BEHAVIOURAL ECOLOGY OF COLONY FORMATION AND FUNCTION OF COLONIAL BREEDING IN CHESTNUT-HEADED BEE-EATER

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Certificate

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CONTENTS

Page no.

CERTIFICATE i

ACKNOWLEDGEMENTS ii

LIST OF TABLES vi

LIST OF FIGURES vii

LIST OF PLATES viii

SUMMARY ix

1. INTRODUCTION 1

    1.1 Colonial breeding 1

        1.1.1 Framework I- Individual level approach 2

        1.1.2 Framework II- Population-level approach 4

    1.2 Study animal – Chestnut-headed bee-eater (CHB) 6

        1.2.1 Phylogeny 6

        1.2.2 Status, distribution and habitat 7

        1.2.3 General habits 7

        1.2.4 Breeding habits 8

        1.2.5 Previous studies on behavioural ecology of bee-eaters 8

    1.3 Objectives 9

2. STUDY AREA 12

3. METHODS 14

    3.1 Habitat characteristics and availability of nesting substrate 14

    3.2 Measurement of morphological features 15

    3.3 Nest monitoring 15

    3.4 Provisioning behaviour observations 16

    3.5 Data analysis 16

4. RESULTS 20

    4.1 General behavioural observations 20

    4.2 Habitat characteristics and availability of nesting substrate 21

    4.3 Morphological measurements 22

    4.4 Nest survival 22

Page no.

4.5 Synchronicity of breeding 25

4.6 Spatial positioning 31

4.7 Provisioning behaviour 31

5. DISCUSSION 35

5.1 Insights into colony formation in CHB 35

5.2 Why colonial breeding in CHB 37

5.3 Conclusion 38

REFERENCES 40

APPENDIX 1 Ring numbers and measurements of all the captured birds 45

APPENDIX 2 Detailed results of all the nest survival models run in MARK 48

APPENDIX 3 Summary of selected Generalized Linear Models made before arriving at the final model. 57

LIST OF TABLES

Page no.

Table 4.1 Comparison of habitat characteristics of solitary and colony nests in chestnut-headed bee-eaters in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). 23

Table4.2 Morphometric differences between colony nesting and solitary nesting chestnut-headed bee-eaters in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). 23

Table 4.3 Factor loadings of various morphological features of chestnut –headed bee-eaters to the extracted principal components. Study was conducted in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). 24

Table 4.4 Summary of nest survival model results of chestnut-headed bee-eater nests in Haliyal and Karwar divisions, Karnataka using program MARK. 26

Table 4.5 Beta estimates of nest survival from all the models for chestnut -headed bee-eater breeding. Study was conducted in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). 27

Table 4.6 Parameter estimates for the most parsimonious model explaining the frequency of provisioning in chestnut-headed bee-eater nests in Haliyal and Karwar divisions, Karnataka (Dec.2010- May 2011). 33

LIST OF FIGURES

Page no.

Figure 2.1. Map of study area 13

Figure 4.1 Dispersion of individual chestnut-headed bee-eaters along principal component axis 1 and axis 2 consisting of a combination of morphometric variables. Study was conducted in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). 24

Figure 4.2 Plot of model {Bage^2, nestno}. Change in Daily survival rate (DSR) of CHB nests as the age of the nests increases, considering that colony size influences DSR. Study was conducted in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). 28

Figure 4.3 Mean daily survival probability estimate with 95% confidence interval of nests in different colony sizes in chestnut-headed bee-eater in Haliyal and Karwar divisions, Karnataka (Dec.2010- May 2011). 29

Figure 4.4 The distribution of nest initiation dates across one, three and six colony sizes, and a randomly generated order of initiation dates in chestnut-headed bee-eaters in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). 30

Figure 4.5 Difference between expected (for random distribution of initiation dates) and observed mean inter-nesting interval in chestnut-headed bee-eater in Haliyal and Karwar divisions, Karnataka (Dec.2010- May 2011). 32

Figure 4.6 Average inter-nest distance for successful and unsuccessful nests in chestnut-headed bee-eater in Haliyal and Karwar divisions, Karnataka (Dec.2010- May 2011) 32

Figure 4.7 Provisioning frequency for three hour periods, with increase in colony size in chestnut-headed bee-eater in Haliyal and Karwar divisions, Karnataka (Dec.2010- May 2011). 33

Figure 4.8 Change in provisioning frequency for three hour intervals in different observation periods in chestnut-headed bee-eaters in Haliyal and Karwar divisions, Karnataka (Dec.2010- May 2011) 34

LIST OF PLATES

Plate 1- A photograph of chestnut-headed bee-eater (*Merops leschenaulti)* and its distribution map.

Plate 2- View of Kali river from Ganeshgudi bridge; Solitary nesting site at Kodli roadside, a nest tunnel entrance is shown with a red circle; View of Bison mine site colony

Plate 3- A captured CHB; Checking for wing moult in a captured bird; Probing the nest hole with the 'burrowscope

SUMMARY

Breeding in densely distributed territories that contain no other resources apart from breeding site is known as colonial breeding. Despite several long-term investigations, there are several questions regarding colony formation, the function of coloniality and the variation in colony sizes that remain unanswered. Chestnut-headed bee-eaters (*Merops leschenaulti)* are tropical Old World birds (Family Meropidae) that breed both solitarily and in small colonies. Hence they are well-suited subjects for the study of colonial breeding.

This study was conducted for five months from December 2010 to May 2011 in parts of Haliyal division and Karwar division in Uttara Kannada district, Karnataka. It is an attempt to explain the variation in colony size through gaining insights into the behaviour of colony formation and function of colonial breeding. A combination of measuring habitat characteristics, capturing and measuring birds, recording reproductive success of breeding pairs across a gradient of colony sizes and behavioural observations were used. A total of 17 nests were found during the course of the study distributed over three colonies and five solitary nests. No significant difference was found between habitat characteristics at solitary and colony nests. Also, there was no shortage of potential breeding sites, as found by the ratio of number of nests to the amount of substrate available. This suggests that the mechanism of colony formation in CHB is conspecific attraction and is not merely habitat-mediated aggregation. The body size of the colony nesters was found to be greater than the body size of solitary nesters. This implies that the optimum colony-size is different for different individuals, with larger individuals having a preference for colony nesting.

Program MARK was used to analyze nest survival data. It was found that the daily survival rate of nests was not significantly different across colonies of different sizes, lending further credence to the hypothesis that different individuals have different colony-size optima. Colony nests were initiated about a week before the solitary nests and nesting was more synchronous at colony sites. During the nest digging stage of breeding, a number of aerial chases were observed between the birds, which hint at a role for despotism in influencing variation in colony sizes. Provisioning frequency was found to be higher and showing larger variation at solitary nests than at colony nests. A possible explanation for this is that there is greater competition at colony sites. Therefore, colony-nesting must be having some other benefit that compensates for the cost of competition. Further investigations into the conspecific cue that mediates colony formation and the benefit of coloniality need to be carried out. [1]

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[1] The thesis has been written following author guidelines for the journal Animal Behaviour

1. INTRODUCTION

1.1 Colonial breeding

Evolution and maintenance of group living in animals has always interested both scientists and sociologists. The study of social animals is made even more interesting by the fact that the tug of war between cooperation and conflict seen in animal societies has parallels even at the level of genes (Hatchwell 2009). Group-living is known to occur in various taxa including mammals, birds, fishes and insects. Why animals live in groups despite the obvious costs (e.g. increased competition and increased chances of disease and ectoparasite transmission (Alexander 1974)) is indeed intriguing.

Colonial breeding is a form of group-living in which individuals nest in closely spaced breeding territories that contain no resources apart from breeding sites (Perrins & Birkhead 1983). Colonial breeding is widespread in birds, being present in about 13% of all bird species (Lack 1968). However, the occurrence of this behaviour is distributed very asymmetrically among bird taxa. It is especially prevalent in the order Ciconiiformes and relatively rare in Passeriformes (Lack 1968; Wittenberger & Hunt 1985; del Hoyo, Elliott & Sargatal 1992,1995). Siegel-Causey & Kharitonov (1990) found that coloniality in birds has evolved independently at least twenty times. Therefore, the evolutionary forces leading to coloniality and its adaptive significance may be different in different bird lineages (Siegel-Causey & Kharitonov 1990).

There is large variation in colony size among species, ranging from small colonies of a few pairs in some heron species to large colonies of several hundred thousand birds in some penguin species (del Hoyo et al. 1992,1995). Even within the same species, colony size may vary greatly, for example, in bank swallows (*Riparia riparia*) colony size ranges from two breeding pairs to several hundred pairs (Hoogland & Sherman 1976). This plasticity in colony size is especially remarkable considering that there is high selection pressure on breeding behaviour (Brown, Stutchbury & Walsh 1990; Brown & Brown 2001).

Hypotheses to understand variation in colony size can be categorised into two frameworks, one having an individual-level approach to the question and the other having a population-level approach (Safran et al. 2007). The hypotheses under the first framework propose that variation in colony size is a result of the process of colony formation i.e. the individual decision-making processes governing nest-site selection (Brown et al. 1990). Thus, this framework can also be referred to as the commodity-selection framework (Danchin & Wagner 1997). Under the second framework, colony size is hypothesized as varying around an optimal colony size (defined on the basis of reproductive success in colonies of various sizes) i.e. the adaptive function of colonial breeding in a species determines the distribution of colony sizes in it (Safran et al. 2007). Thus, this framework can also be referred to as the economic framework.

1.1.1 Framework I- Individual level approach- Commodity selection

Danchin and Wagner (1997) consolidated a number of hypotheses that focus on colony formation as a "by-product" of individual decision-making under this framework. They proposed that selection of similar 'commodity' by individuals- e.g. habitat or mate leads to colony formation; thus coloniality need not be beneficial.

If habitat quality is the commodity that individuals select for, then density of animals would have a positively linear relationship with habitat quality; i.e. habitat-mediated aggregation would be observed. In this scenario, colony size will vary according to the abundance and distribution of resources. (Danchin & Wagner 1997)

This follows the ideal-free distribution model that predicts that the average fitness over a given period of time would be same in different patches (Fretwell & Lucas 1969). Thus colonies would be formed due to a shortage of breeding sites, in terms of breeding sites per se or food resources and therefore, aggregating won't increase the fitness of individuals (Lack 1968; Wittenberger & Hunt 1985; Kaiser & Forbes 1992). For example, Kaiser and Forbes (1992) showed that colonies of four burrow-nesting alcids i.e. ancient murrelet *Synthliboramphus antiquus*, cassin's *Ptychoramphus aleuticus*, and rhinoceros auklet *Cerorhinca monocerata* and tufted puffin *Fratercula cirrhata*, occur only on less than two percent of the 6,500 islands surveyed and 12 of the largest colonies contained about 83% of the breeding population. They found that occupied islands were located in colder, more saline water, and were subject to less intense rainfall than unoccupied islands (Kaiser & Forbes 1992). More recently, Safran (2004) found that in barn swallows (*Hirundo rustica),* colony size at a site depended heavily on the number of old nests at a site in the beginning of the nesting season; old nests acted as a resource in this species, rather than as an indicator of previous year's nesting success.

The other three hypotheses that have been identified under this category predict additive aggregation of animals i.e. density of animals, might be lower or higher than what is expected, based on habitat quality (Danchin & Wagner 1997): (i) the traditional aggregation (TAG) hypothesis - which proposes that individuals use presence of conspecifics or evidence of former presence as cues (A. R. Kiester & Slatkin 1974); (ii) conspecific reproductive success hypothesis - which suggests that individuals use information on reproductive success of conspecifics at a site in the previous breeding season to select a breeding site (Boulinier et al. 1996; Burger 1982); (iii) sexual selection (hidden lek) hypothesis - which proposes that individuals select breeding sites on the bases of secondary sexual characters of potential mates (Morton, Forman & Braun 1990; Wagner 1993). These hypotheses may be collectively referred to as conspecific attraction (Danchin & Wagner 1997).

Under these hypotheses, variation in group size may be caused by different individuals breeding in different group sizes in accordance with non-heritable (size, condition, age, experience, dominance) (Ranta & Lindström 1990) or heritable variation (Brown & Brown 2000). Effect of a non-heritable factor influencing settlement pattern of individuals and consequently colony sizes is illustrated well by lesser kestrels (*Falco naumanni)* (Serrano et al. 2003). Competitive abilities (represented by arrival date at breeding grounds) influence the ability of lesser kestrels to breed in the better-quality sites. Heritable variation was shown to influence choice of colony size in cliff swallows (*Hirundo pyrrhonota)* in an elegant study by Brown and Brown (2000). They suggested that variation in group sizes maybe because of different individuals differing in ability to breed in larger or smaller groups and thus being genetically predisposed to choosing larger or smaller colonies.

Alternatively, energetic, social or temporal constraints may prevent individuals to gather enough information to choose an optimum colony size, leading to variation in colony size (Brown et al. 1990).

1.1.2 Framework II- Population-level approach- Economic framework

All the hypotheses under this category propose that colonial breeding evolved because the benefits of colonial breeding [e.g. enhanced foraging (Brown 1988), defence against predators by mobbing (Hoogland & Sherman 1976; Wiklund & Andersson 1994), group vigilance(Brown & Brown 1987) or dilution effect (Hamilton 1971; Murphy & Schauer 1996)], are greater than the costs [e.g. increased conspicuousness to predators(Lack 1968; Brunton 1997), increased transmission of diseases and parasites (Alexander 1974; Hoogland & Sherman 1976), increased competition(Alexander 1974; Hoogland & Sherman 1976)].

According to this framework, colony size variation is due to "insider-outsider conflict" i.e. the optimal colony size is not stable because when a colony reaches an optimum size, it may still be more advantageous for an 'outsider' to join the colony than to nest solitarily, thereby reducing the fitness of all the 'insiders' (Sibly 1983; Higashi & Yamamura 1993). Thus, the colony size becomes stable only when the colony becomes so large that it is more advantageous for an 'outsider' to nest solitarily (Sibly 1983). Thus, while the 'insiders' drive colony size towards the optimum, the 'outsiders' drive it towards the stable colony size, with the result that colony size varies between the optimal and stable colony size (Higashi & Yamamura 1993). This conflict is further influenced by many factors including relatedness between individuals, despotism and collective decision making (Brown & Brown 2000).

The benefits and costs of coloniality determine the optimum colony size and therefore, they are briefly discussed here. Whether colonies face less predation due to increased group vigilance and mobbing or they face more predation due to increased conspicuousness has still not been unequivocally answered (Brown & Brown 2001). However, a recent phylogenetic analysis within the order Ciconiiformes, using 'Pagel's general method of comparative analysis for discrete variables', showed that coloniality attracts predators (Varela, Danchin & Wagner 2007).

Enhanced foraging efficiency has been proposed to be a benefit of coloniality, regarding which two hypotheses have been proposed. The first of these is 'Information centre hypothesis' which proposes that coloniality has evolved as an adaptation to patchily distributed and unpredictable food resources (Ward & Zahavi 1973). According to Ward and Zahavi (1973), successful foragers return to the colony after successfully locating and to some extent exploiting a food resource and pass on the information to unsuccessful foragers in the colony. Therefore, the colonies serve as 'information-centres'. The only convincing evidence for this hypothesis comes from a study on cliff swallows carried out by Brown (1986).

Richner and Heeb (1995) pointed out several flaws in this hypothesis including the fact that it fails to explain why successful foragers should incur the costs of returning to the colony and advertising the location of the food resource. They also proposed the 'Recruitment centre hypothesis' which suggests that colonies serve as 'recruitment centres' where successful foragers recruit other foragers to the food patch found, because group foraging is more efficient (Richner & Heeb 1996).

