there was no difference in the relative nest heights between the successful and failed nests (One-Way ANOVA: F = 0.573; p = 0.453, Figure 6.24). The nest height in the successful moss nests was higher than that of the failed nests (One-Way ANOVA: F = 9.465, p < 0.01). All the successful moss nests were placed in the middle of the nesting plant and thus apparently received high concealment over the nest. However, there was no significant difference in the nest heights of successful and failed vine nests (One-Way ANOVA: F = 1.156, p = 0.291).

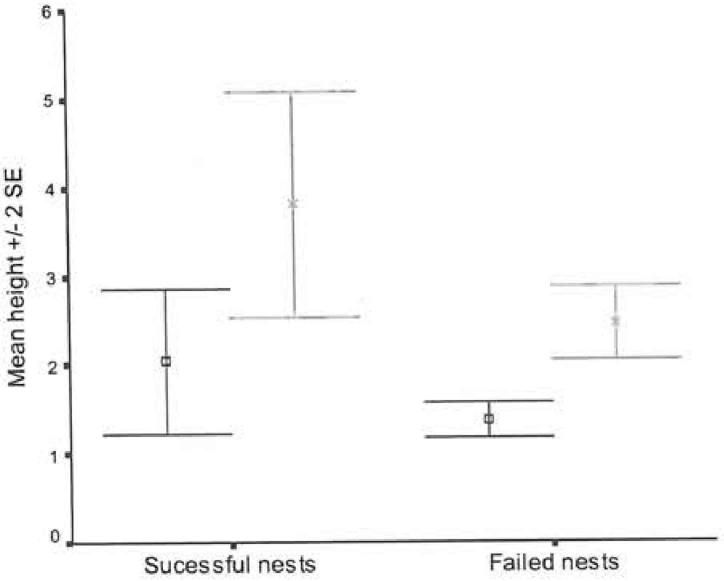

Figure 6.23. Variation in the nest height (□) and height of the nesting plants (x) between successful and failed nests.

Nest concealment, as indexed as a combined variable by the cover in four cardinal directions and cover above and below the nest, was higher for the successful nests (17.28±9.52) than for the failed nests (13.12±7.95). Although it was not statistically significant (One-way ANOVA: F = 1.856, p = 0.180), the concealment index for successful nests was considerably higher than that for both moss (13.56±4.96) and vine nests (13.24±9.11). The nesting success was not influenced by the distance to the nearest foliage edge from the nest in general ($t = -1.009$, $p < 0.318$) and, within the moss ($t = -0.799$, $p < 0.437$) and vine nests ($t = -0.531$, $p < 0.599$). However, all the moss nests were placed within or very close to the foliage compared to the vine nests (3.00±1.41cm *vs*. 8.59±10.32 cm; $n = 17, 32$; $t = -2.212$, $p = 0.05$). Furthermore, the high shrub density in the successful nest sites can be inferred as high foliage or leaf cover over the nests, since all the nests of Grey-headed Bulbul was recorded from the shrub layer.

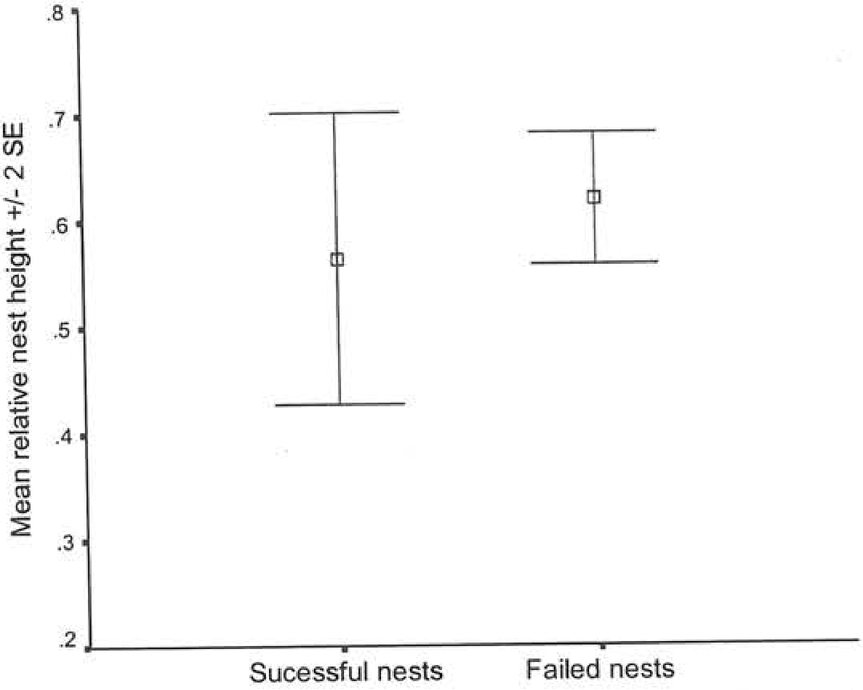

Figure 6.24. Comparison of the relative nest heights between the successful and failed nests of Grey-headed Bulbul.

6.4.13.4. Habitat structure and success

Habitat structure of successful and failed nests was similar in both meso- and micro-scale plots (One-way ANOVA, $p < 0.05$; Tables 6.15, 6.16), except for the nest tree characteristics which is contributed by the general differences in the nest placement among moss and vine nests (see section 6.4.6). A principal component analysis of 15 meso-scale habitat variables resulted in five components that together accounted for 65.60% of the variance (Table 6.17). However, these components were difficult to interpret thus all the variables were included in further analyses. The canonical discriminant function analysis also failed to discriminate the successful nest sites from the failed nest sites. None of the discriminant functions were significant in the analysis of the meso-scale habitat variables (Wilk's Lambda = 0.648, $\chi^2 = 17.588$, $p = 0.285$; Table 6.19).

The 14 original variables included in the principal component analysis were summarised into six PCs with an eigenvalue larger than 1, and these accounted for 72.73% of total variance (Table 6.18). However, the contribution of each variable to these principal components and their influence on the nest success were difficult to interpret. The canonical discriminant function analysis performed to differentiate the successful nest sites from the failed nest sites was unsuccessful and none of the discriminant functions were significant at $p < 0.01$ (Wilk's Lambda = 0.530, $\chi^2 = 26.055$). The structure matrixes of each of the micro-scale variable in this analysis are given in Table 6.19.

Table 6.15. Mean values (±SE) for the habitat characteristics at successful and failed nests of Grey-headed Bulbul measured at the meso-scale.

Variables	Code	Successful nests ($n = 9$)	Failed nests ($n = 41$)	F	p
Mean tree height (m)	MNTHT	11.97±1.10	10.32±0.43	2.439	0.125
Max tree height (m)	MXTHT	22.22±1.77	21.46±0.83	0.150	0.700
Mean tree GBH (cm)	MNTGBH	63.80±10.61	55.90±4.05	0.631	0.431
Tree density (#/plot)	TRDEN	39.22±7.69	42.12±3.64	0.114	0.737
Canopy tree density (#/plot)	CTDEN	18.89±4.56	12.76±1.30	3.110	0.084
Sub-canopy density (#/plot)	SBDEN	18.33±4.60	27.02±3.10	1.548	0.219
Food trees (#/plot)	FTDEN	17.44±5.01	18.76±2.08	0.068	0.795
Food shrubs & liana (#/plot)	FSLDEN	32.00±20.11	20.61±4.65	0.712	0.403
Dead tree density (#/plot)	DDTDEN	0.89±0.42	0.80±0.28	0.017	0.895
Downed tree density (#/plot)	DNTDEN	2.22±0.76	1.17±0.23	2.982	0.091
Percent bare ground	PBG	6.00±4.30	5.17±1.27	0.061	0.806
Percent rock cover	PRC	10.22±5.66	12.24±2.75	0.099	0.755
Percent epiphyte cover	PEPI	0.89±0.31	1.71±0.55	0.468	0.497
Percent canopy cover	PCC	34.44±7.43	35.00±2.86	0.006	0.937
Percent sub-canopy cover	PSCC	56.11±7.06	54.27±3.18	0.060	0.808
Percent shrub cover	PSC	77.78±4.94	73.90±1.93	0.675	0.415
Percent ground cover	PGC	68.33±7.64	70.98±2.88	0.139	0.711

6.4.13.5. Predation risk and success

The daily mortality rates were positively correlated with the predator abundance ($r_s = 0.815$, $n = 33$, $p < 0.001$; Figure 6.25). Successful nest sites had low predator abundance compared to the depredated nest sites (0.70±0.24/count *vs*. 3.04±1.25/count; $t = -5.221, p < 0.001$). The low nest success at the vine nests compared to that at the moss nests can be interpreted as a result of the high predator abundance.

Besides predation, an important cause of nest failure appeared to be the destruction from trampling by the animals. A few nests were found destroyed by the movement of elephants and other large vertebrates such as Sambar Deer *Cervus unicolor*. Nests in the reed patches which are a major feeding ground for the Asian Elephant seemed to be highly vulnerable. Use of steep terrains within the reed patches by Grey-headed Bulbul may be an adaptation against this. Of the nine successful nests, seven were placed on the plants in steep terrains, thus avoid disturbance by animal movement.

Table 6.16. Mean values (±SE) for the habitat characteristics at successful and failed nests of Grey-headed Bulbul measured at the micro-scale.

Variables	Code	Successful nests ($n = 9$)	Failed nests ($n = 41$)	F	p
Nest plant height (m)	HTNP	3.81±0.64	2.47±0.21	6.317	0.015
Nest plant GBH (cm)	GBHNP	6.02±0.99	4.49±0.20	6.102	0.017
Nest plant species density (#/plot)	NPDEN	106.00±40.92	82.17±16.19	0.366	0.548
Sapling density (#/plot)	SAPDEN	19.56±6.33	28.05±3.38	1.180	0.283
Shrub density (#/plot)	SHBDEN	207.11±28.50	179.61±16.95	0.506	0.480
Dominant plant density (#/plot)	DODEN	172.78±26.31	116.41±13.94	3.055	0.087
Co-dominant plant density (#/plot)	CDDEN	29.67±5.74	32.46±3.51	0.122	0.728
Strobilanthes density (#/plot)	SBDEN	19.67±12.27	38.24±7.74	1.548	0.219
Reed density (#/plot)	REETDEN	80.44±33.57	85.51±18.81	0.014	0.907
Live reed density (#/plot)	REELDEN	59.89±25.38	62.07±13.62	0.005	0.945
Dead reed density (#/plot)	REEDDDEN	20.56±9.18	23.44±6.13	0.044	0.836
Pteridophyte density (#/plot)	PTEDEN	5.22±1.73	4.46±0.78	0.172	0.680
Liana density (#/plot)	LNDEN	36.56±26.28	13.80±1.99	3.261	0.770
Litter depth (cm)	LTRDPT	4.67±0.33	4.68±0.22	0.001	0.974
Distance to water (m)	DTWTR	7.75±2.63	9.97±1.45	0.442	0.510
Distance to trek path (m)	DTTKP	25.46±9.59	29.06±6.83	0.550	0.815
Distance to animal trail (m)	DTANT	3.41±0.99	3.49±0.74	0.002	0.961
Distance to adjacent tree (m)	DTNT	2.61±0.51	2.42±0.22	0.143	0.707
Height of adjacent tree (m)	HTNT	11.50±2.66	11.25±0.82	0.014	0.907
GBH of adjacent tree (cm)	GBHNT	52.78±16.02	57.88±5.72	0.128	0.722
Distance to adjacent shrub (m)	DTNS	1.08±1.06	0.70±0.47	2.949	0.092
Height of adjacent shrub (m)	HTNS	2.57±0.43	1.97±0.19	1.698	0.199
GBH of adjacent shrub (cm)	GBHNS	6.22±1.33	4.07±0.38	4.540	0.038

Table 6.17. Results of the principal components analysis of the meso-scale habitat structure.

Variables	PC1	PC2	PC3	PC4	PC5
Eigenvalue	3.448	1.911	1.789	1.48	1.212
Variation explained (%)	22.99	12.74	11.93	9.87	8.08
Cumulative %	22.99	35.73	47.66	57.52	65.60
MNTGBH	-0.855	-0.137	0.094	-0.061	-0.013
TRDEN	0.737	0.528	0.092	0.040	-0.195
MNTHT	-0.718	-0.009	-0.191	0.118	0.053
MXTHT	-0.711	0.379	0.050	0.151	-0.176
PEPI	0.498	0.266	0.306	0.042	0.186
CTDEN	-0.074	0.841	-0.118	0.058	0.085
PCC	0.244	0.797	0.142	0.097	-0.088
PGC	0.013	-0.041	0.879	0.126	-0.075
PSC	0.080	0.039	0.807	-0.097	0.207
FSLDEN	0.300	0.312	0.338	-0.228	-0.276
DDTDEN	0.009	0.053	0.145	0.856	-0.075
DNTDEN	-0.095	0.085	-0.094	0.697	0.040
PBG	0.020	0.136	0.150	-0.229	0.747
PRC	0.260	-0.099	-0.184	0.326	0.608
PSCC	0.421	0.245	-0.210	-0.033	-0.529

Table 6.18. Results of the principal components analysis of the micro-scale habitat structure.

