Behavioural ecology and acoustic communication in a cooperatively breeding paleotropical bird, Jungle Babbler (*Argya striata*)

Yambem Soniya Devi

A thesis submitted for the partial fulfillment of the

degree of Doctor of Philosophy

Department of Biological Sciences

Indian Institute of Science Education and Research Mohali

Knowledge city, Sector 81, SAS Nagar, Manauli PO, Mohali 140306, Punjab, India.

September 2023

Dedication

I dedicate this thesis to my parents and grandparents

Declaration

The work presented in this thesis has been carried out by me under the guidance of Dr. Manjari Jain at the Indian Institute of Science Education and Research Mohali. This work has not been submitted in part or in full for a degree, a diploma, or a fellowship to any other university or institute. Whenever contributions of others are involved, every effort is made to indicate this clearly, with due acknowledgment of collaborative research and discussions. This thesis is a bona fide record of original work done by me and all sources listed within have been detailed in the bibliography.

Y. Soniya

Yambem Soniya Devi

Date: 01-09-2023

Place: Mohali

In my capacity as the supervisor of the candidate's thesis work, I certify that the above statements by the candidate are true to the best of my knowledge.

Manjari Jain

Dr. Manjari Jain

Date: 01/09/23

Place: Mohali

Acknowledgements

I would like to start by expressing my sincere gratitude to the most important person in this long Ph.D. journey, my supervisor Dr. Manjari Jain for her invaluable guidance and support. You opened a new and captivating world of animal behaviour to me, which had previously only existed in my imagination through documentaries on National Geographic or Discovery Channel. I am also grateful to you for helping me understand that the foundation of all applied sciences is based on studying basic sciences. I am truly grateful for your constant input even till the end of writing the thesis, which helped enhance my professional skills, starting from presentation to writing skills. I really appreciate your constant motivation to present my work to both national and international audiences and providing me the precious opportunities to travel and engage with the global scientific communities. Your persistent efforts to challenge me beyond my comfort zone, combined with your unwavering faith in my capabilities, have been an immense source of support and encouragement, especially during moments of self-doubt. I am also grateful to your family for including me in all the celebrations and for all the enjoyable trips, and delightful treats to lunch and dinner. There are not enough words to express my gratitude for everything you have done.

I am also grateful to the members of my supervisory committee, Dr. Mahak Sharma and Dr. Rachna Chaba, for their invaluable feedback and support throughout my Ph.D. program. I would also like to thank Prof. N.G. Prasad for all his encouragement and support. I am also thankful to Prof. Anindya Sinha for his valuable suggestion in the analysis of my scan sampling data for the time-activity budget. I would like to express my appreciation to Dr. V.V. Robin and CK Vishnudas for all the valuable training in bird mist-netting, handling and blood sampling. I am also grateful to all my thesis reviewers for their valuable feedback which have helped in improving the quality of my thesis.

Next, I would like to acknowledge the University Grant Commission (UGC) for funding my Ph.D. and especially for their regular crediting of the fellowship without which my research would have been more difficult to carry out. I am also thankful to IISER Mohali for providing me with all the infrastructure including the environment of the campus which supports a large group of my study species. Other study sites were on the NIPER (National Institute of Pharmaceutical Education and Research) Mohali Campus which also supports a large group of my study species. So, I am grateful to the Director of NIPER for allowing me to carry out my research in their campus. This helped in carrying out my research cost-effectively by avoiding going to faraway field locations and thus also saved time. I am sincerely grateful to the Punjab Forest Department as well as to the Institute Animal Ethical and Biosafety Committee for providing all the necessary permits and approvals to carry out the study. I am also thankful to the Association for the Study of Animal Behaviour, University of Sussex, the Association for Tropical Biology and Conservation as well as IISER Mohali for sponsoring travel grants and giving me the opportunity to present my work to a global audience.

Next, I would like to thank Richa for always being supportive and being patient with me. She was the one who first welcomed me into the lab and made me feel at home. I am from a Botany background and I was really terrified at first to work on this system and she was the one who gave me confidence that I can also do it. She was always there to help me whenever I had problems with anything, whether writing, making ppt or running statistics software. Then Sonam came along. She became my partner in crime :). I am always thankful for all the encouragement and all the fun, adventurous companionship with her. I will always appreciate all her criticism and her opinion which provide me with valuable insights.

I would like to thank all current Ph.D. members, Kanika, Gaurav, Anway and Harish, of the lab for helping me either in the field or in the lab. Especially, I would like to thank Gaurav and Anway for assisting me in the field while conducting playback experiments and for always helping in proofreading. I cannot miss my appreciation to every batch of BSMS students that came to our lab from 2015 to 2023 as an intern or Final year MS students for all their assistance in the field as well as in the lab and for giving me chances to guide them through their beginning journey of research. Particularly, I want to thank Nakul, Jain, Rohit and Deepak, for their priceless assistance in conducting playback experiments in the field. All of my fieldwork could not have been completed without the assistance of field assistants. I owe you for tolerating all the mosquito bites, scorching sun and chilly winter. I am always grateful to Saumya and Lata for their help whenever I had problems in understanding the concepts and to Anindya for all his grammatical corrections. I am also thankful to all the postdocs (Dr. Ranjana, Dr. Mahandran, Dr. Sujata and Dr. Aashish). Especially, I am grateful to Dr. Mahandran for introducing and teaching us how to mist-net.

I would like to extend my gratitude to all the horticulture staff of IISER Mohali and NIPER campus for their indirect assistance in the field and for watching out for me. I am grateful to all the faculty members of IISER Mohali as well as students residing in the hostel for tolerating me while I toiled around the hostel area and staff building with the binoculars in search of my model species. I would like to thank Prof. Bagla for allowing me to enter his house lawn for my observation and always offering me water. I am also thankful to our ex-director Prof. N. Sathyamurthy for always being considerate, giving motivation showing interest in my work and allowing me on the lawn of his residence to carry out my observations as well as experiments.

I met wonderful friends during this journey. I am thankful to Budakoti, Prachi, Ken, Harish, Anish, Sushmit, Sandeep, Tsering and Hari for all their company in making this journey memorable and enjoyable. I would like to acknowledge Dr. Chandrakant's family, Geeta Maam, Cinthoi and Yaichen, for all the tasty Manipuri meals which are not available otherwise and for their constant support. I am also grateful to all the current and ex-IISER Manipuri students, Sunanda, Sushma, Roja, Tarunkishwor, Daimiota, Lisha, Dimpy, Sadananda, Ronald and Narendra for letting me have a break from all the hectic and emotionally exhausting journey of a Ph.D. with a warm meal together, especially Daimiota and Dimpy.

Finally, I am extremely grateful to my family without them, I do not think I would be writing this thesis. Their consistent support and encouragement brought me up till today. They never let me worry about other things than my career and I will always be thankful for that. Thank you, to all my nephews and nieces for being my stress and anxiety relievers. Thank you, Papa, for all your moral advice on how one can be a decent human being. I am always grateful to my elder brother, Tamo, for your constant encouragement to go out from Manipur and for giving me the opportunity to experience that there are larger worlds outside than our hometown to explore. Thank you, my younger brother, Puskin for giving me the strength to push forward and always treating me to a warm, tasty meal whenever I come home during vacation.

I especially want to thank my grandmother for being a modern grandmother and always pushing me out of my comfort zone. Thank you for all your advice about life and how I must accomplish a successful career to earn my freedom as a woman. You are the reason for everything that I am today. I am also grateful to all my aunts for listening to all my complaints. Last but not the least, I am extremely grateful to my husband for all his unwavering moral and emotional support without which it would have been very challenging to continue through the ups and downs of this journey.

Synopsis

Animals exhibit a diverse range of behaviours in their daily lives and over their lifetime in accordance with their socio-ecological environment. These include solitary behaviours that are self-directed and do not require the participation of other individuals and social behaviours that require the interaction between two or more individuals. Social behaviours can be either 'affiliative' or 'agonistic' in nature. The repertoire of behaviour is larger in social animals as they have to perform individual behaviours for their own sustenance as well as social behaviours to coordinate group activities and for sustaining and enhancing the bonds with their group members. Cooperatively breeding species are social animals that are characterized by the long-term or permanent association of the group members who generally live as family units and exhibit repeated interactions with multiple individuals in various contexts. Since cooperative breeders must exhibit both individual and social behaviour, it is important to understand how they partition time between these two categories. Furthermore, communication is a core aspect of social systems that plays an important role in mediating a diverse range of social interactions. Cooperatively breeding animals exhibit alloparental care which aids in increasing the fitness and survival of the young ones. Thus, understanding the diversity of behaviour, partitioning of time between them, communication that mediate these behaviours and the factors influencing cooperative brood care together, provide a comprehensive understanding of the behavioural ecology of cooperatively breeding species.

This thesis focused on various aspects of the social system of a cooperatively breeding bird, Jungle Babbler (*Argya striata*) such as time allocation, communicative complexity, cooperative brood care and brood parasitism. Jungle Babbler is a sexually monomorphic paleotropic passerine that lives in groups of 3 – 20 individuals performing most of their activities together.

They are widespread residents in lowland India preferring closed canopy woodland and scrub vegetation. They are also frequently observed in close proximity to human neighbourhoods such as parks and gardens. **Chapter 1** of the thesis provides a broad overview of various aspects of social behaviour, an introduction to the study system and ends with an outline of the thesis objectives.

The involvement of multiple individuals in various interactions in diverse contexts requires extensive social interactions. This necessitates substantial time allocation to social interactions that would come at the cost of time for activities for sustenance. Thus, it is expected that social animals will exhibit time budgeting between various activities that are required for individual sustenance and those needed for maintaining the stability of the group. Further, these behaviours can vary with environmental factors that change at both diel and seasonal scales. Thus, the first objective of this thesis was to examine the repertoire of behaviours, time allocation between diverse behaviours and temporal variation in these behaviours across days and seasons. All the data were collected through a scan sampling method in the natural habitat of these birds. A total of 12,330 scan samples were recorded across 192 days. From the observations, 13 distinct behaviours including 4 individual behaviours and 9 social behaviours were recorded. Further, it was found that Jungle Babblers devote ~56% of their time budget to foraging and ~13% to other individual behaviours. The remaining ~30% of their time was allocated to social behaviours. This is the cost of sociality which has been quantified in this thesis. Most of the behaviours were found to exhibit diurnal and seasonal variation indicating that the allocation of time is adjusted in accordance with the changing environment. The results of this study are in accordance with studies on social primates, however, similar studies are lacking on social birds. These findings have been presented in **Chapter 2**.

Communication plays a critical role in mediating various interactions in social animals. Given that Jungle Babbler is a cooperatively breeding bird that engages in extensive social interactions, an underlying system of complex communication is expected to coordinate these extensive interactions in accordance with the 'social complexity hypothesis'. Therefore, the second objective of this thesis was to test the prediction of the social complexity hypothesis by investigating the presence of structurally and functionally complex communication systems in Jungle Babblers. Further, I also examined whether the vocalization of Jungle Babblers followed 'Morton's motivational structural rule' which posits that calls produced in similar contexts are structurally similar and calls produced in affiliative contexts are tonal while calls produced in agonistic contexts are harsh and noisy. The work done for this objective is presented in **Chapter 3.** Jungle Babblers were found to produce 15 different types of calls in different functional contexts. From the results of GLMM and further validation of DFA, it was found that all the calls in different functional contexts were also structurally different. These functionally and structurally distinct large repertoires indicate that Jungle Babbler's communicative system upholds the predictions of the social complexity hypothesis. Further, it was also found that calls produced in affiliative contexts are clustered more closely than those produced in agonistic contexts, however, all the calls of Jungle Babbler are mostly harsh and noisy irrespective of the contexts. In so, the findings of this study only lend partial support to Morton's motivational structural rule.

In cooperative breeding, all forms of care such as food provisioning, incubation or brooding, protection from predators, etc. are performed by the breeding pair who are assisted by non-breeding helpers. This cooperative brood care increases the possibility of greater nesting success thereby increasing the direct fitness of the breeders as well as indirect benefit to the non-breeding helpers through inclusive fitness.

However, multiple individuals approaching the nest repeatedly also increases the risk of predation. Thus, the third objective of this thesis focused on different aspects of cooperative brood care such as provisioning, brooding and their association with the time of day, age of the young ones and group size. Further, synchronous provision as a strategy to reduce the chances of exposure to predation was also examined in Jungle Babblers and the diet of adults and young ones of Jungle Babblers was also compared. Lastly, using a combination of field-based observations and manipulative experiments, the communication system between the young ones and adults during provisioning was also examined. This was done in the specific context of the begging response exhibited for different stimuli that may indicate the arrival of an adult with food. Further, the ontogeny of this response was also examined. From the focal nest observation, it was found that the provisioning rate increased and brooding duration decreased with the age of the young ones. This can be explained by the greater requirement of nutrients as young ones develop and a decrease in the requirement of external thermoregulation as the feathers of young ones develop. However, both the provisioning rate and brooding duration did not vary with the time of the day or group size. While the absence of diel patterns in provisioning and brooding in Jungle Babblers can be explained by the ability of the birds to find food at all times of the day and by the presence of a stable thermal environment at the nest, the lack of effect of group size in provisioning rate in Jungle Babblers is not in concordance with findings from other cooperative breeders where larger groups seem to have higher provisioning rate. However, the results are consistent with the 'load lightening' hypothesis which posits that larger groups are at an advantage due to the reduced per-individual load of provisioning on helpers. This is a direct benefit to the non-breeding helpers and is likely to drive patterns of group membership and philopatry. Further, the findings from field observations demonstrate significant synchrony in provisioning which has been proposed as a strategy

in cooperative brood care to reduce the risk of predation by decreasing the chance of exposure. The diet of the young ones varied from the adults of Jungle Babbler wherein, the diet of the young ones contained a significantly higher proportion of invertebrates. Finally, controlled playback experiments on young ones of Jungle Babblers of different age classes revealed a significant begging response to tactile stimulus in the hatchling stage, which decreased significantly at the pre-fledge stage when they are almost ready to fledge out of the nest. This result indicates an ontogenic pattern in their begging response to acoustic and tactile stimuli. **Chapter 4** of this thesis presents these findings in the context of cooperative brood care.

It is known that cooperatively breeding birds are likely hosts of several species of avian brood parasites. This has been linked to the increased provisioning of care by multiple carers. On the other hand, from the perspective of the host, multiple carers in cooperative breeding provide the advantage of multiple defenders that are likely to reduce the incidence of brood parasitism in such species. However, whether and exactly how the host discriminates against the brood parasite (in the absence of host-specific egg signatures) is not understood in Jungle Babblers. Hence, this system is ideal to study the co-evolutionary arms race between cooperatively breeding hosts and their brood parasites allowing a better understanding of such multispecies interactions. Thus, the final objective of this thesis was to examine whether adult Jungle Babblers (host) can discriminate between the young ones of its conspecific and that of the Jacobin Cuckoo (brood parasite) based on acoustic cues. First, I examined the structural difference between the two types of calls (begging call and fledgling close call) of young ones of the host and brood parasite. Then, playback experiments were conducted to examine whether adult Jungle Babblers can discriminate between the calls of their conspecifics and that of brood parasites. From the results of the acoustic analyses, it was found that calls of the young ones of the host at all age classes were structurally different from that of the young ones of the brood parasite. However, playback experiments revealed Jungle Babbler responded by approach with a call almost 100% of the time to the begging calls of conspecifics. On the other hand, Jungle Babbler approached the begging calls of the Jacobin cuckoo all the time but only about 50 % of the time they approached with a call and the remaining time they approached silently (similar to their approach behaviour to heterospecific competitors, Large Gray Babbler). Further, they do not respond to the calls of the fledglings of the brood parasite 40% of the time and even when they approach, they do so silently in 40% of the trials. This result indicates some level of discrimination against the brood parasite by Jungle Babbler. At the same time, they do not always exhibit a differential response toward the calls of the heterospecific brood parasite. Moreover, the result also suggests that while there are sufficient differences between the calls of the host and the parasite, the host is unable to utilize this information in the signal at all times, thereby allowing the brood parasite to continue to live in the host's nest. **Chapter 5** of this thesis focuses on these findings.

Chapter 6 provides an overall summary of this thesis. The thesis represents a comprehensive understanding of the various aspects of the social and vocal behaviour of the cooperatively breeding bird, Jungle Babbler. The findings of this thesis support the prediction of the social complexity hypothesis by demonstrating that the cooperatively breeding bird, Jungle Babbler, exhibited functional and structural complexity in its vocal repertoire. Further, this thesis also provides a detailed behavioural investigation on alloparental care and the factors that may or may not drive it. Finally, this thesis revealed the presence of information in the vocal signals may enable the host to discriminate against and thus reject brood parasites. However, the hosts do not seem to utilize this at all times. This thesis not only provides a fundamental understanding of the behavioural ecology of the Jungle Babbler but also provides a platform for future comparative studies on various aspects of social systems including multispecies interactions as well as on the evolution of a complex social and communicative system.

Table of Contents

	Acknowledgements	i
	Synopsis	vii
	List of Publications	xvii
	List of Figures	xix
	List of Tables	xxv
	Chapter 1. General Introduction	1
1.1	Ethology: a conceptual framework	3
1.2	Animal communication	11
1.3	Cooperative breeding	17
1.4	Brood parasitism	21
1.5	Study species	22
1.6	Thesis objectives	24
	Chapter 2. Behavioural repertoire and temporal variation of different behaviours	27
2.1	Introduction	29
2.2	Materials and methods	32
2.3	Results	37
2.4	Discussion	49
2.5	Appendix A	58
	Chapter 3. Functional and structural complexity in the vocalizations of Jungle Babbler	61
3.1	Introduction	63
3.2	Materials and methods	66
3.3	Results	72
3.4	Discussion	81
3.5	Appendix B	87
	Chapter 4. Understanding alloparental care in Jungle Babbler and the ontogeny of begging behaviour	89
4.1	Introduction	91
4.2	Materials and methods	96
4.3	Results	104

4.4 Discussion 111
4.5 Appendix C 118
Chapter 5. Vocal discrimination by Jungle Babbler between the young ones of conspecific and brood parasite 123
5.1 Introduction 125
5.2 Materials and methods 130
5.3 Results 133
5.4 Discussion 137
5.5 Appendix D 142
Chapter 6. Conclusions and Future directions 145
6.1 Conclusions 147
6.2 Overall summary 152
6.3 Future directions 152
References 157
List of Awards 194

List of Publications

Published

Yambem SD, Chorol S, Jain M (2021) More than just babble: functional and structural complexity of vocalizations of Jungle babbler. Behav Ecol Sociobiol 75(8): 1-14.

Yambem SD, & Jain, M (2022). Temporal variation in the behaviour of a cooperatively breeding bird, Jungle Babbler (*Argya striata*). Trop Ecol, 1-13.

Manuscripts in preparation

Yambem SD and Jain M. Examining the effect of group size on alloparental care in a paleotropical cooperative breeder, Jungle Babbler.

Yambem SD and Jain M. Ontogeny of begging behaviour in relation to acoustic and tactile stimuli in Jungle Babbler (*Argya striata*).

Yambem SD and Jain M. Examining host discrimination against brood parasite in paleotropical cooperative breeder Jungle Babbler (*Argya striata*).

List of Figures

Figure 1.1 Proximate and ultimate causes of behaviour, an adaptation from Alcock 2001. 4

Figure 1.2 Different kinds of social behaviour. An adaptation from Hamilton 1964 and West et al. 2007. '+' indicates benefit and '-' indicates cost. 8

Figure 1.3 Spectrogram of **a)** song of Purple sunbird and **b)** contact call of Jungle Babbler. 15

Figure 1.4 From left to right: JBs perching and clumping on the branch of *Callistemon* sp. and a map showing their distribution. 24

Figure 2.1 **a.** The map shows the distribution of JB and a red mark indicating the study location. **b.** The map shows the three study sites: two on IISER Campus and one on the NIPER campus. 33

Figure 2.2 Ethogram along with the illustrations of JB with 13 behavioural repertoires. Behaviours with blue shaded boxes are those behaviours that are included in the time-activity budget. The letter 'I' in the parenthesis represents 'individual' behaviours. * Indicate behaviours which are grouped into 'other' behaviour. 40

Figure 2.3 Amount of time (represented in percentage) allocated to each behaviour, calculated from 18,418 behavioural records collected from 192 days between October 2016 and September 2017. **a.** Amount of time spent on 'individual' vs 'social' behaviours. **b.** Amount of time allocated to 'affiliative' vs 'agonistic' behaviour among 'social' behaviours. 42

Figure 2.4 Mean ± SE of the proportion of time allocated to each behaviour across different times of the day (5:00-20:00): a) 'individual' behaviours (foraging, grooming and rest); b) 'social' behaviours (allogrooming, movement, sentinel and 'other'). 'other', includes most of the 'social' behaviours 43 (play, mobbing and inter-group fight) except ‘shower’ which is ‘individual’ behaviour.

Figure 2.5 Mean ± SE of the proportion of time allocated to each behaviour across different seasons: **a)** ‘individual’ behaviours (foraging, grooming and rest); **b)** ‘social’ behaviours (allogrooming, movement, sentinel and ‘other’). 45

Figure 2.6 Mean ± SE of the proportion of time spent on sentinel, while other members foraged, across different seasons. Different letters indicate a significant difference with p <0.05. 46

Figure 2.7 **a.** Mean ± SE of the timing of emergence and roosting in relation to the time of sunrise and sunset respectively across different seasons. **b.** Mean ± SE of the light intensity in lux unit at the time of emergence and roosting. The number of days of observation for the light intensity at the time of emergence and roosting were 50 and 53 respectively. Different letters represent significant differences with p<0.05. 48

Figure A2.1 Some of the habitats of the different locations of the study site. 58

Figure A2.2 Different roosting sites in the three locations of the study. 59

Figure 3.1 A fledgling with an adult showing different colours of iris. **a** fledgling and **b** adult 67

Figure 3.2 Figure 3.2 Schematic representation of spectrogram of **a** monosyllabic; **b** multisyllabic and **c** chorus call (Illustration by Deepuraj). 68

Figure 3.3 **a.** Spectrogram of 7 monosyllabic calls and **b.** plot of Linear Discriminant Analysis (LDA) of 7 monosyllabic calls showing first two linear discriminants (LDs). Colour ellipse denotes a 95% confidence interval. 77

Figure 3.4 **a.** Spectrogram of 6 multisyllabic calls and **b.** plot of Linear Discriminant Analysis (LDA) of 6 multisyllabic calls showing first two linear discriminants (LDs). Colour ellipse denotes a 95% confidence interval. 78

Figure 3.5 Spectrogram of 2 chorus calls. 79

Figure B3.1 Distribution of the duration of interval (in seconds) in between calls (inter-call interval) and between notes in a call (inter-note interval). 87

Figure B3.2 Power spectrum (on the left) and spectrogram (on the right) showing different parameters used in the analysis. **a.** an element/ a note; **b.** inter-call interval; **c.** call duration; **d.** frequency 95% **e** bandwidth 90%; **f.** frequency 5% and **g.** peak frequency. 87

Figure 4.1 Sites of the nests found during the study. **a)** sites of the nest found in the both IISER and Niper Campus. Different colours indicate different months: Feb-violet, March-brown, Apr-blue, May-green, June-yellow, July-orange, August-red, Sept-pink, Nov-grey. **b)** zoom in picture of the nests site in the IISER campus showing details of the nest with brood parasitism (BP), unsuccessful nests due to snake predation (P), Wind (W) and unknown reason (UN). 98

Figure 4.2 Spectrograms of the calls used in the playback experiments. **a.** Prompt call; **b.** Flight call and **c.** Contact call. 100

Figure 4.3 Stages of the young ones of JB. **a.** Hatchling; **b.** Nestling and **c.** Pre-fledgling. 101

Figure 4.4 Correlation between the provisioning rate and **a)** time of the day, **b)** group size and **c)** days to fledge and **d)** comparison between the provisioning rate of the nest without brood parasite (JB) and with brood parasite (JBJC) showing mean ± sd. * indicates the significant difference. 105

Figure 4.5 Comparison of the different categories of diet content of the young ones and adults. * Indicates significant difference. 106

Figure 4.6 Correlation between the duration in brooding and **a)** time of the day, **b)** group size, **c)** number of young ones and **d)** days to fledge (age of the young ones). **e)** comparison of the proportion of duration in brooding between the nests without 107 brood parasite (JB) and with brood parasite (JBJC) showing mean ± sd.

Figure 4.7 **a)** Difference in the percentage of the number of synchronized feeding (SF) and non-synchronized feeding. * indicates the significant difference. Correlation between the proportion of synchronized feeding and **b)** group size, **c)** number of young ones and **d)** days to fledge. 108

Figure 4.8 Correlation between the proportion of **a)** prompt call (PC) and the age of the young ones, **b)** begging response to prompt call and the age of young ones and **c)** begging response to adult movement (AM) and the age of young ones. 110

Figure 4.9 The proportion of begging response to the different stimuli at different stages of the young ones: **a)** hatchling, **b)** nestling and **c)** prefledge. Bar indicates the proportion of begging responses and points indicate the number of raw data of no response at 0.0 and response at 1.0 at the Y-axis. BS – Branch shake; BS+F – Branch shake+Flight; BS+P – Branch shake+Prompt; C – Contact; P – Prompt; F – Flight. 110

Figure C4.1 Proportion (in percentage) of different order in the category of invertebrates: **a)** young ones and **b)** adults. 118

Figure C4.2 Percentage of response and no response to adult movement and prompt call. 118

Figure 5.1 **a.** Eggs of only JB in a nest, **b.** eggs of both JB and JC in the same nest. 129

Figure 5.2 Fledgling of JB (left) and JC (right). 129

Figure 5.3 Spectrograms of begging call of young ones of **(a)** JB, **(b)** JC and **(d)** CM and fledgling close call of **(d)** JB and **(e)** JC. 132

Figure 5.4 Linear Discriminant Analysis (LDA) plot of the first two linear discriminants (LDs) of call types of young ones. The colour ellipse indicates a 95% confidence interval. 134

Figure 5.5 Proportion of response towards each call type of the young ones. **a)** proportion of response by approaching towards the speaker and no approach and **b)** proportion of response with call and without call while approaching towards the speaker. 136

Figure 5.6 Variation in the latency of response to the begging call of young ones of JB and JC and fledgling close call of JB and JC. Different letters denote the significant difference. 137

Figure D5.1 Location of the groups of JBs where the playbacks were conducted. All the points are marked with a short name. DH-Director house of IISER Mohali, H5-Hostel 5 of IISER Mohali, H7-Hostel 7 of IISER Mohali, MPH-Main pump house of IISER Mohali, 66- Sector 66 in Mohali, Railway-on the side of railway track in Mohali, NIPER - National Institute of Pharmaceuticals and Education Research Mohali, GV- Garden Valley in Mohali, AP-Animal park in Chandigarh, GC- Garden of conifer in Chandigarh, GFP-Garden of Fragrance Chandigarh, CTP- Children traffic park, SKP-Shanti kunj park, CC_Citco, LV- Leisure valley, BP-Bougainvillea park. 142

List of Tables

Table 1.1 Different signalling modalities and some of their functions. 12

Table 1.2 Number of species reported for the cooperative breeding system in different taxa. 17

Table 1.3 Studies reported on brood parasitism and their respective hosts. 22

Table 2.1 Summary of GLM results for the influence of predictor variable time and length of the day on the proportion of time allocated to different behaviours. 44

Table 2.2 Summary of **a.** Kruskal-Wallis examining the effect of season on the proportion of time spent on different behaviours and the timing of emergence and roosting **b.** Mann-Whitney U test (p values) for pairwise comparison between different seasons for the proportion of time spent on different behaviours and the timing of emergence and roosting **c.** Mann-Whitney U test (p values) for pairwise comparison between different seasons for the proportion of time spent on sentinel duty while foraging. 46

Table A2.1 Number of days and scans for every sampling hour. 59

Table A2.2 Number of days and scans for each month. 60

Table A2.3 Number of days of observation for the timing of emergence and roosting behaviours for different seasons. 60

Table 3.1 Call types along with its associated behavioural contexts. Contexts of the calls were inferred from the behaviour of 69 both the caller and the receiver. Percentage (%) indicates the frequency of a particular context associated with a certain call and it may add to be > or < 100% in cases when the contexts were not mutually exclusive.

Table 3.2 Brief descriptions of the acoustic parameters. 70

Table 3.3 Mean ± SD of the temporal and spectral characteristics of 15 call types of all the categories. N and n represent the number of recordings and number of calls analysed for each call types respectively (a recording can have multiple calls). Green colour filled cells represent the affiliative call category and unfilled represent the agonistic call category. * indicates onomatopoeic description used by Gaston (1977). 80

Table 3.4 Results of a) Generalized Linear Mixed Model (GLMM) and b) Likelihood Ratio Test (LRT) for the models with random effect (RE) and without random effect. 81

Table B3.1 Result of cross-validated DFA across all the call types showing the ratio of correctly classified calls to the total number of calls analysed (RCC) and the percentage of correctly classified calls (CC%). 88

Table 4.1 Stage of the young ones based on the count of number of days to fledge and number of nests used in the analyses of the playback experiment for each stage. 101

Table 4.2 Summary of the results of Spearman Rank Correlation test between **a)** the provisioning rate **b)** the proportion of duration in brooding **c)** the proportion of synchronized 108 feeding and with the factors: the time of day, group size, number of young ones and age of the young ones.

Table 4.3 Summary of the chi-square test for comparison between the proportion of different diet contents of young ones and adults. 109

Table 4.4 Summary of the Chi-square test for the proportion of begging response and the proportion of no response to the playback stimuli at different stages of the young ones: **a)** hatchling, **b)** nestling and **c)** prefledge. BS – Branch shake; BS+F – Branch shake+Flight; BS+P – Branch shake+Prompt; C – Contact; P – Prompt; F - Flight. +ve implies that the subjects exhibited begging significantly more than chance alone and -ve implies absence of begging. NS indicate no statistical significance. 111

Table C4.1 Nests without brood parasitism. Number of nests and hours of observation used in analyses for food provisioning **a)** for each group size of the adults **b)** at different ages of the nest (days to fledge). Numbers in bold and italics were not used in the analyses. 118

Table C4.2 Nests with brood parasitism. Number of nests and hours of observation used in analyses for food provisioning **a)** for each group size of the adults **b)** at different ages of the nest (days to fledge). Numbers in bold and italics were not used in the analyses. 119

Table C4.3 Number of nests and number of hours of observation for each day before the nestlings fledge for the nest **a)** without brood parasitism and **b)** with brood parasitism. Numbers in bold and italics were not used in the analysis due to its small sample. 120

Table C4.4 Number of nests used in the analyses for the begging response to natural prompt call and adult movement. **a)** total number of nests used for overall comparison irrespective of age and number of nests used for age-related analyses and **b)** number of nests used for the analysis of response to natural prompt call and adult arrival (tactile movement) for each day before the nestling fledges. Numbers in bold and italics were not used in the age-related analyses. 121

Table C4.5 Result of **a)** Generalized Linear Mixed Model (GLMM) and **b)** Likelihood Ratio Test (LRT) for the model with and without random effect (group Id of the calls used in the playback experiment). 122

Table 5.1 A summary of the statistical analysis of the comparison of different call types based on 5 acoustic parameters. **a)** Kruskal-Wallis test and **b)** P value of the multiple pairwise comparisons of different call types of the young ones of different acoustic features (with p-value adjustment method: BH). NS represent not significant. 134

Table 5.2 Values showing the number of correctly classified calls to each call type from the cross-validated results. Number of 135 samples assigned by Linear Discriminant analysis to each call group and percentage of correct classification (CC). Correctly assigned samples are marked in red colours.

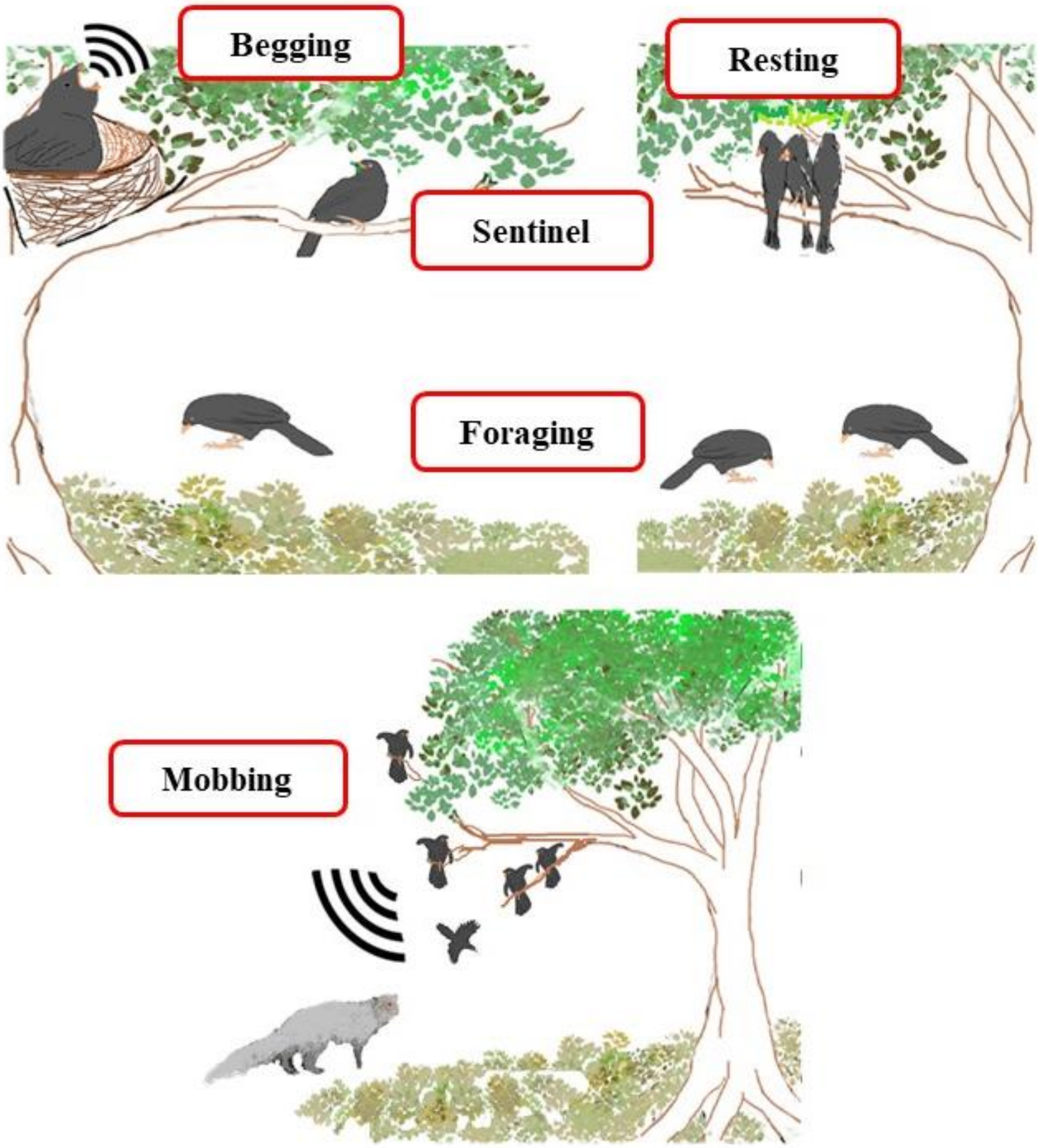
Table D5.1 Number of different nestlings (N) from which recordings were collected and number of calls (n) which are used in the acoustic analyses. 142

Table D5.2 Mean ± SD of the acoustic parameters used in analysing the structure of the call of the young ones of JB and JC. 143

Table D5.3 P values of multiple pairwise comparisons of the latency to response towards different calls of the young ones. 143

Chapter 1

General Introduction



1.1 Ethology: a conceptual framework

Ethology, as defined by Tinbergen (1963), is “the biological study of behaviour” with a particular focus on species-specific ‘instinctive’ behaviours. It starts with observing the behaviour of animals in their natural habitat and if this is not possible, then make the observations in semi-natural conditions. However, there exists no consensus on how to define behaviour. Tinbergen (1955) defined behaviour as “the total movements made by the intact animal”. This would exclude physiological responses such as sweating during hot summer, and would also exclude behaviours such as resting, sleeping and cognition that do not involve movement. Daniel Levitis et al. (2009) executed a survey of the existing literature on the definition of behaviour and came up with a consistent/compatible definition as follows: “Behaviour is the internally coordinated response (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes”. This, however, would exclude mechanistic and ontogenic underpinnings of behaviour. In so, a broad definition regarding the use of the term behaviour has been a conundrum for the researchers and a discipline-wide accepted definition of behaviour is largely lacking. Yet, Tinbergen (1963) proposed a framework for the study of animal behaviour. According to Tinbergen, the way an animal behaves can be explained by two causal mechanisms: proximate and ultimate causes which are interlinked with one another (Figure 1.1, Alcock 2001). Proximate causes of behaviour comprise of developmental, physiological, genetic and environmental factors that can initiate, cause, develop or cease diverse behaviours. These include questions on the mechanism/causation of behaviour and the ontogeny of behaviour that allows us to understand how behaviour develops over the lifetime of an animal. Whereas, questions that address ultimate causes include survival values or function and the evolutionary origin of diverse behaviours (Tinbergen 1963; Alcock 2001).

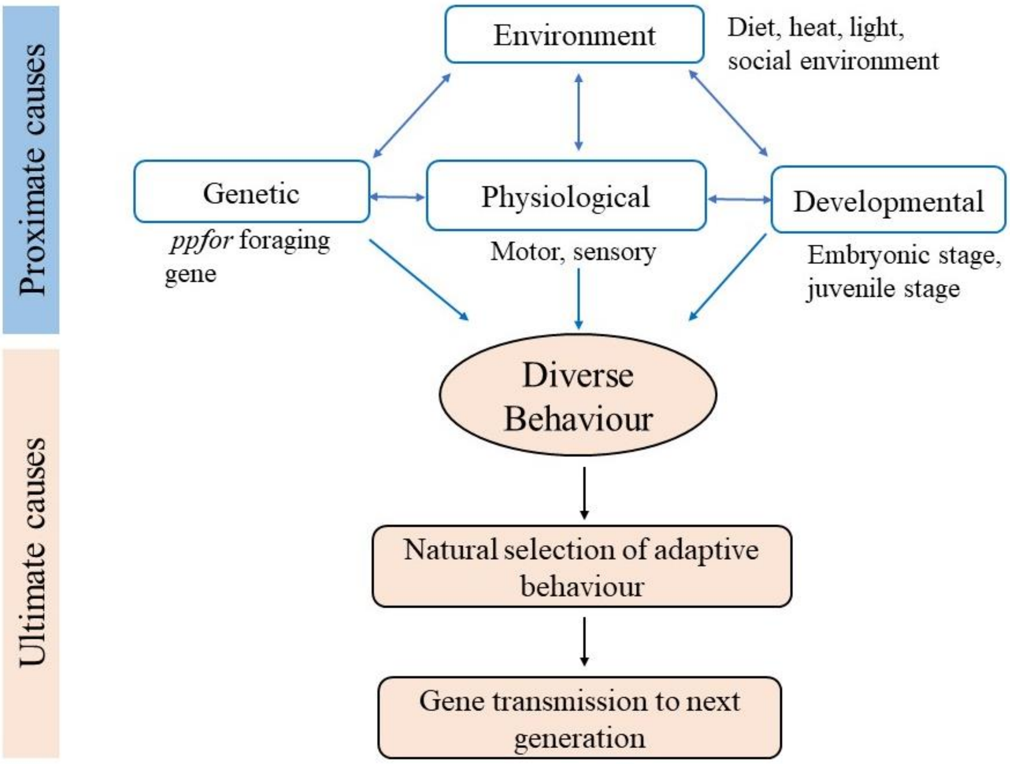


Figure 1.1 Proximate and ultimate causes of behaviour, an adaptation from Alcock 2001.

1.1.1 Diversity of behaviour: transforming observations into patterns

Animals across taxa display a diverse range of behaviours from self-directed behaviours (individual behaviours) to behaviour that involves interaction with another individual (social behaviours). Some of these behaviours may have evolved to enhance survival and would be essential for sustenance while other behaviours may have evolved for a better chance of reproduction of the animals. Further, different species may have evolved to exhibit different behaviours to serve the same function in a manner that is adapted to their specific ecological niches and survival strategies, whereas, the same behaviour may be exhibited across different species but may serve different functions (Alcock 2001). For example, migration may serve different functions in different species. Some species such as monarch butterfly, wildebeest and many passerines may migrate long distances to escape harsh environmental conditions and in search of food, whereas others such as Christmas

Island red crab and Salmon may do so to breed. Similarly, the same function may be served in different species by exhibiting different behaviours. For instance, several ungulate species exhibit fleeing as an escape strategy to avoid a predator whereas some others such as Meerkats may exhibit mobbing behaviour as an antipredator strategy. Finally, the same behaviour may serve multiple functions in the same species. For instance, allogrooming behaviour may have evolved to enhance social bonding but may also serve an immediate function of removing ectoparasites (Radford and Du Plessis 2006). Thus, a variety of proximate and ultimate causes have driven the enormous diversity of behaviours that we see in animals in our natural world. This makes the study of animal behaviour very rewarding but also challenging since one has to find a way to unravel complex behaviours through observations that should result in quantifiable traits that allow unbiased analyses.

The first step towards a comprehensive understanding of the behavioural pattern of an animal involves making observations of the animal and building an ethogram of all behaviours. An *ethogram* is a standardized system for cataloguing and describing all observed behaviours of an animal in its natural or captive environment. By quantifying and describing animal behaviours, an ethogram allows researchers to identify the diversity of behaviours an animal exhibits, provide an operational definition of all behaviours and allow an analysis of behaviour patterns within and across different species comparatively (Lescak 2017). This helps in investigating the relationships between behavioural patterns and social or ecological factors. It allows us to document and subsequently quantify the variations in behaviour patterns across space, time and social settings, highlighting the influence of the environment on behavioural patterns (Bezerra et al. 2011). Ethograms, therefore, provide valuable information for a better understanding of the behavioural ecology of species as well as for future comparative studies. Subsequent to building an ethogram, one can follow behavioural sampling protocols (*Ad libitum*, Focal Animal, Scan Sampling, All Occurrence:

Altmann 1974) to study the behaviours of animals in acute detail and quantify them to make the observations analysable. The method adopted depends on the question being asked, the category of behaviour being analysed (individual versus social behaviour) and the study species. Specifically, social animals may exhibit significant differences from solitary species in the repertoire of behaviours that they exhibit. The next section will focus on social behaviour and the types of social systems in animals.