In a recent paper Safran *et al* (2007) suggested that research on colonial breeding must integrate individual-level and population-level approaches. Individual decision-making processes leading to colony formation need to be identified as the proximate mechanisms; and the costs and benefits of those decisions need to be studied to explain the patterns existing at the population-level to give the ultimate explanation for this behaviour (Safran et al. 2007). Overall, four hypotheses have been suggested to explain variation in colony size i.e. colony size is habitat mediated; optimum colony size is different for different individuals; individuals are constrained from gathering sufficient information to make choices about optimum colony size by social, temporal or energetic factors; despotic behaviour of some individuals forces other individuals to make sub-optimal choices of colony sizes (Brown et al. 1990)

1.2 Study Animal

Chestnut-headed bee-eater (*Merops leschenaulti)* (referred to as CHB in this thesis) is a slender green coloured bird with a rich chestnut-coloured head and a yellow throat with a narrow black and rufous gorget. The back, rump and uppertail-coverts are bright pale blue coloured. The bill is slender, curving, pointed and black in colour (Ali & Ripley 1970). It is the only *Merops* bee-eater outside Africa that does not have elongated central tail streamers (Fry, Fry & Harris 1992). Sexes are similar. Juveniles can be easily distinguished by their green head and the rufous of upper back being well mixed with green. Also, they have a smaller bill and the black and rufous gorget is not clearly defined in them. (Ali & Ripley 1970) [Ref. Plate 1]

There are three sub-species that vary in the amount of rufous in the ear coverts and throat. *M.l.leschenaulti,* the nominate race found all over the range of the species except Andamans, Java and Bali has a black mask and rufous lower throat. *M.l.andamanensis,* found in Andamans, has a rufous mask with a black border towards the cheek and the side of the breast is rufous. *M.l.quinticolor,* distributed in Java and Bali, has rufous mask and yellow lower throat with a blue tail. (Fry et al. 1992)

1.2.1 Phylogeny

Bee-eaters (Order Coraciiformes, Family Meropidae) are non-passerine tropical Old-world birds that have been aptly named for their skill of catching bees and other hymenopterans and carefully removing their sting before eating them (Fry et al. 1992). In the family Meropidae, there are 25 species in 3 genera *Nyctyornis, Meropogon, Merops* (Dickinson 2003). Six species of bee-eaters are distributed in India (5 *Merops* and 1 *Nyctyornis*) (Ali & Ripley 1970). According to a recent molecular phylogenetic study on bee-eaters, CHB is a sister species of blue-throated bee-eater *Merops viridis,* that is distributed in China and South-east Asia. *M.leschenaulti* and *M.viridis* share a common ancestor with green bee-eater *M.orientalis* (Marks, Weckstein & Moyle 2007).

1.2.2 Status, Distribution and Habitat

This species is classified as 'Least Concern' by BirdLife International (2011). It is a widespread species found in India, Sri Lanka, Nepal, Bangladesh, Myanmar, Thailand, Malaysia, Vietnam, Java, Bali, Andamans, Great and Little Cocos and Strait islands. Recently, they seem to be colonising Sumatra as deforestation is creating more habitat for them. (Fry et al. 1992)

It is a resident species in India that emigrates from heavy rainfall areas during the monsoon months. In India it is distributed in submontane tracts of Himalayas from Dehradun eastwards to North-eastern India and Orissa and in Western Ghats from Goa southward (Ali & Ripley 1970). The habitat preferred by this species is mixed deciduous forests by the side of rivers and hill streams (Ali & Ripley 1970). This species is often found in forested hill areas having forest patches interspersed with grassy clearings (Fry et al. 1992).

1.2.3 General habits

CHBs are mostly seen in small flocks. Bare branches at the top of the canopy and telegraph wires are among the favourite perches (Ali & Ripley 1970). Like all bee-eaters, they catch insects in mid-air and then go back to the perch and beat it before swallowing it. They spend a lot of time sunbathing especially in the early morning (Fry et al. 1992). They bathe by gliding slowly into still water and then return to a perch to preen. Communal roosting is also seen in this species. The roost is a place of great activity in the evening (Fry et al. 1992). Bees, dragonflies and butterflies are the main prey species, though they will eat almost any flying insect (Ali & Ripley 1970). They are quite vocal and have a 'pruik' or 'churit' or 'djewy' call, very similar to the call given by european bee-eater. They also have trilling calls like other bee-eaters. (Fry et al. 1992)

1.2.4 Breeding habits

It nests in horizontal tunnels up to 2 m long that it makes in sandy banks of streams or sandy level ground (Ali & Ripley 1970) and in road cuttings. It nests both solitarily and in small colonies of 4-8 breeding pairs (Grimmett, Inskipp & Inskipp 1998). Occasionally, colonies of hundreds of nests have been found. Both sexes are involved in excavating nests, incubation and provisioning of chicks (Fry et al. 1992). It has also been reported to be a cooperative breeder with 'helpers' at the nest (Sridhar & Karanth 1993a; Burt 2002). The breeding season of this species is from February- June with the peak breeding activity in March and April (Ali & Ripley 1970).

1.2.5 Previous studies on behavioural ecology of bee-eaters

As bee-eaters show wide variation in their social and breeding organisation (Fry 1972a), they have attracted considerable interest of behavioural ecologists. However, no study has been done on CHB. There have been a few studies on cooperative breeding in bee-eaters [white-fronted bee-eater *Merops bullockoides* by (Emlen & Wrege 1986; Emlen et al. 1991; Wrege & Emlen 1991); green bee-eater by (Burt 2002; Sridhar & Karanth 1993b)].

Colonial breeding has been studied in european bee-eater (Hoi et al. 2002), however that study used only the population-level approach. They found a negative relationship between reproductive success and colony size and suggested that some resource constraints may be responsible for coloniality in their study population. However, they did not investigate the proximate mechanisms of colony formation.

1.3 Objectives

The objectives of the study were-

1. To explore factors leading to colony formation in CHBs.
2. To assess colonial breeding in CHBs in terms of the costs and benefits to colony nesting pairs versus solitary nesting pairs.

Research Questions

1. To explore factors leading to colony formation in CHBs.

a. Do habitat characteristics of sites having solitary nests differ from sites having colonies?

If habitat-mediated aggregation is responsible for colony formation, then the habitat characteristics of sites having solitary nests must be less suitable for breeding than at colony sites, provided that there is no shortage of potential breeding sites. Based on previous studies on breeding biology and nest site-selection in bee-eaters, the following variables were measured to characterise habitat- soil penetrability, slope, per cent vegetation cover around nesting tunnel entrance, distance to nearest used perch, height of embankment, distance to nearest water source (Boland 2004; Yuan et al. 2006; Heneberg 2009; Asokan et al. 2009).

b. Is there a shortage of potential breeding sites?

If there is a shortage of potential breeding sites, then all the breeding sites should be occupied up to their carrying capacity. In such a case, there may not be a difference in habitat characteristics of colony sites except for the amount of nesting substrate available. Thus, if shortage of potential breeding sites is responsible for colony formation, then the number of nests in a site should be proportional to the amount of substrate available, as was found to be the case in rainbow bee-eater (Boland 2004).

c. Do morphological features of solitary nesting individuals differ from colony nesting ones?

Morphological features are a measure of the physical condition and age of the individuals. Thus, if morphological features vary between solitary nesters and colony nesters, then choice of colony size may be getting influenced by condition or age of individuals.

2. To assess colonial breeding in CHBs in terms of the costs and benefits to colony nesting pairs versus solitary nesting pairs.

a. Does the nesting success of colony nesting pairs differ from that of solitary nesting pairs?

If nesting success of colony nesting pairs is lower than that of solitary nesting pairs, then colony formation may be due to shortage of nesting sites. On the other hand, if colony nesting pairs are more successful, colony formation may be due to the advantage of coloniality and driven by conspecific cues and solitary nesters may be weaker or late arriving individuals who could not find a place in the colony. And if the nesting success of colony nesting pairs and solitary nesting pairs is same, then colony formation may be habitat-mediated or the optimal colony size for individuals in different conditions may be different.

b. Is the breeding more synchronous in colony nesters than in solitary nesters?

Breeding synchronicity may be a benefit of colonial breeding that can act either by reducing predation risk by swamping the predator (Murphy & Schauer 1996) or by the advantage of group foraging (Emlen & Demong 1975). If breeding is more synchronous in colony nesters, but the nesting success is not higher, the post-fledging success may be higher and maybe responsible for the synchronicity. Alternatively, if breeding is less synchronous in colonies, it may be a strategy to reduce chances of extra-pair copulation and intra-specific brood parasitism.

c. Is nesting success influenced by the position of the nest with respect to other nests in the area?

If nests having lower average inter-nest distances are more successful, then grouping may be beneficial and thus colony formation may be due to benefits of coloniality and vice versa. No difference in average inter-nest distance of successful and unsuccessful nests may be due to habitat-mediated colony formation or the optimum inter-nest distance being different for different individuals.

d. Does the provisioning frequency differ between solitary and colony nests?

Provisioning frequency is dependent on the abundance and distribution of resources over space and time. It also depends on the condition and efficiency of provisioning individual and also on whether or not helpers are present and/or the social facilitation of foraging. If provisioning frequency is consistently higher at a site, then either resources are more abundant there or parents are more efficient foragers and are probably assisted. The converse is true if provisioning frequency is consistently lower. Additionally, if provisioning frequency shows a wide variation at a site, the resource availability there may be temporally highly variable.

2. STUDY AREA

The study was conducted in Jagalbet Range of Haliyal division and Joida range of Karwar division in Uttara Kannada district, Karnataka. 6900 Km^2 of area in Uttara Kannada is under forest cover and forms the largest contiguous expanse of tropical humid forest in peninsular India (Gadgil 1992). The district is highly biodiverse and boasts of 1741 species of flowering plants and 403 species of birds (Gadgil 1992). The study area is adjacent to Dandeli-Anshi tiger reserve and is located in the Western Ghats mountains, biogeographic province no.5B (Rodgers & Panwar 1988). The latitude of the study area ranged from N 15.2876 to N 15.1410 and the longitude ranged from E 74.493 to 74.5500. Altitude of the area ranges from 500-600 m. The terrain is hilly with a mix of gentle slopes, steep slopes and plateaus. Soil is deep and loamy. Annual precipitation in the area is around 4000mm. The forest type in the area is 3B (South Indian moist deciduous forest) /C1b (Moist teak forest) (Champion & Seth 1968). Apart from teak *Terminalia paniculata, T.bellerica, T.tomentosa, Dalbergia latifolia, Xylia xylocarpa, Lagerstroemia lanceolata, Salmalia malabarica, Bambusa arundinacea* and *Dendrocalamus strictus* are the dominant tree species (Champion & Seth 1968). Forest fires are common in the dry months i.e. March and April.

Mining of manganese ore was carried out at many places in this area till mid 1990's. There is only one river that passes through the area, river Kali. A dam called Supa dam has been constructed on the river by Karnataka Power Corporation at Ganeshgudi; it is the second largest dam in Karnataka. The erstwhile mining areas provide a good habitat for nesting bee-eaters as there are many vertical cuttings available and also the soil is quite loose. Two of the colonies found in this study [Bison mine site (6 nests) and Hudsa (3 nests)] and two of the solitary nests (Rafting jetty mine site and Kodli mine site) were located in abandoned mines. The forest department has been planting *Acacia auriculiformis* in many of the abandoned mine sites, which might render them unsuitable for nesting by bee-eaters and other birds like nightjars that use small clearings. One colony [Jungle lodges colony (3 nests)] and one solitary nest (Kodli roadside) each were made on the mud cuttings by the roadside. Two solitary nests (Right Bank and Nagoda) were made on sloping grounds near the backwaters of Supa Dam. [Ref. Plate 2]

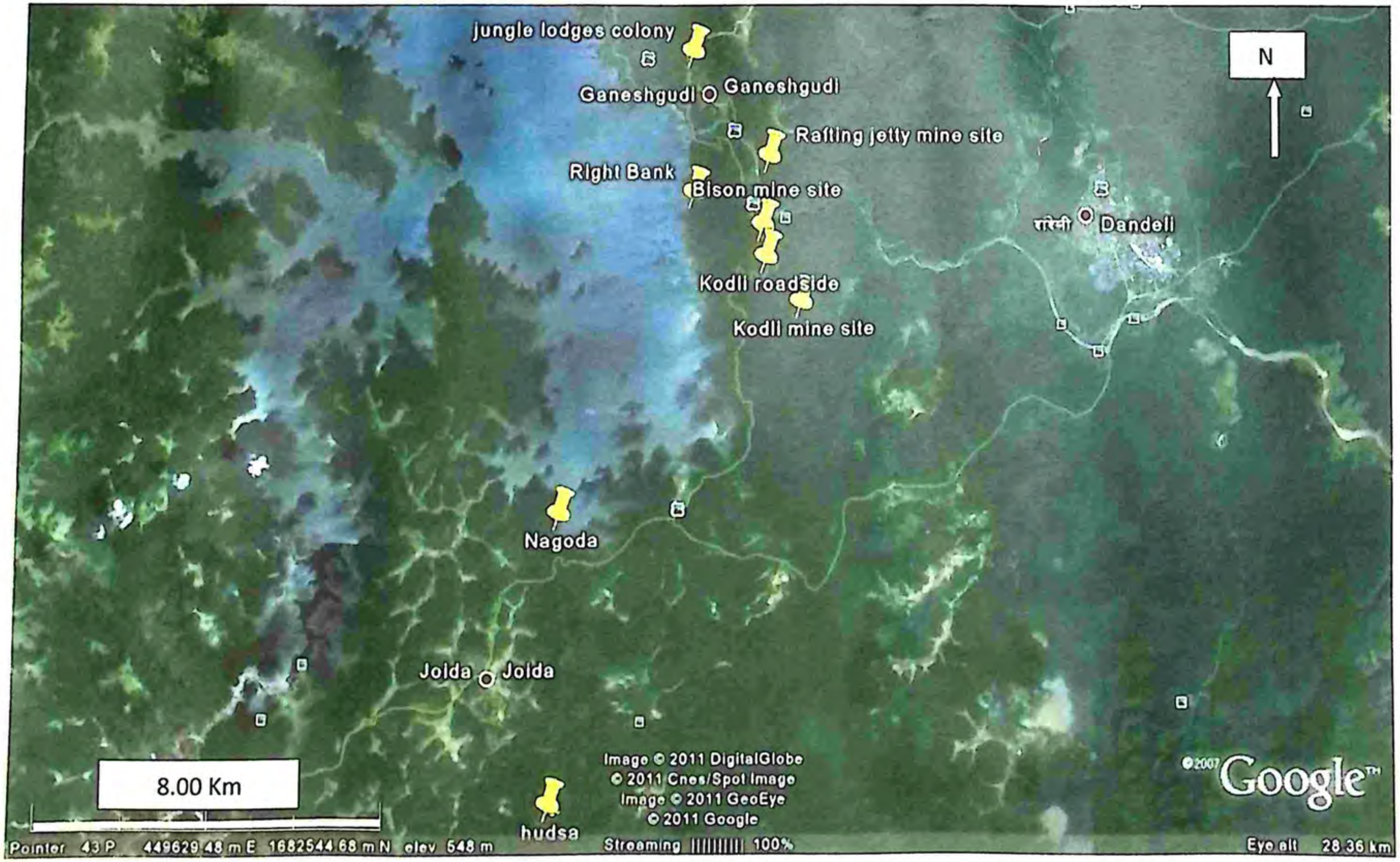

Figure 2.1 Map of the study area – Moist deciduous forest in Haliyal and Karwar division, Karnataka. Latitude of the study area ranged from N 15.2876 to N 15.1410 and the longitude ranged from E 74.493 to 74.5500

3. METHODS

The study was conducted for five months from December 2010- May 2011. The study site had four nature resorts that had naturalists and visitor bird watchers who were regularly observing birds. The naturalists and bird watchers were contacted and initial information on foraging sites, breeding season and nesting sites of CHBs was gathered. Information on foraging and nesting sites of CHBs was gathered from local birdwatchers. Ad libitum observations were made at Bison mine site and Jungle lodges colony site in early January for about ten hours. Towards, the end of January as the birds started showing breeding related behaviours, again ad libitum observations were made for about ten hours at the same sites and at Kodli roadside. About nine hours of observations were made at the same sites and at Hudsa and Nagoda in March. The duration of ad libitum observations vary from ten minutes (if the birds disappeared from view) to three hours. Focal animal samples (about 20 hours) and all occurrences observations (about 46 hours) were recorded at Jungle lodges colony, Bison mine site, Hudsa and Kodli roadside from mid-February to mid-April by two observers. The duration of a focal sample was ten minutes or till the bird disappeared from view whichever was earlier. The duration of all occurrences session was usually about three hours. The data from these focal samples and all occurrences sessions has not been analysed for this thesis.