Variables	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	3.317	1.857	1.559	1.353	1.056	1.040
Variation (%)	23.69	13.26	11.13	9.67	7.54	7.43
Cumulative %	23.69	36.96	48.09	57.76	65.30	72.73
NPHT	0.732	0.335	0.412	0.085	0.054	0.071
DTTKP	0.715	-0.058	-0.102	0.084	-0.056	-0.018
NPGBH	0.676	0.309	0.176	-0.143	0.048	0.165
SAPDEN	-0.521	-0.058	0.233	0.461	0.021	0.016
CDDEN	-0.474	0.468	0.377	-0.027	-0.361	-0.113
SHBDEN	0.043	0.950	0.007	-0.060	0.033	0.028
REETDEN	0.344	0.776	-0.149	-0.206	0.154	-0.078
DTANT	-0.054	-0.087	0.801	0.058	-0.118	-0.104
HTNS	0.212	0.034	0.627	-0.132	0.517	-0.164
LNDEN	0.123	-0.102	-0.006	0.854	-0.115	0.016
HTNT	0.318	0.226	0.313	-0.493	-0.146	0.434
DTNS	-0.058	0.105	-0.065	-0.047	0.871	0.056
DTWTR	0.134	-0.015	-0.316	-0.050	0.006	0.813
DTNT	0.405	0.239	-0.198	-0.326	-0.314	-0.500

Table 6.19. Summary of the discriminant function analysis of habitat features at successful and failed nest sites of Grey-headed Bulbul.

Meso-scale		*Micro-scale*	
	DF1		DF1
Canonical correlation	0.594	Canonical correlation	0.686
Wilk's lambda	0.648	Wilk's lambda	0.530
Chi-square	17.588	Chi-square	26.055
Eigenvalue	0.544	Eigenvalue	0.888
Significance level	0.285	Significance level	0.025
Variables entered	Structure matrix	Variables entered	Structure matrix
CTDEN	0.345	NPHT	0.386
DNTDEN	0.338	NPGBH	0.378
PSC	0.225	DTNS	0.304
PSCC	0.178	LNDEN	0.277
FSLDEN	0.165	HTNS	0.200
MNTHT	0.161	SAPDEN	-0.166
MNTGBH	0.155	SHBDEN	0.109
PRC	-0.103	DTWTR	-0.102
PBG	-0.091	DTNT	0.058
MXTHT	0.076	CDDEN	-0.054
TRDEN	-0.066	DTTKP	-0.036
PCC	-0.031	HTNT	0.018
PEPI	-0.030	REETDEN	-0.018
DDTDEN	0.026	DTANT	-0.008
PGC	-0.012		

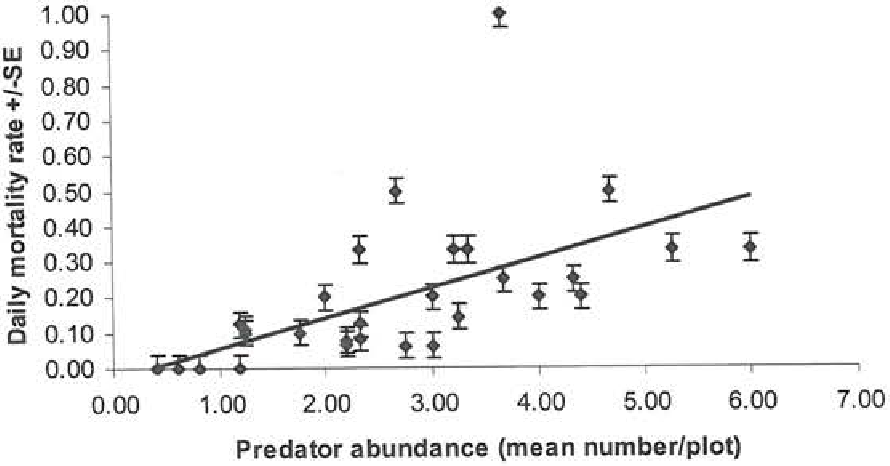

Figure 6.25. Predator abundance and daily mortality rates for Grey-headed Bulbul nests.

6.4.13.6. Inter and intra specific proximity of nests

No overlap with the neighbouring pairs was recorded because of the dispersed distribution of Grey-headed Bulbul. Minimum neighbour distance was at least 500 m for all the live nest sites. Availability and patchiness of the suitable habitats determined the distribution of breeding Grey-headed Bulbuls. Although they avoided the patches occupied by other bulbul species, nesting of species such as Dark-fronted Babbler, Emerald Dove, Mountain Imperial Pigeon, Green Imperial Pigeon and Brown-cheeked Fulvetta was recorded within 30 m radius of Grey-headed Bulbul nests with an average of 1.00±1.11 nests. Minimum distance from Grey-headed Bulbul nest to the nearest nest of other species was five metres (nest of Dark-fronted Babbler). The distances to the closest Yellow-browed and Black Bulbul nests were 43 m and 32 m respectively. The mean number of nests of other species was low as 0.04±0.20 nests within 10 m of Grey-headed Bulbul nests. However, the daily mortality rate was significantly correlated with the number of other species nests with in 30 m radius of Grey-headed Bulbul nests ($r_s = 0.326$, $n = 48$, $p < 0.05$; Figure 6.26). This shows that the nests placed in patches not exploited by other breeding birds had higher chances of survival.

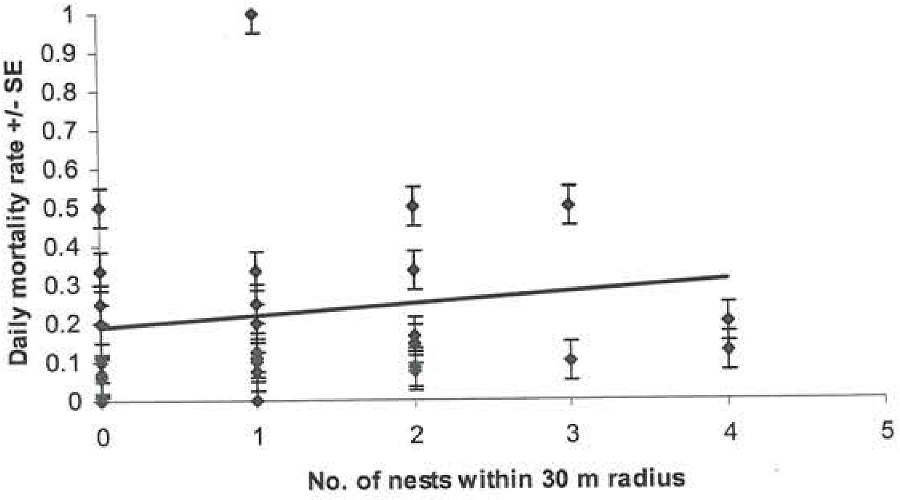

Figure 6.26. Correlation between the number of other species' nests and daily mortality rates for Grey-headed Bulbul nests.

6.4.14. Parental care

6.4.14.1. General patterns

Nest attentiveness progressed from an average of 64.10% on the 1st day to a maximum of 89.10% on the 12th day of incubation. In general, percentage nest attentiveness was higher (48.88±36.93%; range: 2.78-95.00%) during morning hours, and least (40.99±31.23%, range: 2.50-83.89%) during 09.00-12.00 hrs. Results of the repeated-measures ANOVA show a significant variation in the nest attentiveness between the incubation and nestling phases in different daylight hours ($F = 14.07$, $p < 0001$; Table 6.20). The attending parent bird spent an average of 75.12±7.35% of daylight hours at the nest during incubation and 14.22±3.50% during the nestling period.

Mean on-bout and off-bout periods (attentive and inattentive periods) were 26.39±24.01 min and 17.45±5.25 min respectively, for the entire nesting period. On-bout durations were longer (33.00±29.74 min; range: 0.25-85.50 min) during 06.00-09.00 hrs and least (20.34±19.30 min, range: 0.24-63.50 min) during 09.00-12.00 hrs. The mean number of nest visits/hr was 2.60±2.23. There was a significant variation in the on-bout durations between the nesting phases across the different daylight hours ($F = 15.72$, $p < 0.0001$, Table 6.20). However, there was no difference in the off-bout durations between the nesting phases ($F = 1.05$, $p = 0.364$). This indicates that the birds took larger foraging bouts to meet their energy needs during both the phases of nesting. Maximum number of trips was in the evening hours 15.00-18.00 (3.15±2.78; range: 0.33-7.67 trips/hr) and minimum (2.05±1.82; range: 0.33-5.33 trips/hr) during 12.00-15.00 hrs. Mean number of trips/hr was very high during the chick rearing phase (1.00-7.67 trips/hr) compared to the incubation stage (0.33-1.33 trips/hr) across different times of the day ($F = 29.89$, $p < 0.0001$, Table 6.20).

Table 6.20. Comparison of the parental care patterns between the nesting phases across different daylight hours.

Source	Dependant variable	Type III Sum of squares	Df	Mean square	F	p
Daylight hours	Attentiveness	982.97	3	516.71	14.07*	0.001
	On-bout duration	1876.91	3	625.63	15.72	0.001
	Off-bout duration	60.57	3	26.04	1.05*	0.364
	Nest trips	21.90	3	7.30	29.89*	0.001

6.4.14.2. Parental care patterns of broods with different clutch sizes

6.4.14.2.1. Incubation stage

Comparison of the parental care patterns between the nests with different clutches revealed a significant difference (repeated–measures ANOVA, $p < 0.01$; Table 6.21) in all the parameters, except off-bout duration across daylight hours (Figures 6.27, 6.30). During the incubation period the birds were most attentive (80.32±6.28%) during 06.00-09.00 hrs and least attentive (66.00±7.56%) during 09.00-12.00 hrs (Figure 6.27). During the daytime, incubation was intermittent with relatively longer bouts of incubation being interspersed with bouts of foraging during which the clutch is left unattended. Mean attentive periods (on-bout durations) for the nests with two eggs were significantly higher (53.33±11.84 min; range: 25.25–87.00 min) than the nests with single egg (39.69±7.91 min; range: 21.50–84; Figure 6.29). The mean off-bout durations were 21.34 min for nests with 2 eggs and 20.81 min for nests with single egg. The birds with single egg made more trips (0.79±0.23 trips/hr) than the birds incubating two eggs (0.66±0.11 trips/hr; Figure 6.28).

Table 6.21. Comparison of the parental care patterns of Grey-headed Bulbul with different clutch sizes across daylight hours and different days during incubation period (**F* statistics after Greenhouse-Geisser adjustment).

Source	Dependant variable	Type III Sum of squares	Df	Mean square	*F*	*p*
Daylight hours	Attentiveness	3568.43	3	1189.47	45.49	0.001
	On-bout duration	6465.00	3	3033.60	14.65*	0.001
	Off-bout duration	403.27	3	178.74	2.82*	0.062
	Nest trips	2.10	3	0.70	13.25	0.001
Incubation days	Attentiveness	2148.50	12	179.04	9.74	0.001
	On-bout duration	6866.94	12	572.24	2.98	0.005
	Off-bout duration	883.19	12	73.60	1.18	0.331
	Nest trips	1.05	12	0.087	1.83	0.081

Almost similar parental behaviour were seen in different days of the incubation period (repeated–measures ANOVA, $p < 0.01$; Table 6.21). The nest attentiveness increased with the progress of incubation for both type of nests (Figure 6.31). Mean nest attentiveness was marginally higher in nests with single egg than in nest with two eggs (range $_{\text{two egg}}$ = 54.53–75.84%, range $_{\text{one egg}}$ = 60.28 – 86.39%). However, the average attentive periods (on-bout duration) were significantly higher in nests with two eggs ($F = 0.98$, $p = < 0.01$; range $_{\text{two egg}}$ = 39.17–82.63 min, range $_{\text{one egg}}$ = 28.13–63.25 min; Figure 6.33). The off-bout durations (range $_{\text{two egg}}$ = 14.75–26.92 min, range $_{\text{one egg}}$ = 17.08–23.00 min) and nest trips/hr (range $_{\text{two egg}}$ = 0.33–0.83 trips/hr, range $_{\text{one egg}}$ = 0.42–1.17 trips/hr) were not differed among the nests with different clutch sizes (Table 6.21; Figures 6.32, 6.34). This shows that the time devoted for foraging was independent of the progress in incubation, although foraging bouts varied significantly within the day.

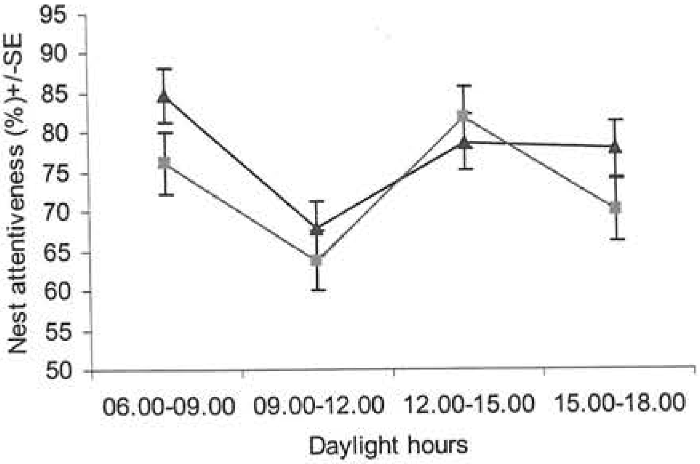

Figure 6.27. Nest attentiveness of Grey-headed Bulbul during incubation across daylight hours (■: nest with one egg; ▲: nest with two eggs).

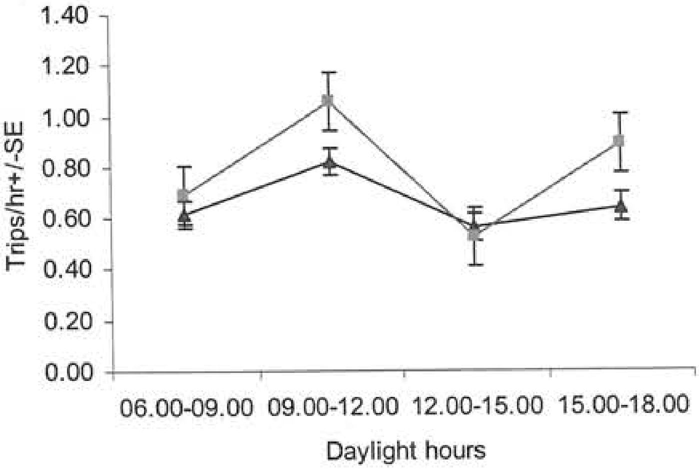

Figure 6.28. Mean nest trips/hr of Grey-headed Bulbul during incubation across daylight hours (■: nest with one egg; ▲: nest with two eggs).