1.1.2 Social behaviour and social animals

Behaviour can be exhibited by animals individually or when they are interacting with other individuals. For this thesis, the convention I have followed is as follows: *Solitary behaviours or individual behaviour* are those behaviours that are exhibited independently by an individual and no other participant is involved. For example, foraging, resting, grooming etc. when exhibited independent of the presence or involvement of other individuals (conspecific or heterospecific).

Social behaviours are those behaviours in which two or more individuals are involved (dyadic, triadic and multi-individual interactions). The association between individuals can range from temporary associations formed for specific contexts (such as mating, breeding, migration, and foraging) to longer-term associations across different contexts (stable social groups in the case of group-living organisms).

Social behaviours can be broadly classified into '*affiliative*' and '*agonistic*' depending on the type of interactions. Affiliative behaviours are those behaviours in which the recipient of an interaction is benefitted and such behaviours involve 'friendly' interactions that facilitate the development, maintenance and enhancement of social bonds such as allogrooming and play (Jasso del Toro and Nekaris 2019). On the other hand, agonistic behaviours are those in which the recipient of interaction is harmed and such behaviours involve aggression, fighting, threatening and submission (Young 2019). Depending on the lifetime fitness impact on the actor and recipient, 'social' behaviours can be further categorized as mutualistic, altruistic, spiteful and selfish (Figure 1.2) (Hamilton 1964; 1970; West et al. 2007). Allogrooming is a good example of mutualistic social behaviour wherein both the actor and recipient gain benefit from the interaction by getting rid of parasites and enhancing their social bonds (Radford and Du Plessis 2006). In altruistic social behaviour, the recipient gains benefit from the interaction while the actor is harmed (pays a cost). Sentinel behaviour is an example of altruistic behaviour in which the sentinel watches out for the rest of the group members and produces an alarm call in the presence of a potential threat. In doing so the sentinel must forego foraging while on duty and by producing an alarm call it is likely to become more conspicuous to the predator. In effect, this is likely to decrease the chance of survival of the sentinel while the recipient gains the benefits of vigilance provided by the sentinel to escape from the predator without having to invest in vigilance itself (Ridley et al. 2013). Selfish social behaviours are those behaviours in which the actor gains benefits while the recipient is harmed. A classic example of such behaviour is 'kleptoparasitism' which is exhibited by Fork-tailed drongo (*Dicrurus adsimilis*), a vocal mimic. During foraging, they mimic the alarm calls of other birds following which these birds drop their meal and flee for cover while the Fork-tailed drongo swoops in to steal the food (Flower 2011). Lastly, spiteful social behaviour is when an individual acts to harm another, even if it incurs a cost itself. This kind of social behaviour is not common and a very rare example of spiteful behaviour had been reported in Western gull (*Larus occidentalis*) in which breeding pairs who have lost their offspring attack other conspecific breeders (sometimes even killing their chicks). In the process, attackers as well as those who are being attacked bear the cost of risk of injury and thereby reduced fitness (Pierotti 1980). Social systems in animals can range from temporary interactions to lifetime associations. Based on this an entire spectrum of social systems exists in which animals can be categorised as solitary, gregarious or social/group living. For the purpose of this thesis, the convention I have followed is given below:

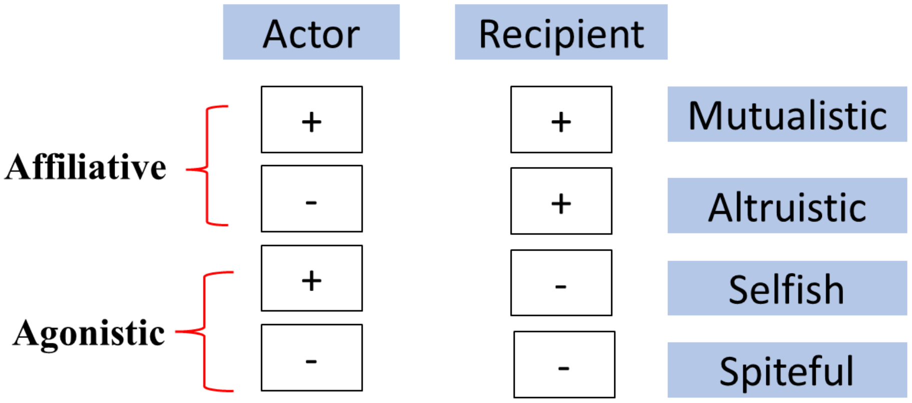


Figure 1.2 Different kinds of social behaviour. An adaptation from Hamilton 1964 and West et al. 2007. '+' indicates benefit and '-' indicates cost.

Solitary animals are those that exhibit a solitary existence and pair up or form groups only in the context of mating and breeding (Caro and Collins 1987; Logan and Longino 2013). Polar bears (*Ursus maritimus* Phipps), for example, show parental care during breeding season when the young ones are being nursed and provisioned for almost up to 2 years and social interaction during the ice-free season (Latour 1981; Owen 2021).

Gregarious animals are those that come together as groups for a specific context (for foraging or roosting) or during a specific time of the year (for migration). There can be heterospecific or conspecific aggregates in which individuals form a temporary association (Buckley 1996; Adamczewska and Morris 2001; Sridhar and Guttal 2018). For example, the terrestrial crab *Gecarcoidea natalis*, an endemic to the forests of Christmas Island, migrate in groups with number ranging from 0.09 to 0.57 crabs per square meter, each year at the arrival of monsoon to the coast to breed (Adamczewska and Morris 2001).

Social animals are those that form permanent or long-term associations usually within a family unit in which group members maintain social bonds over an extended period of time. The African elephant *Loxodonta africana*, for instance, lives as one family unit consisting of 10-20 females and their offspring led by a matriarch (Wilson 1971). Such systems are characterized by individuals frequently interacting with each other in various behavioural contexts, often repeatedly (Freeberg et al. 2012). The diversity of behaviour increases as interactions between individuals become more frequent, particularly in social animals living in stable social groups. The spectrum of the social system in animals illustrates the diverse nature of social behaviour and highlights the importance of social interaction in shaping animal behaviour.

The highest level of social organization is called eusociality. The term 'eusocial' was coined by Suzanne Batra (1966) to describe the way Halictine bees nest. The three characteristic features for the species to be considered eusocial are: 'Cooperative brood care', 'Reproductive caste differentiation' and 'Overlap between generations' (Wilson 1971; Gadagkar 1987). Eusocial systems have been reported mostly in arthropods, especially in Hymenoptera and Isoptera and rarely in other groups (review in Anderson 1984; Clarke and Faulkes 1997; Krasnec and Breed 2012). However, based on the classic definition, Naked mole-rat *Heterocephalus glaber*, and Damaraland mole-rat *Cryptomys damarensis* have also been considered as eusocial animals (Jarvis and Bennett 1993). There has, however, been considerable debate on this (Burda et al. 2000). According to the 'eusociality continuum' proposed by Gadagkar (1994) and Sherman et al. (1995), other cooperatively breeding taxa in mammals (Meerkat *Suricata suricatta*; Clutton-Brock et al 2004), birds (Arabian babbler *Argya squamiceps*, Florida scrub jay *Aphelocoma coerulescens*; Koenig and Dickinson 2004) and crustaceans (Sponge-dwelling shrimps *Synalpheus regalis*; Duffy et al. 2000) should also be considered as eusocial animals since the same characteristic features of eusociality are also exhibited across these taxa (except for temporary non-breeding helper instead of permanent sterile workers). It has been argued that similar behaviour and ecological factors may have driven the evolution of non-reproductive helpers across all these taxa (reviewed in Anderson 1984). These will be discussed in the next section.

1.1.3 Factors influencing behaviour

Various ecological factors influence the behaviour of an animal (Alcock 2001). These include the availability and distribution of resources such as food and mate. These may drive competition and impact the potential for monopolizing resources and have been proposed as an important driver of mating systems in animals (Emlen and Oring 1977). For example, if the distribution of resources (food and mate) is clumped then the availability of multiple mates in a clumped resource is likely to be higher, thereby driving the potential for polygamy. However, poor resource availability will limit the potential for polygamy since both parents have to provide parental care for successfully raising the offspring thereby driving monogamy in this condition. Further, various studies have shown the association between resource availability and distribution and breeding system in various taxa (Emlen and Oring 1977; Howard 1978; Wong et al. 2005; Martin and Martin 2007; Hatchwell and Komdeur 2000). For instance, limited availability of suitable territories, scanty resources or harsher environmental conditions may drive philopatry (delaying of dispersal) and thereby cooperative breeding (Hatchwell and Komdeur 2000; Wong et al. 2012) (covered in detail in section 1.3).

Time is also an important and limited resource which imposes a constraint on animals for finding other resources such as food or mate. Wilson (1971) put forward the importance of the variation in the allocation of time to self-directed behaviours and social behaviours in maintaining a social system. Given that time is an important and limited resource, its allocation for different behaviours can affect individual fitness as well as impact social bonding in group-living animals (Dunbar 1991; Korstjens et al. 2006; Pollard and Blumstein 2008). For instance, with the increase in group size, time spent per individual in scanning for predator reduces whereas time spent on foraging, resting and social interaction may increase (Caraco 1979; Pollard and Blumstein 2008). Thus, both individual survival and group stability may also depend on the time devoted to the individual versus social behaviours. Finally, the crucial role of communication in coordinating social behaviour has been emphasized in several studies and deserves a separate discussion, done in the next section.

1.2 Animal communication

To coordinate various inter-individual interactions, communication plays an important role. Communication can be defined as “the action of, or cue given by one organism (the sender) is perceived by and thus alter the probability/pattern of behaviour in another organism (the receiver) in a fashion adaptive to either one or both of the participants” (Wilson 1975). Most importantly in social animals, communication plays a vital role in facilitating different behaviours that are crucial for cooperation and maintaining group cohesion as well as social bonds (Cheney and Seyfarth 2018). Animals communicate using *signals* which can be defined as “any act or structure which alters the behaviour of other organisms, which evolved because of that effect and which is effective because the receiver’s response has also evolved” (Smith and Harper 2003). On the other hand, a *cue* is defined as an inadvertent by-product of other behaviours of an individual which is not targeted towards any ‘intended’ receiver but can be utilized by unintended receivers for their benefit. While cues do not have intended receivers or defined functions, it is expected that signals must be directed to ‘intended’ receivers and must possess distinct functions (Smith and Harper 2003).

Signals play an important role in communication as they convey information about an animal’s identity, fitness, reproductive status, location, environmental condition etc. which help in facilitating their social and reproductive interactions. There are different signalling modalities through which animals can exchange information effectively depending on different situations (Alcock 2001; Bradbury and Vehrencamp 2011). Different signalling modalities and some of their functions reported in different taxa are given in Table 1.1. Among all the signal modalities, auditory signal can be utilised to convey information in different habitats such as terrestrial, aerial or aquatic since sound can travel through solid, air and water. Further, acoustic communication is independent of light so it can be utilised by both diurnal and nocturnal animals. Acoustic signals can carry a wide variety of information and can be used in long-range communications effectively. Moreover, because of its potential for a rapid signal shift, acoustic signals can be more effective during urgent situations (Alcock 2001; Davies et al. 2012). Thus, it is unsurprising that a wide range of animal taxa including insects, crustaceans, fishes, amphibians, mammals and birds, employ acoustic signals for communication (Bradbury and Vehrencamp 2011).

Table 1.1. Different signalling modalities and some of their functions.

Signalling modalities	**Functions**	**Taxa, species**	**References**
Auditory	Mate attraction: males produce different types of mating calls in long and short range	Field cricket (*Acanthogryllus asiaticus*)	Singh and Jain 2021
	Territory defence: male and female song maintain territory	White-bellied antbird (*Myrmeciza longipes*), Great tit (*Parus major*)	Fedy and Stutchbury 2005; Krebs et al. 1978
	Predator avoidance: alarm call informing different types of predators	Noisy miners, (*Manorina melanocephala*); Vervet monkeys (*Chlorocebus pygerythrus*)	Cunningham and Magrath 2017; Ducheminsky et al. 2014
	Group cohesion: contact calls used in contacting conspecific and reunion of the group members	Birds and mammals	Reviewed in Kondo and Watanabe 2009
Visual	Nest Defence: ‘shimmering behaviour’, a	Asian giant honeybee (*Apis dorsata*)	Vijayan et al. 2022

	coordinated defence mechanism in open-nest is modulated by ambient light condition Indication of male quality: males with contrasting colours on their bodies indicate their physiological state with the lower testosterone level Mate attraction: a combination of colour and pattern of the wing is more successful in attaining mates	Indian rock agama (*Psammophilus dorsalis*) Passion-vine butterfly (*Heliconius erato)*	Amdekar and Thaker (2022) Finkbeiner et al. 2014
Olfactory	Assessing reproductive status: Male can assess the reproductive phase of the female by possibly detecting a pre-ovulatory pheromone released in dung Exerting dominance: The application of non-volatile pheromones on the nest indicates the presence of the dominant queen without any physical interaction Territory maintenance: the rate of scent marking increases with the increase in the number of neighbouring males	Asian elephant (*Elephas maximus*) eusocial wasp (*Ropalidia marginata*) African antelope (*Ourebia ourebi*)	Ghosal et al. 2012 Bhadra et al. 2007 Brashares and Arcese (1999)
Tactile	Territory defence: Resident males use aerial chasing and scuffling to defend their territories against conspecific	Purple-throated caribs (*Eulampis jugularis*)	Gowda et al. 2012

	males, females or heterospecific Navigations: "Tandem running", characterized by two individuals walking one behind the other, maintaining physical contact by tapping, is used as navigation for the recruitment to a new location	Indian queenless ant (*Diacamma indicum*)	Kaur et al. 2017

Avian systems are known for using vocalization as an important signalling modality. In birds, vocalization is generated by the expiration of air through the syrinx and trachea (Gaunt and Gaunt 1985). The smallest vocal unit produced by a bird is called a '*note*' which forms a '*syllable*' consisting of two to three notes that then combine to form a '*phrase*'. Depending on the number of notes present, vocalization can be either *monosyllabic* (only one note) or *multisyllabic* (multiple notes) (Catchpole and Slater 2010) which are described in detail in Chapter 3. Avian vocalization can be categorized as either songs or calls (Figure 1.3). Songs are typically longer duration display vocalizations and are generally produced in the context of mate attraction or territory maintenance (Catchpole and Slater 2010). On the other hand, calls are relatively shorter vocalizations with definite functions associated with them (Ehrlich et al. 1988). Depending on the broad contexts, calls can be either 'affiliative' such as contact calls and recruitment calls which are produced in contacting and recruiting conspecific or 'agonistic' such as alarm calls and mobbing calls which are produced to provide information about potential predators and recruiting members to chase away the predators etc. (Marler 2004).

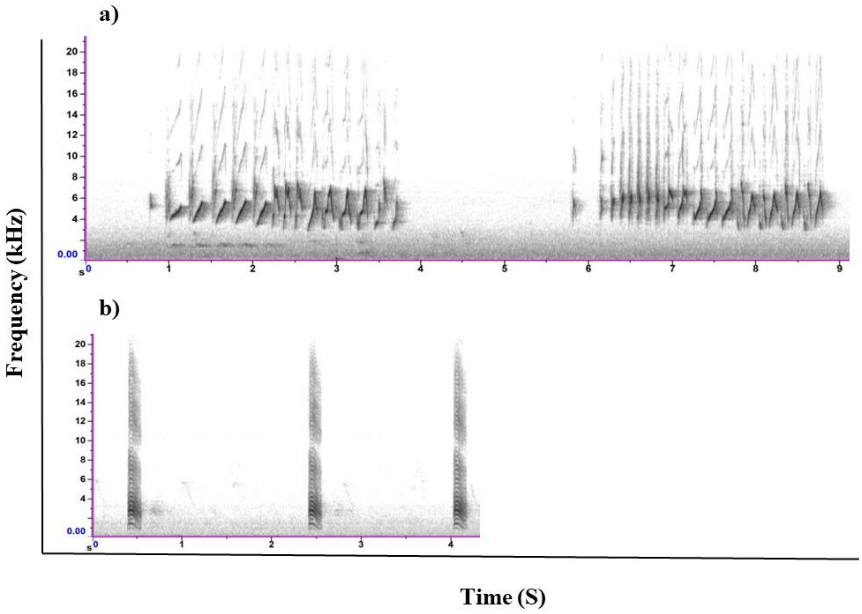


Figure 1.3 Spectrogram of **a)** song of Purple sunbird and **b)** contact call of Jungle Babbler.

1.2.1 Complexity in acoustic communication

Communication is considered complex if the signal "possesses a large number of bits of information (number of distinct notes or arrangement of these notes) or a large number of structurally and functionally different vocalizations (repertoire size)" (Wilson 1971; Freeberg et al. 2012). Additionally, employing multimodel signals can also be considered a complex communication system since they generate a number of signals that enables the transmission of separate pieces of information such as sender's size and motivation. This increases the amount of information that is conveyed to the receiver (reviewed in Peckre et al. 2019). There are various factors that can influence the evolution of complex communication such as predation pressure, habitat structure, sexual selection, species recognition, sociality etc. For example, a study by Leighton (2017) on 253 species from 59 families showed that many species produced a large number of vocalizations toward vigilance contexts increasing the overall repertoire size. This increase in repertoire size may be explained by the imposed requirement of the production of distinct and reliable alarm calls that allow the receiver to efficiently discriminate between the type of predators and the level of urgency allowing them to employ the proper escape strategy and increasing the chances of survival (Manser 2001). Animals that rely on vocal signals as a display for mate attraction can also have a large vocal repertoire since having a large repertoire is expensive and mate choice decisions are often dependent on the repertoire size of the males. For instance, a large syllable repertoire in male Great reed warblers *Acrocephalus arundinaceus* increases the chances of extra-pair fertilization; a large song repertoire of both male Red-winged blackbirds *Agelaius phoeniceus* and Song sparrow *Melospiza melodia* is known to attract more mates (reviewed in Nowicki and Searcy 2004). Thus, the discriminability of selecting complex songs due to female preference can lead to the evolution of complex songs.

Communication is an integral aspect of the social system without which proper sustenance and facilitation of social interaction are not possible/feasible (Wilson 1971; Bradbury and Vehrencamp 2011; Kappeler 2019). The ‘Social complexity hypothesis’, posits that animals living in a comparatively more complex social system will possess a more complex communicative system (Freeberg 2006). Correspondingly, a complex social system is associated with enhanced and sophisticated communication and a complex signalling repertoire (Blumstein and Armitage 1997; McComb and Semple 2005). Various studies have reported that with the increase in the complexity of the social system, there is greater variability in the type and number of associations and thus the requirement for a greater number of distinct signals to enhance and maintain social stability (reviewed in Peckre et al. 2019). For example, Carolina chickadees (*Poecile carolinensis*) produce signals with a larger number of elements in the larger group size which is required to maintain comparatively larger interaction (Freeberg 2006). Cooperative breeding (discussed in detail in section 1.3) is an example of greater complexity in a social system owing to the involvement of individuals of different sex and breeding status (breeders versus nonbreeders), involved in various interactions such as provisioning and caring for the young ones. Thus, it is likely to serve as an important driver of communicative complexity (Freeberg et al. 2012). For example, a study by Leighton (2017) on 253 species of birds provided evidence for the support of “social complexity hypothesis” by demonstrating that the species engaged in cooperative breeding have more functional communicative repertoire than those that do not engage in cooperative breeding.

1.3 Cooperative breeding

Cooperative breeding is a kind of social system characterized by the presence of one or more individuals (generally referred to as ‘helper’ or ‘helper-at-the-nest’) other than the breeding pair in assisting breeders in raising their young ones (Cockburn 1998; Royle et al. 2012). This type of care is known as alloparental or cooperative brood care. The helpers are exhibiting altruistic behaviour by providing care to the offspring of the breeding pair that promotes or aids in the survival and fitness of the offspring at the cost of their own reproduction (Clutton-Brock 1991). These helpers provide care to young ones in the form of incubating eggs, provision of food, brooding of the nestlings, removing faecal matter from the nest and protection from predators. However, the extent to which the helpers provide and forms of parental care may vary between systems (Clutton-Brock 2019).

There are various advantages that are associated with the cooperative breeding system. They provide the advantages of an increase in nesting success through an increase in the provisioning of food, avoidance and protection from predators or brood parasites through multiple defenders (Valencia et al. 2006; Kingma et al. 2010; Feeney et al 2013). For example, Purple crowned-fairy wrens showed an increase in the survival of fledglings through an increase in the provisioning rate with the increase in number of helpers and the workload on the breeders was also reduced in the presence of the helpers irrespective of the group size (Kingma et al. 2010).

The cooperative breeding system is widespread and found across different taxa (Table 1.2). However, such altruistic behaviour in which an individual forgoes its own reproduction and instead assists in raising the young ones of the breeding pair would not have evolved as according to Darwin (1859): “If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection”. Thus, the cooperative breeding system has been a puzzle to behavioural ecologists and evolutionary biologists as to how such altruistic behaviour which does not give benefit to its bearer but costs its reproductive success would have been selected and evolved.

Table 1.2 Number of species reported for the cooperative breeding system in different taxa.

Taxa	**Number of species**	**References**
Birds	9% (852 out of 9456 species)	Cockburn 2006
Mammals	2% (34 out of 1874 species)	Lukas and Clutton-Brock 2012
Fishes	<0.1% (25 out of 32,700 species)	Taborsky 2016
Insects (specially hymenopterans)	<0.1% (thousands of species).	Eggert 2014

One of the most significant and broadly accepted theories in the evolution of helping behaviour is the Hamiltonian kin selection (1964). It posits that a gene can be favoured by natural selection if it promotes reproduction and survival of the individual who also carry the same gene. Most of the cooperative breeding systems are found to consists of closely related family members thus, supporting the inclusive or indirect fitness theory which states that the helpers can increase their indirect fitness by helping relatives (Clutton-Brock 2002; Griffin and West 2003; Green et al. 2016;). Studies in Long-tailed tit *Aegithalos caudatus* showed that the helpers can manipulate their investment on the aiding behaviour in accordance to relatedness within the group member by increasing the helping behaviour with the increase in the relatedness of the recipient of their investment (Nam et al. 2010). Nevertheless, there are rare social systems which are composed of unrelated individuals and altruistic behaviour cannot be explained by inclusive fitness alone. For example, helpers in Fairy-wren *Malurus cyaneus* (Dunn et al. 1995), Dwarf mongoose *Helogale parvula* (Rood 1978), Cichlid *Neolamprologus pulcher* (Zöttl et al. 2013), Paper wasp *Polistes dominula* (Field and Leadbeater, 2016) were often found providing parental care to the unrelated broods. In such cases, direct fitness benefits also play a key role in the evolution and maintenance of a cooperative breeding system and this direct fitness may serve in the form of future breeding opportunities, benefits of group living, acquisition of skill for reproduction (reviewed in Cockburn 1998; reviewed in Riehl 2013; Kingma 2017).

Cooperative breeding systems in which individuals other than the parents are involved in caring of the young offer the feasibility of multiple levels of interaction. For example, in a cooperative breeder, Bell miner (*Manorina melanophrys)* there is a diverse range of patterns of care and association where individuals from the same coterie (group of individuals sharing and defending a territorial space) may help in raising young ones of the same coterie but not of other coterie but individuals of different coterie provide defence against the intruder or predator (Clarke 1984; Clarke and Fitzgerald 1994; Painter et al. 2000). Even within the same coterie, the range of pattern of care is diverse depending on age, sex and breeding status as male and unmated helpers give more aid in assisting raising young ones and that increases with the age (Clarke 1989).

Furthermore, there are extensive varieties in the social system of cooperative breeding where the same species exhibit communal breeding (a system in which more than one breeding pairs share parentage in a single brood and are involved in raising the brood) as well as the assistance of non-reproductive helpers and there are also systems where there is presence of both related and unrelated helpers as well (reviewed in Riehl 2013). Thus, finding routes to the evolution of cooperative breeding become more complicated offering more platform to understand this complex system. Several factors such as life-history traits, ecological constraints, or a combination of these factors have been shown to associate with the evolution of cooperative breeding (Pen and Weissing 2000; reviewed in Hatchwell 2009). A comparative study across 95% of world bird species reported that the uncertainty in the environment may lead to the variability of the social system in the cooperative breeding animal (Jetz and Rubenstein 2011). Another comparative study across the family of African starling by Hatchwell (2007) has also shown that unpredictable environments led to cooperative breeding. In addition, a study by Hatchwell and Komdeur (2000) has also reported that both ecological and life history traits complement each other in the evolution of cooperative breeding and the diversity in the cooperative breeding system might be due to the different selective pressure by these traits.

Given the vast diversity of social systems in the cooperative breeding systems, there are still many unexplored questions on the evolution of this complex society despite several decades of study. This provides the opportunity for future research and it also serves as a good model system to study the evolution of cooperative behaviour. Moreover, according to the ‘eusociality continuum’ as mentioned in the earlier section, a cooperative breeding system can be considered as a eusocial system, a highly advanced social system. Thus, this system imparts a great potential to find the possibility of the existence of an advanced social system in other taxa as well, in addition to the known Hymenoptera. Furthermore, cooperative breeding systems also incur the cost of attracting predators through repeated number of nest visits by multiple carers that might elicit conspicuous begging calls making it more prone to predation (Martin et al. 2000; Haff and Magrath 2011). Besides predators, there are brood parasites which also take the advantages of the presence of multiple carers in cooperative breeders. Thus, brood parasitism may represent a cost to cooperative breeders and it may be expected that cooperative breeders, in turn have evolved mechanisms to discriminate against brood parasites. This has been discussed in detail in the following section.

1.4 Brood parasitism

Parental care is costly owing to the high level of energy and time requirement that comes at the cost of the parent's own survival and future reproduction (Clutton-Brock 1991; Royle et al. 2012). An alternative breeding system to escape from this expensive behaviour is brood parasitism. Brood parasites do not build their nest but lay eggs in the nest of the host species and let the host raise their young ones. This system is reported to mostly occur in the avian system (Table 1.2). Furthermore, cooperative breeders are hosts for many brood parasites owing to their cooperative brood care (Feeney et al. 2013). A study by Feeney et al. (2013) on the geographical distribution and phylogenetic distribution of avian brood parasites and cooperative breeders showed that there is a tight association between avian brood parasitism and cooperative breeding. Feeney et al. 2013 proposed three possible explanations for the association between cooperative breeding and brood parasite: i) advantages to the offspring of brood parasites by having multiple carers, ii) an increase in the number of helpers around the nest make it more noticeable for brood parasites and iii) hosts that are likely to be parasitised would benefit from having multiple individuals to defend their nests from being target by brood parasites thereby driving the evolution of cooperation. They also provided evidence for these explanations by conducting experiments on Superb-fairy wren which showed that the increase in host group size also results in an increase in the growth and development of chicks of brood parasite. At the same time, they also showed that cooperative breeders with larger group sizes showed a reduction in the incidence of brood parasitism. In brood parasitism, the cost and effort of raising the young ones are imposed on other unrelated conspecific or heterospecific. Thus, to avoid the heavy cost of parental care directed towards a parasite, hosts may develop a range of strategies to avoid parasitism including increased distinctiveness of the egg to recognize the difference in egg size, colour and pattern. Hosts may also evolve to recognize the songs or calls of brood parasites and respond aggressively to them. Brood parasites, in turn, have evolved the mechanism to overcome these defences by mimicking the colour and pattern of host eggs, mimicking begging calls and gape marking of the host chick etc. (Feeney et al. 2014). Thus, this system offers to be a good model system to study the co-evolutionary arms race (Rothstein 1990).

Table 1.3 Studies reported on brood parasitism and their respective hosts.

Brood parasite	**Host**	**References**
50% of cuckoo species, five Cowbirds species, Honeyguide, two genera of finches and a duck	Birds (many passerines)	Reviewed in Payne 1977
Cuckoo catfish *Synodontis multipunctatus*	Fish (Cichlid)	Blažek et al. 2018
Cuckoo bumblebee *Bombus* (*Psithyrus*) *vestalis*	Insects (Bumblebee *Bombus terrestris)*	Erler and Lattorf 2010

Brood parasitism offers an avenue to explore the complex system associated with multispecies interactions at different stages of the life cycle of an animal. A study done by Kennerley et al. (2022), reported that 83% of the recorded brood parasites are found to parasitize two or more host species whereas 31% of the host species have been observed to be parasitized by two or more brood parasites. Moreover, they also reported that brood parasite and host interaction at the multispecies level can give rise to complex association accounting for as complex as 241 interactions irrespective of the species richness whether it is brood parasite or host or both, suggesting that brood parasite and host interaction is not straightforward but rather complex.

1.5 Study species

Jungle Babblers (*Argya striata*) belong to the order Passeriformes and the family Leiothrichidae (Cai et al. 2019). They were placed under the genus *Argya* only after the study on molecular phylogenetics done by Cibois et al. (2018) who proposed for the revision of the taxonomy but earlier they were placed under the genus *Turdoides*. Jungle Babblers (JBs) are sexually monomorphic with rounded wings, long tails, stout yellow bills and eyes with creamy white iris (Figure 1.4). Young ones or subadults can be distinguished from adults by the iris colour which is dark brown in the former until they are two months old. Additionally, the first-year juveniles can be identified by the presence of more rounded tips in their primaries. Given their wing morphological features, they are weak flyers and non-migratory (Andrew and Naik 1965, 1970). Birds of this family had been reported to show an average life span of 10 years and JBs have been observed to live up to 16 years on average (Flower 1937). They live in a group of 2-20 individuals exhibiting most of their daily activities in close proximity. Nevertheless, Andrew and Naik (1970) reported that the group may break up and become small during the breeding season. They are common residents throughout lowland India (Figure 1.3) with a special preference for closed-canopy woodland and scrub vegetation. They are commonly observed in the proximity of human neighbourhoods and often seen in parks and gardens (Andrews and Naik 1970; Gaston 1977; Zacharias and Mathew 1988). They are omnivores, mainly feed on insects (both adult and larvae) and may also have fruits like wild figs, berries and grains and their diet may vary according to season and availability (Narang and Lamba 1986; Jose 2004). They forage by hopping on the ground and searching for food mostly among leaf litter by flipping the leaf litter using their beak (Zacharias and Mathew 1988; Jose 2004).

They maintain and defend territory ranging from 0.0014 to 0.016 km^2 (Andrew and Naik 1970). According to different studies and observations, the breeding season of JBs may vary. Ali (1964) reported that they may breed irregularly throughout the year while based on other observations by Dharmakumarsinhji (1954), Whistler (1949) and Andrew and Naik (1970), the breeding season may range from March to October. Nest of JBs are brood parasitized by the migratory bird, Pied crested cuckoo or Jacobin cuckoo (*Clamator jacobinus*) during monsoon season when this brood parasite migrates to breed and by another brood parasite, Hawk cuckoo (*Cuculus varius*) (Gaston 1976). They are cooperatively breeding birds and are assisted by helpers during nest construction, incubation, brooding, provisioning and defending the group from predators or intruders and are known for their conspicuous vocalizations (Andrews and Naik 1970; Gaston 1977). However, a detailed study on their acoustic communication, variation in behaviour, alloparental care and defence against brood parasitism is largely lacking. Thus, they offer to be a good model system to examine both cooperative breeding and brood parasitism. In addition, given that they are both social and vocal, they also offer to be a good model system to examine communicative complexity in birds.

Figure 1.4 From left to right: JBs perching and clumping on the branch of *Callistemon* sp. and a map showing their distribution.

1.6 Thesis objectives

In my thesis, I explore/examine different aspects of the social system such as time allocation, vocal communication, parental care and brood parasitism by employing a combination of methods including natural observation of free-ranging birds, field-based acoustic analyses and playback experiments. Inclusive knowledge of these basic aspects of a social system will be useful in understanding the evolution of cooperative breeding in birds as well as allow comparative study in the variation of social systems within species and between species. Broad objectives and sub-objectives of my thesis are outlined below:

Objective 1: Behavioural repertoire and temporal variation of different behaviours

i. What are the different types of behaviours exhibited by JBs?

ii. How do JBs allocate their time to different behaviours?

iii. Does this allocation of time to different behaviours vary at different temporal scales (diurnal and seasonal)?

Objective 2: Functional and structural complexity in the vocalizations of Jungle Babbler

i. Do JBs produce diverse vocalization in different behavioural contexts?

ii. Do the vocalizations produced in different contexts also differ in their acoustic features?

Objective 3: Understanding alloparental care in Jungle Babbler and the ontogeny of begging behaviour

i. Does the provisioning rate and duration of brooding vary with the time of the day, group size, number of nestlings, age of the young ones and brood parasitism?

ii. How does the diet content of the young ones differ from adults?

iii. Do JBS exhibit synchronized feeding and if so, which parameters influence this behaviour?

iv. Does the nature of signals that induce begging response vary with the age of the young ones?

Objective 4: Vocal discrimination by Jungle Babbler between the young ones of conspecific and brood parasite

i. Do the acoustic features of the calls of young ones of the brood parasite share similar features with that of the host?

ii. Can JBs discriminate between the calls of young ones of its conspecific and the brood parasite?

JBs live in a cooperatively breeding group displaying a wide range of behaviours and the results of objective 1 with respect to the diversity of behaviours exhibited, the time activity budget and temporal variation in these behaviours are presented in **Chapter 2**. Maintaining large social groups to stay together and coordinate their behaviours require a strong communication system and thus **Chapter 3** of my thesis focuses on the findings of objective 2 in examining the complexity in terms of distinct calls based on functions and structure. In **Chapter 4**, the results of objective 3 which deals with the three aspects of alloparental care: provisioning, brooding and communication between provider and offspring, are discussed. Findings of objective 4 which investigate whether vocal cues are used as a strategy in discriminating the young ones of its conspecifics and that of brood parasites are presented in **Chapter 5**. In **Chapter 6**, the overall conclusions of my findings from all the above objectives are presented and I have discussed the possible future directions by connecting the findings from this thesis with the available works. The findings of this thesis will provide a foundation for further research on the influence of various ecological and social factors on the evolution of complex communication and drivers of cooperative breeding.

Chapter 2

Behavioural repertoire and temporal variation of different behaviours

Published as: Yambem, S. D., & Jain, M. (2022). Temporal variation in the behaviour of a cooperatively breeding bird, Jungle Babbler (*Argya striata*). Trop Ecol, 1-13.

2.1 Introduction

Animals display a vast array of behavioural states and events every day in a variety of environmental and social circumstances over the course of their existence. Different amounts of time must be allocated to these different behaviours depending on the metabolism and energetic constraints as well as the relative importance of each behaviour in the sustenance of the life of an animal (Halle and Stenseth 2000). The allocation of varying amounts of time to various behaviours is known as a 'time-activity budget'. However, since time is a limited resource, animals have to trade-off between the allocation of time to different behaviours depending on various environmental and ecological factors as well as the physical state of the animal (Pollard and Blumstein 2008). Moreover, in social animals with the increase in the amount of time spent together and opportunities for a diverse array of interactions, the repertoire of behaviours is larger and includes both 'individual' as well as 'social' behaviours.

Depending on the type of association between individuals, 'social' behaviours can be 'affiliative' behaviour which plays an important role in maintaining the social bond (positive interaction) (Sussman et al. 2005) and 'agonistic' behaviours due to competition for resources such as space, food, or breeding partner (negative interaction) (Wilson 1970). Thus, the allocation of time becomes more complicated in social animals considering that, they have to dedicate their time to 'social' behaviours such as allogrooming (Boccia et.al 1982; Dunbar 1991), play (Pozis-Francois et.al 2004) and sentinel duty (Hollén et al. 2008), that helps in maintaining and improving social bond as well as in protecting the group, in addition to the allocation of time towards an individual's sustenance in gathering resources and seeking opportunities for reproduction. For example, foraging is essential to an animal's survival and provides energy for other activities, thus, it is expected that it will take up a larger amount of the animal's time, leaving less time for other activities such as resting and grooming (Kramer 2001). However, in social animals, managing time to devote it to 'social' behaviours that correlate with the direct or indirect fitness of the animal (Silk 2007; Dunbar et al. 2009) is critical as it can influence their social bonding, group dynamics and stability (Dunbar 1992; Radford 2011). In addition, effective time management across different behaviours has an important influence on the optimum number of calories consumed and preventing exhaustion (Capellini et al. 2010).

Animals' behavioural states are classified into two major categories: 'activity' and 'rest.' Foraging, territorial defence, fresh territory exploration, and mate finding, need a disproportionate amount of energy, but resting, sleeping, grooming, and playing require less energy. Even though active behaviour is essential for life, it must be alternated with resting behaviour to replenish energy. This transition from one behavioural state to another throughout a 24-hour cycle results in the formation of a temporal pattern known as diel activity pattern or activity pattern of a species. (Halle and Stenseth 2000). Animals are classified as nocturnal (active at night), diurnal (active during the day), crepuscular (active at twilight), or cathemeral (active approximately equally throughout the day and night) (Ikeda et al. 2016) based on this diel pattern of activity. Nevertheless, these classifications are not comprehensive or generalized because activity patterns vary even among the same species depending on the environment and season (Ikeda et al. 2016). This species-specific diel activity pattern enables behavioural niche partitioning, allowing diverse species to cohabit (Monterroso et.al 2014; Sunarto et.al 2015).

The variation in the diel activity pattern even within a species may arise due to many abiotic as well as biotic factors. Abiotic factors such as seasonal shifts and the time of the day play a pivotal role in significantly influencing the major changes in environmental parameters like light intensity and temperature (Steiger et al. 2013). For example, Dark-eyed juncos (*Junco hyemalis*) adjust their activity depending on the light intensity. They begin foraging early in low light intensity to restore their low stored energy and end their activity at high light intensity before the risk of predation increases (Lima 1988). European ground squirrels (*Spermophilus citellus*) regulate their activity by devoting more time to resting when the ambient temperature is high at noon (Váczi et al 2006). Among the biotic factors, predation pressure (Lima and Dill 1990), presence of humans (Banerjee and Bhadra 2021) and competitors (Blanchet et al. 2008) are factors that have an impact on the activity pattern of an animal and have been studied in many taxa. For example, female Capuchin monkey (*Sapajus* sp.) had been found to engage in a higher rate of allogrooming (one of the signatures of sociality which helps in maintaining social bonds) during their oestrous cycle which in turn affects the activity pattern of remaining behaviours (Bitetti 1997). Furthermore, emergence and roosting behaviour are possibly to be greatly impacted by ambient light conditions which are likely to vary with different seasons.

Comprehensive knowledge of how animals distribute their activity efficiently and how this pattern changes with various factors, will help in a better understanding of the ecology of the animal. Many studies on activity budget and the temporal variation in activity pattern of social animals have been carried out on social insects, primates, dogs, waterbirds etc. (Gadagkar and Joshi 1983; Rasmussen 1984; Isbell and Young 1993; Zhou et.al 2007; Bensizerara and Chenchouni 2019; Li et.al 2019; Banerjee and Bhadra 2021; Back et.al 2019). Even though many avian species are social, to our information, so far studies on time-activity budgets and its temporal variation have not been examined in social birds even though they display a large behavioural repertoire. According to Enright, 1970, "No description of where an animal lives and what it does can be complete without considering when the activity takes place because animals are adapted to perform given activities at given environmental times: certain seasons, times of day, or phases of the tides". Thus, the objectives of this study on Jungle Babblers (hereafter JBs) were as follows:

1) What are different types of behaviour exhibited by JBs?
2) How do JBs allocate their time to different behaviours?
3) Does this allocation of time to different behaviours vary at different temporal scales (diurnal and seasonal)?

2.2 Materials and methods

2.2.1 Study site

The study was executed in a population of JBs inhabiting an urban landscape in the Mohali region, located in the eastern part of the Punjab state in India (30°36' and 30°45'N latitude and 76°38'and 76°46'E longitude). According to the Koppen-Geiger climate classification system, the climate of Mohali comes under the 'Cwa' category (Kottek et al. 2006). 'Cwa' is a humid subtropical climate that is variable throughout the year with a hot summer and cold, dry winter separated by a brief period of tropical monsoon climate (Kottek et al. 2006). Three main sites were selected in this region where the study could be carried out efficiently. Two sites were at the IISER (Indian Institute of Science Education and Research) Mohali campus and the other one at the NIPER (National Institute of Pharmaceutical Education and Research) campus. The distance between each study site was at least 500 m (Figure 2.1b). Both the campus areas are comprised of a mix of plantation, garden, open grassland and natural closed-canopy woodland. Some pictures of the habitat of the study sites where the model organisms are frequent are given in Figure A2.2. The vegetation is predominantly deciduous and weedy, consisting of trees such as *Populus deltoides, Bombax ceiba, Bauhinia purpurea, Schleichera oleosa, Dalbergia sissoo, Ficus religiosa, F. glomerata, F. virens, Vachellia nilotica, Pongamia pinnata, Morus alba, M. nigra, Psidium guajava, Leucaena leucocephala, Chukrasia tabularis,* *Callistemon* sp., and shrubs by bushes of *Lantana camara, Bougainvillea* sp., *Ricinus communis* and *Cannabis* sp.

2.2.2 Data collection

All the data were collected from free-ranging JBs in their natural habitat. Prior to starting collection of the actual data, focal animals were habituated to the presence of the observer by doing *Ad libitum* sampling for at least 5 months and by doing so the observer can also learn about their rough territory size and the pattern of their movement (Altmann 1974). All the data were collected by observing at a distance of > 5m using 10 x 42 binoculars (Nikon Monarch).