3.1 Habitat characteristics and availability of nesting substrate

To investigate if habitat characteristics differ between solitary and colony nests, the following variables were measured at each nest to characterize the habitat :- (i) soil penetrability, was measured using Lang's penetrometer which expresses resistance to penetration in pounds on a scale reading from one to twenty. Greater the penetrability, smaller is the reading of the penetrometer; (ii) slope of the embankment, was measured using a protractor with a string (having a small weight attached at the end) passing through the midpoint between zero and 180 degree graduation; (iii) per cent vegetation cover in 0.5 m radius around the nest tunnel entrance was visually estimated; (iv) distance to the nearest used perch was measured using a measuring tape, but for a few nests it had to be visually estimated owing to difficult terrain; (v) height of embankment, was measured using a Sunnto Tandem Clinometer cum compass; (vi) bearing of nest tunnel was measured using a compass; (vii) distance of nesting site to the nearest water source was either visually estimated (when the site was next to some water body) or measured using Google Earth™ ; (viii) nesting area available at the site was measured using Google Earth™ for the nesting sites in abandoned mine sites. For nesting sites on linear structure like roads and banks, nesting area available was obtained by multiplying the length of the continuous stretch having similar vegetation characteristics with the average height of the road cutting.

3.2 Measurement of morphological features

A total of 18 birds were captured and banded using numbered aluminium rings provided by Bombay Natural History Society (Ref. Plate 3). Mist nets were spread over the nest tunnel entrance on the ground in the early morning hours (0600-0630) and the birds were caught when they exited the nest tunnel. Mist nets were spread over nest tunnel entrance, instead of being erected in front of it; because in the latter case, the birds flew from under or over the net. To enable individual recognition, initially a few birds were marked on their tail feathers and later, a few individuals were marked on scapulars. However, the markings were not visible from a distance and hence individual recognition was not possible. Measurements were made using dial vernier callipers, an ordinary glass scale and a 50 g Pesola™ spring balance. The techniques detailed in the North American Banders' Manual were followed (North American Banding Council 2001). The ring numbers and standard measurements of the birds are given in Appendix.

3.3 Nest monitoring

Once located, nests were checked as frequently as possible. The nests that were easily approachable were checked almost daily. Maximum interval between consecutive checks of a nest was nine days. Nest contents were checked using a 'burrowscope' assembled with a Closed Circuit Television (CCTV) camera attached at the end of a long pipe whose cable was connected to a MP4 player at the other end of the pipe. Because it was dark inside the nest tunnel, a CCTV camera having an in-bulit light sensor tuned on infrared Light Emitting Diodes (LED) was used to capture video stream. This unit was powered by a 12 V battery. The diameter of the 'burrowscope' at its widest portion was 44 mm. The nests were checked in one to three minutes. A nest check was completed when the enlarged chamber at the end of the tunnel was reached and checked well by rotating the camera.[2] The nests in the colonies were mapped by taking the compass bearing and distance from one of the nests or a reference point to all the other nests. Other nests were mapped on a Google Earth image.

3.4. Provisioning behaviour observations

Provisioning behaviour refers to an adult bird entering the nest tunnel with food in its bill, presumably to feed the chicks. Once the eggs hatched, provisioning observations were made at each nest. Each day was divided into four time periods for observation and were referred to as sessions- (i) 630-930 h; (ii) 930-1230 h; (iii) 1230-1530 h and (iv) 1530-1830 h. These sessions were randomly assigned to nests to remove any bias in the data set. The duration in seconds that a bird spends inside the nest after it enters and until it exits the nest was recorded. Whenever it was possible, the identity of the contents in the bill of the bird was recorded. Each nest was observed during different stages after hatching and at least nine hours of observation was made on each nest.

3.5. Data analysis-

Mean and standard deviation of habitat characteristics of solitary nests and colony nests were compared and Mann-Whitney U Test was employed to check if they are significantly different (Siegel & Castellan 1988). To investigate if any of the body size

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[2] Web links to videos of nest checking- video showing eggs inside nest tunnel- http://www.youtube.com/watch?v=WtQDefYdpQU-; video showing chicks inside nest tunnel- http://www.youtube.com/watch?v=1phCQdpMasw; video showing a predator(spectacled cobra) inside nest tunnel- http://www.youtube.com/watch?v=69h4VRruM5U

parameters differ significantly between solitary nesters and colony nesters, a Mann-Whitney U test was used. In both these cases, non-parametric statistics was used because of the small sample size of solitary nests. A Principal Components Analysis (PCA) with the correlation matrix was done with varimax rotation and setting the minimum eigenvalue of inclusion of a variable at one with 25 iterations to get composite variables. A scatter plot of the principal components one and two (as they explain the maximum variance in the data) was made to compare variance between solitary nesters and colony nesters (Quinn & Keough 2002). The software SPSS 16.0 was used for these analyses (2007).

Data obtained from monitoring nests was analysed using Program MARK (White & Burnham 1999) for nest survival models. The nest monitoring data from 16 nests were used for this analysis. Data from one of the nests in Hudsa was not used because the burrow was blocked by a stone and it could not be checked periodically. The effect of colony size on nest success was of primary interest in this study. However, as weight of the parent could influence nest success, it was used as a covariate. With increasing age of the nests, their vulnerability to predation increases and therefore, the influence of age of the nest on daily survival probability was modelled. Further, the difference in survival probability between the egg stage and the nestling stage was also checked using the models.

The synchronicity of nesting between solitary nesters and colony nesters was compared using a scatter plot. Because the exact nest initiation dates were not known they were calculated from the time of hatching of the nests. There are no existing records of incubation period in CHB; in this study, it was found that the incubation period varied between 24 to 33 days in four nests with an average of 27.75. The approximate nest initiation dates for all nests were back calculated by subtracting 24 days (i.e. the minimum incubation period) from the date on which hatching occurred. Minimum incubation period was used instead of average incubation period because the incubation period was determined from only four nests and so, the average may be biased. In cases, where the exact date of hatching was not known, the date of hatching was calculated by assessing the age of chick by comparing it with chicks of known age. Further, two nests had failed at the egg stage. The nest initiation date of these nests was calculated with the assumption that

CHBs lay eggs at 48 h intervals. Other bee-eaters such as the white-fronted bee-eater (*Merops bullockoides)* (Emlen & Wrege 1986) and rainbow bee-eater (*Merops ornatus)* (Boland 2004) lay eggs at 48 h intervals. The date on which the first nest found in the study was back calculated to have been initiated was March 13, 2011 and it was designated as day zero, and all the nesting days were serially numbered. Mean inter-nesting interval i.e. the mean of the number of days between the initiation dates of pairs of consecutively initiated nests for six-nest (Bison mine site), three-nest (Jungle lodges) and solitary nests was calculated. In order to check if the nest initiation dates were random during the nesting period, ten sets of random numbers between 0 and 25 were generated (there was a difference of 25 days between the nest initiation dates of the first and the last nest recorded in the study), for colony size of six (Bison mine site), three (Jungle Lodges) and five solitary nests. The mean of the difference between pairs of consecutive numbers in this random dataset gave the mean inter-nesting interval that is expected if the nest initiation dates were random. One-sample t-test was performed on the sets of ten mean expected 'inter-nesting' intervals to check the probability of getting the observed inter-nesting interval if nest initiation was random (Zar 1996). SPSS 16.0 was used for this analysis (2007).

In order to analyse the effect of position of the nest in space on reproductive success, the nests were divided into two clusters which were considered as two populations because of the distance separating them- Ganeshgudi cluster and Joida cluster. Hudsa colony and the solitary nest at Nagoda were included in Joida cluster and the others in Ganeshgudi cluster. For every nest, the average distance of all the other nests in its cluster was calculated. Mann-Whitney U-test was employed to check if the inter-nest distance was different between nests that failed and those that succeeded. Non-parametric test was used because of the low sample size and the non-normality of data. A box and whisker plot was also made comparing the inter-nest interval between successful and unsuccessful nests.

A generalized linear model (GLM) was used to analyse the influence of coloniality on frequency of provisioning of the nests using Program R (R Development Core Team 2005). Because the age of chicks and number of chicks influence provisioning frequency, they were included as independent variables in the GLM. The observations on provisioning were made in three hour sessions described earlier. The timing of the observation session was also included as an independent variable, as there was change in provisioning frequency during the day. The number of times a nest was provisioned in a three-hour interval was taken as the dependent variable. In five cases, the observation session was shorter (one case) or longer (four cases) than three hours. The count for such sessions was extrapolated or interpolated to give the frequency of visits in a three hour interval and rounded off to the nearest integer for the analysis. The data on provisioning frequency were checked for over dispersion by comparing the variance with the mean. Since the data was over dispersed a negative binomial distribution was used as a descriptor of the variable (Crawley 2007). The global model included all of the aforementioned independent variables and their interactions. However, the timing of the session was not included in any of the interactions as observation timeframe was not thought to be interacting with any of the other independent variables, i.e. age of chick and number of nests. The model was then simplified following steps outlined in Crawley (2007), till the most parsimonious model was reached.

4. RESULTS

4.1 General behavioural observations

Observations on CHBs showed that the initiation of breeding activities took place towards the end of January in the study area. The first incident of breeding activity was observed in Bison Mine colony on 29 January 2011 and in Jungle Lodges colony on 30 January 2011. From this point in time a number of incidences of mating events were seen. Breeding activity typically included the following sequence of events: mounting of the female by the male (presumably, because the sexes were indistinguishable) – male flying upwards for a short distance making trilling calls - alighting on the perch next to the female - pecking by one individual of the pair sometimes accompanied by its mate, at various points on open vertical slopes - switching pecking substrates. An antagonistic behaviour observed was that of aerial chases, that involved two birds flying upwards in circles around each other and then pecking at each other in mid-air a few times. On occasions, five to six birds flew up together performing these behaviours. Greeting behaviour, i.e. one bird calling excitedly and vibrating its tail when another bird would approach it or perch next to it, became more conspicuous in the breeding season.

Breeding related activities were predominant during forenoon and in the afternoon the birds would only forage and preen as usual. Notably, while the birds started showing breeding activities in Jungle Lodges and Bison Mine site by end-January; CHBs were not even sighted at the other colony site i.e. Hudsa, during visits on sixth and 22 February 2011. Breeding activities were observed in Hudsa on the next visit on 16 March 2011. As has been reported for this species (Ali & Ripley 1970; Fry et al. 1992), both the sexes were involved in digging of nests. By 11 February 2011, one of the nest holes being dug at Bison mine site (that was later abandoned) was already about 400 mm long. At Bison mine site colony, sometimes green bee-eaters were also seen sitting on the vertical slopes and pecking. However, CHBs mostly used to chase them away. By first of March, the breeding pair had already started roosting inside the nesting tunnel at night (nest hole was checked at 2000 h) in Bison mine site colony and Jungle Lodges colony. Length of the nesting tunnels showed a wide variation, from about 0.4 m to 1.2 m. The first observation of courtship feeding in the season was made on 18 March 2011 in Bison mine site colony. Courtship feeding coincided with egg laying activity at all nesting sites. While courtship feeding was being performed, female spent extensive amount of time sitting on the same perch, while the male foraged and brought insects to her. Often the male would beat the prey held in its bill on their perch several times before offering it to the female. The female would receive the insect and again beat the prey before consumption. The first nest with eggs was located on 24 March 2011 in Bison Mine site colony. The nests in this colony were initiated between 13 March and 22 March 2011. Clutch size varied from 4-6, and the modal clutch size was 5. During the incubation period, the birds rarely entered the nesting tunnel during day time. This made it difficult to locate nests that had eggs in them. On most occasions, at least one of the parents was observed to be watching over the nest from a high perch opposite the embankment on which the nest was present. In all, seventeen nests were monitored. Duration of incubation varied from 24- 33 days. Egg reduction (reduction in number of eggs observed without any corresponding occurrence of hatching) was observed clearly in at least four cases. Brood reduction was recorded in every nest that was monitored. The chicks were observed using the burrowscope and were active in the nests even when they were featherless. Often, a chick was seen midway through the tunnel when the nests were probed to monitor the status. The nesting tunnel was very clean during incubation and when the chicks were < 10 days after hatching. As the chicks reached about ten days of age, the nesting tunnel was found to be littered with insect remains and even mutilated but living insects were seen. When the chicks approached the age for fledging, they sat near the tunnel entrance and the parents stopped entering the tunnel to provision them.

4.2 Habitat characteristics and availability of nesting substrate

Five solitary nests and 12 colony nests (distributed over three colonies, two of them having 3 nests each and one having six nests) were found during the study. The mean and standard deviation of bearing of the nest tunnels was 183.64 + 104.25 degrees, *N* = 17. Mann- Whitney U-test results showed that only distance to nearest perch differed significantly between solitary nests and colony nests (Table 4.1). Distance to nearest water source for the three colony sites was 10m (Hudsa colony), 620 m (Jungle Lodges colony) and 760 m (Bison mine site colony). Amount of substrate available for the birds showed large variation. The minimum area to nest ratio was in Jungle Lodges colony having three nests in about 50 m^2 area and the maximum was in Hudsa with three nests in about 111840 m^2.

4.3 Morphological measurements-

The measurements of all the birds caught and ringed and the ring numbers are given in Appendix 1. The mean and standard deviation of morphological measurements of solitary and colony nesters is given in the table. Only tarsus length differs significantly between colony nesters and solitary nesters (Table 4.2). A scatter plot of the principal component scores obtained by doing a PCA of the morphometric variables of all the nests shows that the dispersion of morphometric variables in colony nesters is greater than that in solitary nesters (Figure 4.1). This is despite the fact that the sample size is larger for colony nesting individuals. The component scores of the morphometric variables in the principal components axes were used to interpret the subtle differences that solitary and colony nesters had (Table 4.3).

It was the standard deviation in weight, wing length, bill length and tail length that was found to be greater in colony nesters than in solitary nesters. These are features that change over the lifetime of an individual. Skeletal features that are fixed at fledging i.e. tarsus length and bill depth (Freeman & Jackson 1990) did not show much difference in standard deviation when compared across solitary and colony nesters.

4.4 Nest survival

Only nine of the 16 nests monitored were successful i.e. at least one chick fledged from it. On one occasion, a spectacled cobra *(Naja naja)* was found inside a nest tunnel. Also, brood reduction was observed in all the nests. Out of four or five eggs that hatched, only one or two chicks survived till fledging in all but one of the nests.

Habitat Characteristic	Colony (n = 12)	Solitary (n = 5)
	Mean (S.D.)	Mean (S.D.)
Soil penetrability (1-20)	10.58 (3.60)	11.10 (4.04)
Slope (in degrees)	70.00 (8.79)	73.00 (7.58)
% Ground vegetation cover	14.17 (19.05)	5.00 (11.18)
Distance to nearest used perch (m)*	2.26 (1.23)	6.43 (2.04)
Height of embankment (m)	2.06 (52.28)	1.72 (1.13)
Height of nest (m)	1.39 (0.63)	1.31(1.46)

* Mann-Whitney U Test: *U* = 5.00, *N*1=12, *N*2=5, 2-tailed *P*= 0.006

Table 4.1- Comparison of habitat characteristics of solitary and colony nests of chestnut-headed bee-eaters in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011).