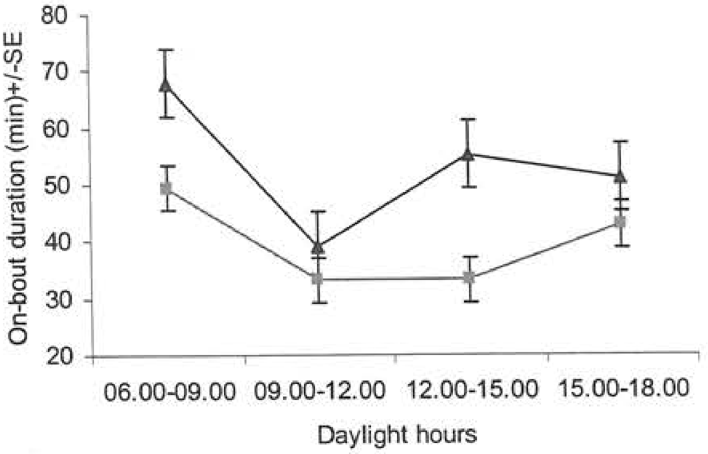

Figure 6.29. Mean on-bout durations/hr of Grey-headed Bulbul during incubation across daylight hours (■: nest with one egg; ▲: nest with two eggs).

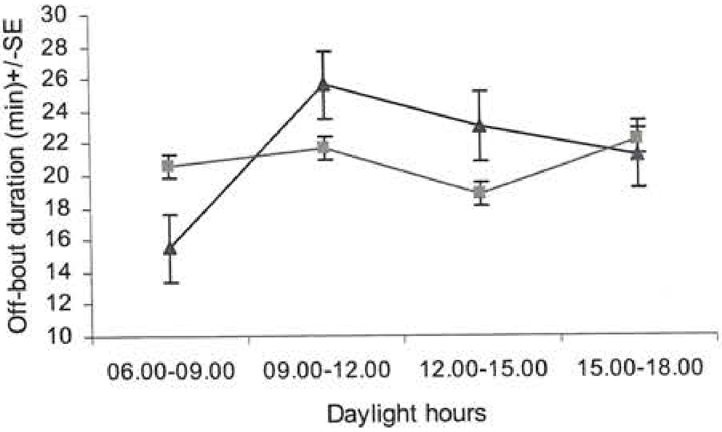

Figure 6.30. Mean off-bout durations/hr of Grey-headed Bulbul during incubation across daylight hours (■: nest with one egg; ▲: nest with two eggs).

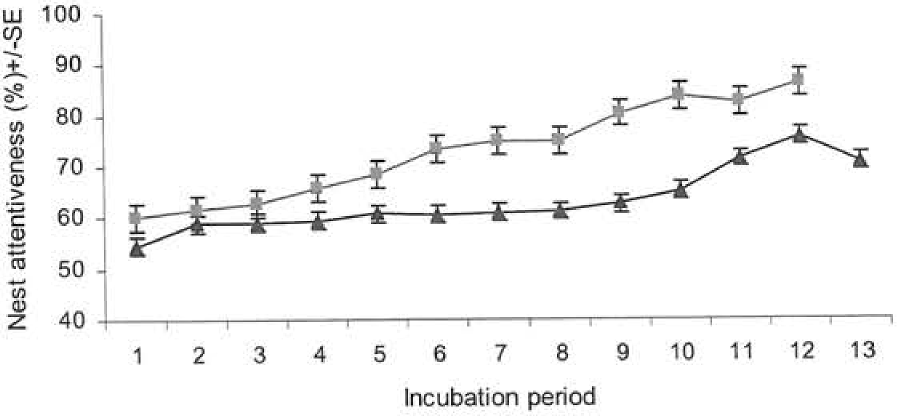

Figure 6.31. Nest attentiveness of Grey-headed Bulbul across different incubation days (■: nest with one egg; ▲ : nest with two eggs).

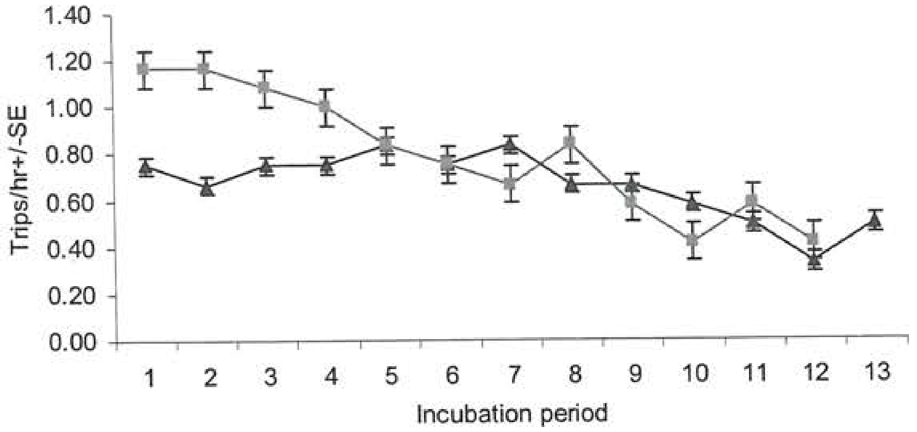

Figure 6.32. Mean trips/hr of Grey-headed Bulbul across different incubation days (■: nest with one egg; ▲: nest with two eggs).

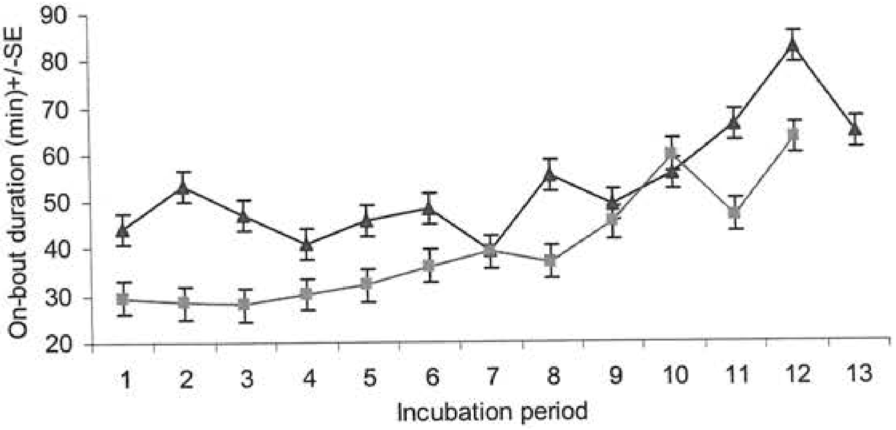

Figure 6.33. Mean on-bout duration/ hr of Grey-headed Bulbul across different incubation days (■: nest with one egg; ▲: nest with two eggs).

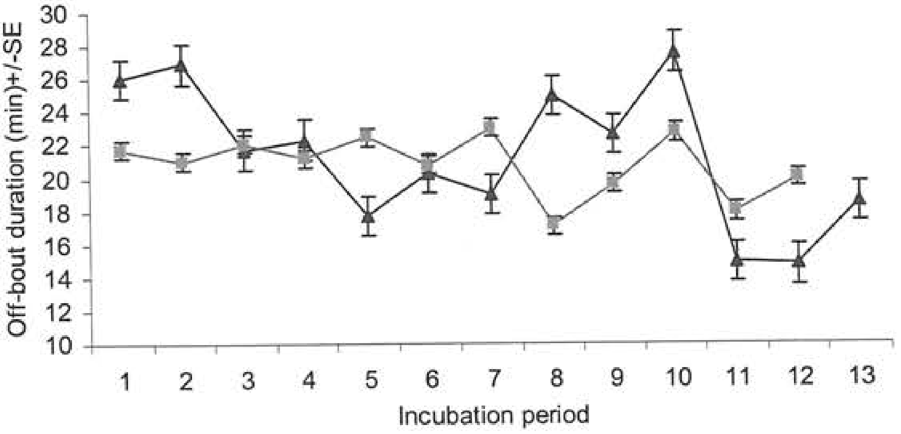

Figure 6.34. Mean off-bout durations/hr of Grey-headed Bulbul across different incubation days (■: nest with one egg; ▲: nest with two eggs).

6.4.14.2.2. Nestling stage

There were no significant differences in the mean attentiveness (17.88±1.96% *vs.* 16.37±1.12%) and on-bout durations (7.75±1.97 min *vs.* 4.71±1.30 min) between the nests with single egg and those with two eggs across the daylight hours (Table 6.22; Figure 6.35, 6.37). During the initial phase of the brooding, attentiveness was higher in both types of nests (65.97%, two eggs; *vs.* 73.19%, one egg), however, it reduced to about 3.33 % (two eggs) and 2.36% (one egg) at the end of the chick rearing period. The mean off-bout durations were significantly higher for the nest with single nestling than the nest with two chicks. In both nest types, birds took larger foraging bouts in the morning 06.00–09.00 hrs ($F = 8.13$, $p < 0.001$; Figure 6.38). Feeding trips varied significantly ($F = 21.00$, $p < 0.001$) among the nest types across the daylight hours with maximum trips during the evening 15.00–18.00 hrs (Table 6.22, Figure 6.36).

Table 6.22. Comparison of the parental care patterns of Grey-headed Bulbul with different clutch sizes across daylight hours and different days during nestling period (**F* statistics after Greenhouse-Geisser adjustment).

Source	Dependant variable	Type III Sum of squares	df	Mean square	*F*	*p*
Daylight hours	Attentiveness	48.00	3	29.39	0.29*	0.700
	On-bout duration	129.60	3	43.20	1.59	0.200
	Off-bout duration	638.88	3	304.25	8.13*	0.001
	Nest trips	59.13	3	28.58	21.00*	0.001
Nestling period	Attentiveness	55047.86	11	5004.35	92.85	0.001
	On-bout duration	14480.28	11	1316.39	48.49	0.001
	Off-bout duration	2585.23	11	235.02	8.98	0.001
	Nest trips	234.56	11	21.32	22.72	0.001

All the behavioural attributes measured to assess the parental care across the nestling period (12 days) varied significantly between pairs with two and single chicks (repeated measures-ANOVA, $p < 0.001$, Table 6.22). The attentiveness varied significantly between nests with single nestling ($F = 92.85$, $p < 0.001$; range: 2.50–73.19%) and with two nestlings (range: 3.33–65.97%; Figure 6.39). On-bout (range: 0.29–55.59 min *vs.* 0.31–32.17 min) and off-bout durations [16.36±7.07 (range: 11.08–35.13 min) *vs.* 11.61±3.83 (range: 8.24–21.71 min)] were significantly higher in the nest with single nestling than with two nestlings (Table

6.22; Figure 6.41, 6.42). Parental visiting rate increased by the progress in nestling stage and was significantly higher at nest with two chicks (4.95±1.78, range: 1.17±7.08) than the nests with single chick (3.85±1.50, range: 0.50–5.75 visits/hr; Figure 6.40). In each trip, the birds brought food to the young ones, thus can be considered as the feeding rate/hr. The identification of the prey-item was extremely difficult because of poor visibility. However, the birds were found carrying caterpillars to the nest. Furthermore, the birds were found feeding both the chicks in a single visit. Thus, estimation of feeding rates / nestling was not attempted in this study.

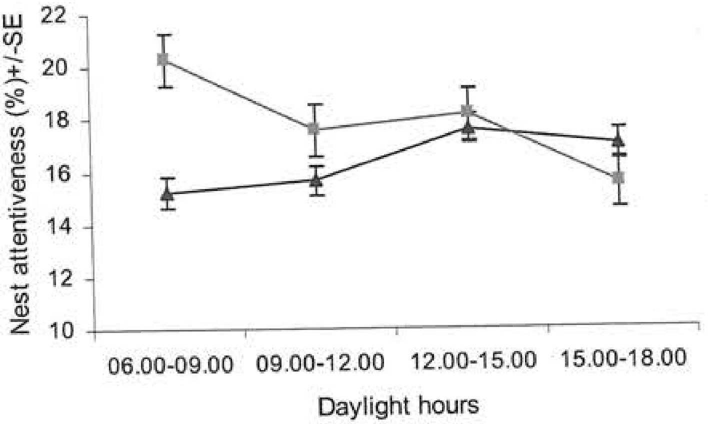

Figure 6.35. Nest attentiveness of Grey-headed Bulbul during nestling period across daylight hours (■: nest with one chick; ▲: nest with two chicks).

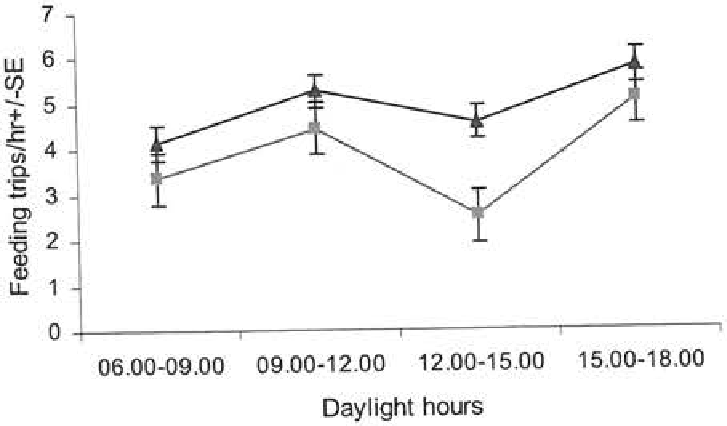

Figure 6.36. Feeding trips/hr of Grey-headed Bulbul during nestling period across daylight hours (■: nest with one chick; ▲: nest with two chicks).