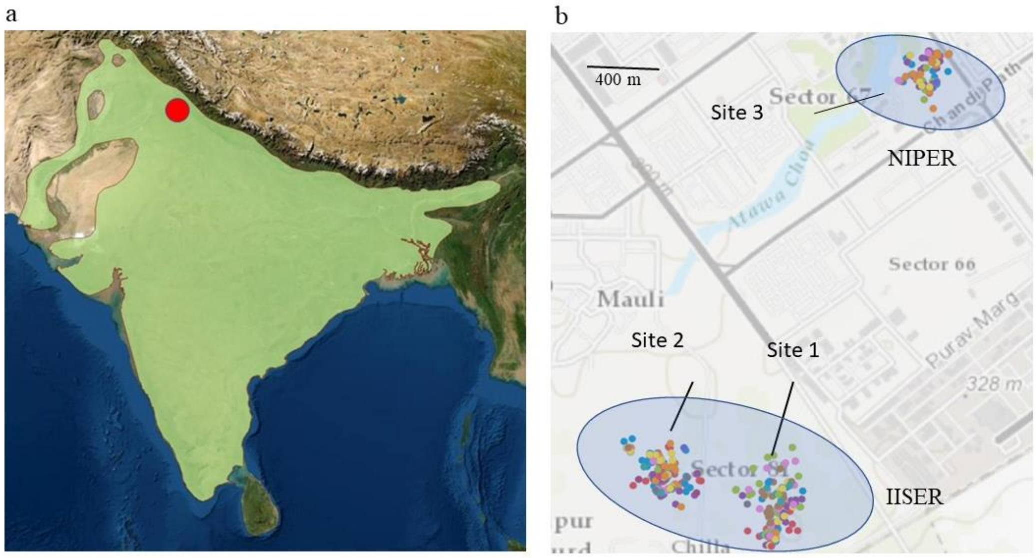


Figure 2.1 **a.** The map shows the distribution of JB and a red mark indicating the study location. **b.** The map shows the three study sites: two on IISER Campus and one on the NIPER campus.

Data collection was carried out between October 2016 and September 2017 for all behavioural data except for the emergence and roosting data which were carried out till February 2018. This study involved multiple groups of JBs from the 3 sites mentioned above. The lists of all the behaviours exhibited during the study period were noted down and these lists of observed behaviours are validated by findings of previous studies in JB (Andrew and Naik 1970; Gaston 1977). Considering that parental care occurs only during a particular season of the year and generally lies between March to October (Andrew and Naik 1970), the parental care activity was not included in the time-activity budget and activity pattern analysis as this study focussed on non-breeding behaviours.

Multiple groups were found to operate in these three sites and *Ad libitum* observations allowed the identification of exact areas where the birds could be found reliably. Observations were carried out between 5:00 to 20:00 to record the activity pattern. Six hours of observations were conducted over 2 sessions in a day with a break of at least 3 hours in between. For each session, three sampling hours were observed where an hour was broken into alternate 5-minute periods of observation and rest to minimize exhaustion during the observation. In order to cover all the time slots from 5:00 to 20:00 at least once a week, the timing of the observations was alternated on different days. Once a group was located, instantaneous scan sampling (Altmann 1974) was used to record all the behavioural activity performed by observable group members as well as the duration of the activity, using a digital stopwatch (Marathon Adanac 3000). If all the focal birds were out of sight before the 5 minutes sampling was completed, then the data from that observation were not included in the analysis to keep the uniformity across sampling times.

To record the time of emergence from the roost site and return to the roosting site, observations were done one hour before the predicted sunrise (5:19-7:21) and sunset (17:32-19:30), respectively. The light intensity at about half an hour after the sunset was enough to carry out the observation. The sites of the roosting and the tree they roosted were also noted whenever it is visible. The time, when all the group members were settled down and clumped together on the same or different branch of the same tree, was noted as the time of roosting. Similarly, the time of emergence was noted down when all the group members flew out from the roosting tree. A light meter (Lutron LX 1102) was used to measure the light intensity at the time of roosting and emergence.

Long-term monitoring data from the lab ascertain previous findings that JB groups are territorial and maintain these territories across years. A large number of JBs have been banded over the years, thus providing information about the identity of the groups that operate in different parts of the landscape. This has been validated by the colour band of several individuals in each group.

2.2.3 Data analyses

From the repertoire of 13 behaviours observed, the time-activity budget was calculated for 10 behaviours shown/listed in Figure 2.2. Analyses for the emergence and roosting data were carried out separately since emergence is an event behaviour while roosting is state behaviour that start at the end of the day and continued throughout the night. The time-activity budget was expressed as the proportion of time spent exhibiting each behaviour which was obtained by dividing the number of scans of a particular behaviour by the total number of scans summed across all behaviours exhibited. The time-activity budget was then represented in percentage values. Ten behaviours used for this study were grouped into two categories: ‘individual’ and ‘social’ behaviour, to investigate if there is any difference in the time allocation to ‘individual’ and ‘social’ behaviours. ‘Individual’ behaviours are assigned to those behaviours that can be executed without any prerequisite for the participation of other individuals whereas, ‘social’ behaviours are designated to those behaviours that require the involvement of other members of the group. Furthermore, ‘social’ behaviours were categorized into ‘affiliative’ and ‘agonistic’ behaviours, to assess the amount of time allocated to each. Behaviour such as allogrooming, movement and play which are required in maintaining social bonds were categorized as ‘affiliative’ behaviours.

On the other hand, ‘social’ behaviours such as sentinel, mobbing and inter-group fight which are prerequisites in defending territories or protecting the group from predators, were assigned as ‘agonistic’ behaviours. In order to examine the diurnal pattern of behaviour, data across all months of the year were pooled and calculated the average proportion of time spent on each behaviour for each of the 15 sampling hours (5:00 – 20:00 hrs). On the other hand, to examine seasonal variation in activity patterns, data across all 15 sampling hours across different days for a given season were pooled and calculated the average proportion of time spent on each behaviour. For the analysis of seasonal patterns, data from one-year observations were grouped into 4 seasons: winter (December to February), summer (March to June), monsoon (July to September), and postmonsoon (October to November). Even though the grouping of the data into seasons leads to inequality of data resulting in fewer days in some seasons and more in others, it would not be a problem for the analysis since the data used were the averaged values.

2.2.4 Statistical analyses

All the statistical analyses were done in R version 4.0.3 (R Core Team, 2020). A Generalised Linear Model (GLM) was run using the R package “MASS” to check the influence of different factors like time of the day, season and length of the day on different behavioural activities. The proportion of time allocated to different behavioural activities: foraging, grooming, rest, allogrooming, movement, sentinel, and ‘other’, was treated as a response variable for the model. Since the response variable was the proportion data, family “quasibinomial” with link “logit” was applied in the model. The Kruskal-Wallis test was done to examine the seasonal variation in the proportion of time spent on behavioural activities. Mann-Whitney U test was run to check the difference between the seasons if any. To test whether the timing of emergence and roosting vary with season, GLM was run using R package “MASS” with the season as a predictor variable and the time as a response variable. Two separate Mann-Whitney U/ Wilcoxon Rank Sum tests were carried out to check the difference between seasons and the difference between the light intensity at the time of emergence and roosting.

2.3 Results

2.3.1 Behavioural repertoire

From the observations, 13 distinct behaviours were recorded. A pictorial ethogram depicting all behaviours is given as an illustration in Figure 2.2. Out of these 13 behaviours, 4 'individual' behaviours: foraging, grooming, shower and rest and 9 'social' behaviours: allogrooming, play, movement, alloparental care, emergence, roosting, sentinel, mobbing and inter-group fight were found. Among these 'social' behaviours, 6 are affiliative behaviours: allogrooming, play, movement, alloparental care, emergence and roosting and 3 are agonistic behaviours: sentinel, mobbing and inter-group fight. As mentioned in the data analyses section, alloparental care was not included in this analysis as it was exclusively studied in detail and the corresponding results are presented in chapter 4. As for the emergence and roosting behaviour, data were analysed separately.

2.3.2 Time-activity budget

In one year, a total of 12,330 scan samples were recorded across 192 days of observation from three locations. After pooling all the scan samples across all behaviours, a total of 18,178 behavioural records were acquired. The precise sample size for each sampling hour and month is provided in Tables A2.1 and A2.2. Time-activity budgets are expressed in percentage (Figure 2.3). From the results, it was found that in JB, most of the time was allocated to foraging (56.6%) followed by sentinel (16.65%). However, while other members foraged, a sentinel was found to be present on duty for only 32% of the time on average. It was also found that an almost equal amount of time ($\chi^2 = 0.047$, df = 1, $p = 0.82$)

was allocated to grooming (10.17%) and allogrooming (9.21%). The least amount of time was spent in movement (3.45%) and resting (1.61%). Behaviours like shower, play, mobbing and intergroup-fight were found very rarely and exhibited in only < 1% of the total activity time. Thus, they were clubbed into 'other' behaviour (Figure 2.3a). After categorising these different behaviours into 'individual' and 'social' behaviours, it was found that JB spent around 69% of the time on 'individual' behaviours such as foraging, grooming, rest and shower which are required for individual sustenance and maintenance (Figure 2.3a). Whereas, the remaining 31% of the time was allocated to 'social' behaviours such as allogrooming, movement, play, sentinel, mobbing and inter-group fight which are essential in maintaining social bonds (Figure 2.3a). Out of these 31% of the time was devoted to 'social' behaviours, 43% was allocated to affiliative behaviours such as allogrooming, movement and play and 57% was spent on agonistic behaviours such as sentinel, mobbing and inter-group fight (Figure 2.3b).

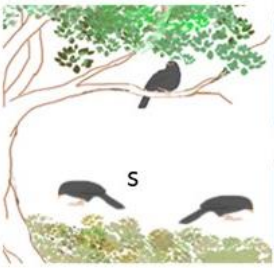
2.3.3 Diurnal and seasonal activity pattern

According to the GLM outputs, foraging, grooming, movement, rest and sentinel showed diurnal activity patterns whereas, allogrooming and 'other' behaviours did not show any diurnal pattern (Figure 2.4 a and b and Table 2.1).

As the time of the day increased, behaviours such as foraging and grooming decreased whereas, sentinel, rest and movement increased (Table 2.1). The diurnal activity pattern of all the behaviours did not vary with the length of the day except for allogrooming, rest and sentinel. Allogrroming and rest increased whereas, sentinel activity decreased with the length of the day (Table 2.1).

According to the results of Kruskal-Wallis test, all behaviours varied with the season (Figure 2.5 and Table 2.2a). Mann-Whitney U test showed that the proportion of time spent in foraging varied significantly across most seasons and was the lowest during winter and highest during postmonsoon (Table 2.2b). The proportion of time allocated to grooming, allogrooming and ‘other’ was found to be significantly high during monsoon whereas, both rest and movement were found to be high during summer (Figure 2.5 a and b and Table 2.2b).

JB showed significant variation in the amount of time allocated to sentinel while other members foraged. They were found to spend around 48% of the time in winter on sentinel duty which significantly dropped to 14% during the monsoon season (Figure 2.6 and Table 2.2c).



Sentinel: One individual remain perched on an elevated platform, higher than the position of the rest of the group, while other group members are foraging, or sometimes grooming, allogrooming on ground.

Foraging (I): Process of finding and obtaining food by hopping and pecking on the leaf litter, foliage, bark crevices and ground.

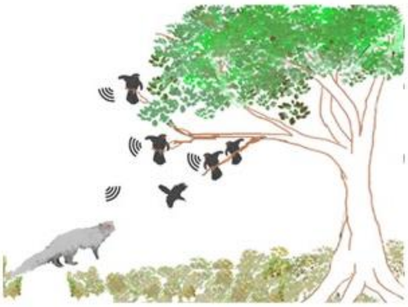
Allogrooming: Two or more individuals groom each other by pecking lightly (mostly on every part of the body).

Grooming (I): Activity of cleaning or maintaining one's own body with its beak.

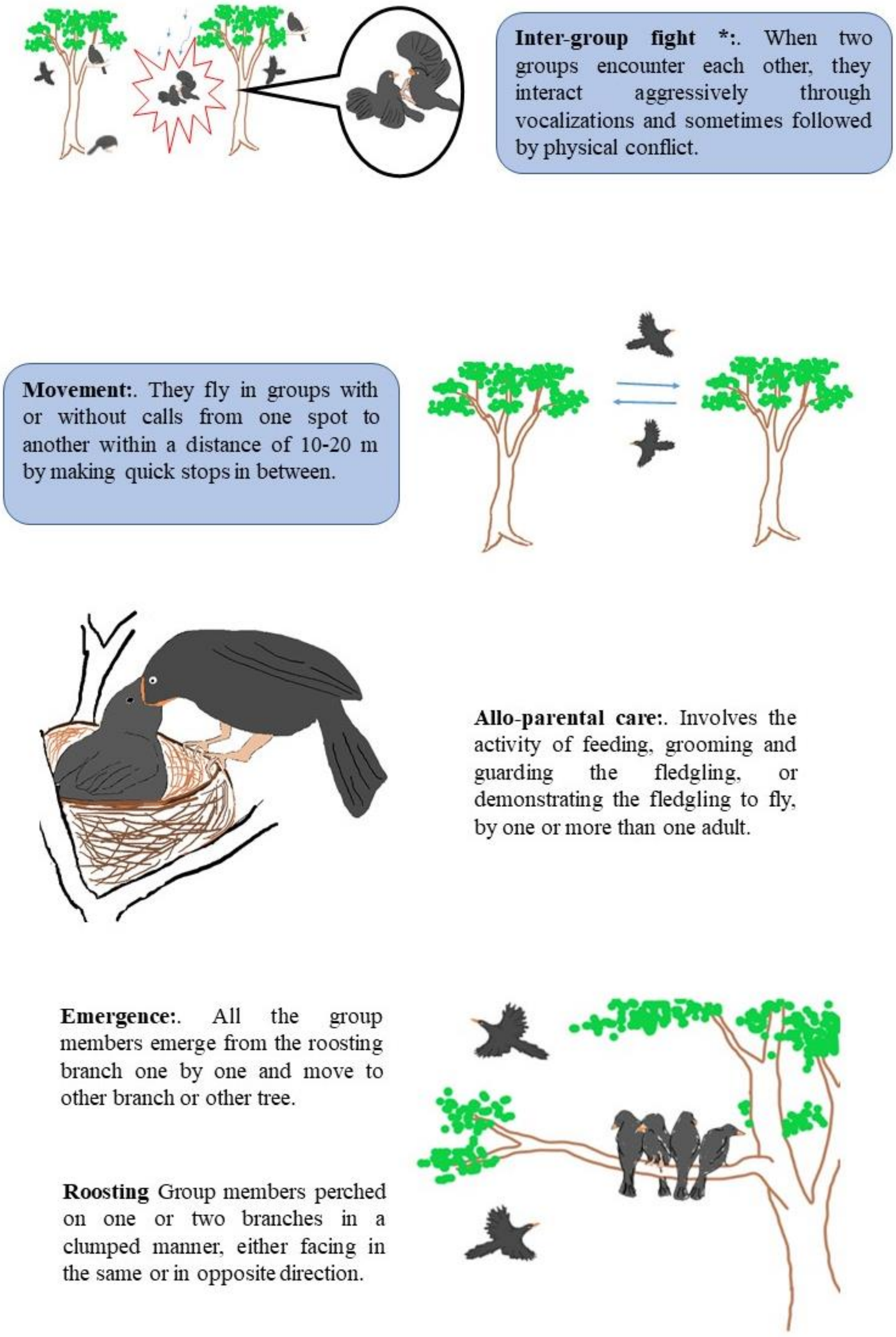
Rest (I): One or more individuals stay next to each other very closely.

Play *:. "Two or more birds engaged in a mock fight in which some lie on the ground more or less passively, while others rolled on top of them, or pecked them deliberately but gently" or sometimes chase one another in the air just above the ground or between the trees. (Gaston 1977).

Shower (I)*:. They quickly dip their body in the shallow pool of water and subsequently shake their feathers.



Mobbing*:. Attacking or chasing the predator, by some individuals or whole group members.



Inter-group fight *:. When two groups encounter each other, they interact aggressively through vocalizations and sometimes followed by physical conflict.

Movement:. They fly in groups with or without calls from one spot to another within a distance of 10-20 m by making quick stops in between.

Allo-parental care:. Involves the activity of feeding, grooming and guarding the fledgling, or demonstrating the fledgling to fly, by one or more than one adult.

Emergence:. All the group members emerge from the roosting branch one by one and move to other branch or other tree.

Roosting Group members perched on one or two branches in a clumped manner, either facing in the same or in opposite direction.

Figure 2.2 Ethogram along with the illustrations of JB with 13 behavioural repertoires. Behaviours with blue shaded boxes are those behaviours that are included in the time-activity budget. The letter ‘I’ in the parenthesis represents ‘individual’ behaviours. * Indicate behaviours which are grouped into ‘other’ behaviour.

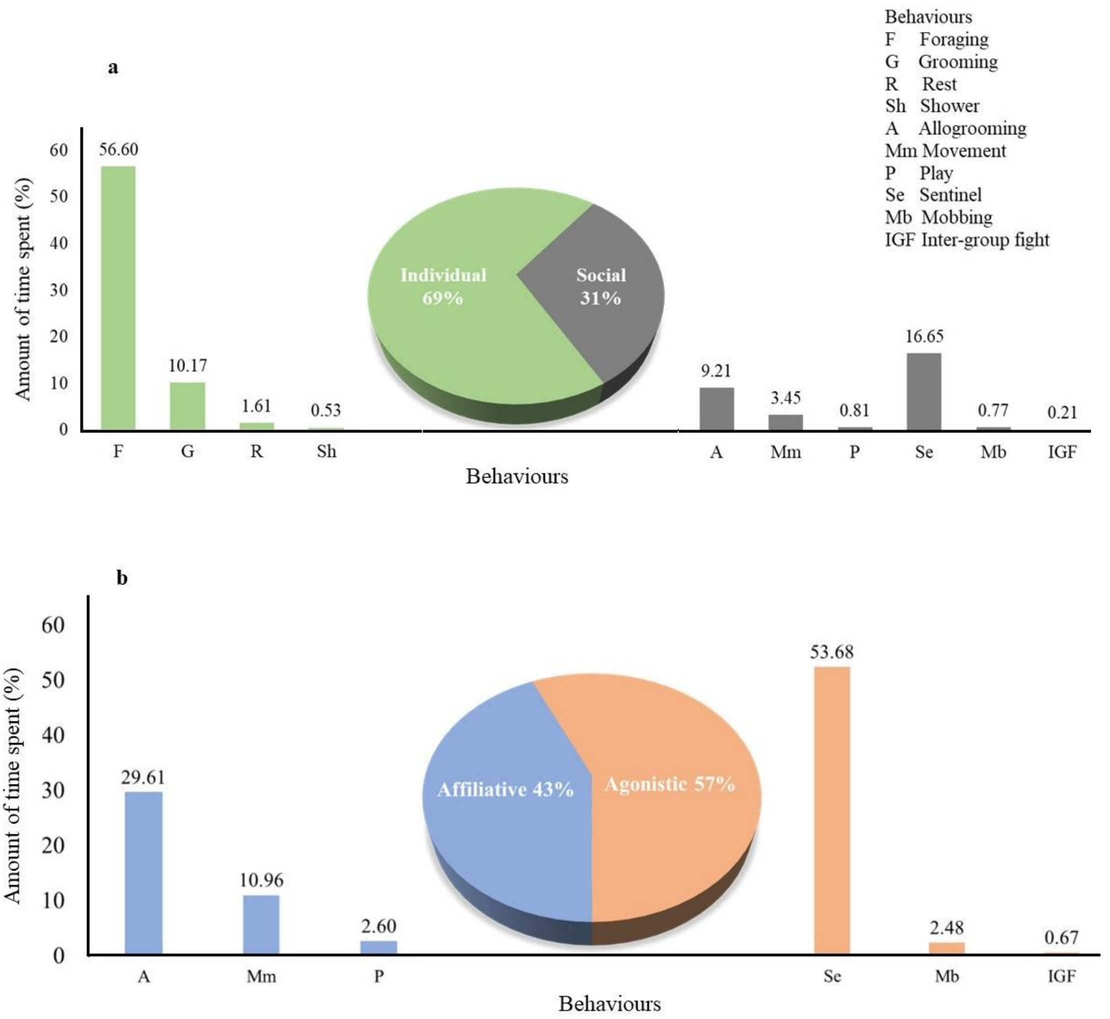
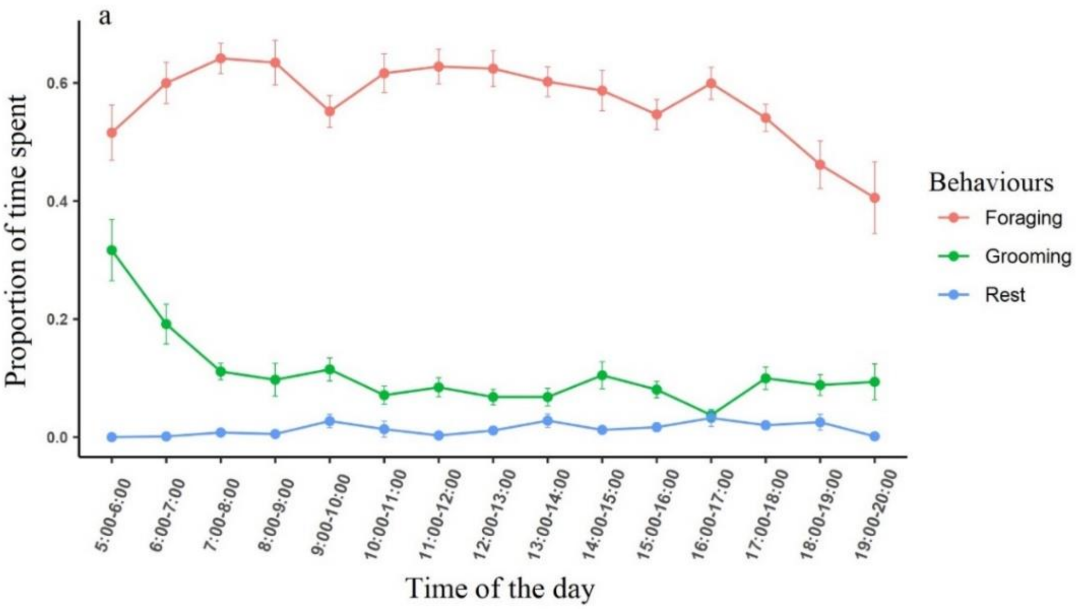


Figure 2.3 Amount of time (represented in percentage) allocated to each behaviour, calculated from 18,418 behavioural records collected from 192 days between October 2016 and September 2017. **a.** Amount of time spent on ‘individual’ vs ‘social’ behaviours. **b.** Amount of time allocated to ‘affiliative’ vs ‘agonistic’ behaviour among ‘social’ behaviours.



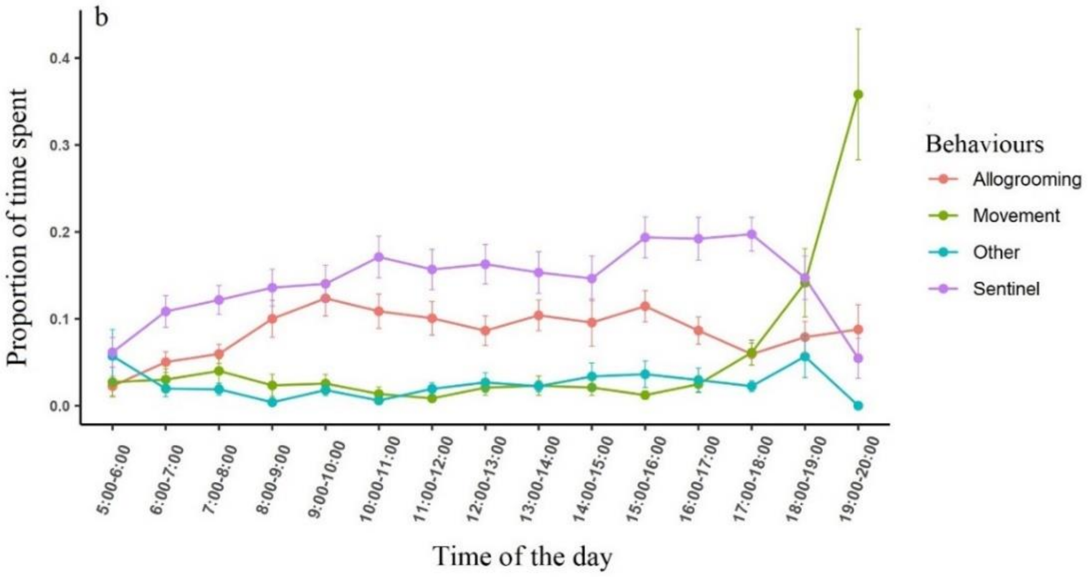


Figure 2.4 Mean ± SE of the proportion of time allocated to each behaviour across different times of the day (5:00-20:00): a) ‘individual’ behaviours (foraging, grooming and rest); b) ‘social’ behaviours (allogrooming, movement, sentinel and ‘other’). ‘other’, includes most of the ‘social’ behaviours (play, mobbing and inter-group fight) except ‘shower’ which is ‘individual’ behaviour.

Table 2.1 Summary of GLM results for the influence of predictor variable time and length of the day on the proportion of time allocated to different behaviours.

Behaviour	**Predictor**	**Estimates**	**Std. error**	***p***
Foraging	Intercept	0.40	0.33	0.23
	Time	-0.03	0.01	<0.0001
	Length	0.03	0.03	0.32
Grooming	Intercept	-1.34	0.58	0.02
	Time	-0.09	0.02	<0.001
	Length	0.02	0.05	0.73
Rest	Intercept	-10.21	1.73	<0.0001
	Time	0.01	0.04	0.01
	Length	0.38	0.13	<0.001
Allogrooming	Intercept	-4.97	0.61	<0.0001
	Time	0.02	0.01	0.259
	Length	0.19	0.05	<0.001
Sentinel	Intercept	0.84	0.42	0.04
	Time	0.05	0.01	<0.0001
	Length	-0.26	0.03	<0.0001
Movement	Intercept	-5.76	1.17	<0.001
	Time	0.20	0.03	<0.001
	Length	-0.001	0.09	0.99
Other	Intercept	-6.45	1.31	<0.001
	Time	0.03	0.03	0.33
	Length	0.19	0.10	0.06

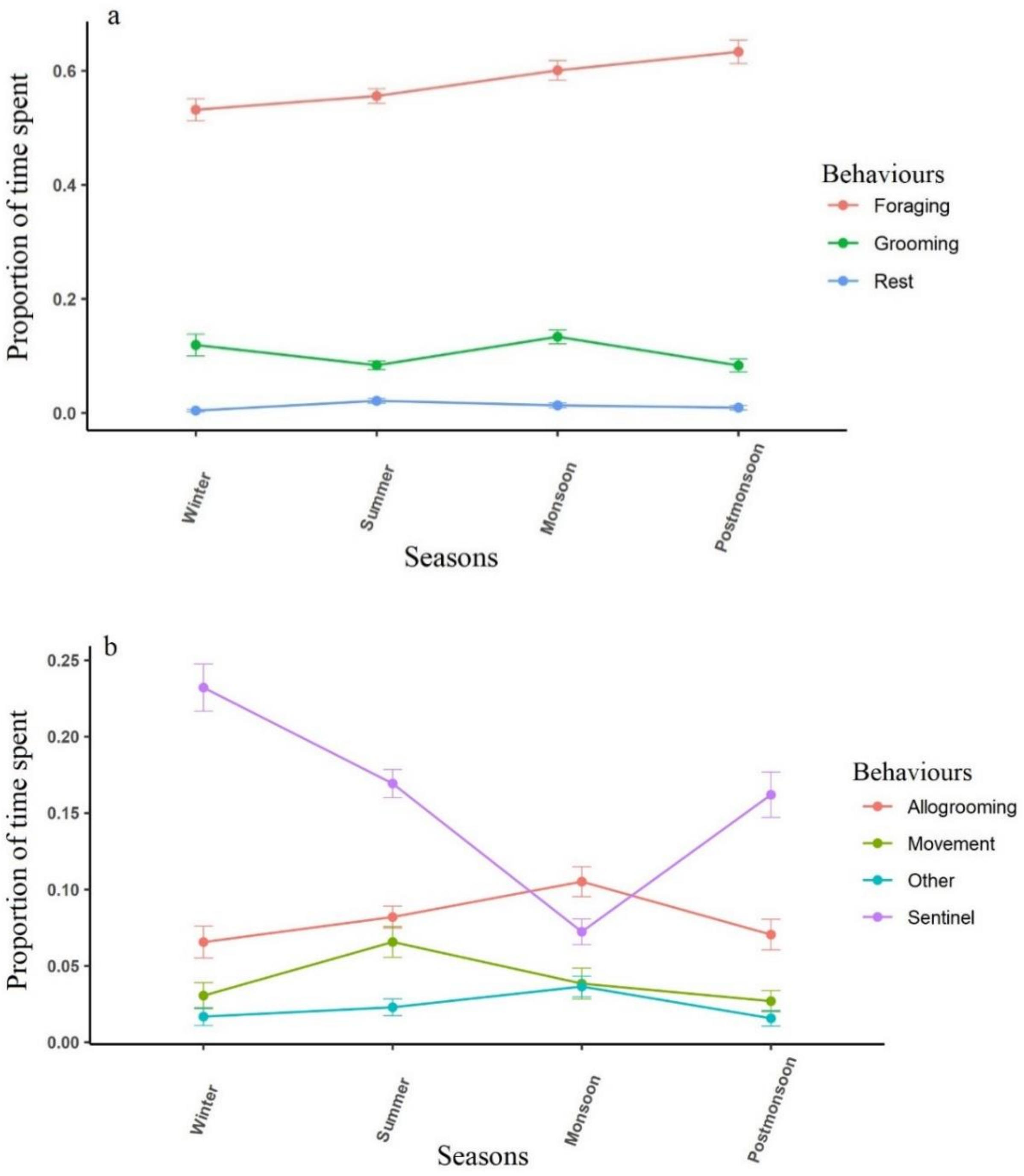


Figure 2.5 Mean ± SE of the proportion of time allocated to each behaviour across different seasons: a) ‘individual’ behaviours (foraging, grooming and rest); b) ‘social’ behaviours (allogrooming, movement, sentinel and ‘other’).

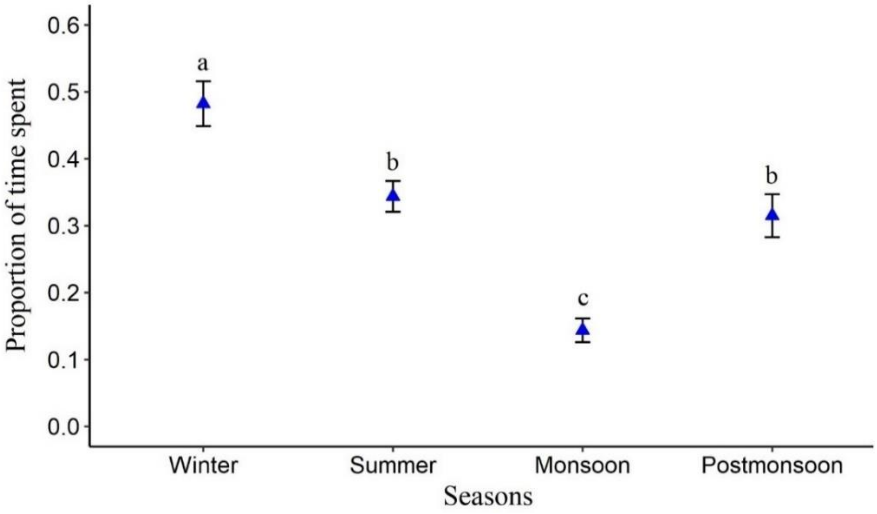


Figure 2.6 Mean ± SE of the proportion of time spent on sentinel, while other members foraged, across different seasons. Different letters indicate a significant difference with *p* <0.05.

Table 2.2 Summary of **a.** Kruskal-Wallis examining the effect of season on the proportion of time spent on different behaviours and the timing of emergence and roosting **b.** Mann-Whitney U test (p values) for pairwise comparison between different seasons for the proportion of time spent on different behaviours and the timing of emergence and roosting **c.** Mann-Whitney U test (p values) for pairwise comparison between different seasons for the proportion of time spent on sentinel duty while foraging.

a.

Behaviour	χ^2	**df**	***p***
Foraging	14.09	3	<0.01
Grooming	9.47	3	0.02
Rest	11.79	3	<0.01
Allogrooming	8.45	3	0.03
Movement	21.32	3	<0.001
Sentinel	93.06	3	<0.001
Other	7.96	3	0.04
Emergence	22.33	3	<0.001
Roosting	14.71	3	<0.01

b.

Activity	Postmonsoon-Winter	Postmonsoon-Summer	Postmonsoon-Monsoon	Winter-Summer	Winter-Monsoon	Summer-Monsoon
Foraging	<0.01	<0.01	0.4	0.31	0.01	0.03
Grooming	0.46	0.99	0.03	0.4	0.12	<0.01
Rest	0.61	0.06	0.99	0.01	0.59	0.01
Allogrooming	0.4	0.4	0.07	0.06	<0.01	0.21
Movement	0.65	<0.01	<0.001	0.03	0.09	<0.0001
Sentinel	<0.01	0.71	<0.001	<0.001	<0.0001	<0.0001
Other	0.91	0.87	0.06	0.77	0.04	0.02
Emergence	0.12	0.03	0.64	<0.001	0.39	<0.001
Roosting	0.26	0.09	<0.001	0.02	0.05	<0.01

c.

Seasons	***p***
Postmonsoon-Winter	<0.001
Postmonsoon-Summer	0.45
Postmonsoon-Monsoon	<0.0001
Winter-Summer	<0.001
Winter-Monsoon	<0.001
Summer-Monsoon	<0.0001

2.3.4 Emergence and roosting

Different roosting sites found during the study are provided in Figure A2.1. Different trees were selected for roosting by JB. The most common trees that are used for roosting by JB during the study were *Leucaena leucocephala* (51%), *Chukrasia tabularis* (22%), *Bambusa* sp. (8%), *Melia azedarach* (4%), *Populus deltoides* (4%), and the remaining, roost on the trees such as *Dalbergia sissoo, Ficus religiosa, Ricinus communis.* These trees are mostly planted or are naturally occurring invasive species. Thus, these results might vary depending on the available trees in other habitats. The total number of days of observation for the timing of emergence and roosting for different seasons are provided in Table A2.3. The outputs of Kruskal-Wallis test revealed that the timing of emergence and roosting varied with the seasons (Figure 2.7a and Table 2.2a). It was found from the pairwise comparison that JB emerged from their roost earliest during summer but returned to their roost earlier in winter and monsoon (Figure 2.7a and Table 2.2b). Light intensity at the time of emergence was found to be significantly lower than at the time of roosting (Mann-Whitney U: W= 470.5, $p<0.001$, Figure 2.7b).

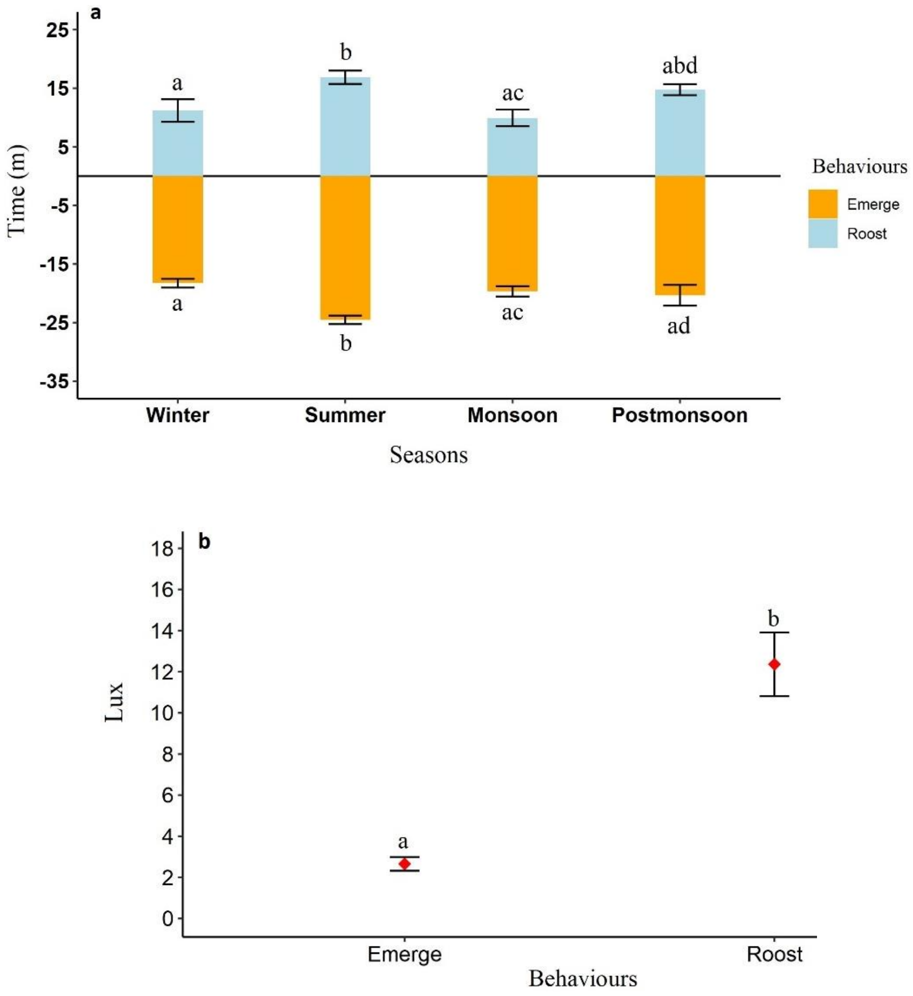


Figure 2.7 **a.** Mean ± SE of the timing of emergence and roosting in relation to the time of sunrise and sunset respectively across different seasons. **b.** Mean ± SE of the light intensity in lux unit at the time of emergence and roosting. The number of days of observation for

the light intensity at the time of emergence and roosting were 50 and 53 respectively. Different letters represent significant differences with $p<0.05$.

2.4 Discussion

2.4.1 Behavioural repertoire

In JB, 13 distinct behaviours were found which were further categorised as ‘individual’ and ‘social’ behaviours. Even though ‘individual’ behaviours such as foraging, shower, grooming and rest do not require the participation of the other member, JB performed most of their activities together in the presence of other group members which may provide social stability through ‘activity synchronization’ (Conradt and Roper 2000). Among ‘social’ behaviours, affiliative behaviours such as allogrooming, movement and play might play an important role in maintaining social bonds (Isbell and Young 1993; Pozis-Francois 2004) whereas, agonistic behaviours such as sentinel and mobbing mediate defence against the predators, and inter-group fights were exhibited for defending territory. A study by Mcgowan and Woolfenden (1989) on Florida scrub jay (*Aphelocoma coerulescens*) showed that the sentinel is the one to detect the predator first and initiate alarm calling. In the case of mobbing, an experimental study conducted on two predators: Little owl (*Athena noctua*) and Tawny owl (*Strix aluca*) revealed that the mobbing caused distress to the predator and even led to abandonment of the place (Flasskamp 1994) and an increase in numbers of mobbers enhanced the effect of mobbing (Krams et al. 2009). Furthermore, a study done on Green woodhoopoe (*Phoeniculus purpureus*) showed that inter-group conflict may enhance social bonding by increasing affiliative behaviour after an inter-group conflict (Radford 2008). In this study, no agonistic behaviours between group members were observed which might partly be explained by the presence of only one pair of breeders in JB as previously reported by Gaston (1977). However, mating behaviour as noted by

Andrew and Naik (1970) and Gaston (1977), was not observed during this study period. Andrew and Naik (1970) also stated that mating behaviour was only observed once during the entire period of their study. It is possible that JB conceals mating as in the case of Arabian babblers (*Argya squamiceps*) and a possible explanation for this behaviour could be given by the 'cooperation maintenance hypothesis' (CMH). CMH posits that concealment of mating prevents arousal in witness, thereby ensuring the breeder's status is unchallenged and that the helpers continue to help (Ben Mocha et al 2018; Ben Mocha 2020).

2.4.2 Time-activity budget

A comprehensive assessment on how animals budget their time to different activities can contribute significantly in understanding which behaviours are of greater importance and even shed light on the relative function of such behaviours. Further, understanding how an animal performs various activities in the limited time available allow may provide fundamental insights into the behavioural ecology of the species, especially for social animals. In a study on social wasps, *Ropalidia marginata,* Gadagkar and Joshi (1983), utilised time-activity budget data to identify behavioural caste in this species which lacks morphological differences between individuals performing different duties. Moreover, a study by Dunbar (1992) reported the importance of the time-activity budget in balancing group stability, as devoting more time to 'individual' behaviour may decrease the time spent on 'social' behaviour that may result in group instability. Thus, the knowledge of the time-activity budget of social animals can contribute to our understanding of the evolution of sociality.

From this study, it was found that JB spent around 70% of their time on 'individual' behaviours and the remaining 30% on 'social' behaviours. This result agreed with the previous study on primates which showed that the time spent on ‘social’ activity is comparatively lesser than ‘individual’ behaviour (Sussman et al 2005). Within the ‘social’ behaviours, an equal amount of time is allocated to both affiliative and agonistic behaviour. This result is in contrast with the previous reports on primates, where the amount of time spent on agonistic behaviour is comparatively less and is around 1% of the time spent on ‘social’ behaviour (Sussman et al. 2005). However, in this study, agonistic behaviour was observed mainly between groups or against predators but not within groups. In most studies on social animals, agonistic behaviour includes aggression between group members, which was not the case with this study. Even though sentinel behaviour is pooled under agonistic behaviour in the context of anti-predatory behaviour for this study, it can be considered affiliative and cooperative as it might be enhancing group coordination for safety during foraging (Mcgowan and Woolfenden 1989). Moreover, sentinel behaviour in JB is found to be associated with soft vocalization (Yambem et al. 2021) and it has been proposed that sentinel soft vocalization in JB may help in enhancing the coordination between the foragers and the sentinel (Wickler 1985). Thus, in comparison with the studies on primates, time spent on agonistic behaviour by JB is also negligible. Gaston (1977) also reported the absence of agonistic interaction among individuals within the group of JB. Comparison of the results of this study with other studies on social birds would have been more meaningful than comparing it with findings in primates. However, such studies on social birds have not been carried out, thereby limiting a more taxonomically relevant comparative discussion of these findings.