Morphological feature	Colony (n = 13)	Solitary (n = 4)
	Mean (S.D.)	Mean (S.D)
Weight (g)#	27.64 (3.23)	25.75 (1.26)
Wing length (mm)	109.54 (3.15)	110.00 (1.15)
Bill length (mm)	32.34 (1.98)	32.42 (2.99)
Bill depth (mm)	5.66 (0.68)	5.44 (0.76)
Tarsus length (mm)*	14.05 (1.41)	12.02 (1.31)
Tail length (mm)	75.00 (3.65)	73.75 (1.26)

#n=14, for colony nesters

*Mann-Whitney U Test: *U* = 8.00, *N*1=13, *N*2=4, 2-tailed *P* = 0.045

Table 4.2- Morphometric differences between colony nesting and solitary nesting chestnut-headed bee-eaters in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011)

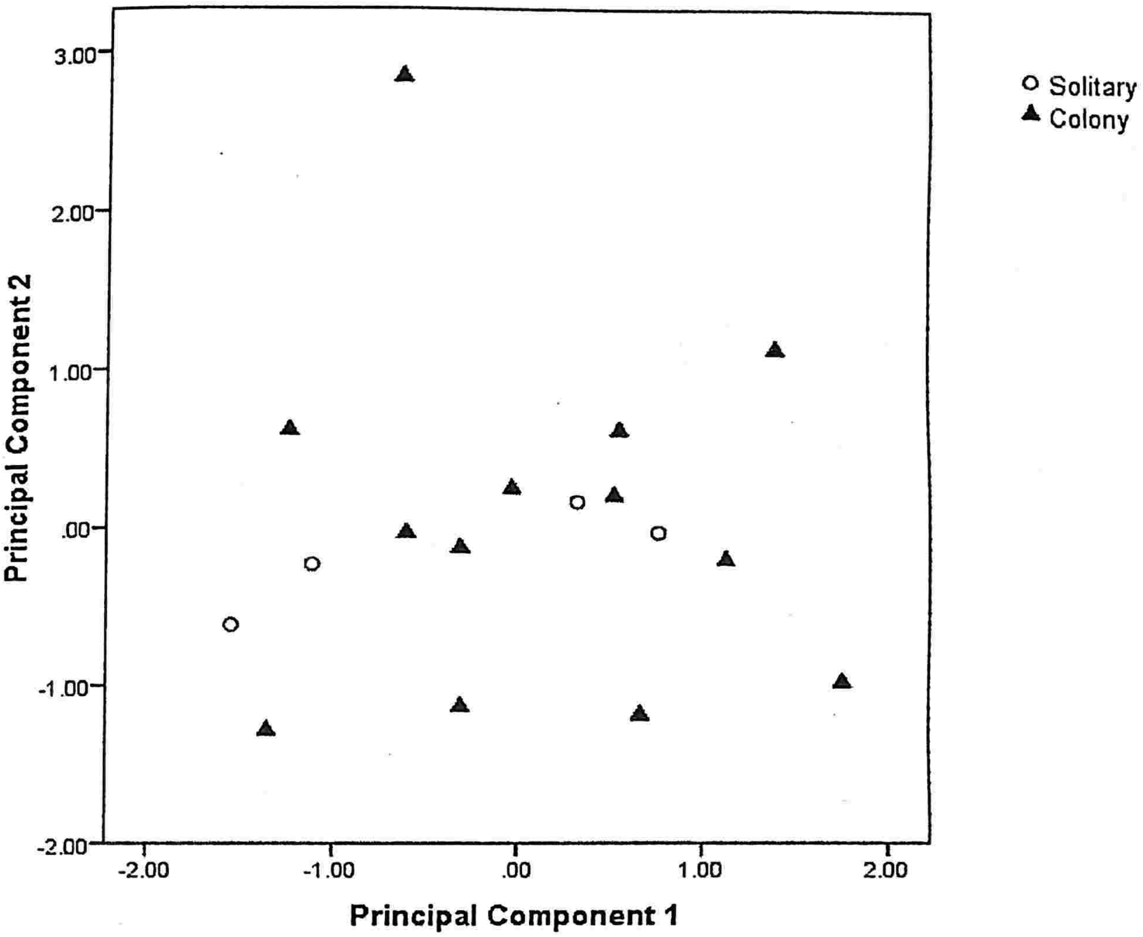

Figure 4.1- Dispersion of individual chestnut-headed bee-eaters (CHBs) along principal component axis 1 and axis 2 consisting of a combination of morphometric variables. The CHBs that were found in solitary and colony nests are shown in different symbols. Study was conducted in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011)

Morphometric features	Component		
	1	2	3
Weight	.63	-.56	-.32
Wing length	.49	.70	-.17
Bill length	.62	-.03	.52
Bill depth	.68	-.41	.37
Tarsus length	.08	.59	.58
Tail length	.60	.42	-.57

Table 4.3 – Factor loadings of various morphological features of CHB to the extracted principal components. The first and second axes explained 30.79 % and 24.78 % of the variation respectively. Study was conducted in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011)

The most parsimonious model for daily survival rate (DSR) of nests was the null model, which suggested that survival probability is constant across all the days of the nesting season and across all nests. The next best model B (age^2, nestno.), suggested that DSR of nests varies as the square of age and linear function of colony size. This model also had a much lower deviance than the null model (Table 4.4). All the competing models that had difference in AIC values of < 2 from the most parsimonious model, also suggests that the age and colony size have significant influence on DSR (Table 4.4). The details of the output from the Program MARK are in Appendix 2. The slope for majority of the models excluding the null model was negative, though not significantly different from zero, suggesting that daily survival rate varies randomly across all nests and over the entire period of the nesting season (Table 4.5). However, it is possible that the influence of the variables taken in the model is not statistically significant because of the low sample size.

The mean and standard error of DSR according to the null model was 0.98 + 0.007, *N* = 16. The models showed that as age and colony size increase, the daily survival rate (DSR) of nests decreases, though the decrease is not statistically significant (Figure 4.2). The mean, standard error and 95% confidence limits of DSR estimates for the three different colony sizes encountered in the study have been shown in Figure 4.3. The mean and standard error of DSR in the egg stage was 0.987 + 0.009, *N*= 16 and in the nestling stage was 0.978 + 0.010, *N* = 13.

4.5 Synchronicity of breeding

Synchronicity of breeding increased with colony size as the distribution of nest initiation dates shows (Figure 4.4). The mean inter-nest interval was only two days for the Bison mine site colony that had six nests. For jungle lodges colony that had three nests, the mean inter-nest interval was five days and that of solitary nests was 3.8 days. When compared with the mean inter-nesting interval that was expected if the nesting occurred randomly during the breeding season, only the colony of six nests had smaller mean inter-nesting interval (One-sample *t*-test: t 9 = 5.38, *P* (one-tailed) < 0.001; Figure 4.5).

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Number of Parameters	Deviance
{Bnull}	59.02	0.00	0.20	1.00	1.00	57.01
{Bage^2,nestno}	59.59	0.57	0.15	0.75	3.00	53.52
{Bage^2}	59.82	0.79	0.14	0.67	2.00	55.78
{Bnestno}	59.88	0.86	0.13	0.65	2.00	55.85
{Bage}	60.34	1.32	0.11	0.52	2.00	56.31
{Bage^2,age}	60.65	1.63	0.09	0.44	3.00	54.58
{Bstage}	60.69	1.64	0.09	0.44	2.00	56.63
{Bweight}	60.66	1.64	0.09	0.44	2.00	56.63

Table 4.4- Summary of nest survival model results of chestnut-headed bee-eater nests in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011), using program MARK. Data from 16 nests was used for this analysis.

Models: Bnull Daily survival rate(DSR) is same over all the days in the nesting season and across nests; **Bage^2,nestno-** DSR varies as the square of age of nest and linear function of colony size; **Bage^2-** DSR varies as a square function of age; **Bnestno-** DSR varies as a function of colony size; **Bage-** DSR varies as a function of age of nest; **Bage^2,age-** DSR varies as the square of age, also having a linear element; **Bstage-** DSR is different in different phases of breeding i.e. egg stage and nestling stage; **Bweight-** DSR varies as a function of weight of parent birds.

Model	Estimate	S.E	Lower C.I	Upper C.I
{Bnull}	1.30	0.05	1.20	1.4
{Bage^2,nestno}	-0.001	0.001	-0.002	<0.001
	-0.33	0.23	-0.77	0.12
{Bage^2}	-0.001	0.001	-0.002	0.001
{Bnestno}	-0.22	0.21	-0.63	0.19
{Bage}	-0.03	0.04	-0.1	0.04
{Bage^2,age}	-0.003	0.002	-0.008	0.001
	0.16	0.14	-0.1	0.43
{Bstage}	-0.53	0.87	-2.24	1.18
{Bweight}	-0.07	0.10	-0.26	0.13

Table 4.5- Beta estimates of nest survival from all the models for chestnut-headed bee-eater breeding. Study was conducted in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). Data from 16 nests was used for this analysis.

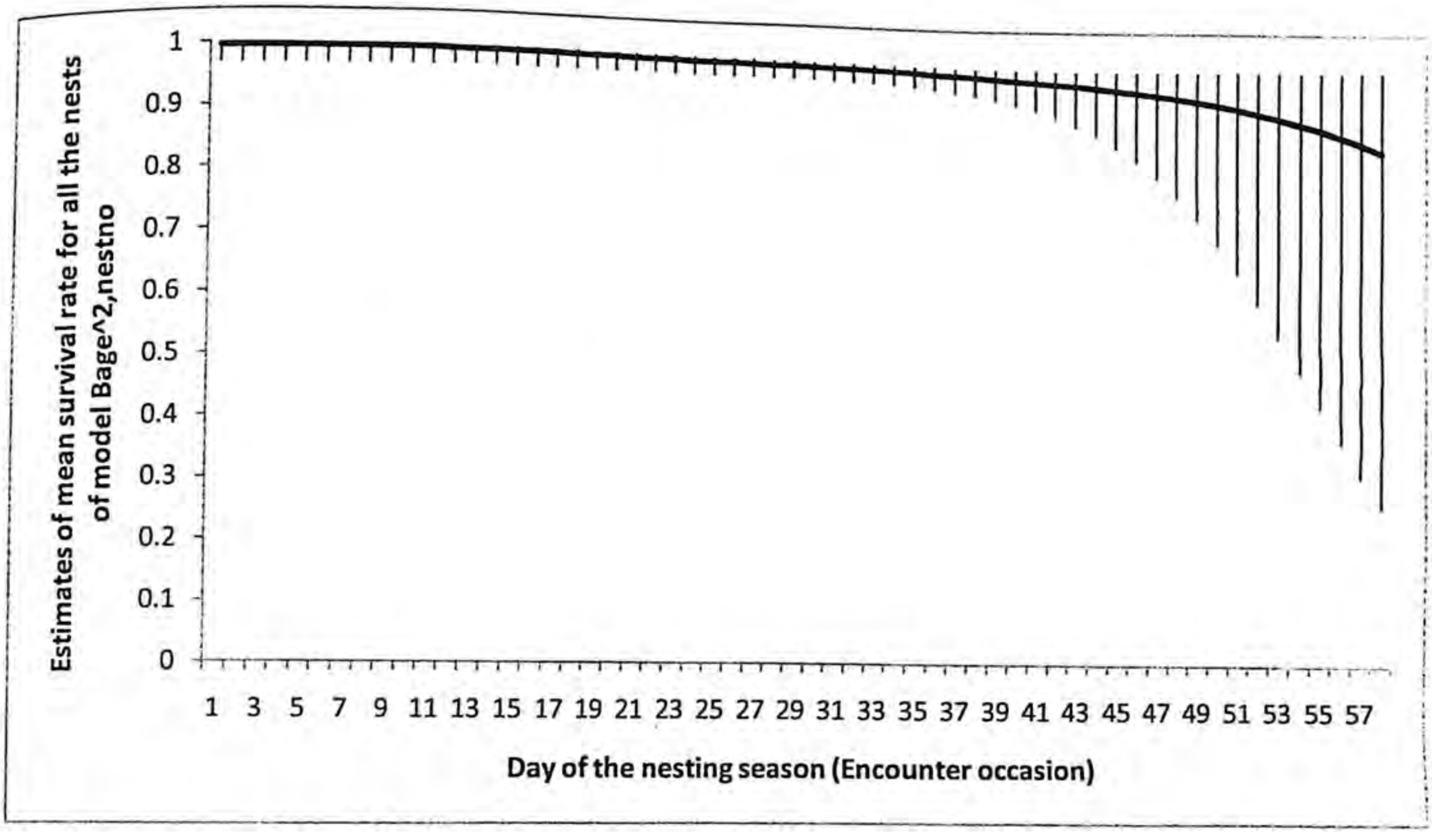

Figure 4.2- Plot of model {Bage^2, nestno}. Change in Daily survival rate (DSR) of chestnut-headed bee-eater nests as the age of the nests increases, considering that colony size influences DSR. Study was conducted in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). Data from 16 nests was used for this analysis.

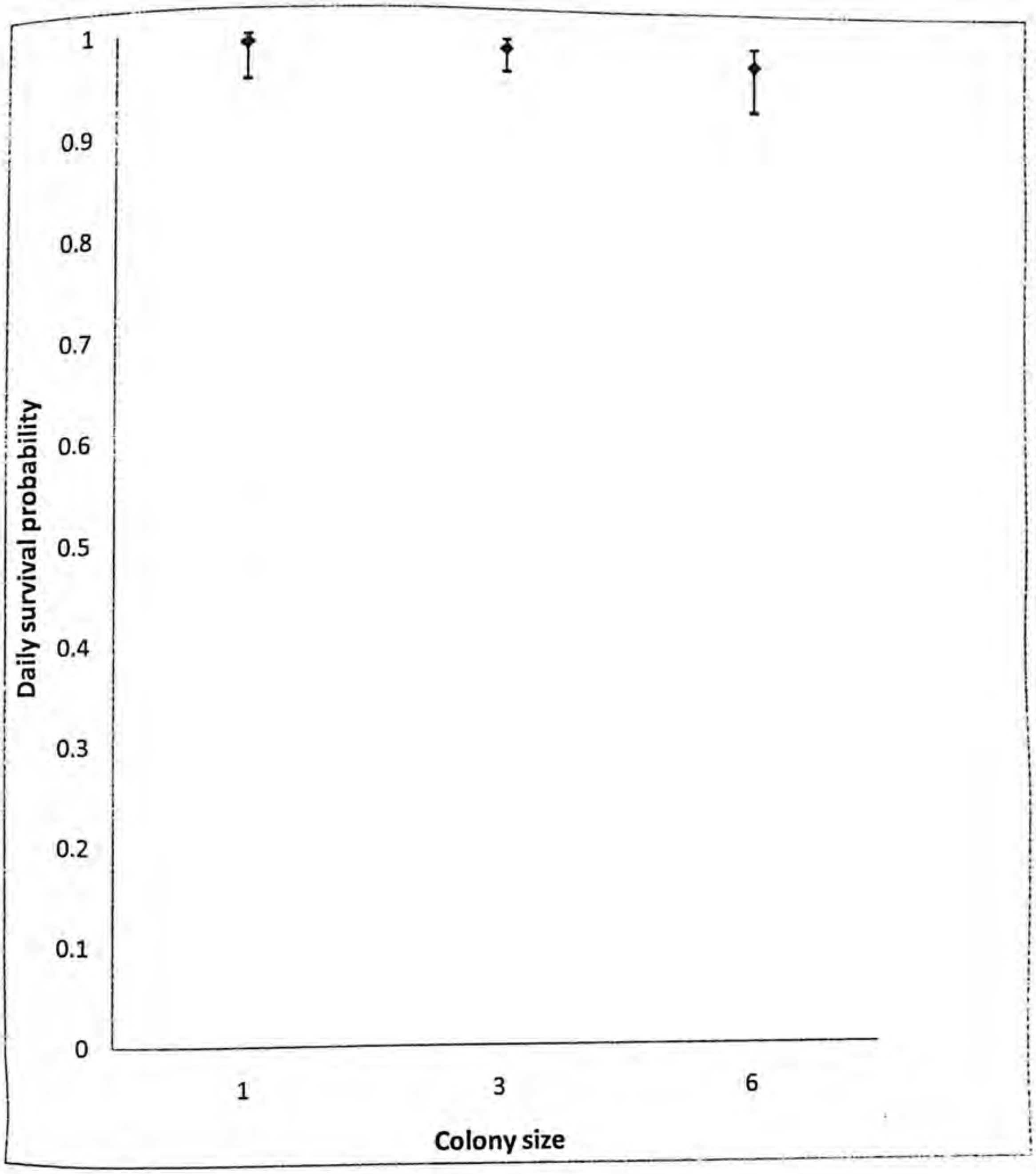

Figure 4.3- Mean daily survival probability estimate with 95% confidence interval of nests in different colony sizes in chestnut-headed bee-eater in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). Data from 16 nests was used for this analysis.