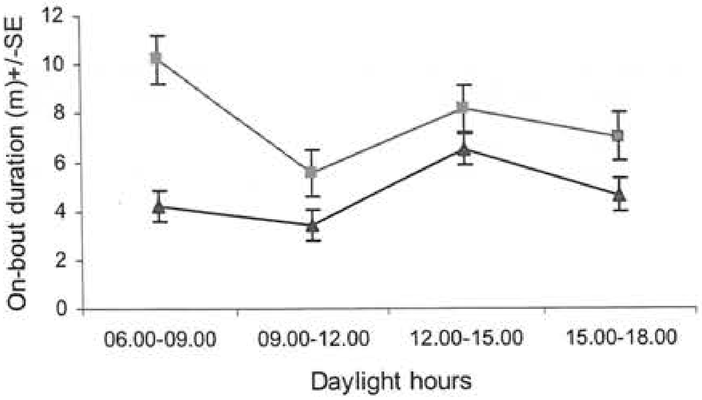

Figure 6.37. Mean on-bout durations/hr of Grey-headed Bulbul during nestling period across daylight hours (■: nest with one chick; ▲ : nest with two chicks).

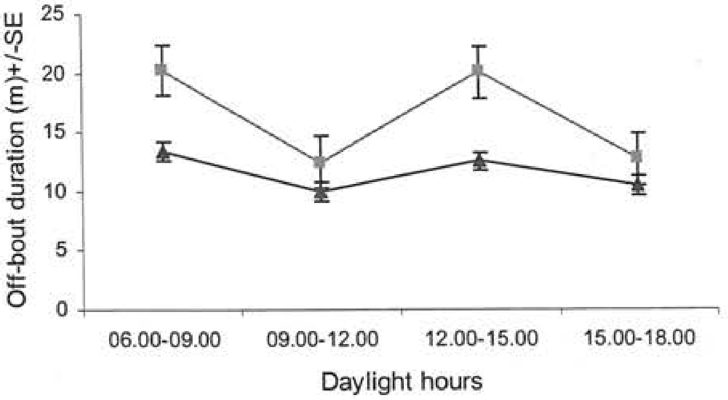

Figure 6.38. Mean off-bout durations/hr of Grey-headed Bulbul during nestling period across daylight hours (■: nest with one chick; ▲ : nest with two chicks).

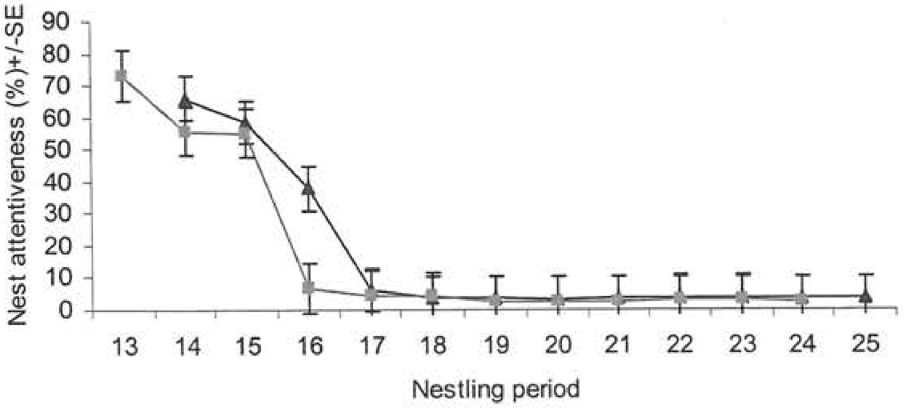

Figure 6.39. Nest attentiveness of Grey-headed Bulbul across different days of nestling period (■: nest with one chick; ▲ : nest with two chicks).

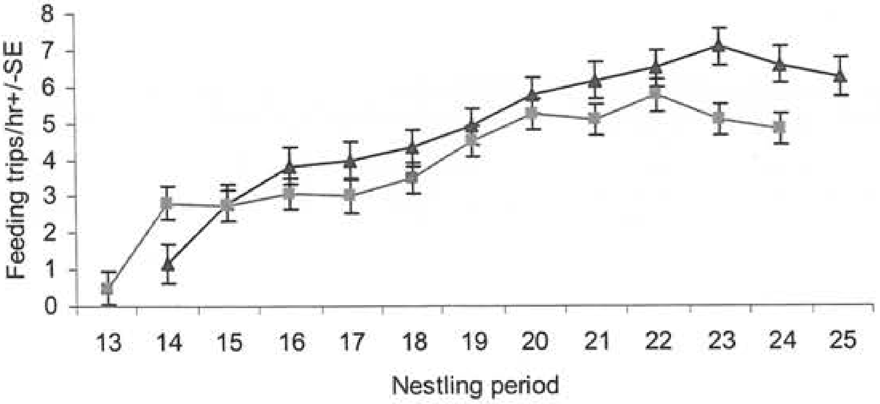

Figure 6.40. Feeding trips/hr of Grey-headed Bulbul across different days of nestling period (■: nest with one chick; ▲: nest with two chicks).

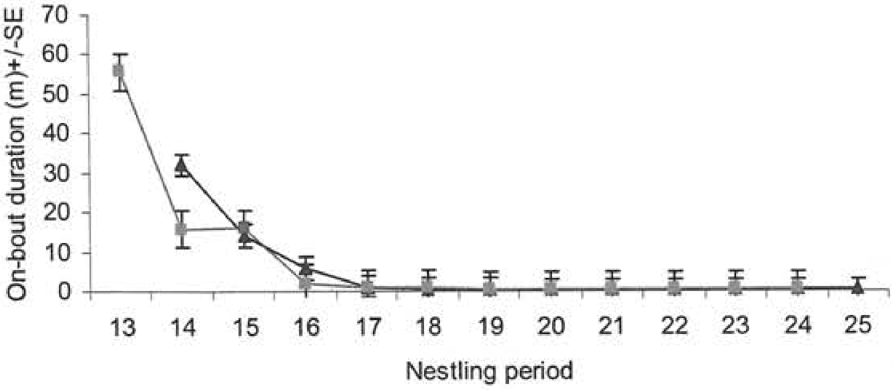

Figure 6.41. Mean on-bout duration of Grey-headed Bulbul across different days of nestling period (■: nest with one chick; ▲: nest with two chicks).

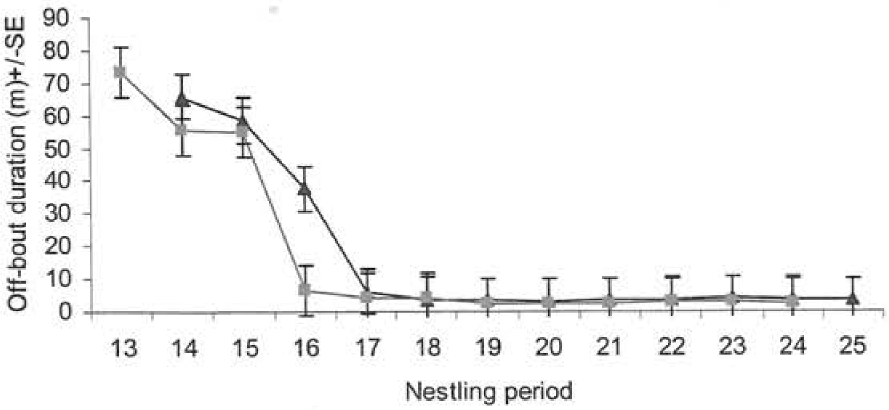

Figure 6.42. Mean off-bout duration of Grey-headed Bulbul across different days of nestling period (■: nest with one chick; ▲: nest with two chicks).

6.5. Discussion

6.5.1. Breeding seasonality

The life-history events in birds are highly environment dependant. The timing of reproduction, migration and feather replacement are thus being regarded as highly adaptive (Immelmann, 1971). In the temperate zones almost all breeding occurs during one period of time, which covers part of the autumn and winter months. In contrast, most parts of the tropics are characterised by a great heterogeneity of breeding seasons (Moreau, 1950; Skutch, 1950; Ali and Ripley, 1987; Wikelski et al., 2000). Several bird species in the equatorial rainforests and tropical islands breed throughout the year (Ali and Ripley, 1987; Wikelski et al., 2000). Food supply, competition, nesting conditions, predation pressure and climatic factors are the ultimate factors known to influence the breeding time. Lack (1968) suggested that the breeding season of birds coincides with the period of maximum food availability for rearing young. Consequently, a large number of studies have examined the relationship between bird abundance or breeding activity and variation in the abundance and exploitation of food resources (e.g., Ward, 1969; Levey, 1988; Poulin et al., 1992; Bancroft and Bowman, 1994; Bancroft et al., 2000; see also Martin, 1987, 1995).

In general, the inhabitants of the rainforests in the equatorial rainforests tend to maximize breeding in the drier months to avoid the heavy annual precipitation. Most birds in the regions with long drier and wet season in a year breed around the rainy season, except a few specialists laying during the dry period (Immelmann, 1971). Pramod and Yom-Tov (1999) have shown that the breeding season of Indian passerines is strongly related to the monsoon during May to June, a month before the peak monsoon, so that the peak food demand of chicks coincides with the arrival of the monsoon (see also Ali and Ripley, 1987).

Many Pycnonotids breed at varying time of the year and are multi-brooded. Numerous open-country *Pycnonotus* species have been recorded in all months and some are known quite commonly to raise three broods in a year, and rarely up to five broods (Ali and Ripley, 1987; Fishpool and Tobias, 2005). The equatorial African species are reported to breed throughout the year and show a peak nesting activity associated with short dry seasons. However, in east Africa the breeding seasons of bulbuls coincide with the main monsoon. Breeding activities in the montane forest species tends to be suppressed during the wet and coldest months (Ali and Ripley, 1987; Fishpool and Tobias, 2005).

The breeding activities of Grey-headed Bulbul in all the three years commenced in the first half of January and ended by mid-May. Ali and Ripley (1987) reported March to May as the breeding season of Grey-headed Bulbul. Of the several correlates tested; rainfall, number of rainy days, and fruit abundance are the major factors that have significant role in controlling the breeding seasonality. Grey-headed Bulbuls preferred drier months with high fruit abundance for breeding. Although there are no detailed studies on the breeding biology of mid and high altitude bulbuls in India, their breeding season is almost consistent and coincides with the drier months (see Ali and Ripley, 1987; P. Balakrishnan, *unpubl. data*). In Silent Valley, two co-existing species, Yellow-browed Bulbul and Red-whiskered Bulbul start breeding in November and peak breeding occurs in January to March. On the other hand, Black Bulbul starts breeding in March and reaches the peak in May. All these species are consistent in their breeding season and no second season as in the case of lowland populations was recorded in Silent Valley. However, seasonality in the lowland forests shows variations from that of higher altitudes. In South India, for example, the breeding season of the Red-vented and White-browed Bulbuls varied annually, depending on the environmental conditions (Vijayan, 1975). In his study, no obvious correlation with rainfall could be discerned, although there was a trend for breeding to coincide with the start of wet season. There was, however, a link between the timing of emergence of caterpillars and the breeding of the Red-vented Bulbul. Although the fruit abundance has been identified as an important factor deciding the breeding season of Grey-headed Bulbul, seasonality of caterpillar or other invertebrates was not explored in this study. Nevertheless, no variation in the abundance of invertebrates was recorded during the breeding months. Furthermore, in the tropics in general, marked periodic flush of insects is not common because of the lesser variation in the seasonal changes in the environment (see Levey, 1988; Loiselle and Blake, 1991; Poulin et al., 1992).

The general breeding patterns of bird community at Silent Valley was highly seasonal during the study period (P. Balakrishnan, unpubl. data; see also Vijayan and Das, 2006). Although a few insectivorous species have shown different patterns, peak breeding occurred during comparatively drier months (December-May). Silent Valley exhibits a bi-model rainfall pattern, with a longer south-west (June-September) and shorter north-east monsoons (October-January). Thus, heavy rainfall during these months restricts the breeding of open-cup nesting species to the drier months. Moreover, breeding of most of the frugivorous species was in the drier months which in turn coincide with the peak fruit abundance. However, because of high abundance of fruits and their ability to exploit invertebrate food resources, bulbuls were not appeared to be constrained by food availability even during the peak breeding of other birds.

Interspecific competition for nest sites seems to be one of the factors controlling the peak breeding time of Grey-headed Bulbul. Competition for nesting substrates in the *Strobilanthes* patches restricts nesting of the species to the reed patches during the early breeding season. However, in the late season they nest in the *Strobilanthes* patches, by when other competitors such as Yellow-browed Bulbul and Brown-cheeked Fulvetta complete their breeding.

Although several proximate factors such as photoperiod are also known to influence the breeding seasonality (see Immelmann, 1971; Wikelski, 2002), role of these factors was not assessed in this study. It has been reported that the photoperiod of tropical or equatorial latitudes would provide no useful seasonal cue, because its changes are supposedly too small to be perceived by tropical organisms (Skutch, 1950; Moreau, 1950; see Dawson et al., 2001 for a review). Wikelski et al. (2000) contradict this by suggesting that day length can be used as long-term cue even in near-equatorial rainforests (see also Hau et al., 1998). However, a study in the tropical habitats provides negative evidence for the influence of photoperiod on the breeding seasonality of bulbuls (Vijayan, 1975). In conclusion, the present study shows that Grey-headed Bulbul is a seasonal breeder during comparatively drier months (January-May), which coincides with high fruit abundance and is negatively correlated with the high rainfall.