Among the ‘individual’ behaviours, the highest proportion of time was dedicated to foraging behaviour. It is expected that time spent on foraging will be disproportionately high as compared to the rest of the behaviours, because foraging activity aids in the acquisition of energy, which is necessary for survival, development, and reproduction

(Kramer, 2001) and to carry out all other behaviours. This result is similar to the findings reported on Urban capuchin monkey (*Sapajus sp.*) and Shelducks (*Tadorna tadorna*) which also spent the majority of their time in foraging which was around 80% and 60% respectively (Back et.al 2019; Bensizerara and Chenchouni 2019). However, findings on Vervet monkeys (*Chlorocebus pygerythrus*) revealed that the time allocated to foraging is only 30-40% which is comparatively less (Isbell and Young 1993). JB spend a lot of their time in grooming preceded by rest and then shower. Grooming and shower behaviours are important for maintaining hygiene by removing dirt and parasite (Clayton and Cotgreave 1994). Similar to the findings by Clayton and Cotgreave (1994) in a comparative survey done on 62 species of birds, which reported that on an average 9.2% of the time was allocated to grooming, JB also spent around 10% of their time on grooming. During the day, JBs were found to spend a small percentage of their time on resting (1.61%). However, it should be highlighted that the period between roosting and emergence is entirely devoted to resting anyway. Moreover, grooming behaviour during the day may have a similar role as rest behaviour, offering a recess from the high activity and so preventing fatigue. Even though it is suggested that resting is important for physiological processes such as digestion and thermoregulation, the time spent during resting is considered to be available for other activities as needed (Herbers 1981; Dunbar 1992). Dunbar and Dunbar (1988) also suggested that in social animals, most of the time available for resting will thus be made available for 'social' behaviours. In JB, around 10% of the time was allocated to allogrooming, a less energy-consuming 'social' behaviour yet, required in maintaining social bonds. In addition to enhancing social bonds (Isbell and Young 1993; Cox 2012; Picard et al. 2020), many studies described the role of allogrooming as being similar to grooming in removing dirt and maintaining hygiene (Sparks 1967; Sachs 1988) proposing that both these behaviours might be serving same ecological function. Moreover, this study revealed that almost an equal amount of time was devoted to both allogrooming and grooming.

Amongst all 'social' behaviours, JB was found to allocate the majority of their time in sentinel behaviour (16.65%, averaged across all months of the year) with reference to time activity budget. This behaviour was mostly performed by one individual and rarely by two individuals on a rotating basis. Furthermore, a sentinel was found to be present on an average of about 32% of the time while others were foraging (data pooled across seasons). This finding is consistent with the findings in Pied Babblers (*Turdoides bicolor*), which reported that only 30% of the time was allocated to the sentinel, during foraging bouts (Hollén et al. 2008). JBs were found to spend only 0.81% of their time in play behaviour despite the suggestion of its contribution to social bonding. This finding might be supported by the fact that JB spends more time in allogrooming which too functions to maintain social bonding, and is a less energy-consuming activity rather than play which is a physically and socially demanding behaviour (Pozis-Francois 2004). A study conducted on Chimpanzee by Lawick-Goodall (1968) also reported that the time spent on play decreases when the amount of time allocated to allogrooming increases. Less amount of time spent on movement (3.45%) by JB can be attributed partially to the fact that for this study only flight behaviour was taken into account as part of movement behaviour whereas walking should be included in the locomotion. However, only flight is considered in movement as the study required only displacement and the locomotion was included in the foraging behaviour. In addition, JB generally has small territory sizes (Andrews and Naik 1970) which restrict the scope for movement and thus affirm the findings. 'Other' behaviour used only 2.32% of the time, even though the 'other' behaviour included four behaviours: shower, play, mobbing and inter-group. This finding might be corroborated by considering the similarity in the functions of the shower to grooming in maintaining hygiene and play to allogrooming in social bonding (Lawick-Goodall 1968; Clayton and Cotgreave 1994; Cox 2012).

2.4.3 Diurnal and seasonal activity pattern

Various environmental factors such as time of the day (Li et al. 2019), season (Ikeda et al. 2016), predation pressure (Lima and Dill 1990) and sociality (Marshall et al. 2012) can influence the activity pattern of an animal. This study demonstrates the variations in the activity pattern in terms of the time of the day and seasons. The majority of the behaviours of the JB were found to vary with time of the day and seasons except for allogrooming and 'other' behaviours and both these behaviours did not show any variation in the diurnal pattern. In JB, the amount of time devoted to foraging was found to vary with the time of the day and season regardless of the length of the day. This is similar to the findings of the study conducted by Reyes-Arriagada (2015) on three species of forest-dwelling passerine, which suggested that the pattern of time spent on foraging was non-consistent throughout the day and also changed according to season and habitat type. It was also found that in JB, time allocated to foraging reduced as the day proceeded. This might be because of the opportunities of obtaining instantaneous energy by engaging in foraging early after a prolonged interval of starvation and drainage of energy through the night-time (Bednekoff and Houston 1994). Regarding the seasonal variation, the foraging behaviour of JB showed the highest peak in postmonsoon (63%) and lowest in winters (53%). Results from the study showed that the amount of time dedicated to foraging was always above 50% and this might be because foraging is required for sustenance. Similar to the findings in Java monkeys (*Macaca fascicularis*) which reported that grooming was higher in the morning than in the evening (Troisi and Schino 1986), JB also showed that grooming behaviour peaked during morning. Additionally, the study revealed that grooming behaviour was more prevalent during the monsoon season, possibly due to the increased likelihood of ectoparasites being present at this time. This is supported by the study in White shifakas (*Verreaux's sifaka*) which reported that the influence of ectoparasite load was found to be greater during monsoon, on the increase in the grooming behaviour to sustain self-hygiene (Lewis 2010). However, examination of the correlation between the parasite load and seasons still remains. Allogrooming in JB was found to show no diurnal pattern but it increased with the increase in length of the day. This may be explained by considering that allogrooming can be executed at any given time of the day (Dunbar 1992) and mainly serve to maintain or establish a social relationship (Picard et al. 2020). Seasonally, allogrooming showed the highest peak in monsoon which may be supported by its function in maintaining hygiene which is similar to the ecological function of grooming. However, this result differed from the findings of Gaston (1977) which showed that allogrooming peaked in the postmonsoon and winter and reduced in summer and monsoon. This could be due to habitat-specific variation in parasite load across seasons.

The proportion of time devoted to sentinel was found to vary across the day and increased during the evening. Gaston (1977) also found a similar result in his study in JB, who reported that the sentinel behaviour increased as the day proceeded and suggested that sentinel behaviour might be associated with the level of satiation attainment that might be correlated with the time of the day. This is supported by an experimental study conducted on Arabian babblers (*Argya squamiceps*) which revealed that fully satiated individuals carried out more sentinel duty implying that sentinel is a state-dependent behaviour (Wright et al. 2001). Seasonally also, there was variation in the proportion of time spent on sentinel in JB which was highest in winter. An investigation by Gaston (1977) on the sentinel behaviour of JB during winter, found that sentinel behaviour was present around 82% of the time. After further examination on sentinel behaviour as a proportion of time present on foraging when the sentinel was present and the variation with the season, it was found that sentinel behaviour showed peak in winter when the sentinel is present around 48% of foraging time and which reduced to 14% in monsoon. This is similar to the findings in Florida scrub jays (*Aphelocoma coerulescens*), which reported that sentinel behaviour during foraging was highest in winter, which is around 75% of the total foraging time and reduced to 33% of the total foraging time in summer (Mcgowan and Woolfenden 1989). There are several factors such as canopy cover, risk of predation and group size, that can lead to the variation in the pattern of sentinel behaviour. In this study, the highest proportion of time spent on sentinel behaviour in winter may be probably explained by exposure to high predation risk due to less canopy cover, which may be attributed to the prevalence of deciduous trees (that shed leaves in winter and early summer) in the study site. Thus, the prevalence of canopy cover might also explain the possibility of the decreased in the sentinel behaviour during monsoon season. In this study, the amount of time spent on rest behaviour increased as the day proceeded when foraging behaviour decreased. These findings support the assumption, that the time for resting will be accessible only when other critical activities required for life sustenance are executed/accomplished (Altmann and Maruthi 1988; Dunbar 1992). It is also possible that other environmental factors such as microclimatic variation of the day can also influence the rest behaviour and thus the rest behaviour increases during the day as the temperature rises. It was found that the movement behaviour showed the highest peak in summer which may be attributed to the possibility of birds spending more time in seeking for nest site, constructing nest etc. that may involve numerous displacements as this time overlaps with the beginning of the breeding season of JB.

2.4.4 Emergence and roosting

In JB, the timing of emergence and roosting with respect to the time of sunrise and sunset were found to vary across different seasons. This finding is similar to the finding in Indian myna (*Acridotheres tristis*) which reported that emergence and roosting behaviour vary with diurnal and seasonal variation, which in turn is affected by environmental, physiological and behavioural factors (Mahabal and Vaidya 1989). Early emergence and late roosting in JB during summer, corresponded to their breeding time. It was also found that the intensity of light during roosting was substantially greater than the emergence time. Similar to this finding, a study done by Swingland (1976) on Rook *Corvus frugilegus* reported that Rook emerges from their roost at low light intensity and return to their roost at high light intensity. These findings may be supported by considering the circumstances under which, at high light intensity finding the roost site might be more efficient.

To our knowledge, this study is the first to provide time-activity budget and temporal variation in 'individual' and 'social' behaviours in a social bird. This study is the only comprehensive examination of the behavioural ecology of JB since the landmark studies by Gaston (1977). In so, it significantly advances our understanding of the ecology of this tropical social passerine. The findings of this study pave the way for future research on the influence of habitat, group size, predation risk etc on the activity pattern of JBs and geographic variation in these.

2.5 Appendix A

Figure A2.1 Some of the habitats of the different locations of the study site.

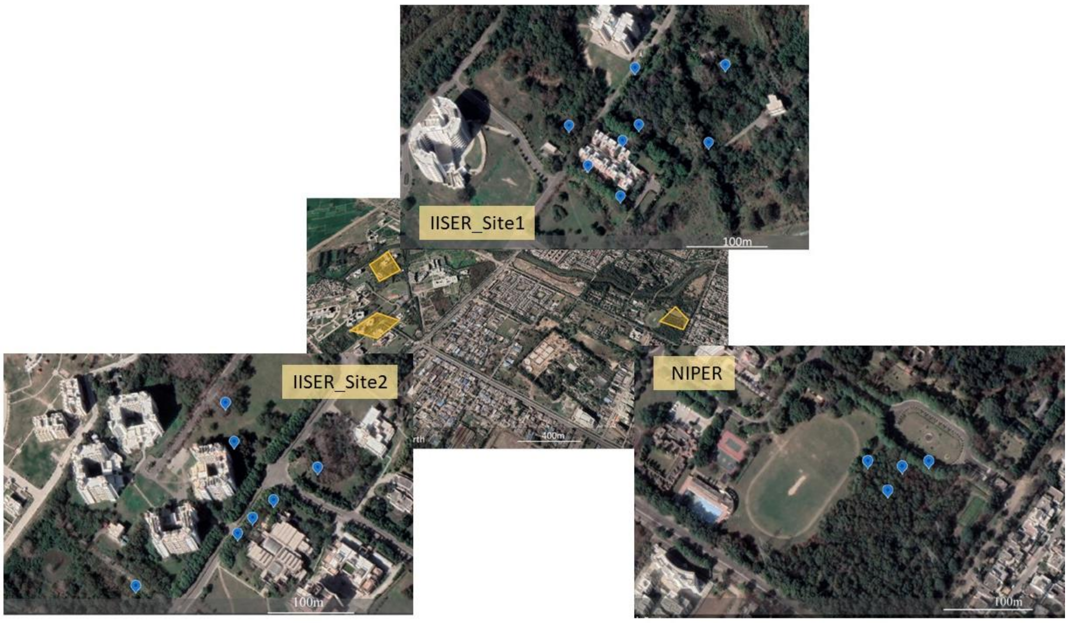


Figure A2.2 Different roosting sites in the three locations of the study.

Table A2.1 Number of days and scans for every sampling hour.

Time	**Days**	**Scans**
5:00-6:00	28	455
6:00-7:00	52	940
7:00-8:00	54	1130
8:00-9:00	36	645
9:00-10:00	40	825
10:00-11:00	37	780
11:00-12:00	50	905
12:00-13:00	49	975
13:00-14:00	43	925
14:00-15:00	44	740
15:00-16:00	47	930
16:00-17:00	42	885
17:00-18:00	62	1145
18:00-19:00	44	790
19:00-20:00	22	260

Table A2.2 Number of days and scans for each month.

Month	**Days**	**Scans**
October	17	980
November	15	870
December	15	930
January	9	385
February	14	495
March	16	865
April	16	1170
May	21	1585
June	17	1380
July	18	1280
August	21	1525
September	13	865

Table A2.3 Number of days of observation for the timing of emergence and roosting behaviours for different seasons.

Seasons	Emergence	Roosting
Winter	25	26
Summer	17	23
Monsoon	15	15
Postmonsoon	12	21

Chapter 3

Functional and structural complexity in the vocalization of Jungle Babbler

Published as: Yambem SD, Chorol S, Jain M (2021) More than just babble: functional and structural complexity of vocalizations of Jungle Babbler. Behav Ecol Sociobiol 75(8): 1-14

3.1 Introduction

Vocal communication plays a critical role in the coordination of different behaviours and in sustaining relationship between individuals which is important for survival and reproduction (Bradbury and Vehrencamp 2011). For example, vocal communication can be used to warn about the danger (Suzuki 2014), for interaction between parent and offspring during parental care (Magrath et al. 2015), in maintaining group coordination (Crane et al. 2016), or as a sexual display or territorial display to attract mates or to confront conspecific and heterospecific rivals (Gill 2007), etc. Thus, the production of distinct vocalizations even within a species inferring a clear and distinct meaning is important. The total number of vocalizations (call types) produced in specific behavioural contexts or unique elements/notes produced by an organism during its lifetime is referred to as the vocal repertoire of a species (Searcy 1992; Bradbury and Vehrencamp 2011). Several studies have demonstrated the importance of having a large repertoire size, being more effective in attracting mates (Catchpole 1987; Robinson and Creanza 2019) or in retaining a territory for a longer duration (Hiebert et al. 1989). Moreover, a larger repertoire size with unique functional contexts helps in maintaining and coordinating group behaviours in social animals (Ficken et al.1978; Seddon et al. 2002; Crane et al. 2016).

In the avian system, there are various factors such as physical environment, motivational state, morphology, social environment or a combination of these factors can also influence the production of numerous distinct vocalizations. For example, a study by Deoniziak and Osiejuk (2019) showed that Song thrush, *Turdus philomelos* in the urban area produced more complex songs than the one in a nearby forested area. Furthermore, according to the motivation-structural (MS) rule hypothesis (Morton 1977), the structure of the vocalization can be influenced by the internal motivation of the individual vocalizing such that the vocalization produced in agonistic contexts will be harsh and lower frequency and those produced in friendly and fearful context will be tonal and high frequency. This also implies that calls produced in similar context should also be structurally similar. Morphological factors such as the morphology of the bill can also influence the frequency range of vocalizations such that the birds with longer beaks vocalize with lower maximum frequency (Giraudeau et al. 2014). Various selection pressure such as predation pressure can also influence the production of complex vocalization. For instance, alarm calls of Meerkats (*Suricata suricatta*) can vary not only depending on the type of predator but also on urgency of the threat (Manser 2001).

The influence of a species' social environment on the evolution of complex vocal communication has long been acknowledged. The 'social complexity hypothesis' postulates that communicative complexity in social animals is disproportionately higher than that in solitary animals (Blumstein and Armitage 1997). This is because, in social animals, as the frequency of interaction between individuals and in different contexts increases, the diversity in communicative system tends to increase in order to coordinate those interactions and deliver meaningful inference of different behavioural context (Freeberg et al. 2012; Krams et al. 2012; Leighton 2017). In this way, the variety of the contexts of vocalizations leads to a greater acoustic repertoire and as a result, communicative complexity of the species increases. Cooperative breeding is one form of social complexity, and it has been shown to be linked with communicative complexity (Crane et al. 2016; Leighton 2017). For example, the Chestnut-crowned babblers (*Pomatostomus ruficeps*) have 18 call types, of which 13 are produced toward alarm, contact and social interactions (Crane et al. 2016). Furthermore, depending on the type of interactions between individuals, calls can be roughly categorized as "affiliative" or "agonistic". "Affiliative" calls are produced in order to preserve social ties, whereas "agonistic" calls are made in order to compete with conspecific and heterospecific competitors (Kondo and Watanabe 2009). This categorization can help in a better understanding of the ecological and social environment the animal lives in.

There are several proxies such as the size of vocal repertoire (number of distinct calls or signalling elements/notes), combinatorial rules underlying the combination of signalling notes (sequential combination or random assemblage of notes), contextual diversity of signaling etc that are used as measures of communicative complexity (Peckre et al. 2019). Moreover, a larger repertoire size is considered more complex compared to a smaller repertoire (Blumstein and Armitage 1997). The study of the vocal repertoire is essential in understanding the behaviour such as the motivational state, and ecology of the animal. Furthermore, a detailed study of vocal repertoire of a species is a prerequisite for comparative studies across different taxa which in turn provides a platform for future studies in understanding the link between social complexity and communicative complexity.

This study focussed on the vocal complexity in Jungle Babblers (*Argya striata*; hereafter JBs) using number of distinct calls with different functions as a proxy for quantifying communicative complexity as this is one of the basic measures that are critical in better understanding of the species as well as their social environment. JB is a cooperative breeder exhibiting many social behaviours such as cooperative brood care, sentinel duty, collective foraging, anti-predator behaviour, allogrooming and intergroup confrontations (Andrews and Naik 1970; Gaston 1977, Yambem and Jain 2023), providing a great system to understand the link between communicative complexity with social complexity. Moreover, onomatopoeic descriptions of some vocalizations of the species in different contexts given by Andrew and Naik (1970) and later Gaston (1977) provided the possibility of complex acoustic communication in this cooperative breeder. However, despite their widespread distribution and the possibility of having a large vocal repertoire in their social system, no study has yet examined complex acoustic communication. Thus, this study aims to investigate the following sub-objectives:

1) Do JBs produce diverse vocalization in different behavioural contexts?
2) Do the vocalizations produced in different contexts also differ in their acoustic features?

3.2 Materials and Methods

3.2.1 Study site

The study was conducted at the same 3 field locations which are mentioned in detail in Chapter 2.

3.2.2 Data collection

All the data collection was carried out between May 2016 and March 2020. All the vocalizations were recorded using a solid-state recorder (Marantz PMD661MKII with frequency response: 20 Hz – 20 kHz), connected to a super-cardioid shotgun microphone (Sennheiser ME66 with K6 PM with frequency response: 40 Hz to 20 kHz), protected by foam windscreen (Sennheiser MZW66). Calls were recorded at the sampling rate of 44.1 kHz and 16-bit depth. While recording the vocalizations, behaviours of the caller as well as that of all group members in sight, any observable changes in the surroundings and any response by any receiver to the signal were also noted and announced at the end of the recording. Sampling and recording methods followed a combination of focal animal and scan sampling (Altmann 1974) and all the behavioural observations were made using 8 x 42 binoculars (Nikon, Monarch 7). All the recordings were focused on a single individual except in the case of chorus calls to ensure minimal overlap between the calls. Vocalizations produced by the individuals trapped in the mist-net and while handled by the extractor to release from the trapped, were also recorded. Recordings of the calls of nestlings and fledglings were made from when they were inside and outside the nest respectively. Identifications of the fledglings were done based on the iris colour as the iris colour of a fledgling is black while that of adult is pale while (Figure 3.1). The behaviour of the signaller was recorded using focal animal sampling and scan sampling was carried out when multiple individuals were vocalizing. In all cases a scan of the environment was carried out to establish the context of vocalization and to assess the response of receivers.

Figure 3.1. A fledgling with an adult showing different colours of iris. **a** fledgling and **b** adult.

3.2.3 Acoustic analyses

In the first step, calls were categorized based on the functional contexts which were deciphered based on the proportion of time a specific call was produced in association with a specific behaviour (Table 3.1). All the calls were analyzed in Raven Pro 1.5 (Cornell Laboratory of Ornithology, USA) using Hann window function, size 512 with a 50%

overlap. A total of 549 call samples with minimum overlap and high signal-to-noise were obtained for further analysis except for the chorus call. A catalogue of the vocalizations listed by Andrews and Naik (1970) and Gaston (1977) helped in proving inference in verifying the lists of calls recorded in this study. The second step after the generation of the spectrogram was to differentiate the calls based on visual and aural inspection. Further, the calls were then classified on the basis of the time gap between the notes (inter-note interval) and if the inter-note interval was > 0.1 s (Figure B3.1), then calls were categorized as "monosyllabic" and when it was <= 0.1 s followed by a longer silent interval, then the calls were considered to be "multisyllabic" call (Catchpole and Slater 2010; Figure 3.2). Those calls in which multiple individuals vocalize at the same time were categorized under a third category as "chorus" call (Figure 3.2). The last step on classification of calls was to characterize call based on 6 acoustic parameters: a) spectral parameters: i) frequency 5% ii) frequency 95%, iii) bandwidth 90% and iv) peak frequency; b) temporal parameters: v) call duration and C), vi) total number of notes in a call (for multisyllabic calls). Detailed description and illustration of the acoustic parameters are given in Table 3.2 and Figure B3.2, respectively. For the analyses of the chorus calls, only spectral parameters were considered, as signal overlap from different callers made analyses of temporal features unreliable.

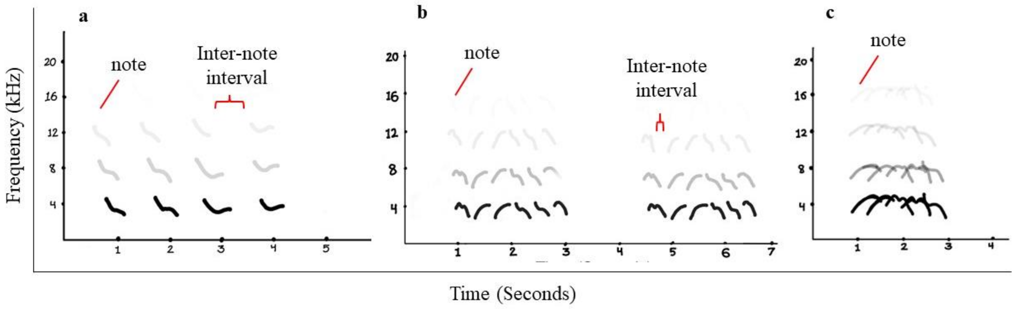


Figure 3.2 Schematic representation of spectrogram of **a** monosyllabic; **b** multisyllabic and **c** chorus call (Illustration by Deepuraj).

Table 3.1 Call types along with its associated behavioural contexts. Contexts of the calls were inferred from the behaviour of both the caller and the receiver. Percentage (%) indicates the frequency of a particular context associated with a certain call and it may add to be > or < 100% in cases when the contexts were not mutually exclusive.

Call	**Number of callers**	**Caller and its behaviour**	**Response by group member**
Contact	One caller (88%); intermittent calling by other members (12%)	Individual perched alone (75%); in presence of group member (28%)	Approach (41%); same call (50%)
Foraging	One caller (24%); intermittent calling by other members (76%)	Individuals foraging in group (100%)	No visible change in behaviour (100%)
Prompt	One caller (87%); intermittent calling by other members (13%)	Adult giving food to fledgling (72%); to nestling (28%)	Begging call (77%)
Prompt flight	One caller (84%), intermittent calling by other members (16%)	Adult around fledgling (52%); around nestling (48%)	Fledgling/nestling close call (46%), begging call (23%), follow adult (8%)
Flight	One caller (43%); intermittent calling by other members (57%)	Any member initiates calling and repeats. Other members may join vocalization.	Group displacement (70%), no response (30%)
Fledgling close	One caller (100%)	Fledgling in presence of adult (78%); in absence of adult (22%)	No visible change in behaviour (100%)
Begging	Could not be determined easily	Produced in presence of adult by fledgling (71%); by nestling (29%)	Food provision (79%); no food given (21%)

Sentinel soft	One caller (100%)	Sentinel (58%); individual near nest (31%); individual perched alone (11%)	No visible change in behaviour (100%)
Threat	One caller (78%), intermittent calling by other members (22%)	Produced in response to sudden appearance of any intruder; foragers (89%)	Startle or take refuge under foliage (78%)
Distress	One caller (100%)	Any member entrapped in mist-net (100%)	Response by group member/s by approaching trapped individual (30%)
Alert	One caller (100%)	Sentinel (55%); individual near nest (30%); any member (15%); towards human observer (50%) and non-urgent threat or unknown behaviour (50%)	Group displacement (10%)
Harsh	One caller (94%); intermittent calling by other members (6%)	Sentinel (42%); adult without food near nest (28%); adult with food (19%); any member (11%)	No visible change in behaviour (100%)
Intermediate alert	One caller (95%); intermittent calling by other members (5%)	Sentinel (74%); any members (26%); towards observer (16%)	No visible change in behaviour (84%); group displacement (16%)
Mobbing	One caller (7%); chorus (93%)	Any member/s towards potential predator or brood parasite (80%); toward observer (7%); unknown behaviour (13%)	Group member/s join caller 100%
Intergroup fight	Chorus (100%)	Any member/s from different group	Response with call only (57%); call with physical fight (43%)

Table 3.2 Brief descriptions of the acoustic parameters.

Acoustic Parameters	Descriptions

1. Frequency 5%	It is the frequency that lies at 5% of the energy in the call
2. Frequency 95%	It is the frequency that lies at 95% of the energy in the call
3. Bandwidth 90%	Represents frequency bandwidth between frequency 95% and frequency 5%
4. Peak frequency	Represents the frequency where maximum energy lies
5. Call duration	The time duration between the beginning and the end of a call
6. Total number of notes in a call	Total number of notes in a multisyllabic call as it is a composition of more than one notes

3.2.4 Statistical analyses

All the statistical analyses were executed in R (version 4.0.3, R Development Core Team 2020). Generalized Linear Mixed Models (GLMMs) (lmer in R package lme4, Bates et al. 2015) with gamma family and log-link function were run to check whether the call types classified based on behavioural contexts, are also acoustically distinct. Call types were considered as fixed/independent variables and acoustic parameters as dependent variables. Different location used in the study site were considered as random variables. To examine if there is any effect of sampling location on the call types, a likelihood Ratio Test (LRT) (lrtest in R package lmtest, Zeileis and Horthorn 2002) was also performed. Furthermore, a Discriminant Function Analysis (DFA) (lda in R program using package MASS, Ripley et al. 2013) was conducted to support our call classification based on behavioural context within each call category (monosyllabic, multisyllabic or chorus calls). Finally, to improve the dependability of the classification, a leave-one-out cross-validation DFA was carried out.

3.3 Results

3.3.1 Contextual complexity of vocal repertoire/vocalization

From the result of assigning call types to its associated behavioural contexts, JB was found to produce 15 functionally diverse call types (Table 3.1). These 15 call types can be broadly put under 2 broad functional contexts: affiliative and agonistic. The frequency of producing a particular call, in association with a particular behaviour is given in Table 3.1 and the brief description of the behavioural contexts under which the signallers produced these diverse vocalizations are given below.

3.3.1.1 Affiliative calls

Contact (Chack) call: JB produces this call while contacting conspecifics under the circumstances of an individual being separated from the group. Any member of the group can respond to this call by producing the same type of call (50%) and can sometimes approach towards the signaller (41%) leading to a reunion of a diverted individual with the rest of the group (Table 3.1).

Foraging (Cuk) call: This call is produced during foraging on the ground/leaf litter. Either one (24%) or more than one individual (76%) of the group can produce this call. In response to this call, no unique response was observed as the group continues to forage (Table 3.1).

Prompt (Ca-ca-ca) call: This call is used during food provisioning of the young ones. It is given by an adult with food in its mouth while progressing towards nestlings (72%) or fledglings (28%). Nestlings or fledglings respond to this call (77%) with a ‘Begging call’ (Table 3.1).

Prompt flight (Long cu-cu-cu) call: This call is typically produced by one adult (84%) or sometimes by more than one adult (16%) when they are in proximity to young ones. While making this call, adults take short flights from one position to another fluttering their wings and back to the young ones. the adult gives this call generally around the nest when the young one (nestlings, 48%) are about to fledge or are already fledging (fledglings, 52%). Young ones may respond to this call by producing a Fledgling close call (46%) and Begging call (23%). In response to this call, young ones are also observed to move out of the nest or move from their current location to another (8%) (Table 3.1).

Flight (Cu-cu-cu) call: The production of this call is generally initiated by one individual (43%) and sometimes the rest of the group members also join in vocalizing (57%), leading to group movement and displacement of group (70%) (Table 3.1).

Fledgling close (Chack) call: This vocalization is exclusively produced by fledglings or juveniles when adults are generally close-by (78%). No observable response by the adults, in close proximity to fledgeling, was found towards this call (Table 3.1). Nevertheless, it can be speculated that there may be a response same as contact call if the adult is far away.

Begging call: This vocalization is produced by nestlings or fledglings when an adult approached the nest with food (79%) or when an adult with food approaching towards nest produces prompt call (23%). While producing this call, the involvement of behaviour such as vigorous flapping of wings and the wide opening of beak were also observed (Table 3.1).

3.3.1.2 Agonistic calls

Sentinel soft (Low chack) call: This is a soft vocalization that is given by a sentinel (58%), an individual perched on an elevated platform watching out for any threat/ risk when the rest of group members forage (Andrews and Naik 1970). The caller is typically not alert when vocalizing and at times, the caller could even groom. No visible response of behaviour of group members was observed in response to this call (Table 3.1). Even though the caller does not show any aggressive behaviour, it is considered under agonistic for this study because of its function in anti-predatory contexts. However, this call can also be placed under affiliative and cooperative as explained in chapter 2.

Threat (Shriek) call: JB make this call when a raptor flew over them or when there is sudden approach of a potential threat (89%). The caller as well as the receiver responds with a startle or take shelter in closest tree or foliage (78%) as soon as the call is made. After some time, they could begin grooming or allogrooming within the cover or they might resume the behaviour they were doing earlier which is generally foraging (Table 3.1).

Distress (Kya-kya-kya) call: This call is produced persistently by an individual when trapped inside the mist-net or when the individual was being held for banding and releasing (100%) that might cause distress. In response to this call, group members may approach towards the caller (30%) (Table 3.1).

Alert (Cackle) call: This call is usually produced by the sentinel (55%) or may be given by any individual near the nest (30%) who is on the perch, in the presence of an intruder such as human observer (50%) or any non-urgent threat (50%). While they produced this call, they look very alert and involve the movement of body side by side along with fluttering of wings, jerking of tail up and down. The production of this call sometimes might attract others members of the group to join in the vocalization (10%) and sometimes there was no visible response or reaction from the group members (Table 3.1).

Harsh (Khack) call: Sentinel (42%) produces this call in the event of any intrusion such as the observer that poses no immediate threat. This call is also produced by the individual (s) approaching towards nest with food and waiting for provisioning (19%) or by the one near the nest without food (28%). There is no visible response by group members in response to this call (Table 3.1).

Intermediate alert (Khack cackle) call: Sentinel (74%) produce this call, sometimes in presence of the observer (16%) and in other cases no clear intruders or potential predators could be ascertained even after thoroughly scanning the environment. While producing this call, the intensity of the behaviour of the caller is somewhat intermediate to the behaviour exhibited while producing Harsh and Alert calls. This call did not seem to elicit any visible response (Table 3.1). While the exact context of this call could not be established unambigulously, it was certain a call produced in relation to vigilance behaviour.

Mobbing (Wheezy cackle) call: This vocalization is produced by more than one individual at a time when there is a potential predator (93%). This vocalization is observed to be produced in the presence of an immediate and proximate predator (80%) such as domestic/feral cats, Indian Grey mongoose, Greater coucal, Spotted owlet, Barn owl, snakes, and Rhesus macaque. While vocalizing, all involved individuals, flutter around and ‘harass’ the potential predator until the predator retreats. However, any involvement of direct physical interaction with the predator is not observed. Sometimes, the group may occasionally leave the area if the predator does not move from its position. Additionally, the production of the loud call may also influence the neighbouring heterospecific birds in joining the mobbing of the predator (Table 3.1).

Intergroup fight (guttural noise) call: This call is also produced by more than one individual when two different groups of JBs come in contact with each other. They make this vocalization as they chase each other from one tree to the next. Along with this vocalization, individuals occasionally get into physical battles in mid-air (43%), falling to the ground and attacking each other with their beaks and claws before disengaging. While vocalizing, the rest of the members of both groups surround the fighting pair and sometimes, both the group members position themselves facing each other on different trees making this call without physical interaction. However, it should be recognized that intergroup fights were uncommon. (Table 3.1).

3.3.2 Complexity on structural basis at the call level

The vocalizations of JB were found to be comprised of 7 monosyllabic, 6 multisyllabic and 2 chorus calls (Figure 3.3, 3.4, 3.5 and Table 3.3), according to the inter-note interval

(Figure B3.1). The results of GLMM indicated that there was a significant difference in acoustic parameters between call types within each category - monosyllabic, multisyllabic and chorus call (GLMM; $p << 0.001$, Table 3.4a). According to LRT results, sampling location did not show any effect on acoustic parameters across call types (Table 3.4b). Furthermore, the results of DFA help in the validation of the call types within each category, classified based on behavioural contexts. For monosyllabic call categories, the first Linear Discriminant Functions (LD1) accounted for 79% of the total variance and combining both LD1 and LD2 accounted for 93% of the total variance (Figure 3.3b). The variance in the monosyllabic calls was contributed mostly by call duration and bandwidth 90%. Similarly, for multisyllabic calls, 83% of the total variance is accounted by LD1 and combining both LD1 and LD2 accounted for 97% total variance (Figure 3.4b). Acoustic parameters such as call duration and the number of notes accounted for most of the variance. Moreover, within the multisyllabic call, calls such as Prompt, Prompt flight and Flight belonging to similar broad behavioural contexts of affiliation are found to be clustered together closer to each other and the same was true for calls such as Alert, Harsh and Intermediate alert belonging to the agonistic contexts (Figure 3.4b). Finally, the results of the cross-validated DFA also supported the classification of all monosyllabic, multisyllabic and chorus calls by presenting the accuracy of the classification to be 78%, 70% and 79% respectively (Table B3.1).

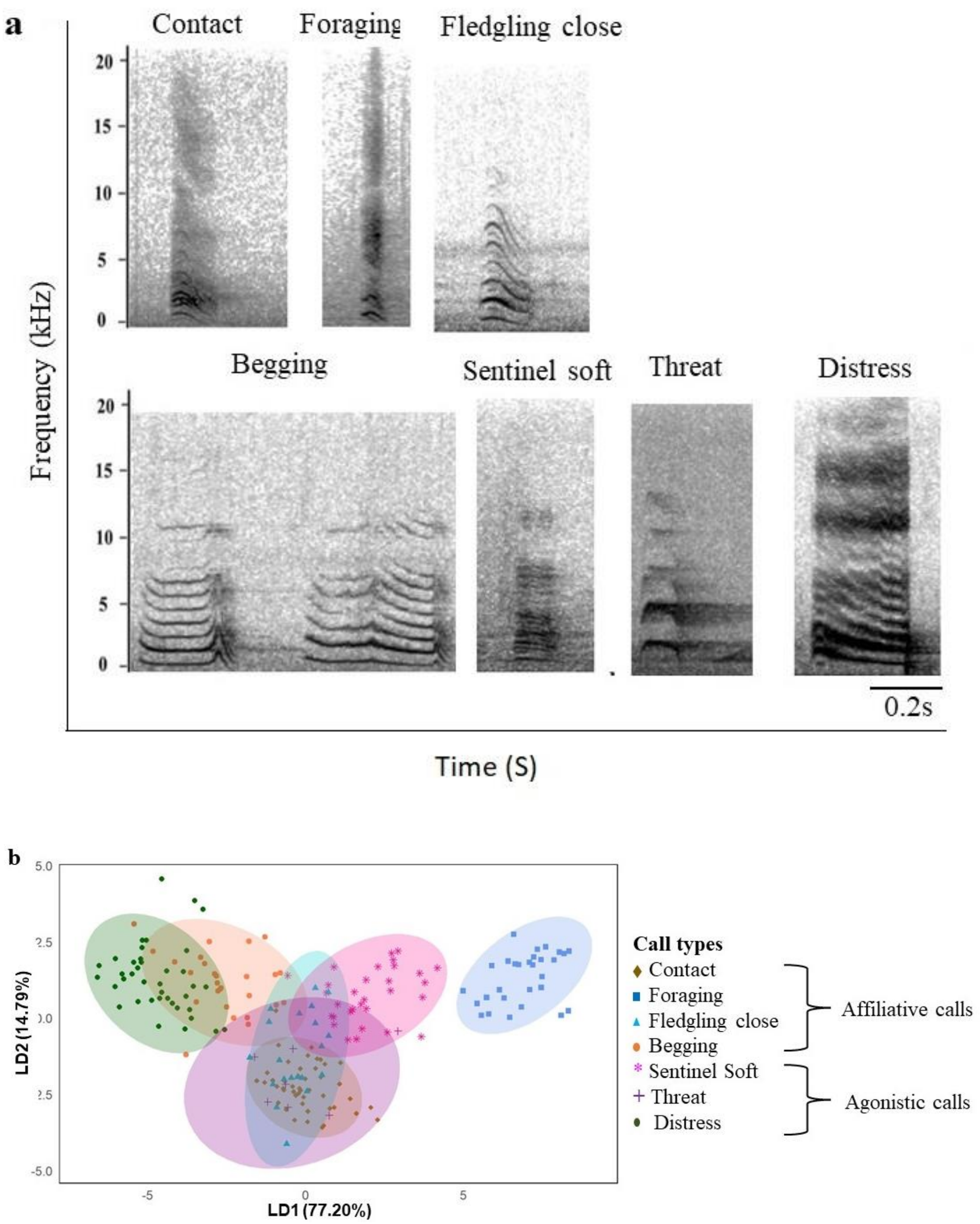


Figure 3.3 **a** Spectrogram of 7 monosyllabic calls and **b** plot of Linear Discriminant Analysis (LDA) of 7 monosyllabic calls showing first two linear discriminants (LDs). Colour ellipse denotes a 95% confidence interval.

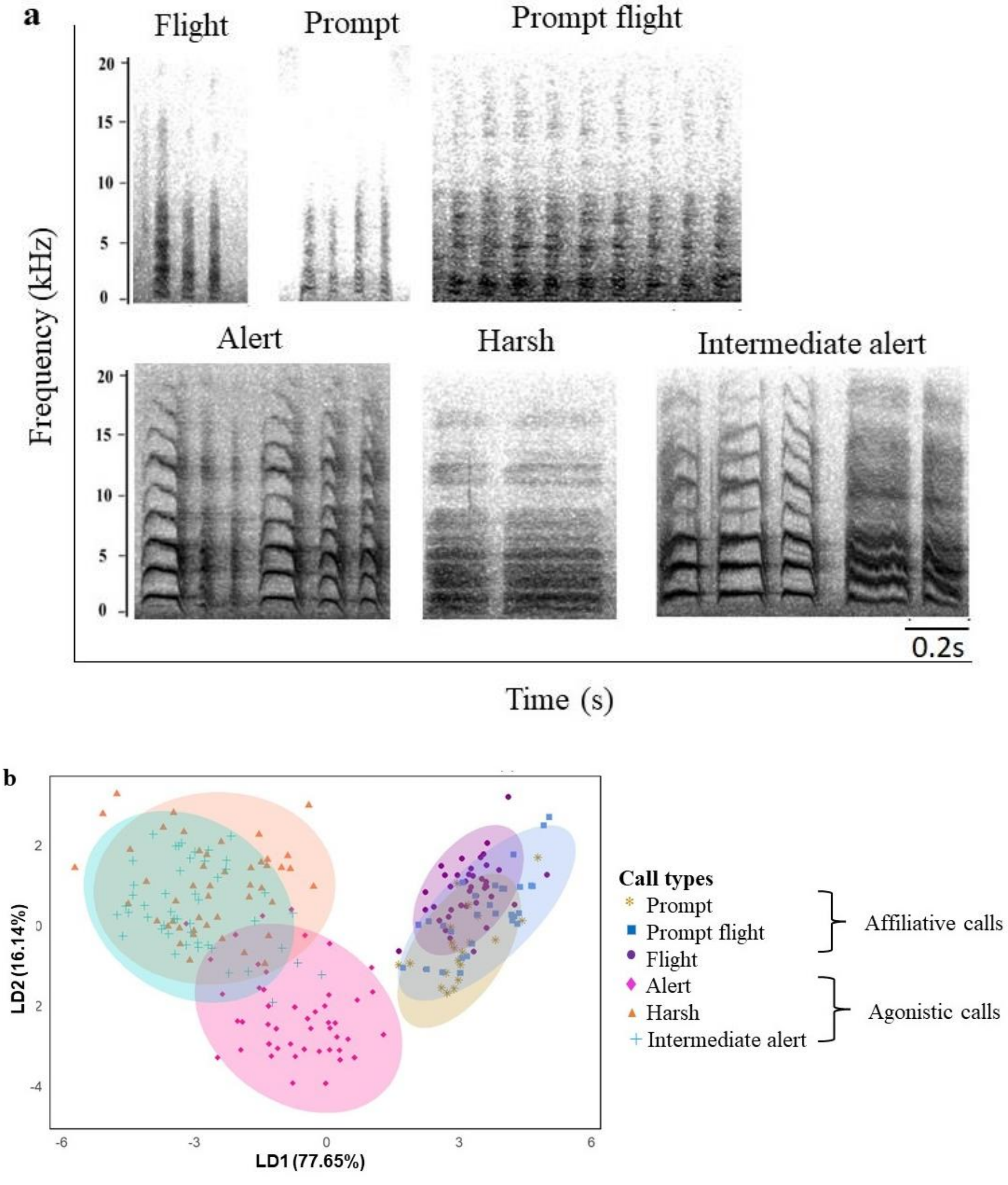


Figure 3.4 **a** Spectrogram of 6 multisyllabic calls and **b** plot of Linear Discriminant Analysis (LDA) of 6 multisyllabic calls showing first two linear discriminants (LDs). Colour ellipse denotes a 95% confidence interval.