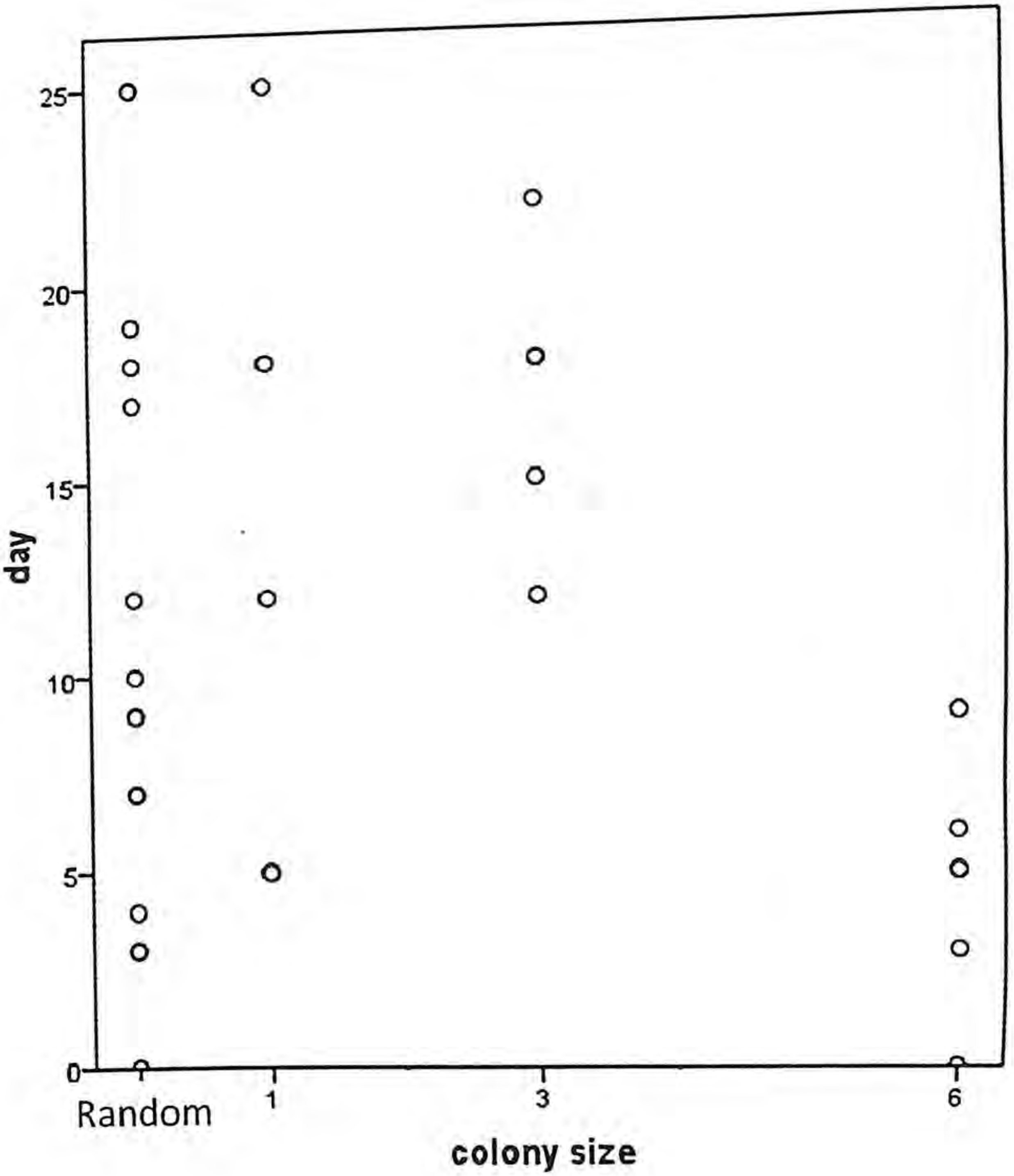

Figure 4.4- The distribution of nest initiation dates across one, three and six colony sizes, and a randomly generated order of initiation dates in Chestnut-headed bee-eaters in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). Day zero on the Y axis represents 13 March, 2011. Data from 16 nests was used for this analysis.

4.6. Spatial positioning

The average inter-nest distance did not differ significantly between nests that succeeded and those that failed (Mann-Whitney U Test: $U = 22$, $N1 = 10$, $N2 = 7$, 2-tailed $P = 0.230$). However, the median inter-nest distance of unsuccessful nests was lower than that of successful nests, though not significantly so (Figure 4.6).

4.7 Provisioning behaviour

In the most parsimonious model (Table 4.6), frequency of nest provisioning varied as a function of colony size and the time interval in which the observations were made. The summary of all the models obtained before meaningfully reducing the independent variables and arriving at the most parsimonious one is given in Appendix 3. Colony size negatively influenced provisioning frequency (Figure 4.7). Observation periods of 630-930 h, 930-1230 h, 1230-1530 h and 1530-1830 h were called as time1, time2, time3 and time4 in the model. Provisioning frequency varies between these time intervals of the day as shown in Figure 4.8.

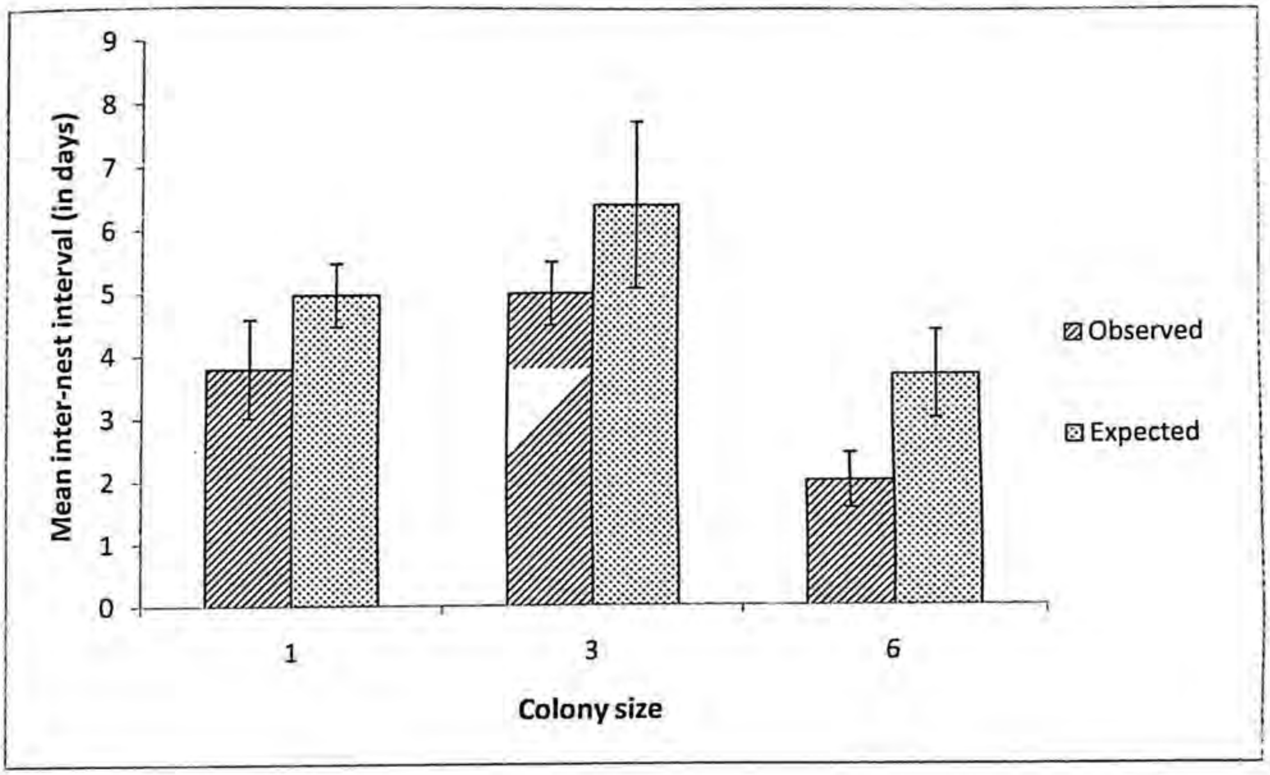

Figure 4.5- Difference between expected (for random distribution of initiation dates) and observed mean inter-nesting interval in Chestnut-headed bee-eater in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). (N= 16 nests).

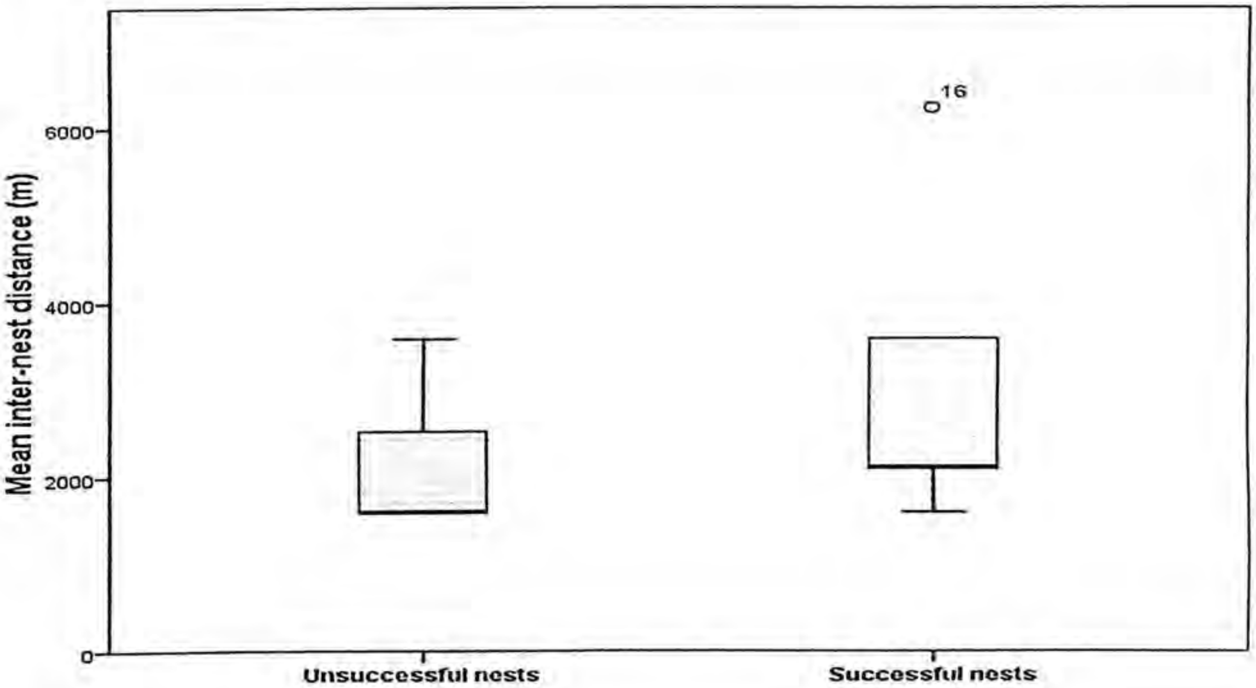

Figure 4.6- Average inter-nest distance for successful and unsuccessful nests in Chestnut-headed bee-eater in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). (N= 16 nests)

	Estimate	S.E.	z	P
(Intercept)	2.71831	0.26765	10.156	< 0.01
nestno	-0.15303	0.06173	-2.479	< 0.05
time2	0.73774	0.28012	2.634	< 0.01
time3	0.29284	0.27451	1.067	0.28
time4	-0.96088	0.30969	-3.103	< 0.05

Table 4.6- Parameter estimates for the most parsimonious model explaining the frequency of provisioning in Chestnut-headed bee-eater nests in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). Total number of provisioning observation sessions = 40.

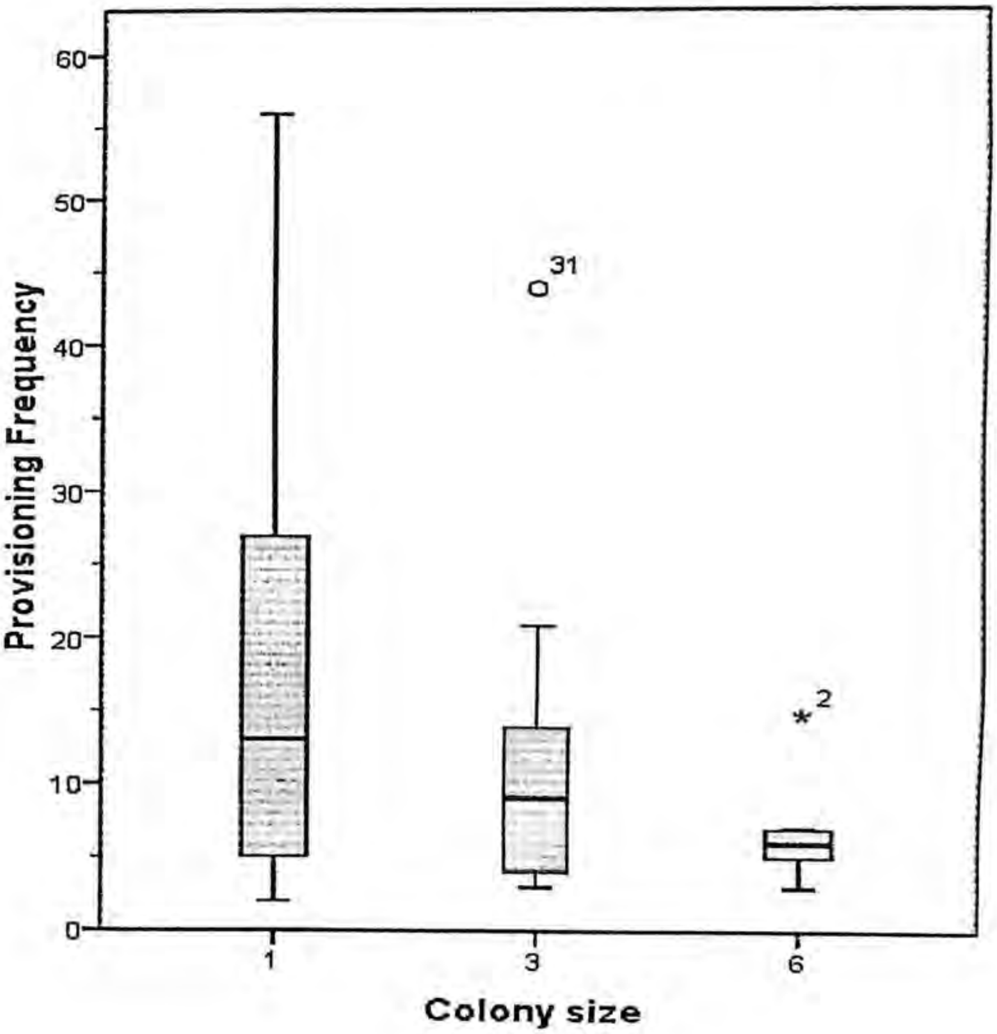

Figure 4.7- Provisioning frequency for three hour periods, with increase in colony size in Chestnut-headed bee-eater in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). Total number of provisioning observation sessions = 40.