6.5.2. Nest construction, placement and reproductive phenology

Most species of bulbuls are monogamous as the case of vast majority of birds. A unique exception is Yellow-whiskered Greenbul, which is polygamous and non-territorial in Gabon, but studies elsewhere in its range such as Kenya and Nigeria, indicate that the species is monogamous and territorial in these regions (Fishpool and Tobias, 2005). Grey-headed Bulbul is a monogamous species (Ali and Ripley, 1987). Territorial fights or aggressions were not recorded for Grey-headed Bulbul, may be due to the sparse distribution of the species.

The period of nest construction appears to vary in Grey-headed Bulbul based on the nest types; usually 3-5 days for vine nests and 6-8 days for the moss nests. Similar figures are reported for other species as well: 2-5 days for Red-vented Bulbul, 3-8 days for Yellow-throated Bulbul, 3-7 days for Yellow-browed Bulbul, 3-5 days for Black Bulbul (Ali and Ripley, 1987; Venkataswamappa and Chaitra, 1999; Chaitra et al., 2000; P. Balakrishnan, unpubl. data), about six days for Flavescent Bulbul in Myanmar, 2-10 days for Cape Bulbul, about four days for Streak-eared Bulbul and, 6-10 days for Seychelles Black Bulbul (Fishpool and Tobias, 2005).

The differential nest placement attributes of Grey-headed Bulbul in reed and *Strobilanthes* patches are adaptive to the respective microhabitats. The moss nests in the reed patches are placed above 2-m well inside the foliage and thus camouflaged from the predators. On the other hand, the nests in the *Strobilanthes* patches are placed around one meter high in a pale background surrounded by dry stems and lianas. However, in both the habitats, nests were placed in the middle of the nesting plants. The uniform orientation of nests around the nest plants was towards the leeward directions of the nest sites.

Grey-headed Bulbul used at least 12 plant species for nesting. This is too low compared to other species of bulbuls. In the mid-elevation forests, species such as Yellow-browed and Red-whiskered Bulbuls seem to be generalists in the nest plant selection. Vijayan et al. (2000) recorded 15 species as nesting plants for Yellow-browed Bulbul in the southern tropical moist deciduous forests of Bolampatty Reserved Forest. In Silent Valley National Park, Yellow-browed Bulbul nested on 32 plant species (n = 153 nests), and most of them were rare sites in their nest sites (see also Chapter 4). On the other hand, the Black Bulbul, which breeds in the mid- and higher elevations selected comparatively fewer number of plant species. Many restricted range bird species of the Western Ghats are known to use several indigenous and exotic plants for nesting and seem to be highly generalists in the nest plant selection. For example, Islam (1985) reported 26 nesting plants for Nilgiri Laughing Thrush, which include four exotic species. Ahmed (2005) recorded 25 species of nesting plants for the same bird species. Similarly, Black and Orange Flycatcher is known to use 21 plant species for nesting which constitute about 27% exotics (Khan, 1977), whereas Nilgiri Wood

Pigeon used at least 23 species (Somasundaram, 2006). However, further studies in other breeding sites of Grey-headed Bulbul are required to determine the degree of nest plant specialization and the reasons for the same.

The nest plant selection in both the reed and *Strobilanthes* patches appeared to be adaptive. Besides giving enough support for nest placement, the high foliage cover on the *Ochlandra* provides a camouflaging background to the moss nests. On the other hand the liana draped *Syzygium* saplings with a dull background form a better camouflaged environment for the vine nests. Although reed and *Strobilanthes* microhabitats are entirely different from each other, selection of nest plant and nest site in these habitats supports the 'background matching hypothesis' (Hansell, 2000; see also Martin, 1998). The nests placed on the abundant plant species in the reed patches (*Ochlandra*) had significantly higher survival. This observation is in agreement with the 'needle in a haystack' or 'potential prey-site' hypotheses. In the *Strobilanthes* patches birds placed nests on rare plant species. However, they had lower survival rates and this pattern disagrees with the predictions of 'rare site hypotheses'. On the other hand, nests placed on rare sites like *Oreocnide integrifolia, Calamus pseudo-tenius* and an un-identified shrub had high success, and thus agreeing with the 'rare site hypotheses'. Similar contrasting patterns were reported in many studies (Martin and Roper, 1988; Martin, 1993a; Filliater et al., 1994; Tarvin and Garvin, 2002) and suggest that differences in search strategies among local predators may constrain the ability of birds to optimize nest-plant selection. Species occur in the lowland scrub forests such as Red-vented and White-browed Bulbuls prefer thorny plants for nesting and this was attributed to the higher nesting success (Vijayan, 1975, 1980).

Grey-headed Bulbul had 53% of its nests with two eggs and the remaining was with one egg during 2003-2005. Ali and Ripley (1987) also reported the clutch size as one and some cases two. Davidson (1898) once recorded three eggs in a nest in Siddapur (Karnataka). However, this seems to be an exceptionally rare case. In most of the African and Asian species of bulbuls, the clutch usually consists of two eggs and some times three. However, Pycnonotus species not uncommonly lay four or five eggs (see Ali and Ripley, 1987; Fishpool and Tobias, 2005). Regional and seasonal variation in the clutch size is common in many species of bulbuls. Red-vented Bulbul in the Himalayas lay larger clutches than those from the hotter lowlands of Southern India (Ali and Ripley, 1987). Several studies provide evidence that the evolution of an optimum clutch size may have been influenced by a variety of factors (Lack, 1947-48, 1954, 1968; Martin, 1987, 1995; Møller, 1991; Roff, 1992; Martin et al., 2000a; see Godfray et al., 1991 for a review). Food limitation is widely considered as a major determinant of clutch size and other life-history traits ('food limitation hypothesis': Lack, 1947-48; see also Martin, 1987 for a review). However, food does not explain considerable variation in reproductive strategies within and among species (Martin, 1995; Martin et al., 2000a; Ferretti et al., 2005). Moreover, comparative and empirical studies suggested that nest sites and associated nest predation play a stronger role than food limitation in life-history evolution (see reviews in Martin, 2004). Vijayan (1975, 1980) reported that both food availability and predation pressure influenced the variations in the clutch sizes of Red-vented and White-browed Bulbuls in South India. The results of present study suggest that predation pressure may be more important than food availability in controlling the clutch size variation in Grey-headed Bulbul. In the predator rich patches (i.e., *Strobilanthes* patches), they produced single clutches, although these patches had comparatively higher food abundance. Moreover, these nests were characterised by longer on- and off-bouts during incubation and lower parental visitation rates to feed nestlings (see section 6.5.2.), which are adaptive strategies to reduce parental activities at the nest sites and thereby reduce the risk of predation (Conway and Martin, 2000a, b; Martin et al., 2000a, b).

In most species of bulbuls, incubation is undertaken by female alone. The males of some species, however, occasionally incubate for short periods, usually no more than a few minutes, although the male Seychelles Black Bulbul may incubate for up to one hour per day (Ali and Ripley, 1987; Fishpool and Tobias, 2005). In Grey-headed Bulbul, only the female probably incubates the eggs, however, the male have significant role in parental care. Their nesting period, from the commencement of incubation to fledging, lasted a mean of 25 days. Incubation averaged 13 days and the nestlings spent an average of 12 days in the nest. It appears to be similar to the patterns recorded for other South Indian bulbuls; incubation period ranges between 11–14 days, except for Yellow-throated Bulbul *Pycnonotus xantholaemus,* which is having a longer incubation period (Vijayan, 1975, 1980; Ali and Ripley, 1987; Venkataswamappa and Chaitra, 1999; Chaitra et al., 2000; P. Balakrishnan, *unpubl. data*). In general, mean fledging period is in the range of 12–16 days, with shorter periods (9–11 days) for White-eared Bulbul and longer periods (21 days) for Seychelles

Black Bulbul. However, all the South Indian bulbuls have short fledging periods ranging 10–13 days (Table 6.23).

Table 6.23. Comparison of the clutch size, incubation and fledgling periods of the South Indian bulbuls (Ali and Ripley, 1987; Vijayan, 1975, 1980; Venkataswamappa and Chaitra, 1999; Chaitra et al., 2000; BirdLife International, 2001; P. Balakrishnan, *unpubl. data*).

Species	Clutch size	Incubation period	Nestling period
Pycnonotus priocephalus	1 / 2	13	12
Pycnonotus melanicterus gularis	2	?	?
Pycnonotus jocosus	3 / 2	12–14	11
Pycnonotus cafer	2 / 3	11–14	12
Pycnonotus xantholaemus	2 / 3	20	13
Pycnonotus luteolus	2	11	10
Iole indica	2 / 3	12	13
Hypsipetes leucocephalus ganeesa	2 / 3	13	12

6.5.3. Phenotypic plasticity in the nest architecture

The birds with altricial chicks have most complex nests in terms of building materials and design. This ensure that chicks are placed in locations which are inaccessible or less visible to predators or protected from climatic extremes in an environment where temperature is regulated and thereby increase the fitness of the breeding pair (Collias and Collias, 1984). This potential to increase reproductive output indicates that nest building behaviour and nest structure are under intensive selective pressures (Nores and Nores, 1994). Nidiculous birds use a variety of material of plant, lichen, fungal and animal origin to build the nest, mostly the readily available material abundant in the immediate surroundings. Grass is a widely used material, reflecting its extensive availability in a great range of habitats, but birds may distinguish different parts of the plant, selecting a part with properties suited to a particular function (Hansell, 2000). High variability of nest material usage was reported in bulbuls. Most bulbul nests consist of an open cup of leaves and thin pliable plant fibres. A number of plant material and rarely spider cocoons were identified from the nests of Grey-headed Bulbul. Material of the structural zone of each nest appeared to be relatively abundant in the immediate surroundings. Of the three types of nests identified based on the material composition, the most common 'vine nests' were made of vine tendrils, dry grass leaves, grass culms and fibre roots of pteridophytes. On the other hand, the 'moss nests' were constituted mainly with the dry leaves and leaf sheaths of *Ochlandra*, the most abundant material at the nest sites. The innermost *lining layer*, which is in direct contact with the eggs and young ones, was made with coma and papus hairs of plants, and fibre roots of pteridophyes in both the nest types. The nests in the reed patches were characterised by a decorative layer with fresh green moss. Different nest materials play different structural and functional roles (Collias and Collias, 1984; Hansell, 2000) and thus, material selection may be highly adaptive. A number of restricted-range and other bird species are known to incorporate moss or other materials in their nests (see Khan, 1977; Islam, 1985; Ali and Ripley, 1987; Ahmed, 2005). However, the structural and functional attributes of these materials were poorly understood. The addition of fresh green plant material to dry nest material is widespread among birds (Wimberger, 1984; Collias and Collias, 1984; Clark and Mason, 1985; Ali and Ripley, 1987; Hansell, 2000). These green materials have different functional roles and often replenished daily during the incubation and nestling stages (Wimberger, 1984; Gwinner et al., 2000; Dawson, 2004). The addition of fresh moss and pale grayish-green lichen in the decorative layer is often regarded as a concealment mechanism provides crypsis by matching with the background (Collias and Collias, 1984; Hansell, 2000). Several species of pathogens and parasites affect the survival of eggs and chicks (Møller, 1990; Martin et al., 2001; see reviews in Fitze et al., 2004). The 'nest protection' hypothesis suggests that volatile compounds in green nest material have biocidal effects on parasites and pathogens (Wimberger, 1984; see also Dawson, 2004). Green nest material could also be used by males to attract females ('courtship' hypothesis and 'male quality' hypothesis see Ali and Ripley, 1987; Gwinner et al., 2000; Brouwer and Komdeur, 2004). Although the biocidal effects of the nest materials used by Grey-headed Bulbul is not known, the courtship and male quality hypotheses are not relevant in the case of this species. Although the vine nests placed in a pale background are devoid of decorative layer, the outer moss layer on Grey-headed Bulbul nests seen in the green backgrounds provides concealment to the nest from predators. Such adaptations were recorded for many other species of bulbuls. For example, the Common Bulbul *Criniger barbatus* of African rainforests works into the rim of its nest with an epiphytic fern that remains green until after the young fledge (see Fishpool and Tobias, 2005). Similarly a number of African forest interior species often incorporate the fungus *Marasmius* into the construction; the black mycelial threads of this fungus grow and ramify through the nest structure, helping to bind the nest to its support. Red-vented Bulbul and many other *Pycnonotus* species often use man-made material, and they vary the make-up of their nests depending on locality and season. Both White-eyed and Cape Bulbuls sometimes incorporate sheep's wool, feathers, paper, string, newspaper, strips of plastic and other human rubbish into their constructions (Fishpool and Tobias, 2005).

The genetic basis of nest building or nest size is poorly known (Møller, 2006). Darwin (1872) noted that nest building by birds is an innate behaviour, by comparing the British and Australian thrushes which build similar nests. Collias and Collias (1984) and Hansell (2000) conclude that nest building is an innate behavior that is performed even by individuals that have not encountered nest building by conspecifics. Naive individuals are able to build species-specific nests of normal size and shape (Collias and Collias, 1984; Hansell, 2000). The nesting behaviour of birds mirror their solutions to the local challenges (Collias and Collias, 1984). Altitudinal and geographical variations in the nest architecture are regarded as phenotypic expressions of genetic differences in the behaviour of individual birds or populations (Kern and van Riper, 1984) to cope with the vegetation structure, adverse climatic effects or reducing predation (Collias, 1964; Collias and Collias, 1984; Hansell, 2000). Studies on nest predation and brood parasitism showed the role of natural selection on the evolution of nest building and nest phenotype (see Møller, 1990; Hansell, 2000). Nest size per se is also expected to affect predation rates, and many tropical bird species which breed especially in predator rich environments have tiny and inconspicuous nests (see Snow, 1978; Collias and Collias, 1984; Møller, 1987, 1990; Hansell, 2000). Nest size in monogamous passerines has recently been hypothesised to be a sexually selected signal of parental quality (Soler et al., 1998). A number of comparative and empirical studies (Soler et al., 1998; 2001; Palomino et al., 1998; De Neve and Soler, 2002) have supported this hypothesis in several species. Moreover, the experimental studies have proved that the females adjust the clutch size based on the nest size (see Soler et al., 2001, De Neve and Soler, 2002) and this in turn affects the final reproductive output. However, although males of most species of bulbuls play an important role in the post-incubation parental care, nest construction and incubation were undertaken by female alone. This is true in the case of Grey-headed Bulbul also and thus the nest size is not related to the male quality.