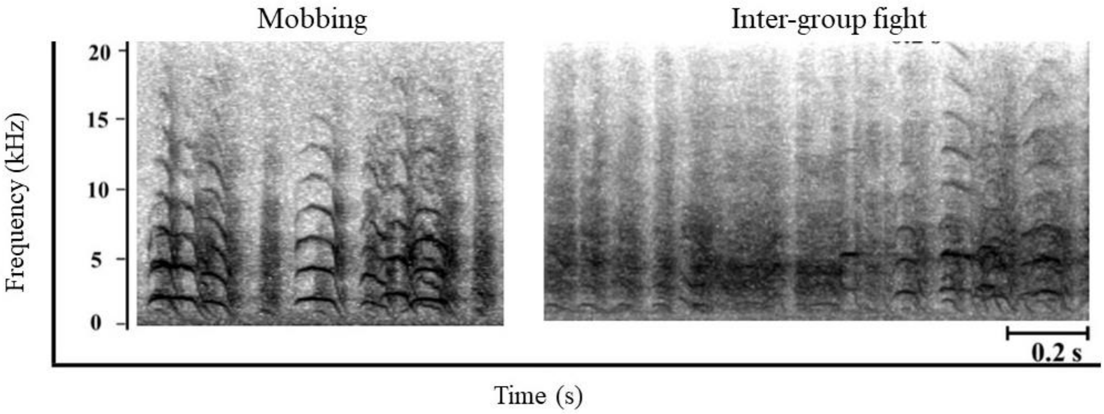


Figure 3.5 Spectrogram of 2 chorus calls.

S.no	Call types		Call Category	N	n	No. of notes	Call duration (s)	Frequency 5% (kHz)	Frequency 95% (kHz)	Bandwidth 90% (kHz)	Peak frequency (kHz)
	Behavioural context	Onomatopoeic description									
1	Contact	Chack *	Monosyllabic	22	57	1	0.14 ± 0.02	1.83± 0.27	3.61 ± 0.28	1.78 ± 0.29	2.69 ± 0.19
2	Foraging	Cuk *		13	36	1	0.05 ± 0.01	0.89 ± 0.15	5.82 ± 0.62	4.94 ± 0.63	1.45 ± 0.39
3	Fledgling close	Fledgling chack		9	26	1	0.15 ± 0.02	1.53 ± 0.38	3.66 ± 0.55	2.12 ± 0.67	2.54 ± 0.29
4	Begging	Rattling squawk*		11	33	1	0.25 ± 0.08	1.39 ± 0.35	4.59 ± 0.61	3.21 ± 0.68	2.70 ± .56
5	Sentinel soft	Low chack		17	38	1	0.11 ± 0.02	1.06 ± 0.18	4.76 ± 0.92	3.69 ± 0.92	2.40 ± 0.26
6	Threat	Shriek *		8	8	1	0.1 ± 0.02	2.39 ± 0.37	5.94 ± 0.93	3.56 ± 0.83	5.13 ± 1.11
7	Distress	Kya-kya-kya*		11	49	1	0.34 ± 0.07	1.80 ± 0.16	5.44 ± 1.63	3.64 ± 1.66	3.34 ± 0.81
8	Prompt	Ca-ca-ca	Multisyllabic	11	25	4.24 ± 1.30	0.29 ± 0.11	0.94 ± 0.22	6.07 ± 0.71	5.13 ± 0.63	1.59 ± 0.24
9	Prompt flight	Long cu-cu-cu		13	37	6.03 ± 2.19	0.46 ± 0.18	0.95 ± 0.20	4.68 ± 0.84	3.73± 0.83	1.79 ± 0.28
10	Flight	Cu-cu-cu *		19	51	3.65 ± 0.80	0.30 ± 0.08	0.95 ± 0.22	4.18 ± 0.57	3.23 ± 0.66	1.86 ± 0.37
11	Alert	Cackle *		15	58	3.79 ± 2.99	0.49 ± 0.44	1.58 ± 0.26	6.47 ± 0.70	4.89± 0.68	3.63 ± 0.62
12	Harsh	Khack		21	58	1.93 ± 1.51	0.46 ± 0.44	1.46 ± 0.28	5.69 ± 0.45	4.23 ± 0.43	2.54± 0.68
13	Intermediate alert	Khack cackle		11	59	3.14 ± 2.16	0.75 ± 0.58	1.60± 0.19	5.86± 0.39	4.25 ± 0.33	2.91 ± 0.64
14	Mobbing	Wheezy cackle *	Chorus	8	8	-	-	1.91± 0.12	6.50 ± 0.68	4.59 ± 0.68	4.20 ± 0.57
15	Inter-group fight	Guttural noise *		6	6	-	-	1.71 ± 0.36	6.05 ± 0.41	4.34 ± 0.31	4.20 ± 0.84

Table 3.3 Mean ± SD of the temporal and spectral characteristics of 15 call types of all the categories. N and n represent the number of recordings and number of calls analysed for each call types respectively (a recording can have multiple calls). Green colour filled cells represent the affiliative call category and unfilled represent the agonistic call category. * indicate onomatopoeic description used by Gaston (1977)

Table 3.4 Results of a) Generalized Linear Mixed Model (GLMM) and b) Likelihood Ratio Test (LRT) for the models with random effect (RE) and without random effect

a

GLMM				
Call categories	**BIC**	**deviance**	**df**	***p***
Monosyllabic	4434.9	4385.4	238	<<0.001
Multisyllabic	5047.0	5001.7	280	<<0.001
Chorus	259.2	248.6	10	<<0.001

b

Call categories	**Model**	**AIC**	**Loglik**	χ^2	***p***
Monosyllabic	~Call types + RE(Location)	4403.1	-2192.7	0	1
	~Call types	4401.1	-2192.6		
Multisyllabic	~Call types + RE(Location)	5018.6	-2502.3	2.9882	0.08387
	~Call types	5017.7	-2500.8		
Chorus	~Call types + RE(Location)	256.6	-124.2	0	1
	~Call types	252.6	-123.3		

3.4 Discussion

Measurements of vocal complexity encompass both functional and structural (repertoire size) aspects of vocalizations (Crane et al. 2016; Holt et al. 2017). Sociality and sexual selection are two of the main contributing factors that can influence vocal complexity (MacDougall-Shackleton 1997; Freeberg et al. 2012). In avian system, cooperative breeding has been regarded as one of the powerful social measures in predicting vocal complexity with large repertoire size (Leighton 2017). Several studies in cooperative birds have also shown that cooperative breeding is linked with the production of numerous functionally and structurally diverse calls (Ficken et al. 1978; Seddon 2002; Warrington et al. 2014; Crane et al. 2016). However, a measurement of the temporal and spectral characteristics of the components (notes) that make up a call or song is also required to evaluate the fine structure of all vocalizations (Yambem et al. 2021, Chorol 2022). The evaluation of vocal complexity in social birds typically lacks this degree of analysis (Greig and Pruett-Jones 2008; Grieves et al. 2015; Crane et al. 2016).

Our results support Andrews and Naik's (1970) and Gaston's (1977) findings that diverse affiliative and agonistic behaviours in JBs are mediated by vocalizations in terms of the functional components of the vocal repertoire. Calls that are meant to coordinate the movement of the group, provisioning of food and brood caring are known as Affiliative calls. For example, in JB, flight calls lead to movement of the member from one area to another in the group and Contact calls are meant for the lost member to rejoin the group. Prompt calls are meant for fledglings to beg and Prompt flight for flying. It is also found that In Pied babblers (*Turdoides bicolor*), displacement of groups can be induced by the ‘clucks’ sound and fledglings would rush towards a food source if ‘purrs’ sound is made. (Engesser et al. 2017). In JB, the true purpose of the Foraging call is still unknown. It is speculated that the purpose of Foraging calls in JB is similar to that of Pied babblers which is to maintain spacing between the foragers so that foraging efficiency can be further improved (Radford and Ridley 2008). Gaston (1977) reported that before any attempt of copulation a type of “Gurgle” call is produced and for rough and tumble behaviour a “Scheer” call is produced. These calls could not be found in our observations and this might be because the behaviour associated with it is exhibited rarely by JBs.

Out of the 15 vocalizations of JBs, 8 vocalizations are produced agonistically towards conspecifics and heterospecifics. Conspecific rivals cause the production of Inter-group fight call (guttural noise). Six other calls which includes Threat, Distress, Alert, Harsh, Intermediate alert and Mobbing calls are mainly produced against the intrusion of heterospecifics mostly potential predator. The reason for exhibiting a disproportionately large number of vigilance calls may be because of the strong selective pressure caused by predation which directly impacts the fitness of an individual (Leighton 2017). During foraging the animals usually scan the environment to look out for predators thereby interrupting their foraging and thus making the vigilance behaviour costly (Wickler 1985). Individuals can reduce the loss or cost of vigilance behaviour by performing acoustic vigilance in a coordinated manner where every individual need not scan for the predator. The mitigation of cost of vigilance depends on the animals producing the reliable alarm calls as the chance of survival increases if the receivers choose the appropriate escape strategy by hearing the reliable calls (Marler 1967). Thus, having a functionally referential alarm vocalization could be adaptive because the receivers are informed by the alarm vocalizations about the category of predator whether aerial or terrestrial or even predator-specific (Seyfarth et al. 1980; Naguib et al. 1999). Encoding the level of urgency (encoding distance of potential threat) would also be adaptive as it allows receivers to respond in an appropriate time (Manser 2001). In cooperative breeders, there is a high chance of an increase in the proportional representation of vigilance vocalizations if all these are combined in their vocal repertoire. For example, Meerkats produce 30 different types of vocalizations and of these 30, 18 call types are produced in relation to vigilance i.e. roughly 60% of the call types are related to vigilance calls). Our findings are also supported by other studies done on cooperatively breeding birds where the majority of the vocalizations tend to be vigilance. For instance, 4 out of 13 calls in Chestnut-crowned babblers (Crane et al.

2016), 5 out of 12 calls in Pale-winged trumpeter, *Psophia leucoptera* (Seddon et al. 2002) and 5 out of 11 calls in Black-capped chickadees, *Poecile atricapillus* (Ficken et al.1978). In addition, cooperative breeders dedicated vigilance-related vocalizations in a significantly higher proportion in their vocal repertoire as found in a study conducted by Leighton (2017) throughout the globe on 253 bird species representing 59 families.

Flee, mob and distress are the three main categories of Alarm calls (reviewed in Magrath et al. 2015). Flee-types calls make the localization difficult due to the production of pure tone calls of short duration (Marler 1955). For example, in Arabian babblers it was found that sentinels were able to sense the threat from the far distance but the foragers were able to see the threat from a nearby distance and thus, foragers produce a much shorter alarm call than the sentinels (Sommer 2011). The results of our study also support that the Threat call of foragers also functions as a flee calls and has the shortest note duration of monosyllable that might help in immediate escape and make it difficult in localization by predators. Nevertheless, multisyllabic calls were also found to be produced by sentinel or individuals on perch in their alarm calls such as Harsh, Intermediate alert and Alert. It is assumed that in different situations of urgency such as low, intermediate and high urgency due to threat, JBs produce alarm calls in different manners i.e., Harsh, Intermediate and Alert respectively but further investigation is needed for exact functional contexts. As reported in other cooperative breeders (Wickler 1985; Manser 1999; Hollén et al. 2008), it is also speculated that the function of the soft call of sentinel is identical to that of the ‘watchman song’. The ‘watchman song’ is a type of acoustic communication that coordinates between vigilant (sentinel) and non-vigilant (foragers) group members that act as a stand-in for the sentinel's presence on duty to the rest of the group (Wickler 1985). Since this call helps in maintaining group cohesion it can be considered as affiliative as well as agonistic and it could also provide information about the predation risk (Kern and Radford 2013).

This study revealed that structurally across calls, 7 monosyllabic and 8 multisyllabic calls were the compositions of the vocal repertoire of JB. This finding of large vocal repertoire fulfills our prediction which has also been reported in most bird species where vocal repertoire exceeds the higher end of the number of distinct vocalizations which ranges from 5 to 15 discrete vocalization (Gill 2007). Moreover, the assumption of the 'social complexity hypothesis' is also confirmed by the results which show calls with distinct functions. Additionally, in all the calls it was also found that each call differed from one another significantly with an overall acoustic difference across the calls except for Fledgling close call. The results of cross-validated DFA revealed that there is often misclassification of this call with Contact call. The reason for this misclassification could be the similarity in function of the calls even if they are produced by different age groups. Moreover, DFA plot of the multisyllabic calls showed that affiliative and agonistic calls within the multisyllabic call category clustered together more closely, supporting Morton's (1977) prediction that there should be structural similarities between calls produced in similar functional contexts. Morton (1977) also proposed that in affiliative contexts, calls would be tonal with high frequency and calls produced in agonistic contexts would be harsher with a lower frequency which is not in accordance with the calls in JB. In JB, the majority of the vocalizations in agonistic contexts exhibited the presence of notes with harmonic structure whereas the structure of the vocalizations produced in affiliative contexts were harsh and showed the absence of tonal structure. Further analyses using pitch saliency or Weiner entropy can be conducted in the future to assign the structure of the vocalizations associated with either affiliative or agonistic contexts as described in a study done on Zebra finch, *Taenjopygia* sp. (Elie and Theunissen 2016).

Quantifying and categorizing all the communication repertoire of a species to its respective behavioural contexts will help in a better understanding of the ecology of species (of species and their association with the environment they lived). Comprehensive knowledge of the vocal repertoire and their associated functional contexts of a species will provide a platform for future comparative studies across taxa in examining factors that are involved in the enhancement of cooperation within that species. Furthermore, the descriptive study of the communication repertoire of a social species will help in cataloguing the diversity of communication of different taxa which in turn might help in the further study of the evolution of communicative complexity.

3.5 Appendix B

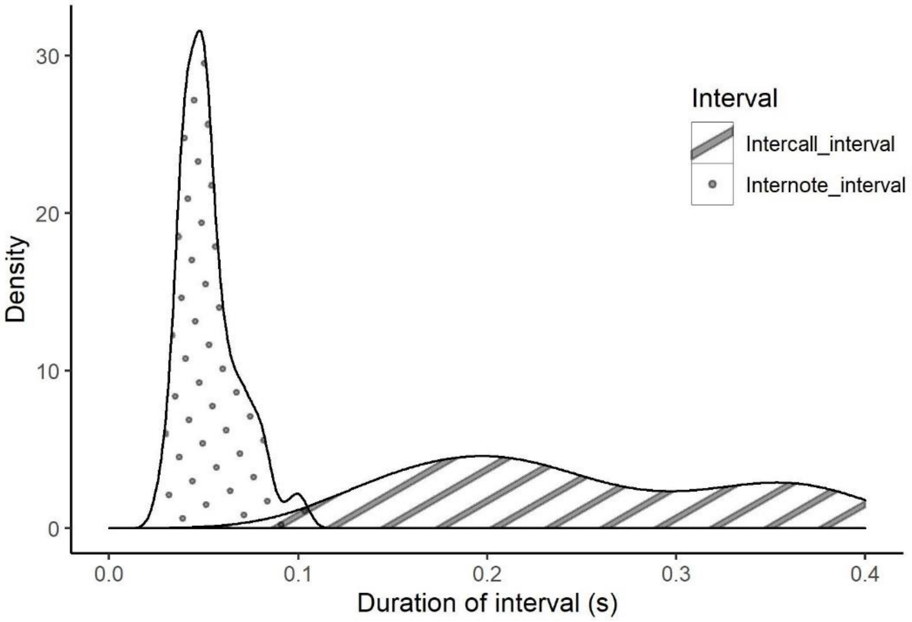


Figure B3.1 Distribution of the duration of interval (in seconds) in between calls (inter-call interval) and between notes in a call (inter-note interval).

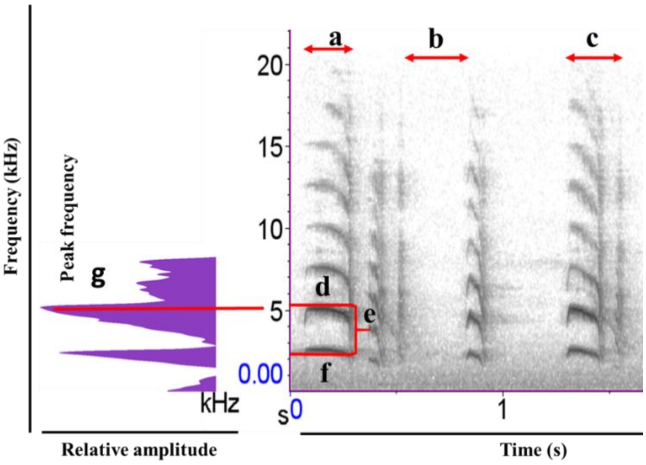


Figure B3.2 Power spectrum (on the left) and spectrogram (on the right) showing different parameters used in the analysis. **a** an element/ a note; **b** inter-call interval; **c** call duration; **d** frequency 95% **e** bandwidth 90%; **f** frequency 5% and **g** peak frequency.

Table B3.1 Result of cross-validated DFA across all the call types showing the ratio of correctly classified calls to the total number of calls analysed (RCC) and the percentage of correctly classified calls (CC%).

Monosyllabic calls			**Multisyllabic calls**			**Chorus calls**		
Call types	**RCC**	**CC (%)**	**Call types**	**RCC**	**CC (%)**	**Call types**	**RCC**	**CC (%)**
Contact	45/57	79	Prompt	21/25	84	Mobbing	7/8	87
Foraging	36/36	100	Prompt flight	14/37	38	Inter-group fight	4/6	67
Fledgling close	4/26	18	Flight	40/51	78			
Begging	22/33	67	Alert	52/58	90			
Sentinel soft	36/38	95	Harsh	40/58	69			
Threat	8/8	100	Intermediate alert	36/59	61			
Distress	43/49	88						

Chapter 4

Understanding alloparental care in Jungle Babbler and the ontogeny of begging behaviour

4.1 Introduction

Parental care is defined as any behaviour by an adult that enhances or increases the fitness and survival of its offspring (Walters 1984; Clutton-Brock 1991). It is exhibited in different forms before or after birth. In precocial species, the young ones at birth are relatively independent as their locomotor activity is more developed. Whereas, altricial species require extensive parental care as their locomotor activity is relatively underdeveloped with closed eyes and no down feather at the time of birth (Starck et al. 1998). In altricial birds, parental care can be displayed in the form of nest-site selection, building nest and preparation of burrows, provision of large and heavily yolked eggs or oviposition, care of the eggs or the young ones inside or outside the nest, provisioning of young ones inside or outside nest (Clutton-Brock 1991; Kölliker et al. 2012). In post-hatchling altricial birds, parental care in the form of provisioning (reviewed in Martin 1987) and brooding are critical factors that can influence the growth and survival of the young ones (Mccarty 2001). Studies within and across species reported the importance of food resources in the growth and development rate (reviewed in Dmitriew 2011). Brooding of newly hatched young ones is crucial as their bodies cannot thermoregulate on their own (Whittow and Tazawa 1991), which can be attributed to their higher body surface-to-mass ratio (Dawson and Evans 1960; Pereyra and Morton 2001) and fewer feathers development (Stephenson et al. 2009).

Several environmental and demographic factors can have an effect on provisioning and brooding, leading to the variation or pattern in the care. Provisioning rate can be influenced by temperature (Pied Babbler, *Turdoides bicolor*, Wiley and Ridley 2016), time (Nashville warbler, *Leiothlypis ruficapilla*, Knapton 1984), predation pressure (study on 64 passerine species, Martin et al. 2011), brood size (House wrens, *Troglodytes aedon,* Bowers et al. 2014), age (Black-throated blue warblers, *Setophaga caerulescens,* Goodbred and Holmes 1996; Chestnut-crowned babbler, *Pomatostomus ruficeps*, Browning et al. 2012), number of providers (Rufous treecreeper, *Climacteris rufa*, Luck 2001), brood parasitism (brood parasitism on Baywing, *Agelaioides badius*, by Screaming cowbirds, *Molothrus rufoaxillaris* and Shiny cowbird *Molothrus bonariensis,* Ursino et al. 2011). In addition to the quantity, quality such as the size of the food items can also influence growth and survival of the nestlings (House sparrow, *Passer domesticus*, Schwagmeyer and Mock 2008). Moreover, different nutritional demands for the growing nestling (Ramsay and Houston 2003) and the handling of the prey items by the young ones (Banbura et al 1999) might lead to the difference in the diet content of the adult and the young ones. The nestlings of a cooperative breeder, Green woodhoopoe (*Phoeniculus purpureus*) showed different diet content from the adults and this changed with their age (Radford 2008). Brooding duration can be influenced by brood size and age. Previous studies on Tree swallow, *Tachycineta bicolor* (Mccarty and Winkler 1999) and House sparrow (Chastel and Kersten 2002) showed that temperature plays an important role in the growth of newly hatched altricial young, based on their homeothermic abilities which can vary with age and brood size influencing brooding duration.

Parental care demands an extensive investment of energy and resources from the carer affecting their fitness and future reproductive success (Clutton-Brock 1991). Moreover, comparative studies on avian systems showed that parental care in the form of provisioning and defence of the nest exerts a huge cost to the carers, which is more than the cost exerted in incubation and nest building (Owens and Bennett 1994). Thus, the carer must invest in such a way that the trade-off between the cost and the benefit of parental care is at an optimum level (Winkler 1987). This optimization of the trade-off between the cost and the benefit also leads to the development of variation in care across taxa and even within the same species, which in turn depends on numerous factors discussed above (Clutton-Brock

1991). This trade-off optimization becomes more complex when there is an involvement of multiple carers (Winkler 1987; Royle et al. 2012; Smiseth 2019).

Cooperatively breeding birds exhibit alloparental care, in which more than two individuals are involved in providing care to the offspring (Stacey and Koenig 1990). The amount of parental effort to be provided may depend on the genetic relatedness of the contributing carers with the young ones (Winkler 1987; Hatchwell and Russell 1996; Houston et al. 2005). Thus, the carers must coordinate to balance their contribution to alloparental care, thereby determining differences in the patterns of care provided to the young ones. Studies on cooperative birds have shown that the workload of parental care is not evenly distributed between the carers depending on the form of care they provide or the relatedness between the carers and the recipients (Valencia et al. 2006; Johnstone 2011). For instance, in Arabian babblers (*Turdoides squamatus*), both parents and helpers who are highly related to each other provision at the same rate (Wright 1998) whereas, in Long-tailed tits (*Aegithalos caudatus*), the parents provide more provisioning than the helpers while the helpers are involved in other forms of parental care such as defence (MacColl and Hatchwell 2003). Study on Azure-winged magpie, (*Cyanopica cyanus*) showed that the parents invest more in provisioning while helpers are engaged in other activities such as nest defence (Valencia et al. 2006).

Furthermore, it has been reported that the helpers in cooperative breeders, may synchronize their behaviour. Two hypotheses have been proposed to explain this synchronization of behaviour. The first is the ‘social prestige’ hypothesis (Zahavi 1995) which posits that synchronized feeding serves as a means to show off the cost of alloparental care to the breeders and other group members and is in line with the ‘pay to stay’ hypothesis (Bruintjes and Taborsky 2008). For example, in Sociable weaver, *Philetarius socius*, it was shown that the helpers wait for the parents and feed the young ones in presence of an audience, thereby conveying a signal of their quality and contribution to alloparental care (Doutrelant and Covas 2007). In Cichlid *Neolamprologus pulcher*, it was reported that the helpers engaged in defence behaviour when the density of the fish was high, in accordance to the 'pay to stay' hypothesis (Bruintjes and Taborsky 2008). The other hypothesis that explains the synchrony in alloparental care posits that synchronized feeding reduces the likelihood of adults making multiple trips to the nest which may make the nest more conspicuous to predators (Strickland and Waite 2001; Martin et al. 2000). Additionally, continuous begging, an energetically expensive behaviour (Rodríguez-Gironés et al. 2001) that helps in communicating their needs with the carers (Kilner et al.1999) also increases the chances of predation (Haff and Magrath 2011). In so, synchronized feeding may reduce the number of instances of begging call production. Given that predation is one of the most crucial factors in the survival of the offspring and a major source of breeding failure in birds (Sullivan 1989; reviewed in Dmitriew 2011), both the carer and the offspring must develop strategies that can promote effective communication between them, yet minimise the risk of predation. Studies have reported that synchronized feeding significantly increases the chances of brood survival. For example, in a cooperatively breeding, Pied babbler, the carers actively synchronize their feeding visits by waiting for the other group members to visit the nest together and this synchronization is associated with an increase in brood survival (Raihani et al. 2010).

Begging behaviour is an important form of communication between the carer and the offspring. Instead of producing conspicuous begging calls indiscriminately, young ones should beg only upon the arrival of an adult. While the young ones can see at the nestling and pre-fledgling stage, their eyes are closed at the hatchling stage. However, they can still perceive the calls of adults and the tactile stimuli from the branch shake when an adult lands near the nest. It is not clear; however, how young ones sense the arrival of adults, what prompts begging response and the ontogeny of begging response in relation to the age of the young ones. They may be utilising a specific signal or a combination of signals to sense the arrival of adults. Such a system would allow economizing begging call production thereby, saving energy and reducing predation risk. Multimodal signals may provide the additional benefit by reducing the probability of deception, minimising errors in perception and enhancing detection (reviewed in Hebets and Papaj 2005). An experimental study by Stynoski and Noble (2012) in tadpoles of Strawberry poison frog, *Oophaga pumilio* showed that tadpoles responded by only swimming when given either a single visual cue or both visual and chemical cues but they responded by begging when presented with a combination of visual, chemical and tactile cues. Studies have been reported on adults producing provisioning calls that announce their arrival with food and this call acts as a signal to the young ones to beg only when adults arrive, which in turn reduces predation risk (Madden et al. 2005a; Raihani and Ridley 2007). For instance, experimental studies on White-browed scrubwren, *Sericornis frontalis* showed that the food call of parents induces more vigorous begging in the nestlings than any other parental vocalization (Magrath et al. 2007).

Studies in cooperatively breeding animals on the patterns of alloparental care provides valuable information on the behavioural ecology of a species and enhances our understanding of the drivers of alloparental care. Moreover, they contribute to future comparative studies and meta-analyses of behavioural strategies that optimize care giving while minimizing risk of predation. In addition, the study on parental care in a cooperative breeding system provides a paradigm for investigating the evolution of cooperation, sexual selection, kin selection and the life history of an organism.

This study aimed to investigate the pattern of alloparental care and some of the factors that might be associated with it in Jungle Babblers (*Argya striata*; hereafter JBs) by focussing on the following objectives:

1) Does the provisioning rate and duration of brooding vary with the time of the day, group size, number of nestlings, age of the young ones and brood parasitism?

2) How does the diet content of the young ones differ from adults?

3) Do JBs exhibit synchronized feeding and if so, which parameters influence this behaviour?

4) Does the nature of signals that induce begging response vary with the age of the young ones?

4.2 Materials and methods

4.2.1 Study site

The study was carried out from August 2016 to April 2021 at IISER Mohali and NIPER Campus, Punjab, India (For climate and vegetation, please refer to Chapter 2). A total of 33 nests were monitored. Of these, 6 were parasitized by Jacobin Cuckoo, and a total of 6 nests were unsuccessful for various reasons. Data from these were, therefore, not included in the analysis. The locations of all 33 nests are given in Figures 4.1a and b.

4.2.2 Provisioning, diet, brooding and synchrony

Observations of the nest for collecting food provisioning data were done using binoculars (Nikon Monarch 10x50) after settling down at a safe place. Most of the nests were found after the eggs had hatched, so the estimation of the stage was by back counting the days from the days the nestlings fledged. There were nests where the access to check nest content was not possible. So, the number of nests used are different for different analysis. Each nest was observed for one hour and all the data collection was done between 6:00 to 17:00 hr randomly. The number of individuals bringing food, the timing of arrival, diet, and the duration of brooding were noted down. In this study, brooding behaviour is defined as the presence of an adult inside the nest who maintain its position so that its wings are flanked above the young ones (Hess et al. 1976). The number of individuals arriving with the food at the same time near the nest or arriving one after another with a large time gap in between was also counted to check whether JB performs the provisioning behaviour in synchrony or not. The content of the nest i.e., the number of eggs or nestlings were also observed using a PC webcam (Intex IT-306 WC) attached to a pole and connected to a laptop via a 5-10 m cable depending on the height of the nest.

4.2.3 Communication during provisioning

4.2.3.1 Behaviour observation

To examine the communication between adult and young ones, I first carried out field-based *ad-libitum* observations on active nests. Observations were carried out after I confirmed the first instance of begging from the young ones. The begging responses could simply be prompted by the visual presence of the adult. However, it was observed that the branch on which the nest is constructed shook lightly upon the arrival of an adult. I hypothesized that this could function as a tactile stimulus indicating adult arrival, thereby prompting the young ones to beg. Further, it was observed that the adults arriving with food at the nest may approach the nest silently or produce a prompt call (Chapter 3; Figure 4.2 a). The young ones could respond to this by begging or remaining silent. So, I wanted to examine the possible stimulus that elicited a begging response from the young ones.

Figure 4.1 Sites of the nests found during the study. **a)** sites of the nest found in the both IISER and Niper Campus. Different colours indicate different months: Feb-violet, March-brown, Apr-blue, May-green, June-yellow, July-orange, Aug-red, Sept-pink, Nov-grey. **b)** zoom in picture of the nests site in the IISER campus showing details of the nest with brood parasitism (BP), unsuccessful nests due to snake predation (P), Wind (W) and unknown reason (UN).

I also wanted to examine if adults are more likely to produce prompt calls for specific age classes of the young ones and if begging response to adults giving prompt call itself vary with the age of the young ones.

In order to examine if the probability of producing prompt calls by adults was dependent on the age of the young ones, the number of adults arriving with food along with or without a call was noted for all nests with young ones of different age classes (calculated backward as the number of days before fledging). The proportion of times, the young ones responded with begging calls to the adults arriving with or without a prompt call was also noted.

4.2.3.2 Playback experiment

Stimuli used for experiments: For tactile stimulus, tapping of the branch was used to simulate the landing of adults at the nest. For acoustic stimuli, three types of call: Prompt, Flight and Contact calls were recorded for use in the playback experiment (Yambem et al. 2021; Chapter 3; section: 3.3.1). From note-level acoustic analyses it has been found that while prompt and flight calls differ acoustically from each other (based on frequency 95% and bandwidth 90%), they also have several acoustic similarities (note duration, frequency 5% and peak frequency; Chorol 2022, Table 4.1). This is probably why they sound almost similar to a human observer. However, whether JBs perceive these two calls as the same is not clear. Thus, flight call was also used in the experiment to check whether the young ones can differentiate between the prompt and the flight call. Contact call on the other hand is distinctly different from both the calls and is produced in affiliative contexts and thus it is used as a negative control. All the recordings were collected by following the same protocol as described in Chapter 3.

Playback experiments were carried out on active nests (N=21) in which tactile stimulus (branch shake) and three acoustic stimuli: flight, prompt and contact call were used to examine whether the begging response from the young is elicited in response to tactile stimulus alone, acoustic stimulus alone or a combination of both the stimuli. The spectrograms of the three acoustic stimuli used are given in Figure 4.2. I also checked whether the response of the young ones to the different stimuli changed depending on the age of the young ones. Three different age classes of the young ones were considered: hatchling, nestling, and pre-fledgling. This categorization of stages is done on the basis of the days they fledged and their morphology (Anava et al. 2001; Jonsomjit et al. 2007), as there is no clear distinction of the range between the stages and sometimes, they either fledged early or late (Figure 4.3 and Table 4.1). Adults become more sensitive during the fledgling stage, the experiment at the fledgling stage could not be carried out. All the calls were digitized in Raven Pro1.5 and only those calls with a high signal-to-noise ratio were selected for the playback experiment. Three to four sample playbacks were created for each call type from different recordings and different nests or different days. One sample playback for each call lasted for 7 to 16 seconds consisting of 6 to 8 calls (some calls were looped where the clean calls were not available). The gap between the calls in each sample is different for different calls to match with the natural calls.

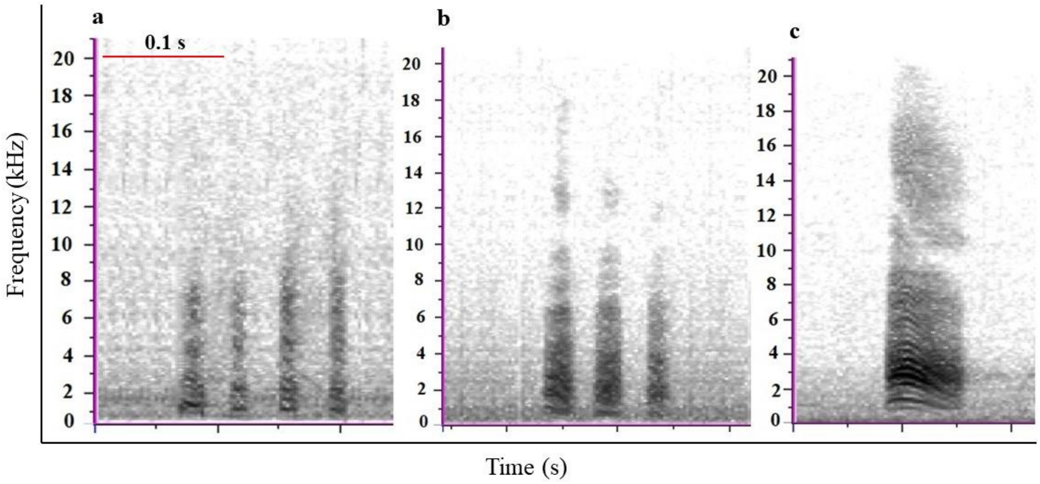


Figure 4.2 Spectrograms of the calls used in the playback experiments. **a.** Prompt call; **b.** Flight call and **c.** Contact call.

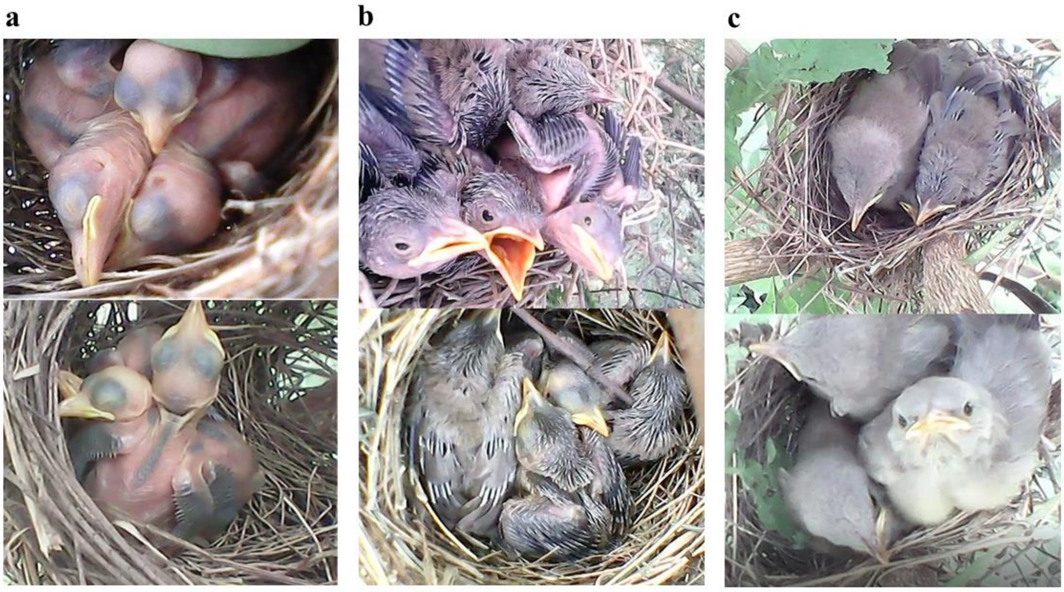


Figure 4.3 Stages of the young ones of JB. **a.** Hatchling; **b.** Nestling and **c.** Pre-fledgling.

Table 4.1 Stage of the young ones based on the count of number of days to fledge and number of nests used in the analyses of the playback experiment for each stage.

Stages of the young ones	**Days to fledge**	**No. of nests**
Hatchling	9-14	7
Nestling	3-9	13
Prefledge	1-4	12

All the calls (playback stimuli) were played back in their original amplitude using a Sony speaker (SRS XB30), connected to a laptop, enabling the observer to control the playback experiment. Prompt and flight calls are soft calls, so the amplitude of both calls was set the same (65-68 dB) while the contact call was set at (75-80 dB) at 1m source. Behaviours of the focal animal were recorded using a portable PC webcam attached to a pole that can reach up to the nest. The webcam was connected to a different laptop using a long cable so that the observer can observe it from the ground without disturbing the nest. Distance between the speaker and the focal animal ranged from 1.5-4m depending on the height of the nest. One set of playback experiments consisted of six stimuli: three with playback calls-prompt call (P), flight call (F), contact call (C), one with a tactile-branch shake (BS), a representative of the adult landing on nest branch and two with both tactile and auditory (call), BS+P and BS+F. The order of the stimuli being presented was randomized. Only one set of playback experiments was carried out on a nest in a day. At least two-day breaks were given between the experiments while carrying out the experiment on the same nest for different stages. The response was considered positive if at least one focal animal (young one) inside the nest responded with a mouth opening showing begging behaviour.

4.2.4 Data analyses

4.2.4.1 Provisioning, diet, brooding and synchrony

The total number of nests found, the number of nests used in the analysis and the hour of observations for both with (total nest = 6) and without brood parasitism (total nest = 21) are given in Tables C4.1 and C4.2a and b. Total number of nests for each group size and age of the young ones were given in Table C4.3a and b. The rate of provisioning was calculated as the number of individuals with food divided by the number of nestlings per hour of observation. Proportion of the duration of brooding was calculated by dividing the total minutes of duration of brooding in 60 min (1 hour) by 60 min. The diet contents were categorized into 4 categories: invertebrates, vertebrates, humanfood and fruits. Invertebrates' categories were further subdivided into orders: Aranea, Hymenoptera, Lepidoptera, Orthoptera, Mantodean, Opisthopora and Odonata. To check for synchrony in provisioning behaviour, the number of individuals arriving with food at the same time near the nest was counted as the total number of synchronized feedings for that particular feeding visit. Then, the proportion of synchrony was calculated by dividing the total number of synchronies per observation by the total number of feeding visits including both synchronized and non-synchronized visits.

4.2.4.2 Communication during provisioning

The total number of individuals with food landing on the nest was counted as the total number of tactile stimuli. Similarly, combining all the instances of the prompt call produced when an individual with food approach toward nest was counted as the total number of prompt call. The total number of nests used in the analyses are given in Table C4.4. The proportion of response by begging to tactile stimuli and prompt call was calculated by dividing the total number of responses to each stimulus (tactile and call) to the total number of adult visit and prompt call respectively. Similarly, the proportion of begging responses to each playback stimulus was calculated by dividing the total number of begging responses to playback trials for each stimulus to the total number of playback trials.

4.2.5 Statistical analyses

4.2.5.1 Provisioning, diet, brooding and synchrony

All the statistical tests were performed in R version 4.0.3 (R Development Core Team, 2020). Shapiro-Wilk test was performed to check the normality of the data. Spearman Rank Correlation test was done to check whether there is a correlation in the provisioning rate with different times of the day, group size and the age of the young ones. A Chi-square test was done to check whether there is a difference in the proportion of different diet contents between the adults and the young ones. Furthermore, to check the correlation between the duration of brooding with the age of the young ones and the number of young ones in the nest, the Spearman Rank Correlation test was run. Mann-Whitney U/Wilcoxon Rank Sum test was carried out to check the difference in the provisioning rate and the duration of brooding between the parasitized and unparasitized nests. Chi-square test was done to check if there is a significant number of synchronized feeding present in the provisioning behaviour of JB. In addition, the Spearman Rank Correlation test was carried out to check the correlation between the number of synchronized feeding and the group size, age of young ones and number of young ones.

4.2.5.2 Communication during provisioning

A Chi-square test was performed to check the significance of begging response to the prompt call and the adult visit. Spearman Rank Correlation test was carried out to check if there is any correlation between the age of the young ones and the proportion of production of the prompt call, proportion of begging response to the prompt call and adult movements. To examine if the group identity from which the different call types (playback stimuli) were recorded to use the min the playback had any effect on the response, a Generalized Linear Mixed Model (GLMM) (lmer in R package lme4; Bates et al. 2015) with binomial family and logit function was carried out. The playback stimuli and the stage of the young ones were considered as independent variables and the begging response to the stimuli as dependent variable. The group ID of the call types (playback stimuli) were considered as random variables. Further, a Likelihood Ratio Test (LRT) (lrtest in R package lmtest; Zeileis and Hothorn 2002) was carried out. Chi-square test was carried out to examine the begging response to the different playback stimuli at different stages of the young ones.

4.3 Results

4.3.1 Provisioning, diet, brooding and synchrony

The provisioning rate was found to be negatively correlated with the days to fledge by the young ones but there was no significant correlation between the provisioning rate and the time of the day and the group size (Figure 4.4a to c and Table 4.2a). There was a significant difference in the provisioning rate between the nest with (JBJC) and without brood parasitism (JB) (W = 1500.5, *p* = 0.01002; Figure 4.4d). It was found that there was a significant difference between the young ones and adults in the category of invertebrate and fruit diet (Figure 4.5 and Table 4.3). In both adults and young ones, the larger proportion of their diet contents was found to be invertebrates which contributed around 66% and 91% respectively (Figure 4.5). Among these invertebrates, the largest contributor in the diet content was Lepidoptera (Figure C4.1). Spearman Rank Correlation tests showed that the proportion of the duration in brooding significantly negatively correlated with the days to fledge, but did not show any significant correlation with the time of the day, group size and young ones (Figure 4.6a to d and Table 4.2b). Mann-Whitney U result showed that there was no significant difference in the proportion of duration in brooding between the nests with (JBJC) and without brood parasite (JB) (W = 2535, *p* = 0.05118; Figure 4.6e). The Chi-square result showed that the percentage of the number of synchronized feeding is significantly higher than the number of non-synchronized feeding (Chi-square test, $\chi^2 = 9.685$, *p* = 0.002; Figure 4.7a). The proportion of synchronized feeding did not vary with the group size, young ones and the age of the young ones (Figure 4.7b to d and Table 4.2c).