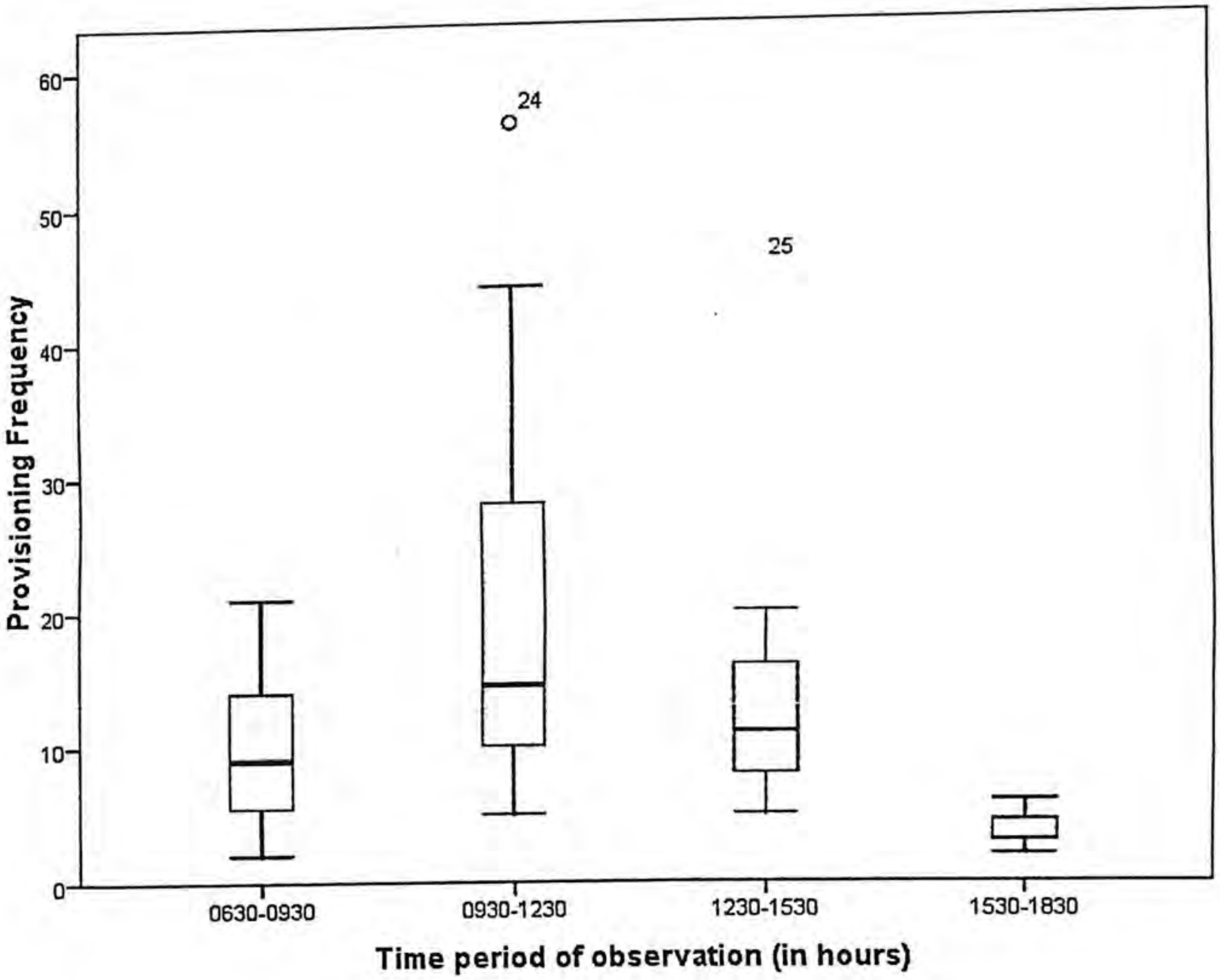

Figure 4.8- Change in provisioning frequency for three hour intervals in different observation periods in Chestnut-headed bee-eaters in Haliyal and Karwar divisions, Karnataka (Dec. 2010- May 2011). Total number of provisioning observation sessions = 40.

5. DISCUSSION

5.1 Insights into colony formation in CHBs

Many studies have examined the factors leading to colonial breeding in birds and broadly, colony formation is either mediated through habitat quality or conspecific attraction. The outcome would depend on whether colony size shows a linear relationship with habitat quality (Danchin & Wagner 1997). Among all the variables measured that characterise the quality of the habitat, only distance to perch site was significantly greater for the solitary nests than for the colony nests. However, this difference seems to be an outcome of coloniality rather than the cause, as there were other perches available in the areas having solitary nests that could have been used by the bird. One possible reason for this difference could be that the individuals nesting solitarily guard the nest from a distance to reduce the chances of being noticed by a predator. Avoiding the nest and staying inconspicuous has been observed to be a nest defence strategy in many bird species (McLean 1987; Burhans 2000). However, the colony nests were conspicuous and hence, guarding a nest from a distance probably was not advantageous.

The large variation in the ratio of number of nests in an area to the amount of substrate available suggests that breeding sites were not limiting in this area. This contrasts with rainbow bee-eater (*Merops ornatus*), where the number of nests in a colony were found to be tightly correlated with the amount of cleared ground cover available for nesting (2004).

One important habitat variable that I could not measure in this study is aerial insect availability. Insect distribution and abundance is influenced by land-use heterogeneity and proximity to water (Brown et al. 2002). Both these factors were uniform in all the breeding sites in the study area as the map shows, and hence insect availability should be similar in all nesting sites. However future studies should empirically verify if this observation is valid. Thus, if insect availability is indeed not different between colony sites and solitary nesting sites, colony formation is not habitat-mediated in CHBs.

Since tarsus length does not change after a bird reaches the fledging age, it is considered to be a very good measure of body size (Freeman & Jackson 1990). The mean tarsus length was found to be different in colony nesters and solitary nesters; the colony nesters being marginally larger. Allometric ratios change during ontogeny and the variation reduces with an increase in the lifetime of an individual (among those measured in this study - wing length, tail length and bill length). These morphometric variables were found to have greater coefficient of variation among colony nesters than among solitary nesters. One plausible explanation for this is that colony nesters comprise of a population belonging to different age-classes, while individuals of a particular age-class (the age class that is nearer to the population mean) constitute the population that made solitary nests. In white-fronted bee-eaters extended family units each consisting of a multi-generation lineage coexisted and formed colonies (Emlen & Wrege 1988). In European bee-eater, breeding among close relatives from different generations has been reported (Lessells, Avery & Krebs 1994). The evidence from this study suggests that colony nesters in CHBs might be related individuals belonging to different age-cohorts. Further studies on this aspect will reveal the role of relatedness among individuals in colony formation in CHBs. It has been established that living in family units facilitates the behaviour of 'helping at the nest', which is common among bee-eaters (Fry 1972b). Because I could not distinguish individuals, I could also not recognise 'helpers' in the colony nests. However, I observed more than two CHBs attending to a nest in two solitary nests (Right Bank and Rafting jetty mine site). A study on CHBs with marked individuals is required to elaborate on the plausible role of helping behaviour.

The results from this study suggest that colony formation in CHBs was not due to habitat-mediated aggregation, but could be due to conspecific attraction. Individuals with larger body size seem to be associated with nesting in colonies. It was observed that individuals that represented an intermediate age were associated with solitary nests. However, since this study had a small sample size, all the conclusions come with a caveat.

Among the conspecific attraction hypotheses, only the traditional aggregation hypothesis and conspecific reproductive hypothesis are likely to apply to bee-eaters. Since, bee-eaters are mostly monogamous and the rate of extra-pair copulations are also low (Fry et al. 1992), the hidden-lek hypothesis of colony formation is ruled out. Conspecific reproductive success hypothesis assumes that reproductive success varies across different sites (Danchin, Boulinier & Massot 1998). In this study, reproductive success was not found to vary among breeding sites and hence conspecific reproductive success could not have acted as a cue for selection of breeding sites. Thus, traditional aggregation seems to be responsible for colony formation in CHBs. The role of previous year's nesting holes (evidence of former presence of conspecifics) as a cue needs to be further examined. All three colony sites and two of the five solitary nests had nest tunnels from the previous breeding seasons. Other studies have also reported presence of previous year's nest tunnels at breeding sites in many species of bee-eaters (Fry et al. 1992; Burt 2002). The presence of former nesting tunnels in breeding sites could also be attributed to site fidelity shown by bee-eaters. During the study, in two separate instances a breeding pair dug a nest in heap of sand meant for construction work. This offers evidence against the role of site fidelity by CHBs at least for solitary nesters.

5.2 Why colonial breeding in CHB?

If colonial breeding is advantageous, then variation in colony size is due to 'insider-outsider' conflict (Higashi & Yamamura 1993). However, if reproductive success of breeding pairs is similar in colonies of various sizes and solitary nests, it means that: (i) colonies are not advantageous and are simply habitat-mediated aggregations (Danchin & Wagner 1997); or, (ii) colony-size optima differs across individuals (Brown et al. 1990). In this study, the daily survival rate of nests did not change with different colony sizes (Figure 4.3). This finding on CHB contradicts the finding that reproductive success declined with colony size in European bee-eater (Hoi et al 2002). Habitat-mediated colony formation does not find support from this study in CHB as discussed previously; it seems more likely that individuals have different colony-size optima.

In all the failed nests, no damage to the structure of the nesting tunnel was observed. Hence, it is likely that snakes have been the predators in all the cases. Brood reduction observed in all the nests could be a consequence of hatching asynchrony. Death of smallest chicks of a brood due to starvation has been reported for european bee-eater

(Lessells & Avery 1989), white fronted bee-eater (Emlen et al. 1991) and rainbow bee-eater(Boland 2004). In case of blue-throated bee-eater, sibling attacks with a developmentally temporary hook at the tip of upper mandible has been reported to cause mortality (Bryant & Tatner 1990). Thus, siblicide is another plausible explanation for brood reduction as observed in this study.

Breeding was more synchronous among colony nesters than among solitary nesters (Figure 4.4). Thus, the fledglings from colony nests may be at a slight advantage due to benefits from social foraging (Emlen & Demong 1975). Nesting success did not differ with respect to position of the nest (Figure 4.6), which indicates that different individuals probably have different inter-nest distance optima in CHB. An earlier study on European bee-eater also found no effect of position on reproductive success (Hoi et al. 2002). Provisioning frequency showed greater variation in solitary nests than in colony nests. This could be attributed to either high temporal variability at solitary nest sites compared to colony nesting sites; or greater competition for food at colony nests than in solitary nests, thereby reducing the provisioning rate and making it consistently small. If aerial insect availability differed between solitary and colony nests and this difference was responsible for colony formation in CHBs, then one would expect the provisioning rate to be similar across nests in colonies of different sizes. However, it seems that colony-living has some other advantage that offsets the cost of competition.

5.3 Conclusions

In the study, it was found that the mechanism of colony formation in CHBs is likely to be conspecific attraction. There are indications of variation in colony size optima among individuals. Variation in colony size is also influenced by despotic behaviour as shown by the aerial chases observed in the beginning of the breeding season when nest building had just been initiated. In the study nesting was initiated seven days earlier in the colony sites than in the solitary sites. Therefore, at least some of the solitary nests might have been made by pairs that could not find a place in the colony during the study. Nest survival probability and nest provisioning rates are measures of reproductive success. It was observed that daily survival probability did not differ between solitary nesters and colony nesters. The nest provisioning rate was found to be greater in solitary nests. For colony nests to have a similar daily survival probability, some other benefit of colony-nesting must be outweighing the effect of lower provisioning rate. Future studies should attempt to document the conspecific cue that leads to colony formation in CHBs and mechanisms that allow colony nesting to persist in CHBs.

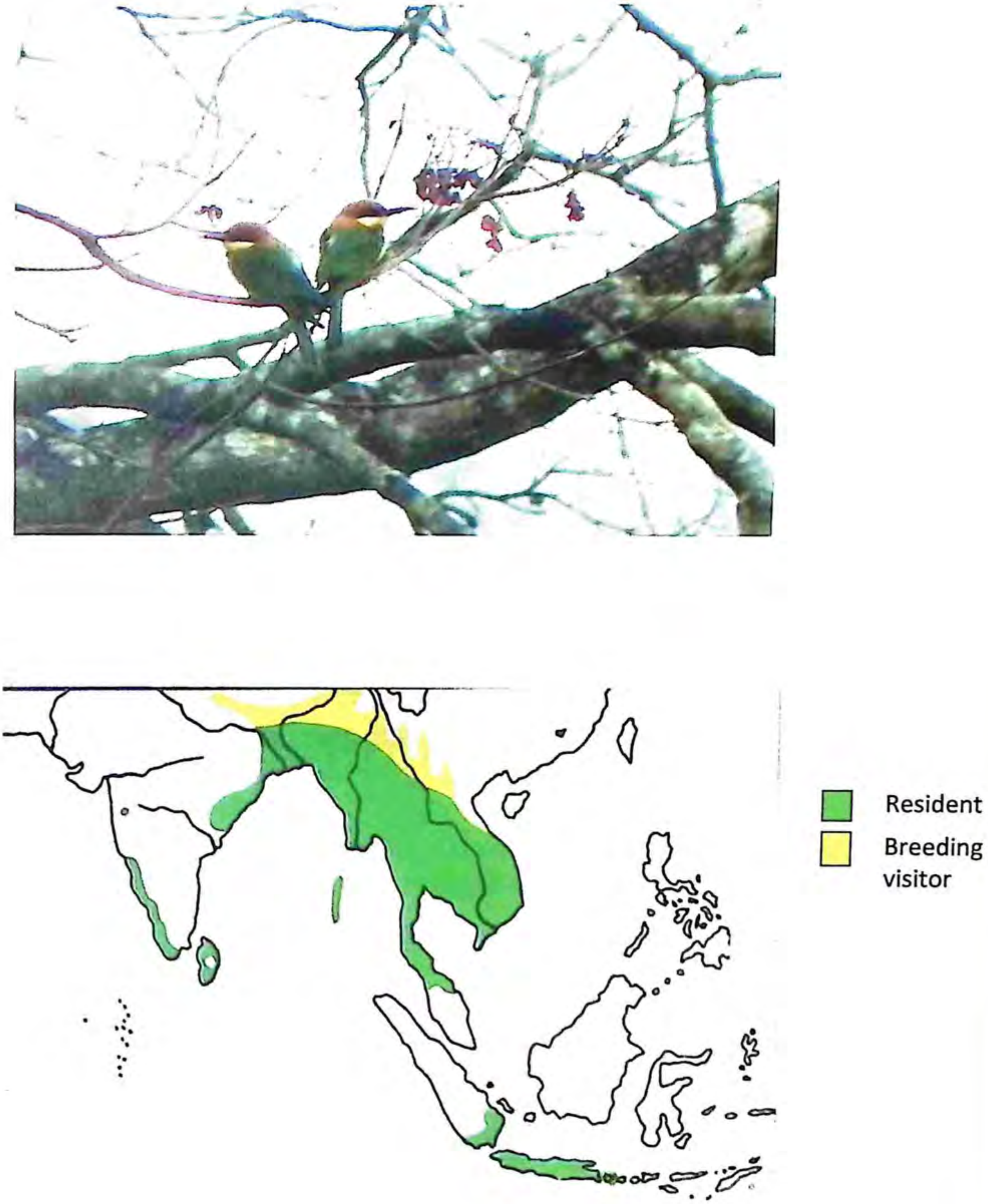

Plate 1- A photograph of chestnut-headed bee-eater (*Merops leschenaultii*) (above) and its distribution map (below) (Fry, Fry & Harris 1992)

Plate 2- View of Kali River from Ganeshgudi Bridge (top); solitary nesting site at Kodli roadside, a nest tunnel entrance is shown with a red circle (middle); View of Bison mine site colony (Below)

Plate 3- A captured Chestnut-headed bee-eater (above left); Checking for wing moult in a captured bird (middle right); Probing the nest hole with the 'burrowscope'(below left)

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APPENDIX 1

Ring numbers and measurements of all the captured birds

Ring no.	Species	Weight(g)	Age	Moult	Plumage	Brood patch	Wing length (mm)	Bill length (mm)	Bill depth (mm)	Tarsus length (mm)	Tail length (mm)	Locality	Habitat	Date
AB168 951	Merops leschenaulti	29	5	1	4	2	107	33.75	6.62	12.92	77	1	1	01-03-2011
AB168 952	Merops leschenaulti	25	5	1	4	2	109	31.23	5.18	15.14	75	2	2	02-03-2011
No ring	Merops leschenaulti	25	5	1	4	2						2	2	02-03-2011
AB168 953	Merops leschenaulti	27	5	1	4	2	110	32.76	4.88	14.81	73	1	1	04-03-2011
AB168 954	Acrocephalus aedon											3	3	04-03-2011
AB168 955	Merops leschenaulti	30	5	1	4	2	109	34.35	6.41	16.2	70	2	2	05-03-2011
AB168 956	Merops leschenaulti	28	5	1	4	2	112	31.42	6.45	14.54	76	2	2	05-03-2011
AB168 957	Merops leschenaulti	25	5	1	4	2	110	32.77	6.35	13.45	69	2	2	05-03-2011
AB168 958	Merops leschenaulti	23	5	1	4	2	111	34.47	5.18	14.91	75	2	2	05-03-2011
AB168 959	Merops leschenaulti	31	5	1	4	2	108	34.44	5.5	12.78	77	2	2	29-03-2011
AB168 960	Merops leschenaulti	36	5	1	4	2	111	34.48	6.42	11.32	79	1	2	30-03-2011
AB168 961	Merops leschenaulti	27	5	1	4	2	117	31.25	5.26	15.1	82	2	2	08-04-2011