The adaptive radiation among species in bird nests in a geographical or altitudinal paradigm has been discussed by several authors (e.g., Schaefer, 1976; Kern and van Riper, 1984; see also Collias and Collias, 1984; Hansell, 2000). Architectural variations in the nests of Grey-headed Bulbul were recorded within the same habitat with significant differences in the vegetation structure and composition. This allowed me to explore the correlates of within-species variation in the nest architecture and to determine their relative evolutionary and ecological importance.

Individuals vary widely, both within and between populations, with respect to life-history traits. For many traits, an individual's phenotype is highly sensitive to the quality of its current physical or biological environment. Phenotypic changes exhibited by an individual or genotype in response to the environment are identified as phenotypic plasticity (Stearns, 1989; Scheiner, 1993; Schlichting, 2002; Pigliucci, 2001, 2005). Much of this variation is the result of direct physiological sensitivity to the environment (phenotypic plasticity) that might be modified secondarily by evolutionary responses that refine phenotype-environment relationships (Ricklefs and Wikelski, 2002). Patterns of population variation play an important role in evolutionary diversification, and many insights into evolutionary processes have come from studies of within-species variation (Badyaev et al., 2000). Numerous experiments have found that morphological and fitness related traits are sensitive to physical (abiotic) conditions, including water and light availability, temperature, and substrate texture, and that traits differ in their sensitivity to these factors (see Pigliucci, 2001). Although a number of studies tested the adaptationist hypotheses in ethology (e.g., Scheiner, 1993; Doughty, 1995; Gotthard and Nylin, 1995; Ghalambor and Martin, 2002), there are only a few systematic studies on the extent of variation in artifacts built by any one species, fewer still on its cause or relative fitness of the variants (Hansell, 2000; see also Reid et al., 2002). Moreover, relatively less attention has been paid to non-genetic responses to the environment, such as adjustment of parental investment in response to perceived risk (Ricklefs and Wikelski, 2002). Among the potential factors that influence the phenotypic variation in nests; role of microhabitat structure, food availability, clutch size, predation pressure and nest site competition were assessed in the present study.

The food abundance in the nesting patches does not explain any variation in the parental investment strategies of Grey-headed Bulbul. The reproductive investment in terms of elaborate nest structure and clutch size in the reed patches was found significantly higher than that in the *Strobilanthes* patches hosting smaller nests with less investment (see section 6.4.4.3). However, food abundance in the reed patches was significantly lower than in the *Strobilanthes* patches. Moreover, the moss nests, placed in the reed patches had more survival than the vine nests in the *Strobilanthes* patches. This shows that the differential investment strategies for the nest construction in these two patches are not influenced by the variation in food abundance.

I found direct evidence for the influence of predation risks on the parental investment for nest construction by Grey-headed Bulbuls occupying different patches. Parental investment for the nests in the *Strobilanthes* patches, which had high predator abundance, was considerably lesser than that in the reed patch nests. The elaborate nest structure of the moss nests requires more time and energy. On the other hand, the vine nests seen in the predator abundant areas were simple and time for construction was also comparatively less. Natural selection plays an important role in the evolution of nest building and nest phenotype (Møller, 2006). Evolution of phenotypic traits is often constrained by costs that act in opposite proximate and evolutionary relationships (Martin et al., 2000b). Parental activity and nest predation are hypothesised to show opposite proximate (positive) and evolutionary (negative) relationships (see Skutch, 1949; Slagvold, 1982; Martin, 1996a; Martin et al., 2000b; Fontaine and Martin, 2006). Moreover, in a recent experimental study, Fontaine and Martin (2006) found that birds can assess nest predation risk at large and the nest predation plays a key role in the expression of avian reproductive strategies.

Given that predation risk appears to be an important factor in the evolution of the nest size, most likely it acts as a selective pressure on the selection of nest material and architectural features to adapt with the micro habitat. Habitat preferences are assumed to be adaptive, such that fitness is higher in preferred habitats, causing natural selection to maintain preferences if they have a genetic basis (Jaenike and Holt, 1991; see also Martin, 1998; Jones, 2001). Moreover, adaptiveness of habitat preferences probably result from adaptiveness of multiple phenotypic traits (e.g., physiological tolerance, background matching, behavioural activity patterns) to preferred habitats (see Martin, 1998). The direct benefits in terms of protection from the predators to the nests may be obtained by placing the nest in a camouflaging background and choosing materials camouflaging in the nest site (Hansell, 2000). The selection of different types of nest materials in two distinct microhabitats may be an adaptation to hide the nests and their contents from the visually hunting predators. In the *Strobilanthes* patches, birds placed the vine nests at the pale stems covered with dry plant parts, whereas the moss covered nests in the reed patches were placed in a green background. Crypsis by background matching (see Collias and Collias, 1984; Hansell, 2000) seems to be important in vine nests than simple foliage cover around the nest. However, in the case of moss nests, the crypsis was attained by adding moss to the outer layer and placing the nest in a green background. In fact, such nests had high foliage cover around them. Indeed this differential architectural attributes are of adaptive nature to reduce predation risks, since nest survival in reed patches was higher than that in the *Strobilanthes* patches. However, lack of evidence for the adaptive fitness of the late season vine nests in the *Strobilanthes* patches should be interpreted cautiously, because as observed in many studies (see Martin, 1987), the nest survival decreased as the breeding season progressed at Silent Valley. Moreover, there was a strong directional preference of reed patches and construction of moss nests in the early breeding season and thus high survival rates are expected. Alternatively, most of the vine nests were placed closer to the ground, and they might be more vulnerable to predation because of the abundance of terrestrial predators at the study site. This is further evident from that the successful vine nests were placed well above the ground compared to the failed nests.

The above observations pose a few questions. Given the high survival advantages in the reed patches, why do Grey-headed Bulbuls shift their breeding to *Strobilanthes* patches in the late season? The ecological interactions of co-existing species may lead to fitness consequences for individuals through their influences on individual reproductive success and/or survival (e.g., Gustafsson, 1987). In a recent experimental study, Martin and Martin (2001) established that interactions between the two species result in substantial fitness costs of coexistence. Because of such fitness costs, natural selection should work towards a divergence of habitat preferences between species (Martin, 1996a, 1998). I found significant overlaps in the nesting resources between Grey-headed Bulbul and co-existing Yellow-browed Bulbul. The latter is an early season breeder, starts breeding in the *Strobilanthes* patches well before the arrival of the local migratory Grey-headed Bulbul. The resource overlaps, and, or the presence of Yellow-browed Bulbul (as a proximate cue that determines fitness by predation risk) may deter Grey-headed Bulbul from nesting in similar patches. Comparatively higher reproductive fitness was observed in the reed patches; however, availability of suitable nest sites in reed patches was less in the study site. Microhabitat shift to the *Strobilanthes* patches was marked by the end of Yellow-browed Bulbul's breeding and start of intermittent rain at the study site. It shows that Grey-headed Bulbul avoid the presence of Yellow-browed Bulbul.

Why do Grey-headed Bulbuls construct simple vine nests during the late breeding season? As explained above the design of the nests placed in the *Strobilanthes* patches could be an interactive effect of predation pressure. Architecture of vine nests ensured maximum crypsis in the pale background. Moreover, the construction time for these nests were considerably less than the more elaborate moss nests, by which the birds reduced their risk in the predator rich microhabitat (see Ghalambor and Martin, 2001). An alternative explanation for the temporal variation in nest design of Grey-headed Bulbul could be a response to the intermittent rainfall during the late breeding season. Although, the bulky moss covered nests may sufficiently camouflage it from the predators, the porosity of such nests may be very poor. On the other hand, the 'vine nests' made with vine tendrils, which are devoid of a moss layer could be capable of drying efficiently after the rain. There is mounting evidence that the need to control the thermal environment may greatly influence the design of nests (Collias and Collias 1984; Collias, 1997; Hansell, 2000; Hilton et al., 2004; Lamprecht and Schmolz, 2004). Moreover, a number of studies explained the variation of nest placement and design as response to local climatic conditions (Schaefer 1980; Walsberg, 1981; Collias and Collias, 1984; Kern, 1984; Møller, 1987). Several studies have shown that although, thermal conductance was significantly related to nest mass and nest dimensions, it was not a simple function of nest size (Kern, 1984; Kern and Riper, 1984), but depended, instead, on the porosity or density of the wall of the nest (Kern, 1984; Kern and Riper, 1984; see also Soler et al., 1998). These observations indicate the role of intermittent rainfall on the design of late season nests. This is further supported by the observation that a few nests recorded in the reed patches during the late season were also typical vine nests.

Møller (2005) after a long-term study on Barn swallows, hypothesised that the temporal change in nest phenotype as a consequence of a microevolutionary change in male tail length and ignored phenotypic plasticity as an alternative explanation. Although the heritable basis of plasticity is not known, the variation in the nest design of Grey-headed Bulbul could be an adaptive phenotypic plasticity to improve fitness in different microhabitats with differential predation pressure.

Equally as interesting as change in nest architecture was the variation in clutch size as a response to predation risk. Grey-headed Bulbuls breeding in patches with high predation risk (i.e., *Strobilanthes* patches) constructed smaller nests and had a single clutch (see sections 6.4.4.3 and 6.4.4.4.). Nest predation has been hypothesised as a major factor influencing clutch size in birds (Martin, 1995; Martin et al., 2000a). Both empirical and experimental studies demonstrated clutch size reduction under high nest predation risk (e.g., Slagvold, 1982) and have been shown to change with differences in nest predation risk across habitat gradients (Ferretti et al., 2005) and among years (Julliard et al., 1997). Such clutch reduction may permit shortening of egg laying, incubation and nestling periods (Martin, 1995), low nest detectability and less conspicuous parental care (Møller, 1990; Martin et al., 2000b; Ghalambor and Martin, 2000, 2002). The smaller nests and clutch size of Grey-headed Bulbul in areas with high predation risk agrees with the view that, longer-lived and less fecund species should be less willing to place themselves at risk compared with their offspring, because investment in current reproduction is reduced and the probability of future breeding opportunities is high (see Dale et al., 1996; Ghalambor and Martin, 2000, 2001; Martin et al., 2000a, 2006; Fontaine and Martin, 2006). As reported for several species, a smaller clutch size during the late breeding season was observed for Grey-headed Bulbul. A number of studies provided evidence for the influence of size of the nest on the evolution of clutch size (e.g., Snow, 1978; Møller, 1982; Slagvold, 1989; Kuleza, 1990; Soler et al., 1998; 2001). The nest cup size-clutch size correlations in Grey-headed Bulbul may be related to the parental investment decisions of birds, since selection favours small nests and clutch to minimize the problem of attracting the attention of nest predators. These observations demonstrate that the nest predation act as a selective pressure on the nest size and design and, clutch size for Grey-headed Bulbul as reported for other species (see Møller, 1982, 1987, 1990; Hansell, 2000; see also Vijayan, 1975).

6.5.4. Nest success and correlates of nest survival

The degree of egg and chick mortality is of interest because fecundity is the primary demographic parameter influencing population dynamics of birds (Newton, 1998). Since measures of nest survival are our most efficacious way of evaluating avian conservation and management practices, these measures need to be as reliable and informative as possible (Jehle et al., 2004). However, avian ecologists are inconsistent in the methodology for nest survival estimates and thus posing difficulties in the comparison of similar species to understand evolution of life-history traits. In the present study I provide three measures of success: the Mayfield nest success, the apparent nest success (number of successful nests divided by the total number of nests) and the percentage of young fledged from the total eggs laid for a comparative purpose. The overall Mayfield nest success of Grey-headed Bulbul was very low as 10.79% with 24.97% at egg stage and 60.01% at the nestling stage. The overall apparent nest success of Grey-headed Bulbul was 19.5%. The overall nesting success was 20.83% when the number of young versus the eggs laid is considered as an index of success. Some authors have reported higher predation rates during the nestling period (see Martin, 1992b for a review). However, I found higher predation during the egg stage as reported by others (e.g., Mermoz and Reboreda, 1998). Nest predation rates are reported higher in the tropics than in the temperate regions (Lack, 1954, 1968; Perrins and Birkhead, 1983; Martin, 1995, 1996b; Robinson et al., 2000; Stutchbury and Morton, 2001). Robinson et al. (2000) found that open cup-nesting temperate zone birds averaged 47% nest loss compared to 71% for tropical birds. There was significant inter-annual variations in the nesting success of Grey-headed Bulbul (see Tables 6.10 and 6.12). Similar variations in the nest survival or predation rates have been reported in several studies (see Perrins, 1970; Mezquida and Marone, 2001). Moreover, nest survival is influenced by a number of factors and the predation rates are likely to vary with habitat, time of the year and possibly altitude (see Stutchbury and Morton, 2001).