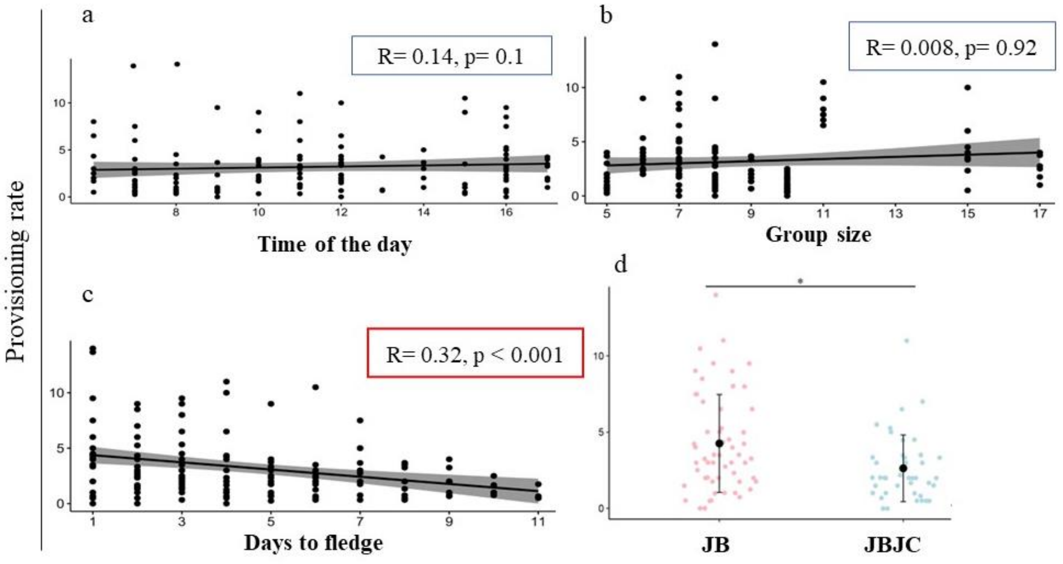


Figure 4.4. Correlation between the provisioning rate and **a)** time of the day, **b)** group size and **c)** days to fledge and **d)** comparison between the provisioning rate of the nest without brood parasite (JB) and with brood parasite (JBJC) showing mean ± sd. * indicates the significant difference.

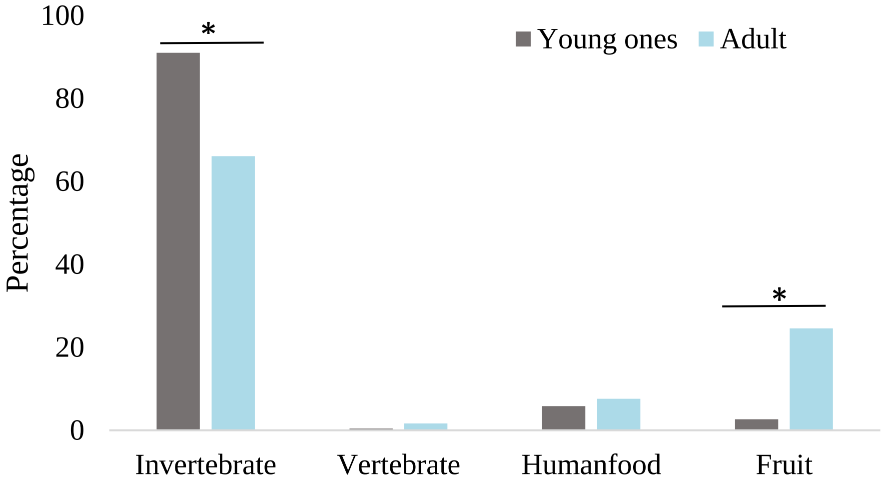


Figure 4.5. Comparison of the different categories of diet content of the young ones and adults. * Indicates significant difference.

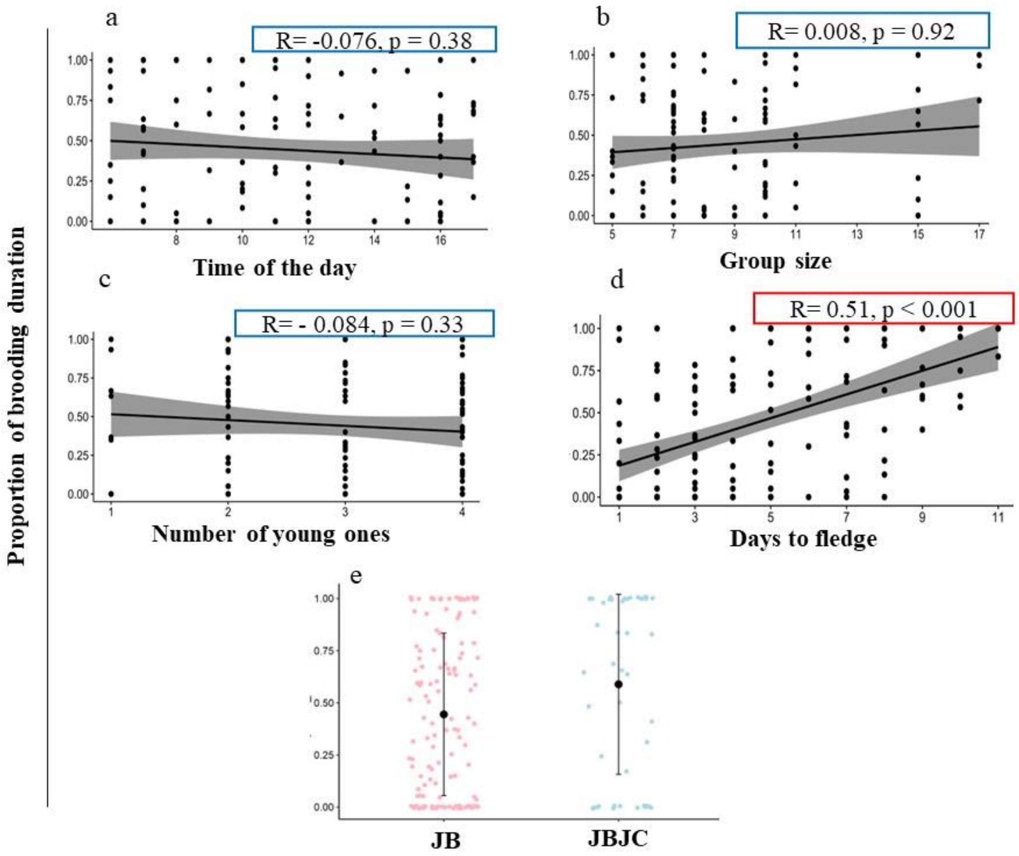


Figure 4.6. Correlation between the duration in brooding and **a)** time of the day, **b)** group size, **c)** number of young ones and **d)** days to fledge (age of the young ones). **e)** comparison of the proportion of duration in brooding between the nests without brood parasite (JB) and with brood parasite (JBJC) showing mean ± sd.

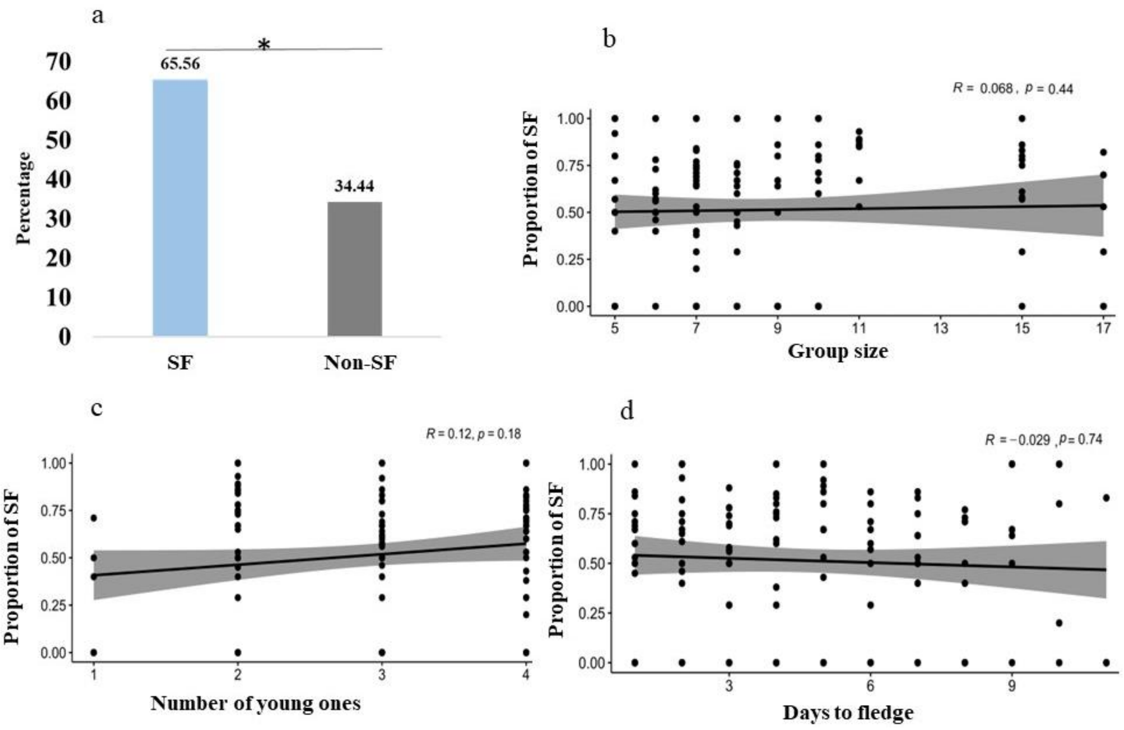


Figure 4.7. **a)** Difference in the percentage of the number of synchronized feeding (SF) and non-synchronized feeding. * indicates the significant difference. Correlation between the proportion of synchronized feeding and **b)** group size, **c)** number of young ones and **d)** days to fledge.

Table 4.2 Summary of the results of Spearman Rank Correlation test between **a)** the provisioning rate **b)** the proportion of duration in brooding **c)** the proportion of synchronized feeding and with the factors: the time of day, group size, number of young ones and age of the young ones.

	Factors	**S**	**R**	***p***
a) Provisioning rate	Time of the day	352	0.141	0.102
	Group size	414	-0.009	0.919
	Age of the young one	540	-0.317	0.0001
b) Brooding duration	Group size	415	0.009	0.918
	Number of young ones	454	-0.084	0.332
	Age of the young one	205	0.511	<0.0001
c) Synchronized feeding	Group size	374	0.068	0.438
	Number of young ones	354	0.117	0.1797
	Age of the young one	413	-0.029	0.738

Table 4.3 Summary of the chi-square test for comparison between the proportion of different diet contents of young ones and adults.

Diet Category	χ^2	**df**	p
Invertebrates	17.002	1	<0.001
Vertebrates	0.027	1	0.869
Humanfood	0.051	1	0.821
Fruit	18.529	1	<0.001

4.3.2 Communication during provisioning

Spearman Rank Correlation results showed that the proportion of prompt call ($R = -0.460$, $p = 0.001$) and begging responses to the prompt call varied significantly with the age of the young ones ($R = -0.351$, $p = 0.019$; Figure 4.8a and b). However, there was no significant correlation in the proportion of begging response to the adult movements ($R = 0.158$, $p = 0.27$; Figure 4.8c). Moreover, there was no significant begging response to both prompt call (Chi-square test, $\chi^2 = 0.04$, $p = 0.842$) and adult movement irrespective (Chi-square test, $\chi^2 = 3.24$, $p = 0.072$) of the age (Figure C4.2). GLMM and LRT results showed that there was no effect of the group Id of the calls used in the playback experiment (Table C4.5a and b). Chi-square results showed that the proportion of begging response towards the BS, BS+F and BS+P was significantly high at the hatchling and nestling stage (Figure 4.9a and b and Table 4.4). There was no significant begging response towards P and F and no response towards C (negative control) (Figure 4.9a to c). The results of the experiment show that call alone, irrespective of the call type, does not elicit begging. Branch Shake (BS), on the other hand is necessary and sufficient to elicit begging until they reach the prefledge stage where begging response, irrespective of stimulus type reduces significantly, indicating an ontogeny of begging response.

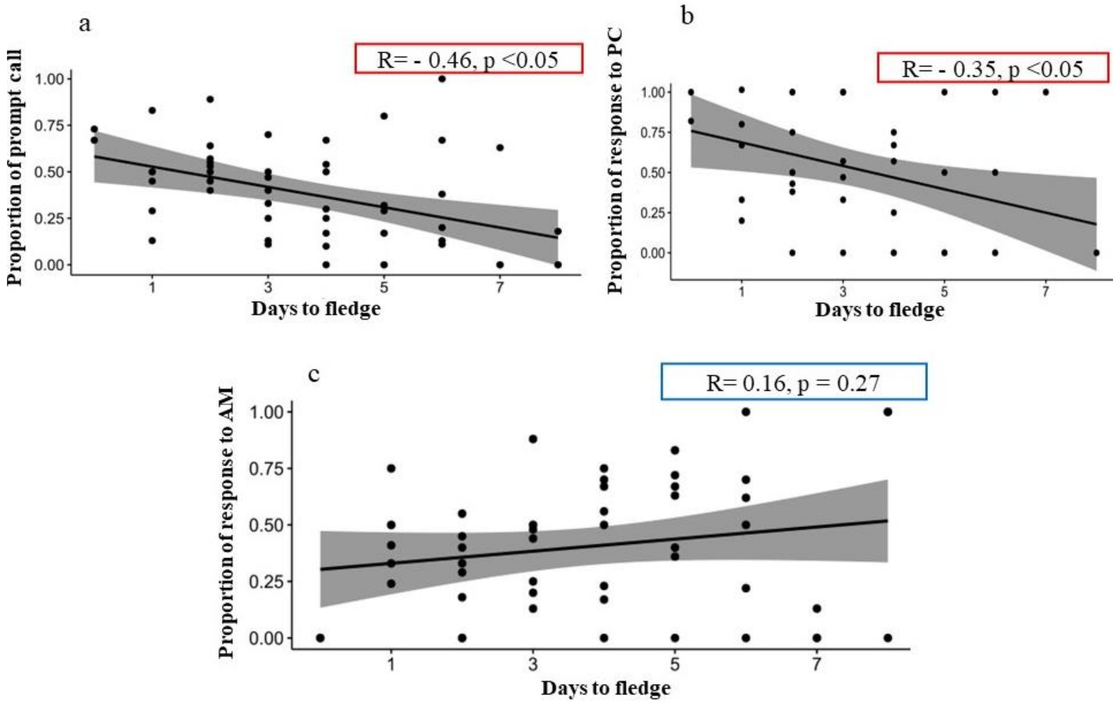


Figure 4.8. Correlation between the proportion of **a)** prompt call (PC) and the age of the young ones, **b)** begging response to prompt call and the age of young ones and **c)** begging response to adult movement (AM) and the age of young ones.

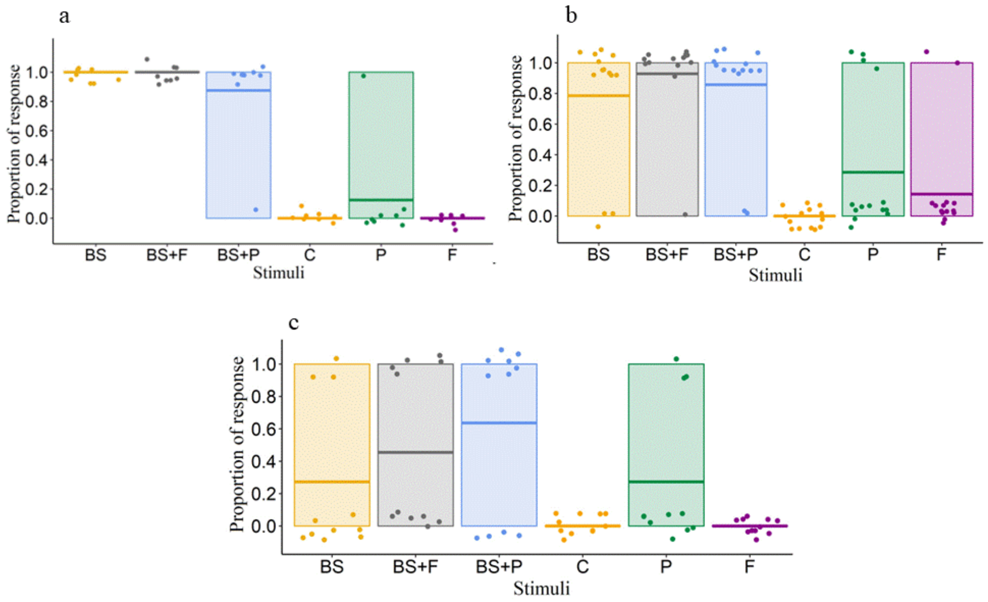


Figure 4.9. The proportion of begging response to the different stimuli at different stage of the young ones: **a)** hatchling, **b)** nestling and **c)** prefledge. Bar indicates the proportion of

begging responses and points indicate the number of raw data of no response at the 0.0 and response at 1.0 at the Y-axis. BS – Branch shake; BS+F – Branch shake+Flight; BS+P – Branch shake+Prompt; C – Contact; P – Prompt; F – Flight.

Table 4.4 Summary of the Chi-square test for the proportion of begging response and the proportion of no response to each playback stimuli at different stages of the young ones: a) hatchling, b) nestling and c) prefledge. BS – Branch shake; BS+F – Branch shake+Flight; BS+P – Branch shake+Prompt; C – Contact; P – Prompt; F - Flight. +ve implies that the subjects exhibited begging significantly more than chance alone and -ve implies absence of begging. NS indicate no statistical significance.

Stages	**Stimuli**	χ^2	**df**	p	**Response type**
Hatchling	BS	33.64	1	<0.001	+ve
	BS+P	51.84	1	<0.001	+ve
	BS+F	92.79	1	<0.001	+ve
	P	51.84	1	<0.001	-ve
	C	33.64	1	<0.001	-ve
	F	33.64	1	<0.001	-ve
Nestling	BS	33.64	1	<0.001	+ve
	BS+P	51.84	1	<0.001	+ve
	BS+F	92.79	1	<0.001	+ve
	P	17.64	1	<0.001	-ve
	F	51.84	1	<0.001	-ve
	C	33.64	1	<0.001	-ve
Prefledge	BS	21.16	1	<0.001	-ve
	BS+P	7.84	1	0.005	+ve
	BS+F	1	1	0.313	NS
	P	21.16	1	<0.0001	-ve
	C	33.64	1	<0.001	-ve
	F	33.64	1	<0.001	-ve

4.4 Discussions

4.4.1 Provisioning, diet, brooding and synchrony

From the results, it was found that both age of the young ones and brood parasitism can influence the variation in the provisioning rate of JB. The provisioning rate increased significantly with the age of the young ones. Similar to our result, Goodbred and Holmes (1996) and Browning et al. (2012) reported that in Black-throated Blue Warblers and Chestnut-crowned babbler, the provisioning rate increased with the age of the young ones. It is speculated that the increase in the provisioning rate is to fulfil the energetic demand of the young ones as they grow which is supported by an allometric study by Weathers (1992) which showed that the daily metabolized energy increased as the nestling grows. The rate of provisioning was found to be higher in the broods without brood parasitism (JB) than in those with brood parasitism (JBJC). From the perspective of the co-evolutionary arm race between the host and the brood parasite, the host will develop mechanisms/strategies to avoid the negative impact on their fitness and in turn the brood parasite will develop counter adaptive strategies to the host's defence mechanism. There are evidences where the host parents are either providing the parasitic nestlings with different diet or a diet of low quality (reviewed in Soler 2009). Studies in a cooperative breeder, Baywing showed that the brood parasitism by Screaming and Shiny cowbirds increased the provisioning rate of the host (Ursino et al. 2011). It was not possible to calculate the difference in provisioning rate between the young ones of conspecific versus that of the brood parasite by the carers due to logistical difficulties such as height of the nests, in making within-nest observations. It can only be speculated that JB can discriminate between their own young ones and that of the parasite (JC) and thereby provision differentially. Further, the ability of adult JB to discriminate may be dependent on the age class of the young ones (see Chapter 5). Thus, further evidence is needed to examine discrimination against brood parasites by JBs and with the limited sample size (5 nests with brood parasites), the evidence for discrimination should be interpreted with caution.

The provisioning rate of JB did not show any variation with the time of the day. There are different results from different studies. Black-throated blue warbler also did not show any variation in the provisioning rate with the time of the day (Goodbred and Holmes 1996) whereas, Rufous treecreeper showed a negative association with the time of the day (Luck 2001). Provisioning rate of JB did not show any variation with the group size. Similar findings have been reported in Rufous treecreeper in which provisioning rate did not change with the increase in the number of helpers. This has been attributed to the ‘load-lightening effect’ wherein the increase in helpers does not alter the provisioning rate but serves to lighten the load of provisioning per individual (Luck 2001). However, in Azure-winged magpie, the provisioning rate increased as the number of helpers increased (Valencia et al. 2006). It is speculated that in JB, the investment by the helpers in provisioning is compensating for the reduction in provisioning rate by the breeders to lighten the load on the breeders and thereby increase the chances of indirect fitness by improving the survival and fitness of the breeder. Further, it is likely that load-lightening may also serve to increase the probability of retaining and attracting helpers who will benefit from the lighter load of provisioning and higher probability of success of the nest. However, this has not been tested in this study and can be taken up for future examination.

The diet content of both adults and the young ones of JB was found to be relatively similar consisting of invertebrates which contributed around 50 % by the Lepidopterans (in this study it is the larva/caterpillar). This result is consistent with the previous study done on Great tits (*Parus major*), where the diet consisted mainly of caterpillars (Wilkin et al. 2009). Even though the diet content was relatively similar, invertebrates’ content in the diet of young ones was significantly higher than the adult. Similar findings have been reported in Bluethroats *Luscinia svecica* spp. *cyanecula* in which diet of the young ones contained more easily digestible prey items such as higher Lepidopteran and Diptera larvae than adults (Orłowski et al. 2014). Diet content of the nestlings may also depend on their nutritional requirements (Ramsay and Houston 2003), or the manageability of the prey item by the young ones (Banbura et al. 1999). For example, carotenoids are important for stimulating the immune system in birds and the diet of nestling of insectivorous birds, Great tits, was reported to contain a higher proportion of Lepidopterans larvae, a carotenoid-rich food item (Eeva et al. 2010). Another study on Blue tits, *Cyanistes caeruleus* revealed that the nestlings at younger ages were fed food items such as spiders that contained a higher level of taurine which is correlated with improved cognitive function and better in handling stressful situations (Arnold et al. 2007).

Duration of brooding showed a positive association only with the days to fledge by the young ones but no correlation with the group size, number of the young ones, the time of day and brood parasitism. The result of the decrease in duration of brooding with the age of the young ones corresponds with the results from the study on the Gray catbird *Dumetella carolinensis* (Johnson and Best 1982) and House sparrow (Chastel and Kersten 2002) which reported a decrease in brooding with the age of nestling. From this result, it can be postulated that with age, the young ones of JB enhance their ability to thermoregulate. However, in the same study on Gray catbird, the brooding duration was associated indirectly with the time of the day in which brooding was high in the early morning and evening which contrasted with the results found in JB. Moreover, in House sparrow, brooding duration decreased in the reduced brood size which also contrasted with the results in this study. No variation in the duration of brooding with time of day and brood size in JB can be attributed to the possibility that the position of the nest is such that there is not much temperature fluctuation (thickly covered foliage) and the brood size used in this study is not variable enough to consider the changes respectively. In addition, group size and brood parasitism did not influence the variation in the brooding duration which can be assigned to the load lightening of the breeder as mentioned earlier. Further, the lack of difference in brooding duration in parasitized and unparasitized nests can be explained by the fact that the parasitized nests also contained JB young ones. Since the exposure of their own offspring cannot be exempted, the cost of not brooding might be higher than brooding. However, the sample size for brood parasitism was not enough to be conclusive about the effect of brood parasitism on brooding duration. In the future, it will be advantageous to check on the nests where there are only young ones of brood parasites.

In JB, the provisioning behaviour was found to be exhibited synchronously for around 65% of the time. This result corresponded with previous studies in Arabian babbler, *Turdoides squamatus* (Carlisle and Zahavi 1986) and Sociable weaver, (Doutrelant and Covas 2007) in which the helper waited with food for the other group members before approaching the nest. These results are attributed to the possibility of the signalling or advertising their participation in provisioning duty (Zahavi 1995). However, a study in Pied babbler does not support the above postulations but the synchrony is explained by the reduction in the risk of predation and the increase of brood survival (Raihani et al. 2010). Furthermore, it was found that the proportion of synchronized feeding did not vary with the group size, number of young ones and the age of young ones. This result is in contradiction with the result found in Pied babblers which showed that feeding visits were more likely to synchronize for older nestlings and larger groups. This synchrony pattern might be explained by the reduction of the possible conspicuousness to predators because of louder begging calls of older nestlings and the reduction of feeding visit (Raihani et al. 2010). However, it will be early to come to any conclusion. So, future studies in investigating the reproductive status of the carer involved in this provisioning behaviour are very important.

4.4.2 Communication during provisioning

From the field observations, it was found that there was no significant response to both adult visits and prompt call irrespective of the age of the young ones. However, the production of prompt call as well as the begging response to the prompt call increased with the age of young ones. Pied babblers also showed increase in the production of ‘purr call’ (call given when feeding young ones) with the nestling age and the experienced nestlings gave a begging response to this ‘purr call’ (Raihani and Ridley 2008). It is speculated that the intensity of begging calls might increase with age, in turn leading to a higher risk of predation (Haff and Magrath 2011). Thus, it will be advantageous for both adults and young ones to effectively communicate about the arrival of food. Nevertheless, it will not be adequate to conclude that the begging response is only due to acoustic signals, as we cannot ignore the signal of tactile stimulus when an adult lands on the nest. To separate the effect of vocal and tactile stimuli on the begging response behaviour, playback experiments were carried out.

From the experiment, it was found that young ones at different stages responded differently to different stimuli. Nestling and hatchling stages responded significantly to both single tactile stimulus (BS) and multimodal stimuli (BS+P and BS+F) indicating that the tactile stimulus might be necessary and sufficient to initiate the begging response at the early stage of young ones of JB. Nestlings of the Black-capped chickadee, *Parus atricapillus*, were found to elicit higher begging response to vibratory stimuli than to vocalization of parents and with age, they started to respond more to the relevant stimuli associated with feeding (Clemmons 1995). At the prefledge stage, tactile stimulus alone did not seem to be adequate to stimulate the begging response as at this stage, the young ones responded significantly only to the multimodal signal with the prompt call. In addition, irrespective of age, there was no response towards contact call as well as the response towards prompt and flight call seemed to differ between different stages even though there were no significant results. An experimental study on Pied babblers showed that the young ones learned to associate the ‘purr call’ with food. This is supported by the results that the young ones who were conditioned to associate the playback call with food responded earlier than the one with only playback call without food (Raihani and Ridley 2008). Previous study by Khayutin (1985) in altricial birds showed that there were different sets of stimuli that induced the begging response at different nestling stages. Nestling at the age of 0-6 days after hatching responded to wide range of sound from the tapping feet on the nest wall, rustling of nest material with the arrival of the adult and the feeding call. As the nestling grew the triggering stimuli changed from visual to both visual and tactile and then to only tactile (adult movement while entering the nest) at the last stage of nestling. These results indicate the possibility of ontogeny in the begging response in terms of their development and they are utilizing these advantages in reducing the cost during provisioning (energetically costly begging, risk of predation, energy-demanding food provision).

This study provides a platform for future studies in cooperatively breeding species in investigating the role of each carer in different forms of parental care such as provisioning, brooding and nest defending. This should be looked at in the context of relatedness to the brood as well as to each other. In addition, this study shows that there are several factors that are associated with the variation in the different forms of parental care. Thus, in future studies, it is recommended to investigate each form of parental care, the factors influencing them, and how the interactions between these factors determine the variation in care. Furthermore, this study provides information for prospects on the employment of multimodal signalling as an extended form of parental care.

4.5 Appendix C

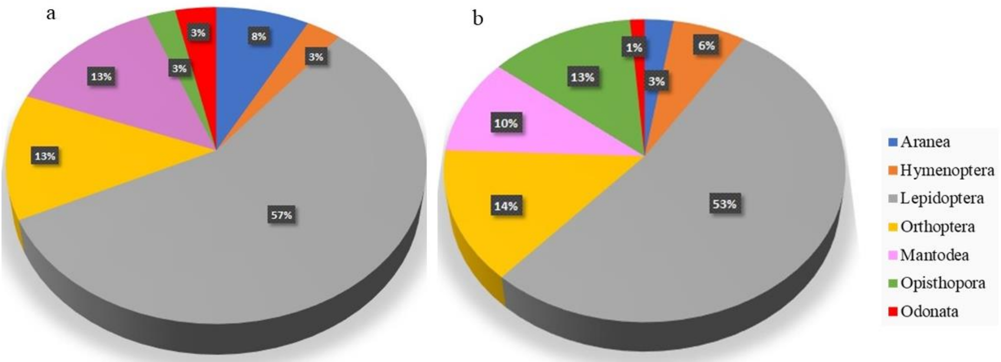


Figure C4.1 Proportion (in percentage) of different order in the category of invertebrates: a) young ones and b) adults.

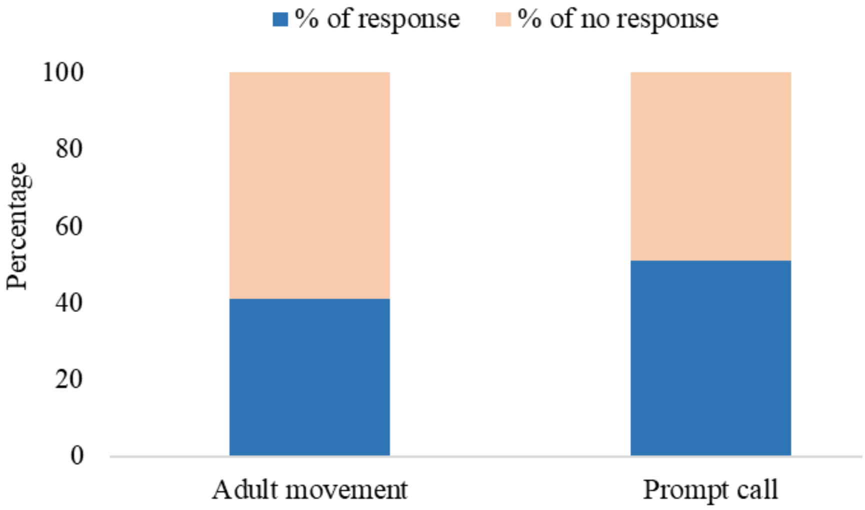


Figure C4.2 Percentage of response and no response to adult movement and prompt call.

Table C4.1. Nests without brood parasitism. Number of nests and hours of observation used in analyses for food provisioning **a)** for each group size of the adults **b)** at different ages of the nest (days to fledge). Numbers in bold and italics were not used in the analyses.

a)

No. of adults	No. of nests	No. of hours of observation
5	3	13
6	2	15
7	4	31
8	4	19
9	1	11
10	2	22
11	1	7
15	3	11
17	1	6

b)

Days to Fledge	No. of nests	No. of hours of observation
1	19	19
2	18	18
3	20	20
4	16	16
5	14	14
6	12	12
7	10	10
8	10	10
9	7	7
10	5	5
11	4	4
12	***2 (1 unhatched)***	***1***
13	***2 (1 unhatched)***	***1***
14	***1 unhatched***	***0***

Table C4.2. Nests with brood parasitism. Number of nests and hours of observation used in analyses for food provisioning **a)** for each group size of the adults **b)** at different ages of the nest (days to fledge). Numbers in bold and italics were not used in the analyses.

a)

No. of adults	No. of nests	No. of hours of observation
7	2	22
8	2	15
11	1	9
12	***1***	***5***

b)

Days to fledge	**No. of nests**	**No. of hours of observation**
1	6	5
2	6	5
3	6	5
4	6	5
5	4	3
6	3	3
7	4	4
8	4	4
9	4	4
10	3	3
11	2	2
12	***1***	***1***
13	***1***	***1***
14	***1***	***1***

Table C4.3 Number of nests and number of hours of observation for each day before the nestlings fledge for the nest **a)** without brood parasitism and **b)** with brood parasitism. Numbers in bold and italics were not used in the analysis due to its small sample.

a)

Days to Fledge	**5 adults**	**6 adults**	**7 adults**	**8 adults**	**9 adults**	**10 adults**	**11 adults**	**15 adults**	**17 adults**
1	1	2	4	4	1	2	1	3	1
2	1	2	4	4	1	2	1	2	1
3	2	2	4	4	1	2	1	3	1
4	2	2	4	1	1	2	1	2	1
5	3	1	3	1	1	2	1	1	1
6	1	2	3	1	1	2	1		1
7	1	1	3	1	1	2	1		
8	2	2	2	1	1	2			
9		1	2	1	1	2			
10			1	1	1	2			
11			1		1	2			
12			***1***						
13			***1***						

b)

Days to fledge	**7 adults**	**8 adults**	**11 adults**	**12 adults**
1	2	2	1	***1***
2	2	2	1	***1***
3	2	2	1	***1***
4	2	2	1	***1***
5	1	1	1	***1***
6	1	1	1	
7	2	1	1	
8	2	1	1	
9	2	1	1	
10	2	1		
11	1	1		
12	***1***			
13	***1***			
14	***1***			

Table C4.4. Number of nests used in the analyses for the begging response to natural prompt call and adult movement. **a)** total number of nests used for overall comparison irrespective of age and number of nests used for age-related analyses and **b)** number of nests used for the analysis of response to natural prompt call and adult arrival (tactile movement) for each day before the nestling fledges. Numbers in bold and italics were not used in the age-related analyses.

a)

No. of nest	**No. of the nest used for age-related analysis**
12	10

b)

Days to fledge	**No. of nest**
0	***2***
1	6
2	8
3	8

4	8
5	7
6	6
7	3
8	3
9	***1***
10	***1***

Table C4.5 Result of **a)** Generalized Linear Mixed Model (GLMM) and **b)** Likelihood Ratio Test (LRT) for the model with and without random effect (group Id of the calls used in the playback experiment).

a) GLMM	**BIC**	**deviance**	**df**	***p***	**b) LRT**	**Model**	**AIC**	**loglik**	**χ^2**	***p***
	197.1	138.8	189	0.012		With random effect	160.81	-69.406	*0*	0.99
						Without random effect	158.81	-69.406		

Chapter 5

Vocal discrimination by Jungle Babbler between the young ones of its conspecific and brood parasite

5.1 Introduction

Obligate avian brood parasites (hereafter brood parasites) do not build their nest and instead lay their eggs in the nest of the host species who bear the cost of parental care (Lyon et al. 2004; Payne and Sorensen 2005). These impose a great cost on the reproductive success of the host more than nest predation in which the host has a chance to restart nesting again (Rothstein 1990) and as a consequence, the host may develop many strategies to defend against brood parasitism. Owing to the benefits of multiple carers providing superior care in cooperative breeders, they offer to be a good host to many avian brood parasites. A comparative study by Feeney et al. (2013) showed that there is a tight association between brood parasitism and the cooperative breeding system in which the brood parasite may be able to get parental care from multiple carers. Conversely, the host may be able to defend against the brood parasite better when multiple helpers are present, thereby driving the evolution of cooperative breeding. In this regard, brood parasitism offers a robust paradigm to explore the complex system associated with the multispecies interactions that may vary further with different stages of the life cycle stages of animals (Kennerley et al. 2022). Moreover, these interactions between the brood parasite and host in avian obligate brood parasitism represent one of the best model systems to study co-evolutionary arms race (Davies and Brooke 1988; 1989; Rothstein 1990).

These co-evolutionary arms races occur at different stages of the breeding cycle, starting at the pre-egg-laying stage (hereafter frontline adaptation) and up to the fledgling stage but comparatively less at the fledgling stage (reviewed in Feeney et al. 2014). Successful parasitism starts from the frontline adaptation when the brood parasite successfully lays eggs inside the host nest by avoiding the chances of being identified (reviewed in Feeney et al. 2014; Feeney 2017). Brood parasites can achieve this by evolving different traits such as cryptic behaviours (watching host's nest from hidden or distant places to optimize the chances of egg-laying without being identified, Honza et al. 2002), plumage mimicry of a dangerous predator or harmless heterospecific species to deter or distract host respectively (Krüger et al. 2007), plumage polymorphism (co-existence of different colour plumage in the same species, Trnka & Grim 2013), etc. As a counter-adaptation to the parasitism, the host also develops many mechanisms such as recognition of the brood parasite (Feeney and Langmore 2013), nesting together with conspecific that eases in-group defense (Clark and Robertson 1979), mobbing or attacking brood parasite (Welbergen and Davies 2009).

After successfully laying eggs in the host nest by parasites, the arms race will continue to the next stage of the breeding cycle (reviewed in Feeney et al. 2014; Yang et al. 2014; Stoddard and Hauber 2017). At the egg stage, the host may defend against parasitism by recognizing and discriminating in accordance with the colour (Spottiswoode and Stevens 2010), shape (Mason and Rothstein 1986), size (Marchetti 2000), pattern (Stoddard et al. 2014), arrangement of eggs (Polačiková et al. 2013), etc. and rejecting the parasite egg (Spottiswoode and Stevens 2010). To counter the defence of the host at the egg stage, the parasite may evolve different adaptations such as mimicry of the host egg in colour (reviewed in Feeney et al. 2014), size (Krüger and Davies 2002), shape (Mason and Rothstein 1986), pattern (Stoddard and Stevens 2010), or even laying non-mimetic eggs of a dark colour that become invisible inside the dark nest of the host (Langmore et al. 2009), or thick-shelled eggs (Brooker and Brooker 1991) that are less likely to crack during laying or being damaged by the host (reviewed in Davies 2011; Stoddard and Hauber 2017).

At the nestling stage, the host may recognize the parasite nestling by different cues such as a longer time to hatch (Grim 2007) or by the presence of a lone chick (Langmore et al. 2003). The host may discriminate against the parasite nestling in the form of abandonment of parasitic young ones (Langmore et al. 2003), evicting the parasite nestling (Tokue and Ueda 2010) or via low quality and quantity of provisioning (Grim et al. 2011). In response to the host defence, the parasite may eliminate the host nestling by evicting them from the nest (Davies 2000) or compete with the host nestling by ensuring proper provisioning which can be achieved by mimicking nestling morphology (Langmore et al. 2011), mimicking of gape marking (Schuetz 2005), mimicking begging call of the host (Anderson et al. 2009), or exaggerated visual or vocal display during begging (Briskie et al. 1994; Tanaka et al. 2011). In an altricial bird species, parental care may be extended even after the nestlings are fledged as the fledglings are not completely independent for a while. Providing parental care to the parasite at the fledgling stage furthers the cost to the host suggesting the existence of interaction between the host and brood parasite at the fledgling stage also (reviewed in Feeney et al. 2014).

However, most of the studies on the relationship between host and brood parasite are on the visual traits and mostly up to the nestling stage (reviewed in Feeney et al. 2014) whereas, studies on counteractive strategies at the fledgling stage, as well as the vocal traits (hereafter begging calls) (Jamie and Kilner 2017), are comparatively less (reviewed in Feeney et al. 2014). Begging call is one of the main vocal traits that are used in the communication between young ones and parents/caregivers (in the case of cooperative breeders) in altricial birds in eliciting parental care (Godfray 1991; Leonard and Horn 2001). This call is produced by the young ones while soliciting food from the caregivers and can be employed as a tool by obligate avian brood parasites in deceiving the host (Jamie and Kilner 2017). Moreover, begging call is one of the important vocal traits that can be mimicked by the non-evictor brood parasite (those brood parasites that do not evict the eggs or nestlings of the host) as a counter-adaptive strategy in evading rejection and in soliciting parental care from the host. Parasitic nestlings may learn to mimic the begging call of the host which allows the parasite nestling to avoid detection and rejection and even elicit more provisioning from the host parent (Wang et al. 2020). Few studies have reported on the plastic nature of the begging call, that it can be learned and that the parasitic nestling can alter the structure of the begging call according to its host (Langmore et al. 2008; Liu et al. 2016). Thus, providing more scope for the parasitic nestling to adapt to the host environment. Despite its promise of being an excellent model system to study adaptation and coevolution, begging calls of about 64% of brood parasites are still unknown and the remaining 34% reported are mostly assessed subjectively or anecdotally (reviewed in Feeney et al. 2014; Jamie and Kilner 2017). This study examined vocal discrimination of the young ones of the brood parasitic Jacobin Cuckoo (*Clamator jacobinus*), by its host Jungle Babblers (*Argya striata*; hereafter JBs).

Jacobin Cuckoo (*Clamator jacobinus; hereafter JC*), also known by different names as Pied crested cuckoo, Pied cuckoo and Black crested cuckoo, is one of the non-evictors obligate avian brood parasites and two subspecies are known in India. One of the subspecies that are found in the study area is *Clamator jacobinus pica* and they arrive in northern India for breeding during monsoon. They are generalist brood parasites parasitizing on JB, Common babbler and Large grey babbler in the study area. Their eggs are of similar blue colour to the host egg but more rounded, less glossy and with harder egg shells (Gaston 1976; Payne and Sorensen 2005) (Figure 5.1). On the contrary, fledgling and pre-fledgling show no sign of host mimicry, possessing easily distinguishable black and white plumage and growing much faster than host nestling (Gaston 1976) (Figure 5.2). Even with their morphologically distinct features, most of the JC nestlings grow up together with the host nestling and even the fledged cuckoos are still fed by the host (Payne and Sorensen 2005). Thus, for the visually distinct parasitic JC nestling to integrate into the host environment without being rejected, it is possible that it exhibits vocal mimicry of the host young ones. Thus, this study had the following objectives

1) Do the acoustic features of the calls of young ones of the brood parasite share similar features with of the host?

2) Can JBs discriminate between the calls of young ones of its conspecific and that of brood parasite?

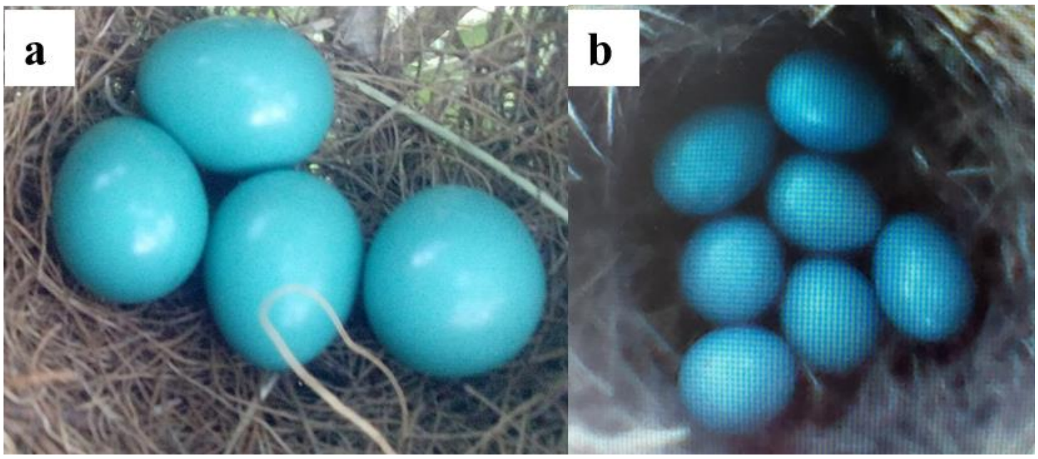


Figure 5.1 **a.** Eggs of only JB in a nest, **b.** eggs of both JB and JC in the same nest.