Ring no.	Species	Weight(g)	Age	Moult	Plumage	Brood patch	Wing length (mm)	Bill length (mm)	Bill depth (mm)	Tarsus length (mm)	Tail length (mm)	Locality	Habitat	Date
AB168962	Merops leschenaulti	26	5	1	4	2	110	30.11	4.78	14.63	77	2	2	08-04-2011
AB168963	Merops leschenaulti	28	5	2	2	2	106	28.11	5.15	12.1	71	1	1	09-04-2011
AB168964	Merops leschenaulti	27	5	1	4	2	104	31.27	5.34	14.72	74	1	1	18-04-2011
AB168965	Merops orientalis	19	5	1	4	2	93	29.47	4.82	10.15	103	4	2	23-04-2011
AB168966	Merops leschenaulti	24	5	1	4	2	111	36.8	5.6	13.22	74	5	2	27-04-2011
AB168967	Merops leschenaulti	27	5	1	4	2	111	31.45	6.44	12.88	75	6	2	03-05-2011
AB168968	Merops leschenaulti	26	5	1	4	2	109	31.42	4.86	11.63	74	7	2	04-05-2011
AB168969	Merops leschenaulti	26	5	1	4	2	109	30.02	4.84	10.34	72	8	2	05-05-2011

Codes

Age- 1- Nestling; 2- Juvenile (first year); 3- Sub-adult; 4- Immature; 5- Adult; 6- Fullgrown but stage unknown

Moult- 1- No moult; 2- Wing moult; 3- Tail moult; 4- Wing and tail; 5- Head; 6- Body; 7- Head and body; 8- General moult

Plumage- 1- Down; 2-Juvenile(first year); 3- Intermediate; 4- Adult; 5- Eclipse; 6- Breeding; 7- Partial breeding

Brood patch- 1- absent; 2- present but details not recorded; 3- Skin smooth, glossy, free of feathers; 4- Skin smooth, network of blood vessels noticeable; 5- Skin thickened, blood vessels not noticeable, fluid layer under epidermis, brood patch resembles a second degree burn; 6- Skin wrinkled, dried up, begins to form scales; 7- Skin becomes smooth, feather calami formed, brood patch begins to be covered up

Locality- 1- Jungle Lodges colony, 2- Bison mine site colony, 3- KPC colony, Ganeshgudi, 4- Kedapani watchtower, 5- Kodli roadside, 6- Right Bank, 7- Nagoda, 8- Rafting jetty mine site

Habitat- 1- Edge of moist deciduous forest; 2- Moist deciduous forest

APPENDIX 2

Detailed results of all the nest survival models run in MARK

1. Bnull

SIN Link Function Parameters of {Bnull}

			95% Confidence Interval	
Parameter	*Beta*	*Standard Error*	*Lower*	*Upper*
1:S	1.2985980	0.0512990	1.1980520	1.3991439

Real Function Parameters of {Bnull}

			95% Confidence Interval	
Parameter	*Estimate*	*Standard Error*	*Lower*	*Upper*
1:S	0.9815911	0.0068958	0.9618880	0.9912013

Survival Estimates of {Bnull}

			95% Confidence Interval	
Group	*Pr. Surviving Duration of Study*	*Standard Error*	*Lower*	*Upper*
1	0.3403889	0.1386942	0.1332756	0.6339450

2. Bage^2,nestno

LOGIT Link Function Parameters of {Bage^2,nestno}

			95% Confidence Interval	
Parameter	*Beta*	*Standard Error*	*Lower*	*Upper*
1:	6.2534927	1.4504677	3.4105760	9.0964095
2:	-0.0010256	0.6587151E-003	-0.0023166	0.2655204E-003
3:	-0.3287872	0.2268646	-0.7734419	0.1158675

Real Function Parameters of {Bage^2,nestno}

Following estimates based on unstandardized individual covariate values:

```
Variable  Value
--------- ------------
AGE      -0.1250000
NESTNO.   3.5000000
WEIGHT    27.812500
```

			95% Confidence Interval	
Parameter	*Estimate*	*Standard Error*	*Lower*	*Upper*
1:S	0.9939566	0.0052474	0.9674080	0.9989039
2:S	0.9939519	0.0052488	0.9674103	0.9989021
3:S	0.9939350	0.0052539	0.9674187	0.9988956
4:S	0.9939055	0.0052628	0.9674332	0.9988843
5:S	0.9938635	0.0052754	0.9674534	0.9988681
6:S	0.9938085	0.0052916	0.9674791	0.9988466

7:S	0.9937403	0.0053114	0.9675098	0.9988198
8:S	0.9936584	0.0053348	0.9675450	0.9987872
9:S	0.9935624	0.0053617	0.9675840	0.9987485
10:S	0.9934516	0.0053919	0.9676260	0.9987030
11:S	0.9933253	0.0054254	0.9676701	0.9986504
12:S	0.9931827	0.0054620	0.9677151	0.9985897
13:S	0.9930229	0.0055016	0.9677598	0.9985203
14:S	0.9928448	0.0055440	0.9678025	0.9984413
15:S	0.9926473	0.0055891	0.9678416	0.9983514
16:S	0.9924289	0.0056367	0.9678748	0.9982496
17:S	0.9921882	0.0056866	0.9678996	0.9981344
18:S	0.9919235	0.0057386	0.9679131	0.9980042
19:S	0.9916330	0.0057927	0.9679118	0.9978571
20:S	0.9913144	0.0058486	0.9678914	0.9976912
21:S	0.9909655	0.0059064	0.9678471	0.9975043
22:S	0.9905835	0.0059662	0.9677726	0.9972938
23:S	0.9901656	0.0060284	0.9676605	0.9970570
24:S	0.9897085	0.0060935	0.9675019	0.9967912
25:S	0.9892086	0.0061625	0.9672855	0.9964935
26:S	0.9886616	0.0062372	0.9669974	0.9961610
27:S	0.9880631	0.0063200	0.9666202	0.9957912
28:S	0.9874079	0.0064145	0.9661322	0.9953821
29:S	0.9866903	0.0065261	0.9655059	0.9949326
30:S	0.9859039	0.0066617	0.9647067	0.9944434
31:S	0.9850416	0.0068314	0.9636909	0.9939168
32:S	0.9840953	0.0070479	0.9624037	0.9933580
33:S	0.9830560	0.0073280	0.9607770	0.9927755
34:S	0.9819137	0.0076922	0.9587269	0.9921806
35:S	0.9806570	0.0081655	0.9561516	0.9915876
36:S	0.9792732	0.0087764	0.9529293	0.9910124
37:S	0.9777481	0.0095571	0.9489160	0.9904706
38:S	0.9760656	0.0105426	0.9439433	0.9899763
39:S	0.9742078	0.0117702	0.9378144	0.9895400
40:S	0.9721545	0.0132800	0.9303000	0.9891682
41:S	0.9698828	0.0151154	0.9211328	0.9888634
42:S	0.9673674	0.0173237	0.9100019	0.9886247
43:S	0.9645794	0.0199583	0.8965487	0.9884488
44:S	0.9614869	0.0230791	0.8803659	0.9883308
45:S	0.9580538	0.0267545	0.8610021	0.9882652
46:S	0.9542397	0.0310623	0.8379750	0.9882462
47:S	0.9499995	0.0360914	0.8107972	0.9882683
48:S	0.9452829	0.0419421	0.7790176	0.9883262
49:S	0.9400338	0.0487279	0.7422817	0.9884152
50:S	0.9341903	0.0565753	0.7004080	0.9885311
51:S	0.9276835	0.0656248	0.6534757	0.9886702
52:S	0.9204380	0.0760303	0.6019067	0.9888291
53:S	0.9123711	0.0879580	0.5465196	0.9890050
54:S	0.9033932	0.1015847	0.4885313	0.9891952
55:S	0.8934076	0.1170938	0.4294849	0.9893976
56:S	0.8823111	0.1346707	0.3711052	0.9896101
57:S	0.8699956	0.1544946	0.3151044	0.9898311
58:S	0.8563485	0.1767289	0.2629831	0.9900590

```
                    Survival Estimates of {Bage^2,nestno}

       Pr. Surviving
       Duration of                        95% Confidence Interval
Group   Study         Standard Error      Lower        Upper
  1    0.1637746      0.2192406           0.0084251    0.8186550
```

3. Bage^2

```
            LOGIT Link Function Parameters of {Bage^2}

                                                95% Confidence Interval
Parameter          Beta            Standard Error      Lower          Upper
  1:             4.6229012          0.7548551         3.1433851      6.1024172
  2:            -.7025744E-003   0.6233646E-003     -0.0019244     0.5192202E-003


            Real Function Parameters of {Bage^2}

Following estimates based on unstandardized individual covariate values:
     Variable  Value
     --------- ------------
     AGE       -0.1250000
     NESTNO.    3.5000000
     WEIGHT    27.812500
                                               95% Confidence Interval
Parameter          Estimate      Standard Error    Lower         Upper
  1:S              0.9902712     0.0072723         0.9586475     0.9977675
  2:S              0.9902661     0.0072722         0.9586579     0.9977645
  3:S              0.9902475     0.0072717         0.9586961     0.9977538
  4:S              0.9902152     0.0072708         0.9587617     0.9977350
  5:S              0.9901692     0.0072695         0.9588544     0.9977081
  6:S              0.9901091     0.0072676         0.9589736     0.9976728
  7:S              0.9900349     0.0072650         0.9591184     0.9976288
  8:S              0.9899461     0.0072616         0.9592879     0.9975755
  9:S              0.9898425     0.0072572         0.9594808     0.9975126
 10:S              0.9897235     0.0072515         0.9596959     0.9974394
 11:S              0.9895886     0.0072443         0.9599314     0.9973552
 12:S              0.9894373     0.0072353         0.9601854     0.9972591
 13:S              0.9892690     0.0072244         0.9604558     0.9971502
 14:S              0.9890828     0.0072112         0.9607402     0.9970275
 15:S              0.9888780     0.0071954         0.9610356     0.9968897
 16:S              0.9886536     0.0071767         0.9613389     0.9967356
 17:S              0.9884087     0.0071550         0.9616465     0.9965636
 18:S              0.9881421     0.0071300         0.9619540     0.9963722
 19:S              0.9878526     0.0071016         0.9622566     0.9961597
 20:S              0.9875388     0.0070700         0.9625486     0.9959244
 21:S              0.9871993     0.0070353         0.9628234     0.9956644
 22:S              0.9868324     0.0069980         0.9630729     0.9953780
 23:S              0.9864364     0.0069592         0.9632879     0.9950636
 24:S              0.9860092     0.0069203         0.9634569     0.9947198
 25:S              0.9855488     0.0068834         0.9635663     0.9943459
 26:S              0.9850528     0.0068517         0.9635994     0.9939417
 27:S              0.9845186     0.0068295         0.9635356     0.9935086
 28:S              0.9839435     0.0068229         0.9633498     0.9930491
 29:S              0.9833244     0.0068396         0.9630111     0.9925682
```

30:S	0.9826578	0.0068899	0.9624817	0.9920732
31:S	0.9819402	0.0069863	0.9617158	0.9915743
32:S	0.9811675	0.0071442	0.9606591	0.9910841
33:S	0.9803354	0.0073810	0.9592478	0.9906177
34:S	0.9794390	0.0077163	0.9574088	0.9901909
35:S	0.9784730	0.0081702	0.9550595	0.9898184
36:S	0.9774317	0.0087633	0.9521083	0.9895125
37:S	0.9763088	0.0095154	0.9484539	0.9892814
38:S	0.9750974	0.0104454	0.9439829	0.9891285
39:S	0.9737898	0.0115717	0.9385678	0.9890529
40:S	0.9723778	0.0129130	0.9320631	0.9890502
41:S	0.9708523	0.0144887	0.9243011	0.9891139
42:S	0.9692032	0.0163199	0.9150888	0.9892359
43:S	0.9674197	0.0184302	0.9042049	0.9894080
44:S	0.9654899	0.0208462	0.8913984	0.9896223
45:S	0.9634005	0.0235982	0.8763897	0.9898712
46:S	0.9611373	0.0267205	0.8588743	0.9901481
47:S	0.9586844	0.0302517	0.8385311	0.9904470
48:S	0.9560248	0.0342354	0.8150371	0.9907628
49:S	0.9531397	0.0387203	0.7880878	0.9910910
50:S	0.9500084	0.0437606	0.7574278	0.9914276
51:S	0.9466086	0.0494167	0.7228871	0.9917695
52:S	0.9429159	0.0557551	0.6844256	0.9921138
53:S	0.9389038	0.0628492	0.6421775	0.9924580
54:S	0.9345432	0.0707789	0.5964901	0.9928002
55:S	0.9298031	0.0796316	0.5479469	0.9931386
56:S	0.9246494	0.0895014	0.4973643	0.9934718
57:S	0.9190458	0.1004897	0.4457552	0.9937985
58:S	0.9129531	0.1127044	0.3942591	0.9941178

Survival Estimates of {Bage^2}

	Pr. Surviving Duration of		95% Confidence Interval	
Group	Study	Standard Error	Lower	Upper
1	0.2116619	0.1979288	0.0255841	0.7330188

4. Bnestno

LOGIT Link Function Parameters of {Bnestno}

			95% Confidence Interval	
Parameter	*Beta*	*Standard Error*	*Lower*	*Upper*
1:	4.8690321	1.0019138	2.9052810	6.8327832
2:	-0.2206635	0.2097576	-0.6317883	0.1904614

Real Function Parameters of {Bnestno}

```
Following estimates based on user-specified individual covariate values not standardized:
     Variable  Value
     --------- ------------
     AGE       0.0000000
     NESTNO.   1.0000000
     WEIGHT    0.0000000
                                                          95% Confidence Interval
Parameter          Estimate       Standard Error     Lower          Upper
  1:S              0.9905136      0.0076295          0.9550802      0.9980536
```

Survival Estimates of {Bnestno}

```
        Pr. Surviving
        Duration of                      95% Confidence Interval
Group   Study        Standard Error   Lower          Upper
  1     0.5753163    0.2570228        0.1470075      0.9141519
```

5. Bage

LOGIT Link Function Parameters of {Bage}

```
                                                     95% Confidence Interval
Parameter              Beta         Standard Error     Lower          Upper
  1:                   4.8154582    1.1441998          2.5728267      7.0580898
  2:                   -0.0301509   0.0365778          -0.1018435     0.0415416
```

Real Function Parameters of {Bage}

```
Following estimates based on unstandardized individual covariate values:
     Variable  Value
     --------- ------------
     AGE       -0.1250000
     NESTNO.   3.5000000
     WEIGHT    27.812500


                                                      95% Confidence Interval
Parameter              Estimate     Standard Error     Lower          Upper
  1:S                  0.9919916    0.0091240          0.9287832      0.9991508
  2:S                  0.9917485    0.0091170          0.9312131      0.9990637
  3:S                  0.9914981    0.0091023          0.9335489      0.9989681
  4:S                  0.9912401    0.0090796          0.9357925      0.9988631
  5:S                  0.9909744    0.0090488          0.9379459      0.9987478
  6:S                  0.9907007    0.0090095          0.9400109      0.9986213
  7:S                  0.9904188    0.0089615          0.9419890      0.9984827
  8:S                  0.9901284    0.0089046          0.9438817      0.9983309
  9:S                  0.9898293    0.0088387          0.9456901      0.9981649
  10:S                 0.9895212    0.0087637          0.9474153      0.9979836
  11:S                 0.9892039    0.0086795          0.9490580      0.9977858
  12:S                 0.9888771    0.0085862          0.9506186      0.9975704
  13:S                 0.9885406    0.0084841          0.9520970      0.9973362
```