The low nesting success of Grey-headed Bulbul is typical of many congeneric relatives, especially common Pycnonotids with higher rates of nest predation. For example, predation rates of Cape Bulbul *Pycnonotus capensis* were 60-83 % with about 70% of these losses due to mammals (Liversidge, 1970; Krüger, 2004). The survival rate of fledglings was estimated to be 18% after one month and 10% after one year (Krüger, 2004). Similarly, predation rates were as high as 74% in Eastern Bearded Greenbul *Criniger chloronotus*, and 82% in Lesser Bristlebills *Bleda notatus* (see Fishpool and Tobias, 2005). In the case of the polygamous Yellow-whiskered Greenbul *Andropadus latirostis* in Gabon, the nesting success varies widely, with predation levels ranging 45-85% with a mean of 75% (Fishpool and Tobias, 2005). In South India, the nesting success of lowland bulbuls was exceptionally low, 13.2% (15 chicks out of 114 eggs) for White-browed Bulbul and 8.3% (11 chicks out of 134 eggs) for Red-vented Bulbul (Vijayan, 1975, 1980) and, this figure drops to 8% in the introduced population of Red-vented Bulbul in Fiji (Walting, 1977, 1983). There are several short notes describing the breeding activities of the Indian bulbuls, however, most of them are based on relatively small number of nests and thus not comparable with the present study. Among all the bulbuls, losses to predation of Common Bulbul *Pycnonotus barbatus* nests were somewhat lower, amounting to 42% (Fishpool and Tobias, 2005). Vijayan et al. (2000) found an exceptionally high nesting success for Red-whiskered Bulbul at Bolampatty Reserved Forest, South India. Of the 105 eggs of 52 nests monitored 91.43% hatched and all the hatched eggs were successfully fledged, thus amounting a success rate of 91.43%. However, the reason for such a high nesting success was not clear.

The nest losses of Grey-headed Bulbul were caused mainly by predation and destruction by trampling of elephants and other large vertebrates. Although the degree of predation by mammals, birds and reptiles was unknown, correlates of high mortality and abundance of the predators belong to these groups in the nest sites was clear (see section 6.4.13.5). Though a list of probable predators is only an indication of what the predator assemblage might be (Vijayan, 1975; Rudnicky and Hunter, 1993; see also Fenske-Crawford and Niemi, 1997); logistics not permitted the identification of the actual predators in the present study. However, the list of probable predators was based on the observations of predation on similar species in the field and previous studies. For example, Vijayan (1975) recorded a number of avian, reptilian and mammalian predators including Common Indian Grey Mongoose *Herpestes edwardsii* on the eggs and nestlings of Red-vented and White-browed Bulbuls. Similarly, Kruger (2004) also reported small mammal predation on Cape

Bulbul. Ali and Ripley (1987) reported that the eggs and nestlings of Red-whiskered Bulbul suffer very heavy predation, principally by cats, crows and Calotes lizards. They report that one nestling of Red-vented Bulbul was consumed by a Saw-scaled Viper *Echis carinatus*. In the present study the direct evidence of predation is restricted to a single observation of egg predation by Jungle Striped Squirrel *Funambulus tristriatus*. However, instances of predation of eggs and nestlings of Yellow-browed and Red-whiskered Bulbuls by Common Vine Snake *Ahaetulla nasuta*, White-bellied Treepie *Dendrocitta leucogastra*, and Greater Coucal *Centropus sinensis* were recorded from the study sites.

Brood parasitism is a major problem for a number African species (e.g., Liversidge, 1970; Kruger, 2004; see also Fishpool and Tobias, 2005). Only two species of Asian bulbuls, Red-vented and Flavescent Bulbuls are reported to be affected by brood parasitism by Pied Cuckoo *Clamator jacobianus*. It is likely that several other Pycnonotids in the region are cuckoo hosts (see Fishpool and Tobias, 2005). However, no brood parasitism was recorded at the nests of Grey-headed Bulbul or other bulbuls in the study sites. Hybridization is common among several species of bulbuls (Keith, 1992; Craig et al., 1997) and it is one of the major reasons for endangerment in some species (e.g., Styan's Bulbul). However, although Sibley and Short (1959) reported hybridization between Red-vented Bulbul and White-cheeked Bulbul in north India, no such information is available from South India.

Many species of bulbuls such as Red-vented and Red-whiskered Bulbuls were known to chase the avian predators. Although Ali and Ripley (1987) reported that Grey-headed Bulbuls energetically defend the nests, at Silent Valley they were found moving away from the nest sites and no mobbing behaviour was recorded. The conspicuous distraction displays to defend the nests or fledglings are reported for several Asian Pycnonotus species including the Himalayan, Red-whiskered, Red-vented, Yellow-vented and White-eared Bulbuls (Vijayan, 1975, 1980; Ali and Ripley, 1987; see also Fishpool and Tobias, 2005). In the case of Himalayan Bulbul, both male and female feign injury, demonstrating that males have a high level of investment in parental care (Fishpool and Tobias, 2005). Ali and Ripley (1987) reported that Red-whiskered Bulbul, when their nests are threatened, drag themselves along the ground with outspread beating wings, screaming piteously. In the case of Red-vented Bulbul, when the nest was approached by a predator, both parents raised a hue and cry and one of them scrambles on the ground and give distress calls and beat its wings. However, no such displays were recorded for Grey-headed Bulbul or other bulbuls at Silent Valley.

The timing of breeding appears to be an important factor determining the nest success of Grey-headed Bulbul. The patterns obtained suggest that the early season nests had less daily mortality rates than the late season nests. Similar patterns of nest success in relation to the laying date have been found in other species. For example, late season nests of Cape Bulbul suffered more predation than the early nests (Kruger, 2004). However, most of the moss nests which had higher survival rates than the vine nests appeared in the early breeding season.

The nest predation rates vary with the attributes of nest placement and concealment (Ricklefs, 1969; Martin, 1993a, b; Collias and Collias, 1984; Martin and Roper, 1988; Møller, 1989; Kulesza, 1990; Martin and Li, 1992). Nest predation commonly differs between nest positions. In general, the nest predation is greater on open nests on the ground than on those off the ground (Ricklefs, 1969; Slagvold, 1982; but see Martin, 1988a). A number of hypotheses were proposed and tested to relate survival rates with the nest placement and concealment attributes. The "nest height" hypothesis (see Li and Martin, 1991; Filliater, 1994) predicts that nests placed high or low relative to the frequency distribution of nest heights in the population will be more successful than those of more typical height. Furthermore, the stereotypy in nest placement could also result in poor reproductive performance (Martin, 1993a). The mean height of the successful nests was well above the median nest height and thus agreeing with the prediction of this hypothesis. The "mid-height" hypothesis predicts that nests placed at mid height in a tree or shrub will be more successful than those placed either higher or lower in the plant (Filliater, 1994). However, since there were no differences in the relative nest heights of the successful and failed nests and since most of the nests were placed in the middle of the nesting plant, a direct test of this hypothesis is not possible.

The structural heterogeneity of vegetation has been considered as a key factor influencing predation rates on nests. The "nest concealment" hypothesis predicts that nests that are concealed regardless of the particular plant structure will be more successful than those that are not so concealed because of reduced auditory, olfactory, and visual cues to potential predators (Martin, 1993a). However, both positive and negative effects of concealment have been regularly found in studies looking at the effects of nest cover on nest survival (e.g., Martin and Roper, 1988; Sedgwick and Knopf, 1992; Estrada et al., 2002; see Martin, 1992a, 1993a; Hansell, 2000; Remes, 2005 for reviews). Although the nest concealment on the successful nests of Grey-headed Bulbul was considerably higher, no statistically significant variation was obtained. A number of other studies have also recorded little relationship between nesting success and nest concealment (Filliater et al., 1994; Howlett and Stuchburry, 1996), probably because some predators use non-visual stimuli for nest detection (e.g., Rangen et al., 1999) or because a trade-off exists between nest crypsis and the ability of parents, at the nest, to detect predators (Götmark et al., 1995; Cresswell, 1997). Moreover, in a recent study, Remes (2005) demonstrated that the absence of positive effects of nest cover on nest survival does not automatically mean a lack of natural selection on higher nest concealment. The trade-offs between nest plant selection and nest placement, and nest success of Grey-headed Bulbul was evident as the pattern either agreed or rejected the hypotheses such as 'needle in a haystack or potential prey site', and 'rare site' in different patches (see section 6.5.2. for a detailed discussion)

Although, Grey-headed Bulbul shows variation in the life-history traits based on the differential microhabitat selection, the contribution to fitness due to these variations are not very clear. The higher levels of nest predation experienced by the study population could be masked the effects of vegetation structure of the nest sites on nest survival. The habitat characteristics were not found to have influenced the nest success. None of the 40 varibles measured at the meso- and micro-scales varied between the successful and failed nests. However, these results should be interpreted cautiously because the non-random patterns in nest site selection itself could be considered as a strategy to improve fitness. The low sample size for successful nests ($n = 9$) and the complex nest site selection processes of Grey-headed Bulbul also posed difficulties in exploring the correlates of habitat structure and nest success. The birds had chosen two different types of microhabitats, which significantly varied in the vegetation structure and composition. However, no variation was found in the habitat structure of successful and failed nests of both nest types, except that the successful vine nests had higher liana density at the micro-scale. The present patterns indicate that regardless of the structural attributes of vegetation, the relationship between habitat and nesting success results either from the overall influence of habitat on predator abundance or distribution, or from more complex interactions between habitat and predator search efficiency (Martin and Roper, 1988; Martin, 1992b; Filliater et al., 1994; Tarvin and Garvin, 2002).

In general bulbul nests are well separated, but in some instances nests are clumped, almost in a loose colony. For example in South India and in Fiji three active nests of Red-vented Bulbul were found with in three metre (Vijayan, 1975; Walting, 1977). Similarly, 2-4 nests of White-browed Bulbuls were recorded within a radius of eight metre (Vijayan, 1975). None of Grey-headed Bulbul nest sites overlapped and the minimum neighbour distance was at least 500 m for all the live nests. However, the proximity of the nests of other species increased the probability of Grey-headed Bulbul nests to predation (see section 6.4.13.6). This agrees with the observation of Martin (1988a, b, 1996a), that the overlap in the habitat characteristics of nest patches among coexisting species can increase risk of nest predation.

In summary, I found that nest survival in Grey-headed Bulbul is comparatively lower than that in several threatened species. Although the nests placed in the *Strobilanthes* patches suffered high predation pressure than those in the reed patches, both meso- and micro scale nest-site characteristics around the nests did not significantly affect nest survival rates. High predation rates could mostly be attributed to the higher diversity and abundance of nest predators. Thus, more information on the predators in different patches, their foraging strategies and their impact on the nests would be important for a better understanding of the differential nest site selection process and its adaptive benefits to Grey-headed Bulbul.

6.5.5. Parental care

Biparental care is almost a norm in birds, as it occurs in about 90% living species (Wesolowski, 1994; Ligon, 1999). Grey-headed Bulbul was no exception. As seen in majority of bulbuls (see Fishpool and Tobias, 2005), the incubation is assumed to be undertaken by female alone. However, the demand of high degree of parental care for the altricial chicks was ensured by the participation of male during the nestling stage. Although, the role of male and female birds may vary in the parental care, in the present case this could not be explored due to the lack of sexual dimorphism. However, the effort of male in feeding the nestlings seems almost equal to that of the female. Moreover, the birds were found making alternative feeding trips continuously, especially towards the end of nestling period.

Thus, the patterns presented for the nestling periods are combined parental investment of male and female birds.

The evolution of parental care strategies is thought to result from the trade-offs between the fitness costs and benefits associated with providing care (Clutton-Brock, 1991; Roff, 1992; Stearns, 1992; Møller and Cuervo, 2000). Various environmental conditions can influence these fitness trade-offs and lead to variation among species and populations in the amount or type of parental care provided (e.g., Clutton-Brock, 1991; Badyaev and Ghalambor, 2001). The optimal division of time is likely to vary with environmental conditions and, indeed, incubation and foraging bout durations have been shown to vary consistently with weather, stage of incubation and time of day (see reviews in Conway and Martin, 2000a).

The temporal variation in the nest attentiveness was prominent during the incubation period. Maximum nest attentiveness was recorded in the morning and evening hours. On- and off-bout durations are often assumed to reflect a tradeoff between energy needs of the adult (food limitation) and thermal needs of the developing embryos (temperature) (see Kendeigh, 1952; Conway and Martin, 2000b). Although, food limitation was not appeared to be a constraint to the breeding Grey-headed Bulbuls, the thermal requirements of the eggs seem to have a significant role in the on- and off-bout durations of incubation. Although the temporal variations in the weather conditions were not recorded, in general, the early morning and late afternoon hours had lower temperatures in the study area. Thus the higher attentiveness in the morning and evening hours ensured the thermal needs of the eggs. Moreover, off-bouts for foraging were significantly higher during 09.00 to 12.00 hrs which coincides with an increase in the air temperature at the study site, and therefore maintaining the optimum temperature requirements of the embryos. Similar patterns were observed during the brooding stage, however, nest attentiveness and durations of on- and off-bouts decreased and number of trips/hr was increased during the nestling phase. The evening hours during the nestling period was characterised by low on-bouts and maximum foraging trips, hence allowing the incubating bird to obtain more food for it and to chicks before roosting.

The nest attentiveness and on-bout durations were increased by the progress in incubation which could be explained by increasing thermal needs of the embryo (see Conway and Martin, 2000a). Nest attentiveness during incubation and brooding represents a parent-offspring conflict; incubating birds must balance a trade-off between caring for embryos or chicks by staying on the nest versus self-maintenance by getting off the nest to forage. For species in which females are the sole incubator, males can potentially affect this trade-off and increase nest attentiveness by feeding incubating females on the nest (Martin and Ghalambor, 1999; Ghalambor and Martin, 2000; see also Parker and Schwagmeyer, 2005). However, no mate feeding was recorded in the case of Grey-headed Bulbul, thus they avoided risk of predation by increased parental activity at the nest site. The initial stages of brooding are characterised by higher nest attentiveness, and larger on- and off-bout durations. Since increase in the age of chicks lead to higher food demands, the number of trips increased significantly towards the end of the nestling period. During this phase, both the birds were found feeding the young.