Figure 5.2 Fledgling of JB (left) and JC (right).

5.2 Materials and methods

5.2.1 Study site

The study site is the same as given in section 2.2.1 of Chapter 2. In addition to the Mohali region, this study was also conducted in the Chandigarh region (Figure D5.1), where the habitat and the climate are almost the same as in Mohali.

5.2.2 Acoustic data collection

Recordings were collected during the breeding season (March to October, Andrew and Naik 1970; Gaston 1976) of 2016 to 2020. All the recordings were collected using a solid-state recorder (Marantz PMD661*MKII*; frequency response: 20 Hz – 20 kHz), connected to a super-cardioid shotgun microphone (Sennheiser ME66 with K6 PM; frequency response: 40 Hz to 20 kHz), covered with a foam windscreen (Sennheiser MZW66) with the sampling rate of 44.1 kHz and 16-bit accuracy. Two types of calls: 1) begging calls and 2) fledgling close calls were recorded from the young ones of JB and JC and only begging call type was recorded from the young ones of Common Myna (CM) for this study. Begging call is the call produced by the young ones associated with a typical behaviour of flapping wings along with the wide mouth opening whereas the fledgling close call is produced mostly by fledgling when an adult is perching on a different branch or tree or not around them when gone in search of food (Leonard and Horn 2001; Yambem et al. 2021). Begging calls in hatchling and young nestling stages were feeble and hard to get good recordings. Thus, begging calls were recorded only from the nestling (with developed feathers and open eyes) as well as from the fledgling stage whereas the fledgling close calls were recorded from the fledgling stage only, when they are out of the nest but still dependent on adults (sample size in Table D5.1).

5.2.3 Acoustic analyses

All the recordings were analyzed using Raven Pro 1.5 (Cornell Laboratory of Ornithology, USA) and spectrograms were generated using the Hann window function, size 512 with a 50% overlap. Only those calls where there was no overlap from other calls, as well as the same call of the brood mates and with a high signal-to-noise ratio, were selected for further analysis. To examine acoustic differences in the call types, the following acoustic parameters were measured: A) spectral parameters- i) frequency 5% (referred to as minimum frequency and represents frequency which lies at 5% of the energy in the call), ii) frequency 95% (referred to as maximum frequency and represents frequency which lies at 95% of the energy in the call), iii) bandwidth 90% (referred to as frequency bandwidth and is the difference between frequency 95% and frequency 5%) and iv) peak frequency (it is the frequency with maximum energy); B) temporal parameter- i) call duration (measured as the difference in time between the onset and offset of a call).

5.2.4 Playback experiment

In order to check whether the adult can discriminate between the calls of young ones of its conspecific and that of a brood parasite, playback experiments were conducted on 16 different groups of JBs. All the playback experiments were conducted between October 2020 to March 2021. One trial consisted of five playback stimuli of the following calls: begging call of 1) host, 2) brood parasite, 3) Common Myna (negative control) and fledgling close call of 4) host and 5) brood parasite. Calls for the playback were generated in Raven Pro1.5. Every playback was constructed in such a way that the rate of calling matches that of a natural call and the duration of each playback was kept at 1 min (Figure 5.3). Each playback was created from calls of 3 different individual nestlings or fledglings.

A group was subjected to a complete set of playbacks and no repeat trials on any group were conducted.

A Sony speaker (SRS XB30) was used to playback the calls by placing either on the ground or tree branch at heights of 1-2 m and at a distance of 5-20 m from the focal animal (≥ 5 ≤ 20). The loudspeaker was connected to an Android smartphone via Bluetooth which enable the observer to control the playback from a safe position. A gap of at least two minutes was kept in between each playback stimulus. The order of the playback was randomized. Calls were played back at the 60-65dB at 5m from the loudspeaker (SPL was measured using Larson and Davis). In order to compare the responses towards different playback stimuli, the following measurements of behaviours following playback were taken: 1) approach towards the speaker (within 3m), 2) nature of approach (with call or silently) and 3) latency of response by noting the time elapsed from the initiation of playback till at least one bird from the focal group started approaching the speaker.

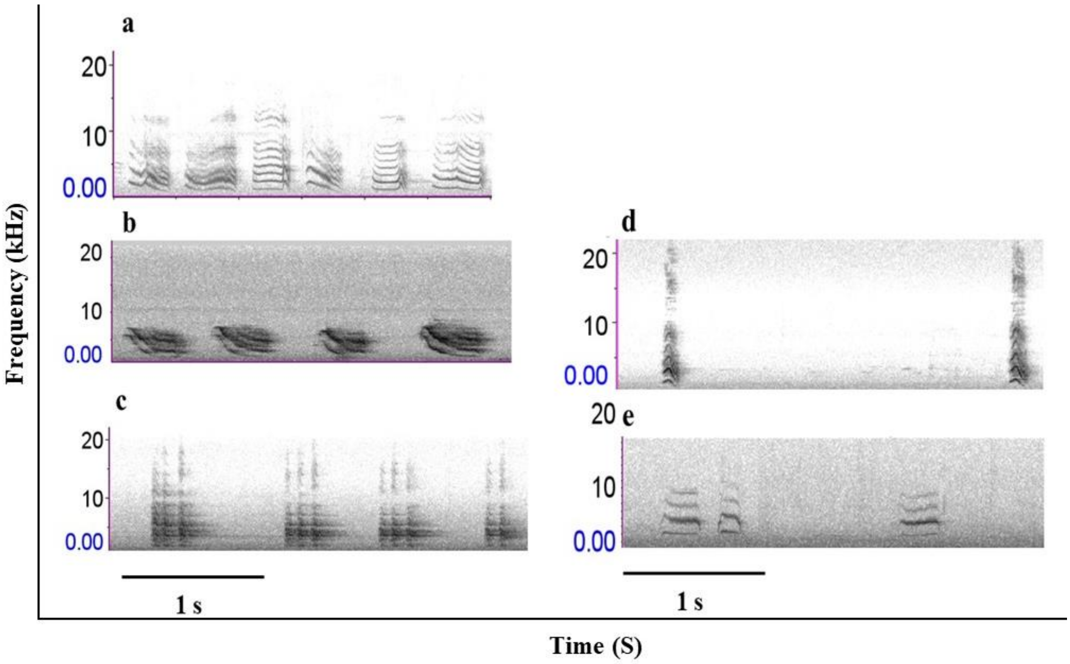


Figure 5.3. Spectrograms of begging call of young ones of **(a)** JB, **(b)** JC and **(c)** CM and fledgling close call of **(d)** JB and **(e)** JC.

5.2.5 Statistical analyses

Statistical tests were performed in R version 4.0.3 (R Development Core Team, 2020). Shapiro-Wilk test was performed to check the normality of the data for acoustic features of all the call types. Kruskal-Wallis test was done for the comparison of an overall difference between all call types, followed by multiple pairwise comparisons between call types using the R function pairwise.wilcox.test (p-value adjustment method: BH). Moreover, Discriminant function analysis (DFA)/Linear discriminant analysis (LDA) was also carried out to check whether the multivariate data (acoustic features) can discriminate between call types. Further, a leave-one-out cross-validation was performed to confirm the classification by DFA. A Chi-square test was done to check whether there is a difference in the frequency of response to playback between call types. Further, Kruskal-Wallis test was done to check the difference in the latency to response between call types, followed by a pair-wise comparison using Mann-Whitney U test/Wilcoxon Rank Sum test.

5.3 Results

5.3.1 Structure of begging and fledgling close calls of host and brood parasite

The structure of the begging call and fledgling close call of the young ones of the host and brood parasite were found to be significantly different (Kruskal-Wallis test, $p < 0.001$; Table 5.1a; Table D5.2). Multiple pairwise comparisons showed that each call is different from each other's by at least three acoustic features (pairwise.wilcox.test, $p < 0.05$; Table 5.1b). DFA result also validates that each call type of the young ones was correctly categorized based on the priori-defined groups, in which 95% of the total variance is explained by the first two LDs (Figure 5.4). The variance in the DFA was contributed mostly by call duration and bandwidth 90%. The cross-validated result showed that each call type of the young ones was correctly classified with an accuracy of > 70% except for the fledgling close call of JB begging call which is 60% (Table 5.2).

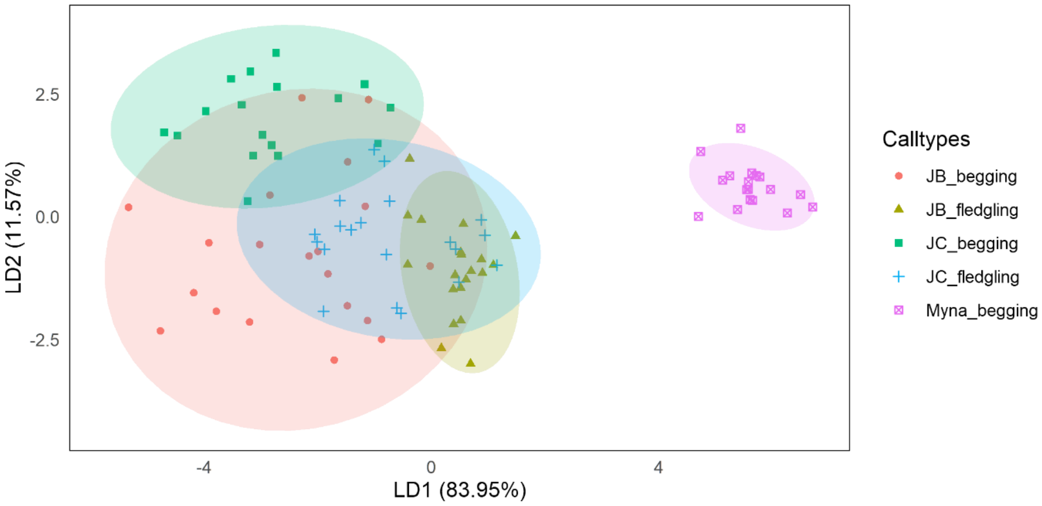


Figure 5.4. Linear Discriminant Analysis (LDA) plot of the first two linear discriminants (LDs) of the call types of young ones. The colour ellipse indicates a 95% confidence interval.

Table 5.1. A summary of the statistical analysis of the comparison of different call types based on 5 acoustic parameters. a) Kruskal-Wallis test and b) P value of the multiple pairwise comparisons of different call types of the young ones of different acoustic features (with p-value adjustment method: BH). NS represent not significant.

a

Call parameters	**χ^2**	**df**	**p**
Call duration (s)	90.88	4	<<0.001
Frequency 5% (Hz)	46.26	4	<<0.001
Frequency 95% (Hz)	57.59	4	<<0.001
Bandwidth 90% (Hz)	53.22	4	<<0.001
Peak frequency (Hz)	51.80	4	<<0.001

b

Comparison of call types	Call duration (s)	Frequency 5% (Hz)	Frequency 95 % (Hz)	Bandwidth 90% (Hz)	Peak frequency (Hz)
Myna_begging vs **JB_begging**	<0.0001	<0.0001	<0.01	NS	<0.05
Myna_begging vs **JB_fledgling**	<0.0001	NS	<0.0001	<0.01	<0.001
Myna_begging vs **JC_begging**	<0.0001	NS	NS	NS	NS
Myna_begging vs **JC_fledgling**	<0.0001	NS	<0.0001	<0.0001	NS
JB_begging vs JB_fledgling	<0.0001	<0.05	NS	NS	NS
JB_begging vs JC_begging	NS	<0.05	<0.001	<0.05	<0.001
JB_begging vs JC_fledgling	<0.001	<0.0001	<0.01	<0.0001	NS
JB_fledgling vs JC_begging	<0.0001	NS	<0.0001	NS	<0.0001
JB_fledgling vs JC_fledgling	<0.0001	<0.0001	NS	<0.01	<0.05
JC_begging vs JC_fledgling	<0.01	NS	<0.0001	<0.001	<0.001

Table 5.2. Values showing the number of correctly classified calls to each call type from the cross-validated results. Number of samples assigned by Linear Discriminant analysis to each call group and percentage of correct classification (CC). Correctly assigned samples are marked in red colours.

Call types	**Myna_begging**	**JB_begging**	**JB_fledgling**	**JC_begging**	**JC_fledgling**	**CC (%)**
Myna_begging	22	0	0	0	0	100
JB_begging	0	15	4	5	1	60
JB_fledgling	0	0	21	0	4	84
JC_begging	0	1	0	19	1	90.47
JC_fledgling	0	0	6	1	17	70.83

5.3.2 Playback Experiment

Results of the chi-square test showed that the JBs significantly responded to both the begging call (Chi-square test, $\chi^2 = 16$, $p < 0.0001$) and fledgling close call (Chi-square test, $\chi^2 = 16$, $p < 0.0001$) of conspecific young ones by approaching towards the speaker (Figure 5.5a). JBs also responded significantly towards the begging call (Chi-square test, $\chi^2 = 16$, $p < 0.0001$) but not to the fledgling close call of the young ones of brood parasite (Chi-square test, $\chi^2 = 1$, $p > 0.05$; Figure 5.5a) and ignored the begging call of Common Myna (Chi-square test, $\chi^2 = 12.25$, $p < 0.001$). Further, JB responded with the call significantly more towards the begging (Chi-square test, $\chi^2 = 12.25$, $p < 0.001$) and fledgling close call (Chi-square test, $\chi^2 = 9$, $p < 0.01$) of the conspecific (Figure 5.5b). However, they responded with call only 50 % of the time to the begging and fledgling close call of brood parasites. Further, the latency of response significantly varied with call type (Kruskal-Wallis, $\chi^2 = 15.332$, df = 2, $p < 0.01$; Figure 5.6). JBs took significantly longer to respond to fledgling calls as compared to the begging calls of its conspecifics. However, it was quick to respond to the calls of the brood parasite's begging as well as fledging call (Multiple pairwise comparisons, Table D5.3).

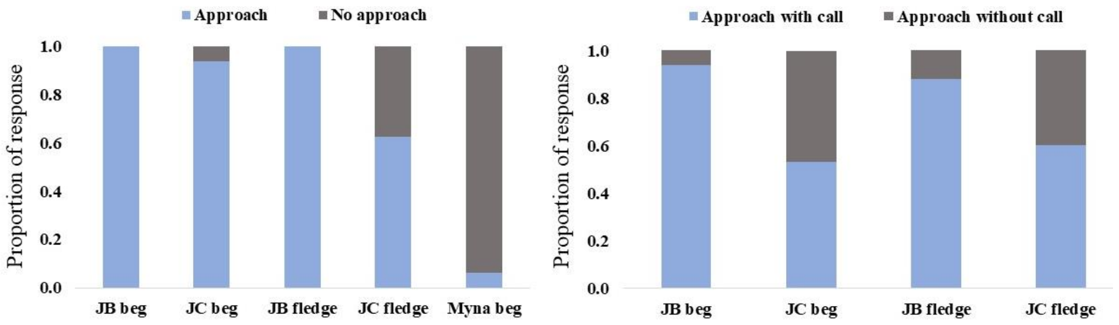


Figure 5.5. Proportion of response towards each call type of the young ones. **a)** proportion of response by approaching towards the speaker and no approach and **b)** proportion of response with call and without call while approaching towards the speaker.

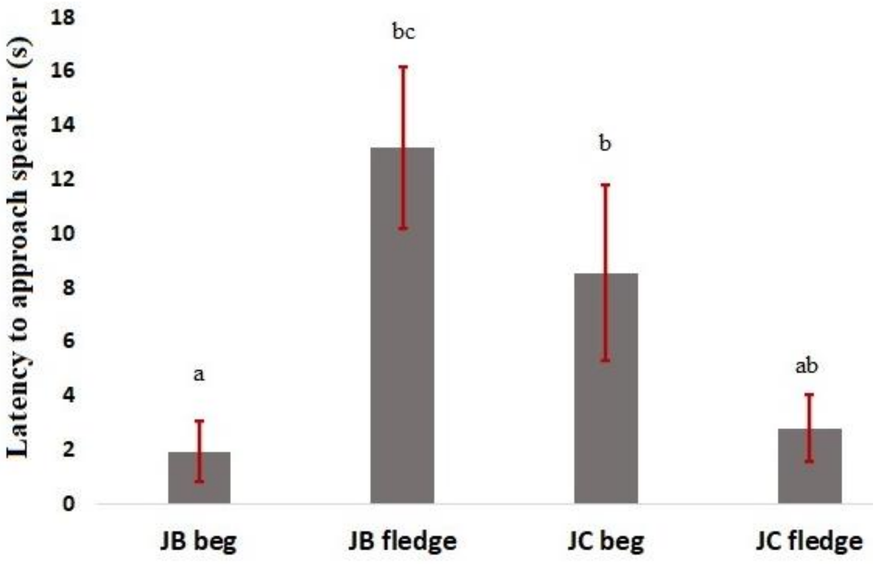


Figure 5.6. Variation in the latency of response to the begging call of young ones of JB and JC and fledgling close call of JB and JC. Different letters denote the significant difference.

5.4 Discussion

Studies examining vocal mimicry between conspecific and brood parasite's begging calls have been carried out in many systems and the results vary considerably from system to system. Payne and Sorensen (2005) proposed that the begging calls of most parasitic cuckoos are likely to differ from that of their host. A study on the Common cuckoo and its 4 different host species showed that the structure of the begging call of the Common cuckoo varied from the begging calls of all 4 of its hosts (Butchart et al. 2003). However, in contradiction, a study by Davies et al. (1998) showed that the begging call of nestling of Common cuckoo mimics the calls of the young ones of its host, the Reed warbler, *Acrocephalus scirpaceus*, thereby ensuring proper parental care. Furthermore, manipulative experiments on a generalist brood parasite, Horsfield's bronze-cuckoo, showed that the parasite's chick mimics different begging calls of its primary host (Superb fairy-wren) as well as its secondary host (Buff-rumped thornbill) (Langmore et al. 2008). Further, a review by Jamie and Kilner (2017) examined the evidence for vocal mimicry in the begging calls of 11 parasitic cuckoos and their host. They reported that out of 11 cuckoo species, 7 showed similarities between the begging calls of the parasitic cuckoos and their respective hosts.

The results of this study provide clear evidence for the presence of vocal signatures in the begging and fledgling calls of JB young ones, wherein their calls were acoustically dissimilar to that of its most common brood parasite JC. This provides a possible strategy for JB to discriminate between the young ones of its conspecific and brood parasites. However, the results from the playback experiments suggest that JB cannot fully discriminate between the calls of conspecific young ones and JC as they always approached the speaker that played back the calls of the brood parasite, although the nature of the approach was different by 50% of the time (silently approach). These findings indicate that, even though vocal signatures of identity are present in the calls of the conspecifics, JB adults are unable to utilize it in order to discriminate against the brood parasite. While this result remains puzzling, it explains the observation of the lack of eviction of brood parasites in parasitized nests. In addition, these also indicate the possibility of the generalization in the calls of the young ones of generalist brood parasites that may allow them to persist in the nest of the host and continue to get benefit from the diverse hosts that they parasitize. A study on a generalist brood parasite, Brown-headed cowbird, *Molothrus ater* revealed that the begging call of their fledgling covered a wide range of frequencies and appeared to be able to emphasize the amplitude and peak frequency in such a way that resembles the vocalization of the begging call of the nestmates they grew up with (Liu et al. 2016). Additionally, JBs could discriminate between the types of calls of the young ones of its conspecific wherein, they took more time to respond to the fledgling close call than the begging call, suggesting that adults are more likely to tend to the calls of hatchlings and nestlings than to fledglings who are likely to be more independent. This is corroborated by my field observations over the entire course of the thesis work.

One instance of JB actively chasing away a fledgling of JC was recorded from the field observations during the breeding period of a group found in the study site. Anecdotal observation by Sanjeeva Raj (1964) also noted that the fledgling of JC was ignored by its foster parent, the Yellow-billed babbler. The incomplete discrimination exhibited by the JB adults is in line with these observations, wherein the host may be able to utilize the differences in the calls of its young ones to occasionally discriminate against the parasite. Co-evolutionary arms race beyond the egg stage has been overlooked and has been given even less attention beyond the nestling stage, which can be attributed to the conundrum that the host has already paid the cost of parasitism by raising up the nestlings of the parasite and the cost of erroneous rejection and discrimination at this late stage might outweigh the benefit of rejection (reviewed in Feeney et al. 2014; Lawes and Marthews 2003). However, the fledglings of altricial birds are still dependent on adults even after they emerge from the nest, so it will be beneficial to the host if they can recognize and discriminate brood parasites to avoid the extra cost of raising parasitic young ones. Recent studies have found evidence for the coevolved adaptation beyond the egg and nestling stage in which the mortality rate of post-fledgling of mimicking Screaming cowbirds was found to be lesser than the non-mimicking Shiny cowbirds (De Mársico et al. 2012). Moreover, anecdotal observation by Hoskin (1989) on Black-eared cuckoo and a variety of species showed that there is a possibility of abandonment of the fledgling of the Cuckoo and in other cases, the Cuckoo continues to receive provisioning from its hosts as well as other species. Such incomplete discrimination is indicative of a possible co-evolutionary arms race between the host and the brood parasite beyond the nestling stage also.

In this study, field observations yielded evidence of the provisioning of JC by JB. 6 nests of JB that were parasitized by JB were studied (Chapter 4; Table 4.2). In all these nests, JB adults provided for the JC young ones. Two of these nests had no JB chicks left (possibly due to host eviction by brood parasite or host chick mortality due to other reasons) and only had JC young ones. In both these cases, adult JB continued to provide for the young JC till they fledged. Gaston (1976) also reported the occurrence of provisioning of fledgling of JC even after two to three weeks of leaving the nest. These observations can be justified by the explanation of 'strategy blocking' (Britton 2007) or the cost of adaptation of rejecting the fledglings of parasites outweighing the benefits of rejection (Lawes and Marthews 2003). Strategy blocking refers that the adaptation at one stage might be blocking the development of adaptation in the next stage of the breeding cycle. At the egg stage, there is an occurrence of adaptation of mimicry of the egg where the eggs of JC resemble that of JB but have more thickened shells which might have developed as an adaptation to these coevolutionary race to avoid cracking of egg while laying eggs in the nest (Gaston 1976). Besides, Gaston (1976) also showed that there was no difference in the growth rate of nestling of JB with and without JC suggesting that the cost of parasitism might not have much impact on the JB. At the same time our results from manipulative playback experiments suggest that while JB adults always responded to the begging calls of the brood parasite, 50% of the time, they would approach silently as they would do to the calls of their sympatric competitor species, Large grey babbler (Chorol 2022).

Previous studies on generalist brood parasites showed that the nest environment modulates the begging behaviour of the generalist brood parasite. For example, generalist brood parasites, Brown-headed cowbird and Shiny cowbird begged more intensely, took less time to beg and increased the duration of begging when they were reared alongside the bigger chicks of the host species (Rivers 2007; Tuero et al. 2016). Flexibility in the begging behaviour might play a bigger role in contributing greater benefit to the generalist brood parasite in successfully parasitizing at a large or diverse range of host species (Tuero et al. 2016). Even though, our study does not account for the begging behaviour other than the vocal trait, it lays the foundation for future investigation regarding the flexibility of the begging behaviour in the generalist brood parasite. This study furthers our understanding of the interrelationship of the structure and function of begging call and fledgling close call (Yambem et al. 2021) of JB and provides insights on a possible ongoing evolutionary arms race in this system. This study also provides a bedrock for further research on the adaptation and the counter adaptation in host and brood parasites beyond the nestling stage.

5.5 Appendix D

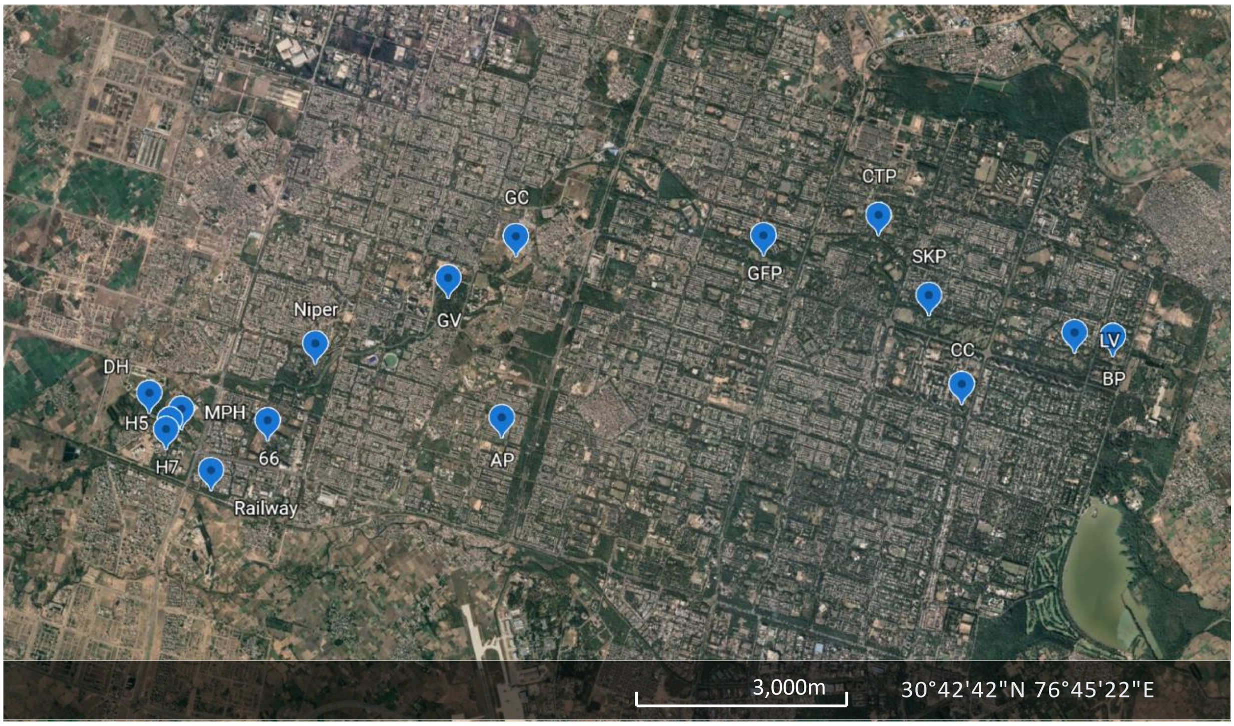


Figure D5.1 Location of the groups of JBs where the playbacks were conducted. All the points are marked with a short name. DH- Director house of IISER Mohali, H5-Hostel 5 of IISER Mohali, H7-Hostel 7 of IISER Mohali, MPH-Main pump house of IISER Mohali, 66- Sector 66 in Mohali, Railway- on the side of railway track in Mohali, NIPER - National Institute of Pharmaceuticals and Education Research Mohali, GV- Garden Valley in Mohali, AP-Animal park in Chandigarh, GC- Garden of conifer in Chandigarh, GFP-Garden of Fragrance Chandigarh, CTP- Children traffic park, SKP-Shanti kunj park, CC_Citco, LV- Leisure valley, BP-Bougainvillea park.

Table D5.1. Number of different nestlings (N) from which recordings were collected and number of calls (n) which are used in the acoustic analyses.

Call types	**N**	**n**
JB_begging	3	25
JC_begging	3	21
Myna_begging	3	22
JB_fledgling	3	25
JC_fledgling	3	24

Table D5.2 Mean ± SD of the acoustic parameters used in analysing the structure of the calls of the young ones of JB and JC.

Call Types	**Note duration (s)**	**Frequency 5% (kHz)**	**Frequency 95% (kHz)**	**Bandwidth 90% (kHz)**	**Peak frequency (kHz)**
JB_fledge	0.17 ± 0.02	1.65 ± 0.38	4.32 ± 0.95	2.66 ± 1.12	2.68 ± 0.43
JB_beg	0.30 ± 0.09	1.44 ± 0.27	4.88 ± 1.70	3.44 ± 1.77	2.89 ± 1.39
JC_fledge	0.23 ± 0.05	2.16 ± 0.28	3.87 ± 0.64	1.70 ± 0.61	3.12 ± 0.65
JC_beg	0.33 ± 0.06	1.95 ± 0.55	6.03 ± 0.46	4.08 ± 0.73	5.15 ± 0.79
Myna_beg	0.07 ± 0.01	2.24 ± 0.32	5.98 ± 0.82	3.74 ± 1.04	3.43 ± 0.72

Table D5.3 P values of multiple pairwise comparisons of the latency to respond towards different calls of the young ones.

Playback	**JB beg**	**JC beg**
JB beg		
JC beg	0.0117	
JB fledge	0.0011	0.1968

Chapter 6

Conclusions and Future Directions

6.1 Conclusions

This thesis presents fundamental findings of the behavioural ecology of Jungle Babblers (*Argya striata*; hereafter JBs) including their behavioural repertoire, communicative complexity, cooperative brood care and host discrimination against a brood parasite. The findings suggest that both individual and social behaviours vary temporally and most of the social interactions are mediated by acoustic communication in this species. Most importantly, this study unravels the intricacies of alloparental care, one of the major components of the social system and the defining characteristics of the cooperative breeding system. Finally, this study also reveals acoustic signals as a possible strategy that might be employed by the host to discriminate against the brood parasites.

Key conclusions from the four work chapters are given below:

6.1.1 Chapter 2: Behavioural repertoire and temporal variation of different behaviours

Time is a limited resource that puts constraints on the activity budget of organisms, thus it must be utilised efficiently in order to balance the needs of social animals towards sustenance and social interactions. In this chapter, the time-activity budget of different behaviours exhibited by JBs was examined. Furthermore, the differential allocation of time for different behaviours with the changing environment across days and seasons was also investigated.

- JBs exhibited 4 individual behaviours (that do not require the participation of other individuals are considered for this study), as well as 9 social behaviours apart from alloparental care (which is limited to the breeding season).
- Time allocation to individual behaviours (~70%) was much more than social behaviours (~30%) and the bulk of this was attributed to the time devoted to

foraging (56%) which is required for the survival of an organism. This implies that JBs devote one-third of their time to social behaviours which comes at a cost to time that could have been devoted to behaviours required for individual sustenance. This quantifies the cost of sociality and is in agreement with findings from studies on social primates.

- In this study, time devoted to affiliative and agonistic behaviours was largely observed in relation to predator avoidance. Interestingly, agonistic behaviours were almost always observed against other group members or against potential predators and intra-group conflict was not observed during this study. This is in stark contrast to the Arabian babblers in which within-group aggression at an early age is common and is a means of establishing dominance within the group.
- The time budget allocated to most of the behaviours showed both diurnal and seasonal patterns indicating the allocation of time is adjusted in accordance with the changing environment. Specifically, variation in the time allocation to sentinel activity (one of the most conspicuous behaviours of some social animals) across days and seasons indicates the possible influence of satiation level and change in canopy cover across seasons, respectively.
- Furthermore, results also showed that the light intensity at the time of roosting was higher suggesting the requirement of light during roost searching.

6.1.2 Chapter 3: Functional and structural complexity in the vocalizations of Jungle Babbler

Communication is associated with the complex social system as it is essential in mediating the interactions required in maintaining social bonds and according to the 'social complexity hypothesis' a more complex social system will have higher complexity in communication. Structural complexity and functional complexity have been regarded as two independent measures of complexity and have been shown to be associated with cooperative breeding. In this chapter, I examined the vocal repertoire of JBs and the function of these vocalizations as measures of complex communication. Furthermore, I examined if functionally similar calls were also structurally similar in accordance with Morton's motivational structural rules.

- From this study, 15 types of vocalizations of JBs, produced in different contexts, were identified. Among these, 7 were produced in affiliative contexts and 8 were produced in agonistic contexts (mostly in the context of inter-group interactions or in the context of predator avoidance). This is in concordance with the predictions of the social complexity hypothesis.
- Of these 15 vocalizations, 13 were produced by adults and 2 by young ones. 7 calls were monosyllabic, 6 were multisyllabic and 2 were chorus calls produced by many group members simultaneously.
- It was also found that all these functionally distinct vocalizations were also structurally distinct, perhaps driven by a prerequisite of sending a distinct signal to infer reliable meaning.
- The study found partial support for Morton's motivational structural rules wherein functionally similar multisyllabic calls were also structurally similar to each other.

6.1.3 Chapter 4: Understanding alloparental care in Jungle Babbler and the ontogeny of begging behaviour

Alloparental care is a major component of cooperative breeders and is likely to be influenced by factors such as group size, age of the young ones and environmental variables. Further, how young ones communicate with adult care-givers is in itself a fascinating behaviour to study. In this chapter, I examined the different aspects of alloparental care such as brooding, provisioning and signalling during provisioning. Specifically, I examined the association of brooding and provisioning rate with group size, the age of the young ones as well as the time of the day. I also examined the evidence for synchronized feeding in JB and compared the diet contents of adults and young ones. Lastly, I examined the ontogeny of the begging response in JB in response to tactile cues and acoustic signals produced by the adults.

- Contrary to the findings in many other cooperative breeders, the rate of provisioning was not related to group size. However, the age of the young ones was a good predictor of both provisioning and brooding duration. The provisioning rate increased with age (indicative of the requirement of more diet to support their growing body) and brooding duration decreased with the age of the young ones (perhaps driven by the reduced requirement of external thermoregulation with the development of feathers). Neither the provisioning rate nor brooding duration varied with the time of the day.
- JB exhibited synchronized feeding which can be attributed to the avoidance of frequent visits that might attract the attention of predators and to the possibility of advertising the quality of parenting behaviour or showing the reciprocity behaviour.
- The diet of the young contained more invertebrates indicative of a protein-rich diet of young ones as compared to adults.

Furthermore, results of the manipulative experiment revealed that tactile stimulus might be necessary and sufficient at the early stage of the young ones (hatchling and nestling) to elicit a begging response whereas, at the prefledge stage, tactile stimulus does not elicit a begging response. Prompt calls only exhibited a weak response during the prefledge stage. These findings indicate an ontogenic pattern in the response to the same stimulus in JB implying that young ones at different ages respond to different signalling stimuli during provisioning. This may be attributed to the process of development of different sensory organs at different stages. Besides, the association between stimuli and response at a stage can be seen as a possible strategy towards predator avoidance.

6.1.4 Chapter 5: Vocal discrimination by Jungle Babbler between the young ones of conspecifics and brood parasite

The association between the brood parasite and the host has been a classic example to study evolutionary arms race. It is in the interest of the host to discriminate against the brood parasite as parental care is an expensive endeavour. However, in the absence of host-specific egg signatures, acoustic and visual cues from young ones may help the host identify brood parasites at the nest. This discrimination may be exhibited at any stage during the stay of the parasite in the host's nest. I tested the possibility of a host-specific vocal signature of young ones in JB which the adults may be utilizing to discriminate against the young ones of Jacobin Cuckoo (its primary brood parasite) both at the nestling and fledgling stage.

- Comparison of calls of both nestling and fledgling of the host and brood parasite revealed that the calls are different structurally by several spectral parameters suggesting the presence of acoustic signatures that can potentially be employed by the host to discriminate against the brood parasite.
- The playback experiment using different call types of both the young ones of the conspecific and brood parasite showed that the adult host responded 100% of the time by approaching with a call to the begging calls of the conspecific. On the other hand, JB approached with calls only 50% of the time when the begging call of the parasite was broadcasted and the remaining time they approached silently as they would for an intruder. This response further reduced when presented the fledgling

calls of the brood parasite. This outcome suggests that JB can discriminate against the brood parasite at some level but not all the time, even though clear acoustic differences exist between the signals of the host and the parasite. This provides a possible mechanism for the brood parasite to persist in the host's nest for longer.

6.2 Overall summary

This study demonstrated the association of various factors that might influence the behaviours of a cooperatively breeding paleotropical bird endemic to the Indian subcontinent. From this study, it can be postulated that, in a cooperative breeding system, there might be an association of social behaviour with time-activity budget and activity pattern. This study lends support to the predictions of the 'social complexity hypothesis' with Jungle Babbler possessing a large repertoire of structurally and functionally distinct vocalizations. In contradiction to the findings in many cooperatively breeding birds, neither the provisioning rate nor the number of young ones fledged is correlated with group size in Jungle Babbler. However, a larger group size would enable "load lightening" in an alloparental care system and may drive patterns of philopatry. Furthermore, this study provides evidence for host-specific acoustic signatures in the calls of the young one and the inability of the host to utilise it completely. In so, the lack of complete discrimination against the brood parasite, despite the presence of vocal signatures, provides a possible mechanism for the persistence of the brood parasite in the nest of the host.

6.3 Future directions

Overall, this study lays the foundation for future comparative studies in the evolution of sociality, communicative complexity and generalization of complex social systems, especially in cooperative breeding systems. Some immediate and some long-term future directions emerge from the current study and these are enlisted below.

Chapter 2: The findings on the time allocation between individual and social behaviours show that about one-third of their time was devoted to social behaviours which probably might enhance maintaining the social bonds. However, this study was carried out at the group level and individual variations in behaviour were not recorded. Thus, further examination on the individual level will give us insights into whether breeders and helpers vary with respect to the time partitioning between individual and social behaviours. Study in the variation of the time-activity budget with respect to the sex of the individual will provide a platform for future studies in the division of labour in this sexually monomorphic species. This might also help in understanding the philopatry system of JB, whether it is female or male philopatry which will further provide a better understanding of the fission-fusion dynamics of the species. Moreover, it is possible that individual variation in social behaviours dictates the reproductive queue in JB and in line with the 'eusociality continuum', there might indeed be permanent non-reproductive castes which can be identified by studying their behaviour. Therefore, future investigation on the presence of reproductive division of labour in JB will offer a great advantage for further research on the comparative study of cooperative breeding birds in terms of eusociality.

Furthermore, to maintain social bonding, they must coordinate to perform their daily activities. Results showed that the time devoted to agonistic behaviour is mostly between groups of JBs and heterospecific (potential predators). The within-group conflict was rarely observed, leaving a gap in the understanding of whether a dominance hierarchy exists in JB and if so, how is it established and maintained.

Chapter 3: The "social complexity hypothesis" has focused on the senders with respect to the repertoire size of behaviours and vocalizations. However, looking at the receiver's side of the perception might give us new insight into the association between communicative complexity and social complexity. This needs to be examined for non-acoustic communication as well. Furthermore, this study provides the platform for further research on the complexity of the graded nature of the call which might be attributed to the ecology and motivational status of an individual.

Chapter 4: Even though the forms and patterns of alloparental care were examined in this study, individual variation in alloparental care was not examined in this study since not all individuals in the group were banded. However, this cooperative parental care might take up most of the time from their daily time budget at the individual level. Therefore, individual-level variation in alloparental care will provide valuable insights into the extent to which an individual of a particular reproductive status invests in alloparental care, its influence on bonding with the group members, the probability of such individuals gaining reproductive status and linking this with relatedness to offspring. Such a holistic investigation can only be done in the long term but will yield valuable insights into the drivers of cooperation in this species.

From this study, it was found that JB synchronized its provisioning behaviour. However, the function of synchrony could not be established. It is possible that synchronized feeding reduces predation pressure or could be a means of advertising an individual's contribution to alloparental care in line with the 'pay to stay' hypothesis (Bruintjes and Taborsky 2008). If the breeder is performing the provisioning behaviour, then there is no need for advertisement as well as no requirement for 'pay to stay' which might be the opposite for the non-breeder. Thus, assessing the reproductive status of carers will be crucial in understanding the function of synchronized feeding.

Furthermore, it was observed that the tactile stimulus (even when the adult is absent) triggered the begging response at the early stage of the young ones. This could be a costly endeavour as the begging calls can attract predator attention. However, the cost of not begging might be perhaps higher due to sibling competition. Thus, manipulative experiments on the effect of the number of young ones on the begging response to the tactile stimulus at the early hatchling stage will provide valuable information on the cost and benefit of begging behaviour.

Finally, in future studies, one should examine whether JB is socially or genetically monogamous. This is likely to impact the relatedness between helpers and young ones and thereby determine the role of kin selection in driving philopatry and thereby cooperative breeding in this species. Furthermore, one can check whether the investments by the helpers also depend on the number of helpers. One can also check whether the quality and quantity of food also depend upon the reproductive status of the provider. One can also examine if there is any association between the diet content of the nestling or the availability of the prey items and the provisioning rate. As mentioned above, the occurrence of dominance hierarchy is low in Jungle Babbler, so examining the criteria other than the dominance hierarchy of mate selection in further studies will provide an avenue on the complexity of the mating system, a component of the complex social system.

Chapter 5: The findings of this chapter suggest that despite the presence of vocal signatures in the calls of the young ones of conspecifics and brood parasites, adult JB does not always manage to discriminate against the brood parasite. From a signal design perspective, it will be interesting to examine if certain features of calls of the brood parasite evoke a response from JBs' adults to attend to them in a manner similar to their own offspring, which the brood parasite may be exploiting to their advantage. However, the study sets the stage for a larger investigation of vocal discrimination of brood parasites by various host species and a specific examination of the evolution of vocal mimicry or convergence of call features in brood parasites across various avian host species and their brood parasites.

References

1. Adamczewska, A. M., & Morris, S. (2001). Ecology and behavior of *Gecarcoidea natalis*, the Christmas Island red crab, during the annual breeding migration. The Biological Bulletin, 200(3), 305-320.
2. Alcock, John, (2001). Animal behavior: an evolutionary approach. Sunderland, Mass.: Sinauer Publishers.
3. Ali, S. (1964). The book of Indian birds: with 66 plates in colour (depicting 264 species), 3 in line, and 22 in half-tone. Bombay Natural History Society.
4. Altmann J. Muruthi P (1988) Differences in daily life between semiprovisioned and wild-feeding baboons. Am J Primatol 15(3): 213-21
5. Altmann, J. (1974). Observational study of behavior: sampling methods. Behaviour, 49(3-4), 227-266.
6. Amdekar, M. S., & Thaker, M. (2022). Colours of stress in male Indian rock agamas predict testosterone levels but not performance. Hormones and Behavior, 144, 105214.
7. Anava, A., Kam, M., Shkolnik, A., & Degen, A. A. (2001). Growth rate and energetics of Arabian Babbler (*Turdoides squamiceps*) nestlings. The Auk, 118(2), 519-524.
8. Anderson, M. (1984). The evolution of eusociality. Annual review of ecology and systematics, 15(1), 165-189.
9. Anderson, M. G., Ross, H. A., Brunton, D. H., & Hauber, M. E. (2009). Begging call matching between a specialist brood parasite and its host: a comparative approach to detect coevolution. Biological Journal of the Linnean Society, 98(1), 208-216.