14:S	0.9881939	0.0083735	0.9534928	0.9970822
15:S	0.9878369	0.0082548	0.9548052	0.9968073
16:S	0.9874693	0.0081289	0.9560326	0.9965108
17:S	0.9870907	0.0079967	0.9571727	0.9961919
18:S	0.9867008	0.0078596	0.9582225	0.9958505
19:S	0.9862993	0.0077194	0.9591778	0.9954866
20:S	0.9858858	0.0075782	0.9600334	0.9951009
21:S	0.9854600	0.0074390	0.9607824	0.9946950
22:S	0.9850216	0.0073053	0.9614164	0.9942714
23:S	0.9845702	0.0071814	0.9619251	0.9938335
24:S	0.9841054	0.0070724	0.9622960	0.9933862
25:S	0.9836269	0.0069845	0.9625142	0.9929358
26:S	0.9831341	0.0069247	0.9625624	0.9924900
27:S	0.9826268	0.0069008	0.9624211	0.9920579
28:S	0.9821046	0.0069211	0.9620685	0.9916491
29:S	0.9815669	0.0069942	0.9614816	0.9912738
30:S	0.9810134	0.0071282	0.9606368	0.9909414
31:S	0.9804435	0.0073304	0.9595102	0.9906596
32:S	0.9798570	0.0076069	0.9580793	0.9904342
33:S	0.9792532	0.0079622	0.9563221	0.9902679
34:S	0.9786317	0.0083992	0.9542183	0.9901607
35:S	0.9779920	0.0089195	0.9517480	0.9901103
36:S	0.9773336	0.0095234	0.9488915	0.9901125
37:S	0.9766560	0.0102106	0.9456282	0.9901617
38:S	0.9759586	0.0109804	0.9419366	0.9902519
39:S	0.9752409	0.0118320	0.9377930	0.9903769
40:S	0.9745024	0.0127645	0.9331718	0.9905310
41:S	0.9737424	0.0137775	0.9280449	0.9907087
42:S	0.9729603	0.0148707	0.9223821	0.9909052
43:S	0.9721557	0.0160443	0.9161509	0.9911163
44:S	0.9713278	0.0172985	0.9093168	0.9913384
45:S	0.9704761	0.0186343	0.9018437	0.9915683
46:S	0.9695998	0.0200525	0.8936944	0.9918036
47:S	0.9686984	0.0215546	0.8848307	0.9920419
48:S	0.9677711	0.0231422	0.8752145	0.9922816
49:S	0.9668174	0.0248169	0.8648083	0.9925210
50:S	0.9658363	0.0265808	0.8535759	0.9927591
51:S	0.9648274	0.0284361	0.8414834	0.9929947
52:S	0.9637897	0.0303853	0.8285003	0.9932271
53:S	0.9627226	0.0324307	0.8146003	0.9934556
54:S	0.9616253	0.0345752	0.7997627	0.9936797
55:S	0.9604971	0.0368216	0.7839736	0.9938990
56:S	0.9593371	0.0391728	0.7672268	0.9941132
57:S	0.9581445	0.0416319	0.7495254	0.9943220
58:S	0.9569185	0.0442021	0.7308826	0.9945254

Survival Estimates of (Bage)

Group	Pr. Surviving Duration of Study	Standard Error	95% Confidence Interval	
			Lower	Upper
1	0.2906532	0.1614138	0.0811592	0.6552671

6. Bage^2, age

LOGIT Link Function Parameters of {Bage^2,age}

Parameter	Beta	Standard Error	95% Confidence Interval Lower	 Upper
1:	2.7242978	1.6270279	-0.4646771	5.9132726
2:	-0.0034965	0.0024550	-0.0083083	0.0013154
3:	0.1604601	0.1350661	-0.1042694	0.4251896

Real Function Parameters of {Bage^2,age}

Following estimates based on unstandardized individual covariate values:

```
Variable  Value
--------- -------------
AGE      -0.1250000
NESTNO.   3.5000000
WEIGHT    27.812500
```

Parameter	*Estimate*	*Standard Error*	*95% Confidence Interval* *Lower*	 *Upper*
1:S	0.9372732	0.0965634	0.3740170	0.9973310
2:S	0.9459369	0.0778181	0.4699296	0.9971125
3:S	0.9531521	0.0628235	0.5634813	0.9968913
4:S	0.9591727	0.0508470	0.6483518	0.9966706
5:S	0.9642079	0.0412889	0.7208419	0.9964545
6:S	0.9684293	0.0336645	0.7799410	0.9962475
7:S	0.9719773	0.0275854	0.8265362	0.9960550
8:S	0.9749667	0.0227422	0.8624584	0.9958831
9:S	0.9774912	0.0188892	0.8897700	0.9957381
10:S	0.9796273	0.0158316	0.9103717	0.9956264
11:S	0.9814376	0.0134151	0.9258481	0.9955534
12:S	0.9829731	0.0115162	0.9374483	0.9955234
13:S	0.9842758	0.0100361	0.9461267	0.9955379
14:S	0.9853798	0.0088940	0.9526009	0.9955952
15:S	0.9863134	0.0080238	0.9574076	0.9956902
16:S	0.9870993	0.0073707	0.9609481	0.9958146
17:S	0.9877564	0.0068891	0.9635237	0.9959579
18:S	0.9882998	0.0065418	0.9653613	0.9961092
19:S	0.9887418	0.0062990	0.9666323	0.9962582
20:S	0.9890922	0.0061371	0.9674660	0.9963964
21:S	0.9893583	0.0060381	0.9679600	0.9965169
22:S	0.9895459	0.0059888	0.9681877	0.9966147
23:S	0.9896590	0.0059793	0.9682043	0.9966863
24:S	0.9896997	0.0060026	0.9680506	0.9967288
25:S	0.9896691	0.0060540	0.9677567	0.9967401
26:S	0.9895664	0.0061301	0.9673437	0.9967178
27:S	0.9893896	0.0062291	0.9668256	0.9966594
28:S	0.9891349	0.0063500	0.9662094	0.9965618
29:S	0.9887969	0.0064925	0.9654958	0.9964208
30:S	0.9883685	0.0066574	0.9646788	0.9962317
31:S	0.9878401	0.0068465	0.9637444	0.9959883
32:S	0.9872000	0.0070630	0.9626691	0.9956834
33:S	0.9864334	0.0073119	0.9614167	0.9953088

```
34:S        0.9855220   0.0076015   0.9599345   0.9948559
35:S        0.9844437   0.0079446   0.9581463   0.9943160
36:S        0.9831712   0.0083611   0.9559436   0.9936829
37:S        0.9816710   0.0088813   0.9531724   0.9929540
38:S        0.9799027   0.0095502   0.9496154   0.9921344
39:S        0.9778163   0.0104333   0.9449679   0.9912394
40:S        0.9753512   0.0116217   0.9388079   0.9902967
41:S        0.9724330   0.0132375   0.9305598   0.9893453
42:S        0.9689706   0.0154381   0.9194507   0.9884299
43:S        0.9648526   0.0184203   0.9044600   0.9875936
44:S        0.9599425   0.0224262   0.8842658   0.9868702
45:S        0.9540735   0.0277530   0.8572058   0.9862805
46:S        0.9470421   0.0347666   0.8212974   0.9858324
47:S        0.9386012   0.0439178   0.7744003   0.9855239
48:S        0.9284527   0.0557576   0.7146351   0.9853466
49:S        0.9162405   0.0709487   0.6411446   0.9852888
50:S        0.9015445   0.0902650   0.5551044   0.9853375
51:S        0.8838790   0.1145714   0.4605277   0.9854799
52:S        0.8626974   0.1447673   0.3641065   0.9857035
53:S        0.8374088   0.1816768   0.2736417   0.9859968
54:S        0.8074113   0.2258661   0.1956535   0.9863495
55:S        0.7721492   0.2773746   0.1335877   0.9867521
56:S        0.7311970   0.3353733   0.0875695   0.9871957
57:S        0.6843702   0.3978069   0.0554266   0.9876726
58:S        0.6318497   0.4611425   0.0340465   0.9881758
```

```
                         Survival Estimates of {Bage^2,age}

      Pr. Surviving
      Duration of                   95% Confidence Interval
Group   Study       Standard Error     Lower          Upper
  1   0.0322678     0.1118057    0.2987083E-004   0.9738352
```

7. Bstage

```
              LOGIT Link Function Parameters of {Bstage}

                                          95% Confidence Interval
Parameter         Beta      Standard Error   Lower          Upper
 1:           4.3001966     0.6996209     2.9289397      5.6714536
 2:          -0.5286660     0.8725925    -2.2389473      1.1816152


              Real Function Parameters of {Bstage}

Following estimates based on unstandardized individual covariate values:
     Variable  Value
     --------- ------------
     AGE       -0.1250000
     NESTNO.    3.5000000
     WEIGHT    27.812500
                                          95% Confidence Interval
```

```
Parameter           Estimate    Standard Error   Lower        Upper
1:S to 26:S         0.9866157   0.0092386        0.9492586    0.9965690
27:S to 58:S        0.9775010   0.0104974        0.9445902    0.9910496
```

Survival Estimates of {Bstage}

```
        Pr. Surviving
        Duration of                95% Confidence Interval
Group   Study       Standard Error   Lower        Upper
  1     0.3400946   0.1386966        0.1330633    0.6337633
```

8. Bweight

LOGIT Link Function Parameters of {Bweight}

```
                                            95% Confidence Interval
Parameter       Beta         Standard Error   Lower         Upper
  1:            5.8486127    2.9826829        0.0025541     11.694671
  2:           -0.0651986    0.1015783       -0.2642922     0.1338949
```

Real Function Parameters of {Bweight}

```
  Following estimates based on unstandardized individual covariate values:
     Variable   Value
     --------   ------------
     AGE       -0.1250000
     NESTNO.    3.5000000
     WEIGHT     27.812500
                                             95% Confidence Interval
Parameter           Estimate    Standard Error   Lower        Upper
  1:S               0.9826264   0.0069029        0.9624119    0.9920594
```

Survival Estimates of {Bweight}

```
        Pr. Surviving
        Duration of                95% Confidence Interval
Group   Study       Standard Error   Lower        Upper
  1     0.3618496   0.1474342        0.1395821    0.6646475
```

APPENDIX 3

Summary of selected Generalized Linear Models made before arriving at the final model

Model name	AIC	Independent variables for the model
glmfull	265.57	Age+nestno+chicks+time+Age:nestno+Age:chicks+nestno:chicks+Age:nestno:chicks
mod1	264.03	Age+nestno+chicks+time+Age:nestno+Age:chicks+nestno:chicks
mod2	264.46	Age+nestno+chicks+time+Age:chicks+nestno:chicks
mod3	262.34	Age+nestno+chicks+time+Age:nestno+nestno:chicks
mod4	263.9	Age+nestno+chicks+time+Age:nestno+Age:chicks
mod5	262.21	Age+nestno+chicks+time+Age:nestno
mod6	262.46	Age+nestno+chicks+time+nestno:chicks
mod7	261.11	Age+nestno+chicks+time
mod8	259.57	Age+nestno+time
mod9	260.65	nestno+chicks+time
mod10	259.15	nestno+time

All the generalised linear models made with their corresponding AIC values

Summary of selected models

1. glmfull

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.877926	1.391746	1.349	0.17723
Age	-0.019417	0.084781	-0.229	0.81885
nestno	0.099180	0.496614	0.200	0.84171
chicks	0.099573	0.456124	0.218	0.82719
time2	0.750560	0.288873	2.598	0.00937 **
time3	0.036021	0.298907	0.121	0.90408
time4	-0.984757	0.315326	-3.123	0.00179 **
Age:nestno	0.006785	0.033705	0.201	0.84046

Age:chicks	0.028072	0.032083	0.875	0.38159
nestno:chicks	-0.035117	0.156106	-0.225	0.82201
Age:nestno:chicks	-0.008213	0.011820	-0.695	0.48718

Null deviance: 101.132 on 39 degrees of freedom

Residual deviance: 37.099 on 29 degrees of freedom

AIC: 265.57

Theta: 5.09

Std. Err.: 1.60

2 x log-likelihood: -241.565

2. mod1

Coefficients:

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	1.136990	1.045584	1.087	0.276851
Age	0.032869	0.042655	0.771	0.440952
nestno	0.396385	0.325301	1.219	0.223027
chicks	0.352981	0.320562	1.101	0.270839
time2	0.764193	0.290760	2.628	0.008582 **
time3	0.020008	0.298739	0.067	0.946603
time4	-1.028212	0.308980	-3.328	0.000875 ***
Age:nestno	-0.016184	0.010608	-1.526	0.127119
Age:chicks	0.008609	0.014846	0.580	0.562011
nestno:chicks	-0.133290	0.094117	-1.416	0.156715

Null deviance: 99.628 on 39 degrees of freedom

Residual deviance: 37.007 on 30 degrees of freedom

AIC: 264.03

Theta: 4.98

Std. Err.: 1.54

2 x log-likelihood: -242.028

3. mod3

```
Coefficients:
                Estimate      Std. Error    z value    Pr(>|z|)
(Intercept)     0.845596      0.985673       0.858     0.39095
Age             0.053876      0.028200       1.911     0.05607 .
nestno          0.381192      0.321243       1.187     0.23538
chicks          0.457001      0.287081       1.592     0.11141
time2           0.779386      0.292866       2.661     0.00779 **
time3           0.072099      0.284850       0.253     0.80018
time4          -1.002417      0.308007      -3.255     0.00114 **
Age:nestno     -0.014385      0.009696      -1.484     0.13789
nestno:chicks -0.133308       0.094108      -1.417     0.15662

Null deviance: 98.476  on 39  degrees of freedom
Residual deviance: 36.891  on 31  degrees of freedom
AIC: 262.34
Theta:  4.90
Std. Err.:  1.50
2 x log-likelihood:  -242.343
```

4. mod 5

```
Coefficients:
                Estimate      Std. Error    z value    Pr(>|z|)
(Intercept)     2.033181      0.473062       4.298     1.72e-05 ***
Age             0.036754      0.024728       1.486     0.13719
nestno         -0.038186      0.113897      -0.335     0.73743
chicks          0.087483      0.114954       0.761     0.44664
time2           0.653517      0.290081       2.253     0.02427 *
time3           0.135367      0.287748       0.470     0.63804
time4          -0.985723      0.314423      -3.135     0.00172 **
Age:nestno     -0.008565      0.008695      -0.985     0.32460

Null deviance: 94.021  on 39  degrees of freedom
```

Residual deviance: 37.034 on 32 degrees of freedom

AIC: 262.21

Theta: 4.58

Std. Err.: 1.38

2 x log-likelihood: -244.211

5. mod7

Coefficients:

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	2.31696	0.39179	5.914	3.34e-09 ***
Age	0.01504	0.01153	1.304	0.19208
nestno	-0.13934	0.06208	-2.244	0.02481 *
chicks	0.07688	0.11443	0.672	0.50167
time2	0.71487	0.27435	2.606	0.00917 **
time3	0.17513	0.28563	0.613	0.53979
time4	-1.01338	0.31576	-3.209	0.00133 **

Null deviance: 92.360 on 39 degrees of freedom

Residual deviance: 37.267 on 33 degrees of freedom

AIC: 261.1

Theta: 4.47

Std. Err.: 1.34

2 x log-likelihood: -245.111

6. mod8

Coefficients:

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	2.48864	0.30538	8.149	3.66e-16 ***
Age	0.01535	0.01163	1.320	0.18667
nestno	-0.13324	0.06149	-2.167	0.03025 *
time2	0.73238	0.27431	2.670	0.00759 **
time3	0.21281	0.28097	0.757	0.44880
time4	-0.96495	0.30483	-3.166	0.00155 **

```
Null deviance: 90.879  on 39  degrees of freedom
    Residual deviance: 37.119  on 34  degrees of freedom
    AIC: 259.57
   Theta:  4.37
    Std. Err.:  1.29
  2 x log-likelihood:  -245.569
```

4. mod10

```
 Coefficients:
             Estimate           Std. Error        z value          Pr(>|z|)
  (Intercept) 2.71831           0.26765           10.156           < 2e-16 ***
  nestno      -0.15303          0.06173           -2.479            0.01317 *
  time2        0.73774          0.28012            2.634            0.00845 **
  time3        0.29284          0.27451            1.067            0.28607
  time4       -0.96088          0.30969           -3.103            0.00192 **

  Null deviance: 86.967  on 39  degrees of freedom
  Residual deviance: 37.040  on 35  degrees of freedom
  AIC: 259.15
  Theta:  4.11
   Std. Err.:  1.19
   2 x log-likelihood:  -247.147

  Significance codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```