Parental care patterns during incubation significantly varied among the broods with different clutches. The nests with two eggs had longer attentive periods (on-bout durations) compared to those with single clutch. However, the off-bout durations across different day-light hours and incubation days were similar among the broods with different clutches. There was no variation in the attentiveness and on-bout durations across day-light hours during the nestling period. However, all the parameters varied among broods with different clutches. The parental effort for the nests with larger clutches was significantly higher than the nests with single clutch.

Longer on- and off-bout durations in general and reduced parental activity at the sites with high predation pressure during the incubation and nestling periods of Grey-headed Bulbul could be a strategy to reduce the risk of predation as has been found in the previous studies For example, Conway and Martin (2000b) in a comparative study on passerine incubation behaviour found that the species with high nest predation take longer on and off-bout durations, despite the fact that increased time off the nest may lengthen the incubation period, which would increase the exposure to nest predation (see also Filliater et al, 1994; Martin et al, 2000a, b; Fontaine and Martin, 2006). However, such a strategy may prevent frequent feeding by adults and thus compromise future reproductive attempts (Conway and Martin, 2000b). In conclusion, the differential parental care strategies of Grey-headed Bulbul seems to be an adaptive behaviour to improve fitness, since the investment in predator rich microhabitats was considerably low.

6.6. Summary

Understanding the population limitations and, life-history traits and its evolution are crucial factors in developing conservation and management of any rare avifauna. However, basic information on the natural history and life-history traits of most bird species in the tropical regions are poorly documented. In this study, I documented the life-history traits of Grey-headed Bulbul and examined the role of several biotic and abiotic factors in the evolution of these traits. The breeding biology of the species was studied at Silent valley National Park and surrounding reserved forests during January 2003-May 2005 using standard methods.

- Breeding season of Grey-headed Bulbul is confined to the drier months (January-May), as reported in several tropical species.
- Peak breeding (April-May) of the species was coincided with high abundance of fruits and absence of rain.
- The nest sites of Grey-headed Bulbul are associated with the reed and *Strobilanthes* patches in the mid-elevation (900-1400m) evergreen forests.
- The architecture of the nests varied, apparently, based on the microhabitat. The dominant (66.04%) typical bulbul nests (*vine nests*) were made mainly of vines and grasses and seen mostly in *Strobilanthes* patches and the second type of nests (*moss nests*) constructed mainly with *Ochlandra* leaves (33.96%) were located mostly in reed patches.
- The architectural variations could be an adaptive phenotypic plasticity evolved to improve the fitness and may have arisen from multiple interacting factors such as differential micro-habitat use to avoid inter-specific competition and predation pressure.
- The breeding phenology of the species was similar to the patterns recorded in other bulbuls; incubation and nestling periods averaged 13 and 12 days respectively.
- Grey-headed Bulbul used 12 plant species for nesting, two species namely *Ochlandra travancorica* and *Syzygium* sp. (saplings) bear 72.22% of nests.
- Nest success of Grey-headed Bulbul was 10.79%, which is comparatively lower than that of several threatened species, but typical of the Pycnonotids.
- The nest losses were caused mainly by predation.

- Nest initiation dates, nest placement, predator abundance and proximity of the nests of other species were important factors in determining the fate of the nests.
- Nest concealment, nest orientation and, nest-site characteristics around the nest did not significantly affect nest survival.
- The early season nests (moss nests in the reed patches) had better survival rates than the late season nests (vine nests in the *Strobilanthes* patches).
- The breeding birds took longer on- and off-bouts during the incubation and nestling periods and the parental activities were significantly low at the sites with high predation pressure.
- Interactive effects of interspecific competition and nest predation resulted in differential microhabitat and nest plant selections and, phenotypic variations in the nest architecture.

With-in species variation in nest sites and nest architecture of Grey-headed Bulbul.

1 a) *Ochlandra* patch

1 b) Moss nest

2 a) *Strobilanthes* patch

2 b)Vine nest

3 a) *Calamus* patch

3 b) Leaf nest

Juveniles of Grey-headed Bulbul.

Chapter 7

Synthesis, management implications, and future research needs for Grey–headed Bulbul conservation

In this dissertation, I examined the status, distribution and ecology of the Grey-headed Bulbul spanning across spatial and temporal scales in the Western Ghats. The present chapter outlines the major findings and conclusions detailed in the previous chapters and examine their implications for the future research and conservation of the species.

Grey-headed Bulbul is a rare species with a patchy distribution in the evergreen forests. The breeding season distribution of the species was restricted to the larger stretches of low- and mid-elevation evergreen forests. The species was also recorded from the moist deciduous and scrub forests, apart from the low-altitude evergreen forests in the rain-shadow areas during the non-breeding season. They were not seen in the shola forests and altered habitats such as plantations. The primary habitat of the species was areas dominated by *Strobilanthes* and reeds characterised by low canopy height, low canopy cover, high shrub cover and presence of wet streams. Grey-headed Bulbul was not seen in areas with wood cutting, mining and other anthropogenic pressures. They showed regular seasonal local migration in response to the variation in fruit abundance and adverse climatic conditions (Chapter 3).

Grey-headed Bulbul displayed non-random habitat selection at all the spatial scales examined. The foraging patches were characterised by higher densities of small trees and lianas, and higher sub-canopy and shrub covers. Interspecific competition for nest sites and other resource and, or simply the presence of Yellow-browed Bulbul has a significant role in the nest site selection of Grey-headed Bulbul. The differential habitat selection (reed patches in early season and *Strobilanthes* patches in late season) could be an adaptation to avoid competition for the nesting resources with Yellow-browed Bulbul and indirect factors affecting the fitness (Chapter 4 and Chapter 6).

Despite the abundance of the fruit bearing plant species in the evergreen forests, the narrow diet and specificity poses several constraints to the species. The non-random spatial distribution of food plants leads to the patchy distribution of Grey-headed Bulbul within the evergreen forests. Moreover, the lack of keystone species and strict seasonality of preferred fruit plants along with the adverse climatic conditions had a significance influence on the local migratory behaviour of the species (Chapter 3 and Chapter 5). The local migration to the lowland habitats with several competitors and predators may increase their vulnerability. Participation of the species in mixed-species flocks seems to be a strategy to override these constraints.

Breeding of Grey-headed Bulbul was restricted to the dry months and peak breeding coincided with high abundance of fruits and absence of heavy rain. The nest architecture of the species varied, apparently, based on the microhabitat. These architectural variations could be an adaptive phenotypic plasticity evolved to improve the fitness and may have arisen from multiple interacting factors such as differential micro-habitat use to avoid inter-specific competition and predation pressure. The nesting success of the Grey-headed Bulbul was typical of the common Pycnonotids. However it is comparatively lower than that of several threatened species.

7.1. Conservation implications

Grey-headed Bulbuls show a number of elements associated with the threatened species, including the restricted range, patchiness in occurrence, low population density, local migratory behaviour, nest site limitations, smaller clutch size, low nesting success, and distinct ecological requirements during different seasons, and need for pristine evergreen forests for breeding. These elements have significant conservation importance.

As in the case of most of the restricted range bird species of Western Ghats, the principal threat to Grey-headed Bulbul is the habitat loss and degradation. Although there are no reliable estimates of the total forest loss for the Western Ghats, several regional studies using satellite data suggest that only about 20% of the natural forest vegetation of the Western Ghats is remaining today, that too in a highly fragmented state (see, Chapter 2). The lowland evergreen forests which are of vital importance to several endemic species in the Southern Western Ghats have been cleared long ago and much of the lowland rainforests at 100 m elevation still exist only in the Southern Districts of Karnataka State. Moreover, most of the existing lowland forests are unprotected and are threatened by various anthropogenic pressures. Owing to the habitat loss, natural patchiness in occurrence and local migratory behaviour of Grey-headed Bulbul it is logical to infer that the species is under threat.

Although the occurrence of the species extends from Belgaum and Goa to Kanyakumari, the actual area of occupancy of this species is noticeably lesser, considering the large tract of unsuitable habitat and the patchy distribution of the species. Even though population estimation by extrapolation is not possible due the distinct microhabitat preferences and nomadic behaviour, the total number of Grey-headed Bulbuls seems to be significantly low. This is further supported by the low encounter rates obtained from both the breeding and non-breeding habitats (Chapter 3).

Conservation of a rare species requires the maintenance of sufficient area of suitable habitat to harbour minimum population size for long term survival. Grey-headed Bulbul's habitat specificity and narrow resource use indicate that the fate of these populations is closely linked to the persistence of suitable habitats. Even though Western Ghats represent maximum number of National Parks and Wildlife Sanctuaries of all the bio-geographic regions of India, most of these were designed based on the ecological requirements of large and charismatic species (Rodgers and Panwar, 1988; Daniels et al., 1991; Nair, 1991; Prasad et al., 1998; Rodgers et al., 2002). Recently, Das et al. (2006) identified areas of high conservation value in the Western Ghats using Red Listed animal species, and endemic tree species of evergreen and semi-evergreen forests as the species surrogates. However, species which are not assessed for threat levels and areas without proper biodiversity documentation are not included in these prioritization exercises. The major gap in the existing Protected Area network is the lack of large heterogeneous forests in terms of vegetation and elevation, especially in the low altitudes. The Grey-headed Bulbul was recorded from only half of the Protected Areas surveyed during this study. Moreover, more than half of the Important Bird Areas which support the Grey-headed Bulbul are unprotected areas (Islam and Rahmani, 2004). This indicates the inadequacy of the existing Protected Areas for the conservation and management of Grey-headed Bulbul and other nomadic species of the Western Ghats. Thus there is a need for developing programmes to protect/restore the low-elevation evergreen forests and, site/species safeguard and management for the effective conservation of Grey-headed Bulbul. Establishment of larger conservation complexes rather than smaller Protected Areas are crucial for the long-term survival of Grey-headed Bulbul and many other species which are seasonal migrants to low altitude forests. The following specific measures are suggested for the conservation of the species.

- Expansion of the Silent Valley National Park by the addition of the contiguous reserved forests (Kalikavu range) of Nilambur South Division; Attapady Reserved Forest and the vested forests of Mannarkkad Division.
- Formation of the Karimpuzha National Park with the New Amarambalam Reserved Forest (26,572 ha) of Nilambur South Forest Division as the core zone.
- Formation of a new Protected Area complex, which includes the Muthikkulam Reserved Forest (Mannarkkad Division) – Dhoni Hills (Chenath Nair Reserved Forest, Palakkad Division) – Bolampatty Reserved Forest (Coimbatore Division).
- Additions of Kottiyoor Reserve to the Aralam Wildlife Sanctuary (Kerala) and, Kemphole Reserve to the Kudremukh National Park (Karnataka).
- Legal protection of Kulathupuzha Reserved Forest in Kerala, Kemmangundi and Bababudan Hills; Castle Rock and Bhimgad in Karnataka.
- Formation of a larger Protected Area in the Palni Hills covering all the habitat types from the lower to the higher altitudes.

Another important aspect for the conservation of Grey-headed Bulbul is the prevention of extensive extraction of reeds (*Ochlandra*), as they form a major nesting plant and microhabitat for the species (see Chapter, 6). In its entire range of the Western Ghats, reed bamboos constitute an important raw material for pulp and paper industry, besides being used in traditional cottage industries such as basket and mat-weaving. During the past three decades, the pulp and paper sector in the Western Ghats states has become the major consumer of reed resources resulting the depletion and degradation of reed habitats (Bhat and Pandalai, 1999). Chundamannil (1989) noted that intensive exploitation of reeds is threatening the regeneration of forests and activating the degradation process. Even though reed breaks are poor in terms of ecological diversity, they form a distinct habitat supporting a number of specialists such as the Grey-headed Bulbul. Currently the reeds are not extracted from the National Parks and Wildlife Sanctuaries. However a sustainable extraction scheme in the un-protected areas is necessary for the preservation of Grey-headed Bulbul and similar habitat specialists. It is suggested that the low lying forests adjacent to National Parks and Sanctuaries and to the major reserve forests may be completely exempted from reed extraction.

The restricted range, patchiness in occurrence, low population density, low breeding productivity and annual recruitment and, the threats to the habitat of Grey-headed Bulbul (Chapter 3 and Chapter 6) make it a right candidate for considering under the "Vulnerable" category of the IUCN. Majority of the low elevation evergreen forests, where the species was once recorded as fairly common have lost the species during the past few decades. Although Grey-headed Bulbuls were recorded from about 33 sites, majority of them are non-breeding sites and are unprotected areas. Even though the number of individuals and the actual areas of occupancy are limited, the nomadic behaviour of the species and its distinct and louder calls might have lead to the erroneous conclusion that the species was very common. It may be noted that Grey-headed Bulbul was listed as a Near-Threatened species in earlier assessments (Collar et al., 1994; Stattersfield et al., 1998). However, in the recent assessments the species was excluded from the list (Birdlife International, 2001; 2004a), although proposals to include them in the IUCN category have been mooted (L. Vijayan, *pers. comm.*).

7.2. Research implications

Although the habitat preservation approaches are of prime importance, the long-term conservation of Grey-headed Bulbul requires further understanding of such life history and other parameters as age of first breeding, lifespan, adult survival rates, annual fecundity; nest survival in unprotected and fragmented areas; movements and demographic trends. Therefore some of the key research perspectives for the conservation of Grey-headed Bulbul are: (1) the status of the species in areas that could not be surveyed during this study, (2) monitoring procedure including marking of individuals to identify population changes in relation to environmental and anthropogenic factors; (3) an in-depth assessment of the protected area coverage especially in the low elevations for the conservation of Grey-headed Bulbul and similar species, (4) phenological patterns of food species, its dependence on insect food and competition with the co-generic species in the non-breeding habitat; and behavioural plasticity to cope with the changing habitat.

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* Originals not referred.