10. Andrew, M. I., & Naik, R. M. (1965). Structural basis of the change of eye colour of the Jungle babbler, *Turdoides striatus* (Dumont), during post-embryonic development. Pavo, 3, 72-74.

11. Andrews, M. I., & Naik, N. M. (1970). The biology of the Jungle babbler. Pavo, 8, 1-34.

12. Arnold, K. E., Ramsay, S. L., Donaldson, C., & Adam, A. (2007). Parental prey selection affects risk-taking behaviour and spatial learning in avian offspring. Proceedings of the Royal Society B: Biological Sciences, 274(1625), 2563-2569.

13. Back, J. P., Suzin, A., & Aguiar, L. M. (2019). Activity budget and social behavior of urban capuchin monkeys, *Sapajus* sp. (*Primates: Cebidae*). Zoologia (Curitiba), 36.

14. Banbura, J., Lambrechts, M. M., Blondel, J., Perret, P., & Cartan-Son, M. (1999). Food handling time of Blue Tit chicks: constraints and adaptation to different prey types. Journal of Avian Biology, 263-270.

15. Banerjee A, Bhadra A (2021) Time-activity budget of urban-adapted free-ranging dogs. Acta Ethol 1-10

16. Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed effect model using lme4. J Stat Softw 67:1-48

17. Bednekoff PA, Houston AI (1994) Avian daily foraging patterns: effects of digestive constraints and variability. Evol Ecol *8*(1): 36-52

18. Ben Mocha Y, Mundry R, Pika S. (2018) Why hide? Concealed sex in dominant Arabian babblers (*Turdoides squamiceps*) in the wild. Evol. Hum. Behav. 39, 575-582.

19. Ben Mocha, Y. (2020). Why do human and non-human species conceal mating? The cooperation maintenance hypothesis. Proceedings of the Royal Society B, 287(1932), 20201330.

20. Bensizerara D, Chenchouni H (2019) Are diurnal time-budgets and activity patterns density-dependent in the Shelduck (*Tadorna tadorna*) wintering in Algeria? An analysis across multiple temporal scales. Avian Res 10(1): 1-5

21. Bernstein, I. S. (1980). Activity patterns in a stumptail macaque group (*Macaca arctoides*). Folia Primatologica, 33(1-2), 20-45.

22. Bezerra, B. M., Barnett, A. A., Souto, A., & Jones, G. (2011). Ethogram and natural history of golden-backed uakaris (*Cacajao melanocephalus*). International Journal of Primatology, 32, 46-68.

23. Bhadra, A., Iyer, P. L., Sumana, A., Deshpande, S. A., Ghosh, S., & Gadagkar, R. (2007). How do workers of the primitively eusocial wasp *Ropalidia marginata* detect the presence of their queens? Journal of Theoretical Biology, 246(3), 574-582.

24. Blanchet S, Loot G, Bernatchez L, Dodson JJ (2008) The effects of abiotic factors and intraspecific versus interspecific competition on the diel activity patterns of Atlantic salmon (*Salmo salar*) fry. Can J Fish Aquat Sci 65(8): 1545-1553

25. Blažek, R., Polačik, M., Smith, C., Honza, M., Meyer, A., & Reichard, M. (2018). Success of cuckoo catfish brood parasitism reflects coevolutionary history and individual experience of their cichlid hosts. Science advances, 4(5), 4380.

26. Blumstein, D. T., & Armitage, K. B. (1997). Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. The American Naturalist, 150(2), 179-200.

27. Boccia, M. L., Rockwood, B., & Novak, M. A. (1982). The influence of behavioral context and social characteristics on the physical aspects of social grooming in rhesus monkeys. International journal of primatology, 3(1), 91-108.

28. Bowers, E. K., Nietz, D., Thompson, C. F., & Sakaluk, S. K. (2014). Parental provisioning in house wrens: effects of varying brood size and consequences for offspring. Behavioral Ecology, 25(6), 1485-1493.

29. Bradbury, J. W., & Vehrencamp, S. L. (2011). Principles of animal communication. 2nd. Sunderland, Massachusetts: Sinauer.

30. Brashares, J. S., & Arcese, P. (1999). Scent marking in a territorial African antelope: I. The maintenance of borders between male oribi. Animal Behaviour, 57(1), 1-10.

31. Briskie JV, Naugler CT, Leech SM. 1994. Begging intensity of nestling birds varies with sibling relatedness. Proc. R. Soc. B-Biol. Sci. 258:73–78

32. Britton, N. F., Planqué, R., & Franks, N. R. (2007). Evolution of defence portfolios in exploiter–victim systems. Bulletin of Mathematical Biology, 69(3), 957-988.

33. Brooke, M. D. L., & Davies, N. B. (1988). Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. Nature, 335(6191), 630-632.

34. Brooker, M. G., & Brooker, L. C. (1991). Eggshell strength in cuckoos and cowbirds. Ibis, 133(4), 406-413.

35. Browning, L. E., Young, C. M., Savage, J. L., Russell, D. J. F., Barclay, H., Griffith, S. C., & Russell, A. F. (2012). Carer provisioning rules in an obligate cooperative breeder: prey type, size and delivery rate. Behavioral Ecology and Sociobiology, 66(12), 1639-1649.

36. Bruintjes, R., & Taborsky, M. (2008). Helpers in a cooperative breeder pay a high price to stay: effects of demand, helper size and sex. Animal Behaviour, 75(6), 1843-1850.

37. Buckley, N. J. (1996). Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures. The Auk, 113(2), 473-488.

38. Burda, H., Honeycutt, R. L., Begall, S., Locker-Grütjen, O., & Scharff, A. (2000). Are naked and common mole-rats eusocial and if so, why? Behavioral Ecology and Sociobiology, 47(5), 293-303.

39. Butchart, S. H. M., Kilner, R. M., Fuisz, T., & Davies, N. B. (2003). Differences in the nestling begging calls of hosts and host-races of the common cuckoo, *Cuculus canorus*. Animal Behaviour, 65(2), 345-354.

40. Cai T, Cibois A, Alström P, Moyle RG, Kennedy JD, Shao S, Zhang R, Irestedt M, Ericson PG, Gelang M, Qu Y (2019) Near-complete phylogeny and taxonomic revision of the world’s babblers (Aves: Passeriformes). Mol Phylogenet Evol 130: 346-56.

41. Capellini I, Preston BT, McNamara P, Barton RA, Nunn CL (2010). Ecological constraints on mammalian sleep architecture. Evolution of Sleep: Phylogenetic and Functional Perspectives, 12-33.

42. Caraco, T. (1979). Time budgeting and group size: a test of theory. Ecology, 60(3), 618-627.

43. Carlisle, T. R., & Zahavi, A. (1986). Helping at the nest, allofeeding and social status in immature Arabian babblers. Behavioral Ecology and Sociobiology, 18(5), 339-351.

44. Caro, T. M., & Collins, D. A. (1987). Male cheetah social organization and territoriality. Ethology, 74(1), 52-64.

45. Catchpole CK (1987) Bird song, sexual selection and female choice. Trends Ecol Evol 2:94-97.

46. Catchpole CK, Slater PJ (2010) Bird song: biological themes and variations. Cambridge University Press, Cambridge.

47. Chastel, O., & Kersten, M. (2002). Brood size and body condition in the house sparrow *Passer domesticus*: the influence of brooding behaviour. Ibis, 144(2), 284-292.

48. Cheney, D. L., & Seyfarth, R. M. (2018). Flexible usage and social function in primate vocalizations. Proceedings of the National Academy of Sciences, 115(9), 1974-1979.

49. Chorol S. (2022). Communicative complexity in avian vocalization [Unpublished doctoral dissertation]. Indian Institute of Science Education and Research Mohali, Punjab, India.

50. Cibois, A., Gelang, M., Alström, P., Pasquet, E., Fjeldså, J., Ericson, P. G., & Olsson, U. (2018). Comprehensive phylogeny of the laughingthrushes and allies (Aves, Leiothrichidae) and a proposal for a revised taxonomy. Zoologica Scripta, 47(4), 428-440.

51. Clark, K. L., & Robertson, R. J. (1979). Spatial and temporal multi-species nesting aggregations in birds as anti-parasite and anti-predator defenses. Behavioral Ecology and Sociobiology, 5(4), 359-371.

52. Clarke, F. M., & Faulkes, C. G. (1997). Dominance and queen succession in captive colonies of the eusocial naked mole–rat, *Heterocephalus glaber*. Proceedings of the Royal Society of London. Series B: biological sciences, 264(1384), 993-1000.

53. Clarke, M. F. (1984). Co-operative breeding by the Australian bell miner *Manorina melanophrys* Latham: a test of kin selection theory. Behavioral Ecology and Sociobiology, 14(2), 137-146.

54. Clarke, M. F. (1989). The pattern of helping in the bell miner (*Manorina melanophrys*). Ethology, 80(1-4), 292-306.

55. Clarke, M. F., & Fitzgerald, G. F. (1994). Spatial-organization of the cooperatively breeding bell miner *Manorina melanophrys*. Emu, 94(2), 96-105.

56. Clemmons, J. R. (1995). Vocalizations and other stimuli that elicit gaping in nestling black-capped chickadees (*Parus atricapillus*). The Auk, 112(3), 603-612.

57. Clutton-Brock, T. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. Science, 296(5565), 69-72.

58. Clutton-Brock, T. (2019). Cooperative breeding. Encyclopedia of Animal Behavior, 31.

59. Clutton-Brock, T. H. (1991). The evolution of parental care. In The Evolution of Parental Care. Princeton University Press.

60. Clutton-Brock, T. H., Russell, A. F., & Sharpe, L. L. (2004). Behavioural tactics of breeders in cooperative meerkats. Animal Behaviour, 68(5), 1029-1040.

61. Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. Annual Review of Ecology and Systematics, 141-177.

62. Cockburn, A. (2006). Prevalence of different modes of parental care in birds. Proceedings of the Royal Society B: Biological Sciences, 273(1592), 1375-1383.

63. Conradt, L., & Roper, T. J. (2000). Activity synchrony and social cohesion: a fission-fusion model. Proceedings of the Royal Society of London. Series B: Biological Sciences, 267(1458), 2213-2218.

64. Cox JA (2012) Social grooming in the Brown-headed Nuthatch may have expanded functions. Southeast Nat 1(4): 771-4

65. Crane JM, Savage JL, Russell AF (2016) Diversity and function of vocalisations in the cooperatively breeding Chestnut-crowned Babbler. Emu 116:241-253

66. Cunningham, S., & Magrath, R. D. (2017). Functionally referential alarm calls in noisy miners communicate about predator behaviour. Animal Behaviour, 129, 171-179.

67. Darwin C. 1859. The origin of species by means of natural selection, or the preservation of favored races in the struggle for life. London: John Murray

68. Davies NB, Brooke, MDL. 1988 Cuckoos versus reed warblers: adaptations and counteradaptations. Anim behav 36, 262-284.

69. Davies NB, Brooke, MDL. 1989 An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. The Journal of Animal Ecology, 207-224.

70. Davies, N. B. (2000). Cuckoos, Cowbirds and Other Cheats. T. & A.D. Poyser, London.

71. Davies, N. B. (2011). Cuckoo adaptations: trickery and tuning. Journal of Zoology, 284(1), 1-14

72. Davies, N. B., Kilner, R. M., & Noble, D. G. (1998). Nestling cuckoos, *Cuculus canorus,* exploit hosts with begging calls that mimic a brood. Proceedings of the Royal Society of London. Series B: Biological Sciences, 265(1397), 673-678.

73. Davies, N. B., Krebs, J. R., & West, S. A. (2012). An introduction to behavioural ecology. John Wiley & Sons.

74. Dawson, W. R., & Evans, F. C. (1960). Relation of growth and development to temperature regulation in nestling Vesper Sparrows. The Condor, 62(5), 329-340.

75. De Mársico, M. C., Gantchoff, M. G., & Reboreda, J. C. (2012). Host–parasite coevolution beyond the nestling stage? Mimicry of host fledglings by the specialist screaming cowbird. Proceedings of the Royal Society B: Biological Sciences, 279(1742), 3401-3408.

76. Deoniziak, K., & Osiejuk, T. S. (2019). Habitat-related differences in song structure and complexity in a songbird with a large repertoire. *BMC ecology*, *19*(1), 1-11.

77. Dharmakumarsinhji, R. S. (1954). Birds of Saurashtra. Times of India Press, Bombay, India.

78. Di Bitetti, M. S. (1997). Evidence for an important social role of allogrooming in a platyrrhine primate. Animal Behaviour, 54(1), 199-211.

79. Dmitriew, C. M. (2011). The evolution of growth trajectories: what limits growth rate? Biological Reviews, 86(1), 97-116.

80. Doutrelant, C., & Covas, R. (2007). Helping has signalling characteristics in a cooperatively breeding bird. Animal Behaviour, 74(4), 739-747.

81. Ducheminsky, N., Henzi, S. P., & Barrett, L. (2014). Responses of vervet monkeys in large troops to terrestrial and aerial predator alarm calls. Behavioral Ecology, 25(6), 1474-1484.

82. Duffy, J. E., Morrison, C. L., & Rí; os, R. N. (2000). Multiple origins of eusociality among sponge-dwelling shrimps (*Synalpheus*). Evolution, 54(2), 503-516.

83. Dunbar, R. I. (1991). Functional significance of social grooming in primates. Folia primatologica, 57(3), 121-131.

84. Dunbar, R. I. (1992). Time: a hidden constraint on the behavioural ecology of baboons. Behavioral ecology and sociobiology, 31(1), 35-49.

85. Dunbar, R. I. M., & Dunbar, P. (1988). Maternal time budgets of gelada baboons. Animal Behaviour, 36(4), 970-980.

86. Dunbar, R. I., Korstjens, A. H., Lehmann, J., & British Academy Centenary Research Project. (2009). Time as an ecological constraint. Biological Reviews, 84(3), 413-429.

87. Dunn, P. O., Cockburn, A., & Mulder, R. A. (1995). Fairy-wren helpers often care for young to which they are unrelated. Proceedings of the Royal Society of London. Series B: Biological Sciences, 259(1356), 339-343.

88. E.O. Wilson. (1971). The insect societies. Cambridge, Massachusetts, USA, Harvard University Press [Distributed by Oxford University Press].

89. E.O. Wilson. (1975). Sociobiology, The New Synthesis. Cambridge, MA: Harvard University Press.

90. Eeva, T., Helle, S., Salminen, J. P., & Hakkarainen, H. (2010). Carotenoid composition of invertebrates consumed by two insectivorous bird species. Journal of chemical ecology, 36, 608-613.

91. Eggert, A. K. (2014). Cooperative breeding in insects and vertebrates. Oxford University Press.

92. Ehrlich, P., Dobkin, D. S., & Wheye, D. (1988). Birder's handbook. Simon and Schuster.

93. Elie JE, Theunissen FE (2016) The vocal repertoire of the domesticated zebra finch: a data-driven approach to decipher the informationbearing acoustic features of communication signals. Anim Cogn 19:285–315

94. Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. Science, 197(4300), 215-223.

95. Engesser S, Ridley AR, Townsend SW (2017) Element repetition rates encode functionally distinct information in Pied Babbler ‘clucks’ and ‘purrs’. Anim Cogn 20:953-960

96. Enright JT (1970) Ecological aspects of endogenous rhythmicity. Annu Rev Ecol Evol Syst 1(1): 221-238

97. Erler, S., & Lattorff, H. M. G. (2010). The degree of parasitism of the bumblebee (*Bombus terrestris*) by cuckoo bumblebees (*Bombus (Psithyrus) vestalis*). Insectes sociaux, 57(4), 371-377.

98. Fedy, B. C., & Stutchbury, B. J. (2005). Territory defence in tropical birds: are females as aggressive as males? Behavioral Ecology and Sociobiology, 58, 414-422.

99. Feeney, W. E. (2017). Evidence of adaptations and counter-adaptations before the parasite lays its egg: the frontline of the arms race. In Avian brood parasitism (pp. 307-324). Springer, Cham.

100. Feeney, W. E., & Langmore, N. E. (2013). Social learning of a brood parasite by its host. Biology Letters, 9(4), 20130443.

101. Feeney, W. E., Medina, I., Somveille, M., Heinsohn, R., Hall, M. L., Mulder, R. A., ... & Langmore, N. E. (2013). Brood parasitism and the evolution of cooperative breeding in birds. Science, 342(6165), 1506-1508.

102. Feeney, W. E., Welbergen, J. A., & Langmore, N. E. (2014). Advances in the study of coevolution between avian brood parasites and their hosts. Annual review of ecology, evolution, and systematics, 45, 227-246.

103. Ficken MS, Ficken RW, Witkin SR (1978) Vocal repertoire of the Black-capped Chickadee. Auk 95:34-48

104. Field, J., & Leadbeater, E. (2016). Cooperation between non-relatives in a primitively eusocial paper wasp, *Polistes dominula.* Philosophical Transactions of the Royal Society B: Biological Sciences, 371(1687), 20150093.

105. Finkbeiner, S. D., Briscoe, A. D., & Reed, R. D. (2014). Warning signals are seductive: relative contributions of color and pattern to predator avoidance and mate attraction in *Heliconius* butterflies. Evolution, 68(12), 3410-3420.

106. Flasskamp, A. (1994). The adaptive significance of avian mobbing V. An experimental test of the 'move on' hypothesis. Ethology, 96(4), 322-333.

107. Flower, S. S. (1937). Further notes on the duration of life in animals. In Proceedings of the Zoological Society of London (Vol. 107, No. 1, pp. 1-40). Oxford, UK: Blackwell Publishing Ltd.

108. Flower, T. (2011). Fork-tailed drongos use deceptive mimicked alarm calls to steal food. Proceedings of the Royal Society B: Biological Sciences, 278(1711), 1548-1555.

109. Freeberg, T. M. (2006). Social complexity can drive vocal complexity: group size influences vocal information in Carolina chickadees. Psychological Science, 17(7), 557-561.

110. Freeberg, Todd M., Robin IM Dunbar, and Terry J. Ord (2012). "Social complexity as a proximate and ultimate factor in communicative complexity." Philosophical Transactions of the Royal Society B: Biological Sciences 367.1597: 1785-1801.

111. Gadagkar R, Joshi NV (1983) Quantitative ethology of social wasps: time-activity budgets and caste differentiation in *Ropalidia marginate* (Lep.) (Hymenoptera: Vespidae). Anim Behav 31: 26–31

112. Gadagkar, R. (1987). What are Social Insects? IUSSI Indian Chapter Newsletter, 1(2), 3-4.

113. Gadagkar, R. (1994). Why the definition of eusociality is not helpful to understand its evolution and what should we do about it? Oikos, 485-488.

114. Gaston AJ (1977) Social behaviour within groups of Jungle Babblers (*Turdoides striatus*). Anim Behav 25:828-848

115. Gaston, A. J. (1976). Brood parasitism by the pied crested cuckoo *Clamator jacobinus*. The Journal of Animal Ecology, 331-348.

116. Gaston, A. J. (1977). Social behaviour within groups of Jungle babblers (*Turdoides striatus*). Animal Behaviour, 25, 828-848.

117. Gaunt, A. S., & Gaunt, S. L. (1985). Syringeal structure and avian phonation. Current Ornithology: Volume 2, 213-245.

118. Ghosal, R., Seshagiri, P. B., & Sukumar, R. (2012). Dung as a potential medium for inter-sexual chemical signaling in Asian elephants (*Elephas maximus*). Behavioural processes, 91(1), 15-21.

119. Gill FB (2007) Ornithology. Macmillan, New York

120. Giraudeau, M., Nolan, P. M., Black, C. E., Earl, S. R., Hasegawa, M., & McGraw, K. J. (2014). Song characteristics track bill morphology along a

gradient of urbanization in house finches (*Haemorhous mexicanus*). *Frontiers in Zoology*, *11*(1), 1-8.

121. Godfray, H. C. J. (1991). Signalling of need by offspring to their parents. Nature, 352(6333), 328-330.

122. Goodbred, C. O. N., & Holmes, R. T. (1996). Factors affecting food provisioning of nestling Black-throated Blue Warblers. The Wilson Bulletin, 467-479.

123. Gowda, V., Temeles, E. J., & Kress, W. J. (2012). Territorial fidelity to nectar sources by purple-throated caribs, *Eulampis jugularis*. The Wilson Journal of Ornithology, 124(1), 81-86.

124. Green, J. P., Freckleton, R. P., & Hatchwell, B. J. (2016). Variation in helper effort among cooperatively breeding bird species is consistent with Hamilton’s Rule. Nature Communications, 7(1), 1-7.

125. Greig E, Pruett-Jones S (2008) Splendid songs: the vocal behaviour of Splendid Fairy-wrens (*Malurus splendens melanotus*). Emu 108:103-114

126. Grieves LA, Logue DM, Quinn JS (2015) Vocal repertoire of cooperatively breeding Smooth-billed Anis. J Field Ornithol 86:130-143

127. Griffin, A. S., & West, S. A. (2003). Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. Science, 302(5645), 634-636.

128. Grim T, Samas P, Mosk ˇ at C, Kleven O, Honza M, et al. (2011). Constraints on host choice: Why do parasitic ´ birds rarely exploit some common potential hosts? J. Anim. Ecol. 80:508–18

129. Grim, T. (2005). Mimicry vs. similarity: which resemblances between brood parasites and their hosts are mimetic and which are not? Biological Journal of the Linnean Society, 84(1), 69-78.

130. Grim, T. (2007). Experimental evidence for chick discrimination without recognition in a brood parasite host. Proceedings of the Royal Society B: Biological Sciences, 274(1608), 373-381.

131. Haff, T. M., & Magrath, R. D. (2011). Calling at a cost: elevated nestling calling attracts predators to active nests. Biology Letters, 7(4), 493-495.

132. Halle S, Stenseth NC (2000) Activity Patterns in Small Mammals: An Ecological Approach. Springer Science and & Business Media

133. Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. Journal of theoretical biology, 7(1), 17-52.

134. Hamilton, W. D. (1970). Selfish and spiteful behaviour in an evolutionary model. Nature, 228, 1218-1220.

135. Hatchwell, B. J. (2007). Avian reproduction: role of ecology in the evolution of cooperative breeding. Current Biology, 17(19), R845-R847.

136. Hatchwell, B. J. (2009). The evolution of cooperative breeding in birds: kinship, dispersal and life history. Philosophical Transactions of the Royal Society B: Biological Sciences, 364(1533), 3217-3227.

137. Hatchwell, B. J., & Komdeur, J. (2000). Ecological constraints, life history traits and the evolution of cooperative breeding. Animal behaviour, 59(6), 1079-1086.

138. Hatchwell, B. J., & Russell, A. F. (1996). Provisioning rules in cooperatively breeding long-tailed tits *Aegithalos caudatus*: an experimental study. Proceedings of the Royal Society of London. Series B: Biological Sciences, 263(1366), 83-88.

139. Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: developing a framework of testable hypotheses. Behavioral Ecology and Sociobiology, 57(3), 197-214.

140. Herbers, J. M. (1981). Time resources and laziness in animals. Oecologia, 49(2), 252-262.

141. Hess, E. H., Petrovich, S. B., & Goodwin, E. B. (1976). Induction of parental behavior in Japanese Quail (Coturnix coturnix japonica). Journal of comparative and physiological psychology, 90(3), 244.

142. Hiebert SM, Stoddard PK, Arcese P (1989) Repertoire size, territory acquisition and reproductive success in the Song Sparrow. Anim Behav 37:266-273

143. Hollén, L. I., Bell, M. B., & Radford, A. N. (2008). Cooperative sentinel calling? Foragers gain increased biomass intake. Current Biology, 18(8), 576-579.

144. Holt J, Barati A, McDonald PG (2017) The complex acoustic repertoire of a highly social species, the Noisy Miner, *Manorina melanocephala*. Emu 117:19-30

145. Honza M, Taborsky B, Taborsky M, Teuschl Y, Vogl W, Moksnes A, Røskaft E. (2002). Behaviour of female common cuckoos, *Cuculus canorus*, in the vicinity of host nests before and during egg laying: a radiotelemetry study. Animal Behaviour. 1;64(6):861-8.

146. Hoskin ES. 1989. A black-eared cuckoo and white-breasted wood swallows. Aust. Birds 2:35–36

147. Houston, A. I., Székely, T., & McNamara, J. M. (2005). Conflict between parents over care. Trends in Ecology & Evolution, 20(1), 33-38.

148. Howard, R. D. (1978). The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution, 850-871.

149. Ikeda, T., Uchida, K., Matsuura, Y., Takahashi, H., Yoshida, T., Kaji, K., & Koizumi, I. (2016). Seasonal and diel activity patterns of eight sympatric mammals in northern Japan revealed by an intensive camera-trap survey. PloS one, 11(10), e0163602.

150. Isbell, L. A., & Young, T. P. (1993). Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. Behavioral ecology and sociobiology, 32(6), 377-385.

151. Jamie, G. A., & Kilner, R. M. (2017). Begging call mimicry by brood parasite nestlings: adaptation, manipulation and development. In Avian brood parasitism (pp. 517-538). Springer, Cham.

152. Jasso del Toro, C., Nekaris, K.AI. (2019). Affiliative Behaviors. In: Vonk, J., Shackelford, T. (eds) Encyclopedia of Animal Cognition and Behavior. Springer, Cham.

153. Jetz, W., & Rubenstein, D. R. (2011). Environmental uncertainty and the global biogeography of cooperative breeding in birds. Current Biology, 21(1), 72-78.

154. Johnson, E. J., & Best, L. B. (1982). Factors affecting feeding and brooding of Gray Catbird nestlings. The Auk, 99(1), 148-156.

155. Johnstone, R. A. (2011). Load lightening and negotiation over offspring care in cooperative breeders. Behavioral Ecology, 22(2), 436-444.

156. Jonsomjit, D.A., Jones, S.L., Gardali, T., Geupel, G.R. & Gouse, P.J. (2007) Guide to Nestling Development and Aging in Altricial Passerines. Biological Technical Publication. US Department of Interior Fish and Wildlife Service, Washington, DC.

157. Jose, B (2004). Ecological isolation of Babblers (*Turdoides* sp.) [Doctoral dissertation, Department of Zoology, St. Berchmans College, Changanacherry].

158. Kappeler, P. M. (2019). A framework for studying social complexity. Behavioral Ecology and Sociobiology, 73(1), 1-14.

159. Kaur, R., Joseph, J., Anoop, K., & Sumana, A. (2017). Characterization of recruitment through tandem running in an Indian queenless ant *Diacamma indicum*. Royal Society open science, 4(1), 160476.

160. Kennerley, J. A., Somveille, M., Hauber, M. E., Richardson, N. M., Manica, A., & Feeney, W. E. (2022). The overlooked complexity of avian brood parasite–host relationships. Ecology Letters, 25(8), 1889-1904.

161. Kern JM, Radford AN (2013) Call of duty? Variation in use of the watchman's song by sentinel Dwarf Mongooses, *Helogale parvula*. Anim Behav 85:967-975

162. Khayutin, S. N. (1985). Sensory factors in the behavioral ontogeny of altricial birds. In Advances in the Study of Behavior (Vol. 15, pp. 105-152). Academic Press.

163. Kilner, R. M., Noble, D. G., & Davies, N. B. (1999). Signals of need in parent–offspring communication and their exploitation by the common cuckoo. Nature, 397(6721), 667-672.

164. Kingma, S. A. (2017). Direct benefits explain interspecific variation in helping behaviour among cooperatively breeding birds. Nature Communications, 8(1), 1-7.

165. Kingma, S. A., Hall, M. L., Arriero, E., & Peters, A. (2010). Multiple benefits of cooperative breeding in purple-crowned fairy-wrens: a consequence of fidelity? Journal of Animal Ecology, 79(4), 757-768.

166. Knapton, R. W. (1984). Parental feeding of nestling Nashville Warblers: the effects of food type, brood-size, nestling age, and time of day. The Wilson Bulletin, 594-602.

167. Koenig, W. D., & Dickinson, J. L. (Eds.). (2004). Ecology and evolution of cooperative breeding in birds. Cambridge University Press.

168. Kölliker, M., Royle, N. J., Smiseth, P. T., & Royle, N. J. (2012). The evolution of parental care. The Princeton Guide to Evolution, 663.

169. Kondo, N., & Watanabe, S. (2009). Contact calls: information and social function. Japanese Psychological Research, 51(3), 197-208.

170. Korstjens, A. H., Verhoeckx, I. L., & Dunbar, R. I. (2006). Time as a constraint on group size in spider monkeys. Behavioral Ecology and Sociobiology, 60(5), 683-694.

171. Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift, 15(3), 259-263.

172. Kramer, D. L. (2001). Foraging behavior. Evolutionary ecology: concepts and case studies. Oxford University Press, New York, 232-246.

173. Krams I, Krama T, Freeberg TM, Kullberg C, Lucas JR (2012) Linking social complexity and vocal complexity: a parid perspective. Phil Trans R Soc B 367:1879-1891

174. Krams, I., Bērziņš, A., & Krama, T. (2009). Group effect in nest defence behaviour of breeding pied flycatchers, *Ficedula hypoleuca*. Animal Behaviour, 77(2), 513-517.

175. Krasnec, M. O., & Breed, M. D. (2012). Eusocial evolution and the recognition systems in social insects. Sensing in nature, 78-92.

176. Krebs, J., Ashcroft, R., & Webber, M. (1978). Song repertoires and territory defence in the great tit. Nature, 271(5645), 539-542.

177. Krüger, O., & Davies, N. B. (2002). The evolution of cuckoo parasitism: a comparative analysis. Proceedings of the Royal Society of London. Series B: Biological Sciences, 269(1489), 375-381.

178. Krüger, O., Davies, N. B., & Sorenson, M. D. (2007). The evolution of sexual dimorphism in parasitic cuckoos: sexual selection or coevolution? Proceedings of the Royal Society B: Biological Sciences, 274(1617), 1553-1560.

179. Langmore NE, Hunt S, Kilner RM. 2003. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. Nature 422:157–60

180. Langmore, N. E., Maurer, G., Adcock, G. J., & Kilner, R. M. (2008). Socially acquired host-specific mimicry and the evolution of host races in Horsfield's bronze-cuckoo *Chalcites basalis*. Evolution: International Journal of Organic Evolution, 62(7), 1689-1699.

181. Langmore, N. E., Stevens, M., Maurer, G., & Kilner, R. M. (2009). Are dark cuckoo eggs cryptic in host nests? Animal Behaviour, 78(2), 461-468.

182. Langmore, N. E., Stevens, M., Maurer, G., Heinsohn, R., Hall, M. L., Peters, A., & Kilner, R. M. (2011). Visual mimicry of host nestlings by cuckoos. Proceedings of the Royal Society B: Biological Sciences, 278(1717), 2455-2463.

183. Lawes, M. J., & Marthews, T. R. (2003). When will rejection of parasite nestlings by hosts of nonevicting avian brood parasites be favored? A misimprinting-equilibrium model. Behavioral Ecology, 14(6), 757-770.

184. Leighton, G. M. (2017). Cooperative breeding influences the number and type of vocalizations in avian lineages. Proceedings of the Royal Society B: Biological Sciences, 284(1868), 20171508.

185. Leonard, M. L., & Horn, A. G. (2001). Begging calls and parental feeding decisions in tree swallows (*Tachycineta bicolor*). Behavioral Ecology and Sociobiology, 49(2), 170-175.

186. Lescak, E. (2017). Ethograms. In: Shackelford, T., Weekes-Shackelford, V. (eds) Encyclopedia of Evolutionary Psychological Science. Springer, Cham. https://doi.org/10.1007/978-3-319-16999-6_2743-2

187. Levitis, D. A., Lidicker Jr, W. Z., & Freund, G. (2009). Behavioural biologists do not agree on what constitutes behaviour. Animal behaviour, 78(1), 103-110.

188. Lewis, R. J. (2010). Grooming patterns in Verreaux's sifaka. American Journal of Primatology, 72(3), 254-261.

189. Li, Y., Huang, Z., Zhou, Q., Ma, G., & Huang, C. (2019). Daily activity pattern in Assamese macaques inhabiting limestone forest, southwest Guangxi, China. Global Ecology and Conservation, *20*: e00709.

190. Lima, S. L. (1988). Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. Oikos, 3-11.

191. Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Canadian journal of zoology, 68(4), 619-640.

192. Liu, W. C., Rivers, J. W., & White, D. J. (2016). Vocal matching and intensity of begging calls are associated with a forebrain song circuit in a generalist brood parasite. Developmental neurobiology, 76(6), 615-625.

193. Logan, C. J., & Longino, J. T. (2013). Adult male coatis play with a band of juveniles. Brazilian Journal of Biology, 73, 353-355.

194. Luck, G. W. (2001). Variability in provisioning rates to nestlings in the cooperatively breeding Rufous Treecreeper, *Climacteris rufa*. Emu, 101(3), 221-224.

195. Lukas, D., & Clutton-Brock, T. (2012). Cooperative breeding and monogamy in mammalian societies. Proceedings of the Royal Society B: Biological Sciences, 279(1736), 2151-2156.

196. Lyon BE, Eadie, JM. 2004 An obligate brood parasite trapped in the intraspecific arms race of its hosts. Nature 432, 390-393.

197. MacColl, A. D., & Hatchwell, B. J. (2003). Sharing of caring: nestling provisioning behaviour of long-tailed tit, *Aegithalos caudatus*, parents and helpers. Animal Behaviour, 66(5), 955-964.

198. MacDougall-Shackleton SA (1997) Sexual selection and the evolution of song repertoires. Curr Ornithol 14:81–124

199. Madden, J. R., Kilner, R. M., & Davies, N. B. (2005). Nestling responses to adult food and alarm calls: 1. Species-specific responses in two cowbird hosts. Animal Behaviour, 70(3), 619-627.

200. Magrath, R. D., Pitcher, B. J., & Dalziell, A. H. (2007). How to be fed but not eaten: nestling responses to parental food calls and the sound of a predator's footsteps. Animal behaviour, 74(5), 1117-1129.

201. Magrath, R.D., Haff TM, Fallow PM, Radford AN (2015) Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. Biol Rev 90:560-586

202. Mahabal A, Vaidya VG (1989) Diurnal rhythms and seasonal changes in the roosting behaviour of Indian myna *Acridotheres tristis* (Linnaeus). Proceedings: Anim Sci 98(3): 199-209

203. Manser MB (2001) The acoustic structure of Suricates' alarm calls varies with predator type and the level of response urgency. Proc R Soc Lond B 268:2315-2324

204. Manser, M. B. (1999). Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*. Proceedings of the Royal Society of London B: Biological Sciences, 266(1423), 1013-1019.

205. Marchetti, K. (2000). Egg rejection in a passerine bird: size does matter. Animal Behaviour, 59(4), 877-883.

206. Marler P (1955) Characteristics of some animal calls. Nature 176:6-8

207. Marler P (1967) Animal communication signals: we are beginning to understand how the structure of animal signals relates to the function they serve. Science 157:769-774

208. Marler, P. (2004). Bird calls: their potential for behavioral neurobiology. Annals of the New York Academy of Sciences, 1016(1), 31-44.

209. Marshall, H. H., Carter, A. J., Rowcliffe, J. M., & Cowlishaw, G. (2012). Linking social foraging behaviour with individual time budgets and emergent group-level phenomena. Animal Behaviour, 84(6), 1295-1305.

210. Martin, J. K., & Martin, A. A. (2007). Resource distribution influences mating system in the bobuck (*Trichosurus cunninghami*: Marsupialia). Oecologia, 154, 227-236.

211. Martin, T. E. (1987). Food as a limit on breeding birds: a life-history perspective. Annual review of ecology and systematics, 18(1), 453-487.

212. Martin, T. E., Lloyd, P., Bosque, C., Barton, D. C., Biancucci, A. L., Cheng, Y. R., & Ton, R. (2011). Growth rate variation among passerine species in tropical and temperate sites: an antagonistic interaction between parental food provisioning and nest predation risk. Evolution: International Journal of Organic Evolution, 65(6), 1607-1622.

213. Martin, T. E., Scott, J., & Menge, C. (2000). Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society of London. Series B: Biological Sciences, 267(1459), 2287-2293.

214. Mason, P., & Rothstein, S. I. (1986). Coevolution and avian brood parasitism: cowbird eggs show evolutionary response to host discrimination. Evolution, 40(6), 1207-1214.

215. Maynard Smith, J. and Harper, DGC 2003. Animal signals. Oxford University press, Oxford.

216. McCarty, J. P. (2001). Variation in growth of nestling tree swallows across multiple temporal and spatial scales. The Auk, 118(1), 176-190.

217. Mccarty, J. P., & Winkler, D. W. (1999). Relative importance off environmental variables in determining the growth off nestling Tree Swallows *Tachycineta bicolor*. Ibis, 141(2), 286-296.

218. McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. Biology letters, 1(4), 381-385.

219. McGowan KJ, Woolfenden GE (1989) A sentinel system in the Florida scrub jay. Anim Behav 37: 1000-6

220. Monterroso, P., P. C. Alves, and P. Ferreras. 2014. Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. Behav. Ecol. Sociobiol. 68, *1403*– 1417.

221. Morales Picard A, Mundry R, Auersperg AM, Boeving ER, Boucherie PH, Bugnyar T, Dufour V, Emery NJ, Federspiel IG, Gajdon GK, Guéry JP (2020) Why preen others? Predictors of allopreening in parrots and corvids and comparisons to grooming in great apes. Ethology 126(2): 207-28

222. Morton ES (1977) On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. Am Nat 111:855-869

223. Naguib M, Mundry R, Ostreiher R, Hultsch H, Schrader L, Todt D (1999) Cooperatively breeding Arabian Babblers call differently when mobbing in different predator-induced situations. Behav Ecol 10:636-640

224. Nam, K. B., Simeoni, M., Sharp, S. P., & Hatchwell, B. J. (2010). Kinship affects investment by helpers in a cooperatively breeding bird. Proceedings of the Royal Society B: Biological Sciences, 277(1698), 3299-3306.

225. Narang, M. L., & Lamba, B. S. (1986). Food habits of jungle babbler *Turdoides striatus* (Dumont) and its role in the ecosystem. Indian Journal of Ecology, 13(1), 38-45.

226. Nowicki, S., & Searcy, W. A. (2004). Song function and the evolution of female preferences: why birds sing, why brains matter. Annals of the New York Academy of Sciences, 1016(1), 704-723.

227. Orłowski, G., Rusiecki, S., & Karg, J. (2014). Partial dietary segregation between adult and nestling Bluethroats *Luscinia svecica*. Acta Ornithologica, 49(1), 107-118.

228. Owens, I. P., & Bennett, P. M. (1994). Mortality costs of parental care and sexual dimorphism in birds. Proceedings of the Royal Society of London. Series B: Biological Sciences, 257(1348), 1-8.

229. Painter, J. N., Crozier, R. H., Poiani, A., Robertson, R. J., & Clarke, M. F. (2000). Complex social organization reflects genetic structure and relatedness in the cooperatively breeding bell miner, *Manorina melanophrys*. Molecular Ecology, 9(9), 1339-1347.

230. Payne, R. B. (1977). The ecology of brood parasitism in birds. Annual review of ecology and systematics, 1-28.

231. Payne, R. B., & Sorensen, M. D. (2005). The cuckoos (Vol. 15). Oxford University Press.

232. Peckre, L., Kappeler, P. M., & Fichtel, C. (2019). Clarifying and expanding the social complexity hypothesis for communicative complexity. Behavioral Ecology and Sociobiology, 73(1), 1-19.

233. Pen, I., & Weissing, F. J. (2000). Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. Proceedings of the Royal Society of London. Series B: Biological Sciences, 267(1460), 2411-2418.

234. Pereyra, M. E., & Morton, M. L. (2001). Nestling growth and thermoregulatory development in subalpine Dusky Flycatchers. The Auk, 118(1), 116-136.

235. Pierotti, R. (1980). Spite and altruism in gulls. The American Naturalist, 115(2), 290-300.

236. Polačiková, L., Takasu, F., Stokke, B. G., Moksnes, A., Røskaft, E., Cassey, P., ... & Grim, T. (2013). Egg arrangement in avian clutches covaries with the rejection of foreign eggs. Animal cognition, 16(5), 819-828.

237. Pollard, K. A., & Blumstein, D. T. (2008). Time allocation and the evolution of group size. Animal Behaviour, 76(5), 1683-1699.

238. Pozis-Francois, O., Zahavi, A., & Zahavi, A. (2004). Social play in Arabian babblers. Behaviour, 141(4), 425-450.

239. R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

240. Radford AN (2011) Preparing for battle? Potential intergroup conflict promotes current intragroup affiliation. Biol Lett 7(1): 26-29.

241. Radford, A. N. (2008). Age-related changes in nestling diet of the cooperatively breeding green woodhoopoe. Ethology, 114(9), 907-915.

242. Radford, A. N. (2008). Duration and outcome of intergroup conflict influences intragroup affiliative behaviour. Proceedings of the Royal Society B: Biological Sciences, 275(1653), 2787-2791.

243. Radford, A. N., & Du Plessis, M. A. (2006). Dual function of allopreening in the cooperatively breeding green woodhoopoe, *Phoeniculus purpureus*. Behavioral Ecology and Sociobiology, 61, 221-230.

244. Radford, A. N., & Ridley, A. R. (2008). Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Animal behaviour, 75*(2), 519-527.

245. Raihani, N. J., & Ridley, A. R. (2007). Adult vocalizations during provisioning: offspring response and postfledging benefits in wild pied babblers. Animal Behaviour, 74(5), 1303-1309.

246. Raihani, N. J., & Ridley, A. R. (2008). Experimental evidence for teaching in wild pied babblers. Animal Behaviour, 75(1), 3-11.

247. Raihani, N. J., Nelson-Flower, M. J., Moyes, K., Browning, L. E., & Ridley, A. R. (2010). Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. Journal of Animal Ecology, 79(1), 44-52.

248. Ramsay, S. L., & Houston, D. C. (2003). Amino acid composition of some woodland arthropods and its implications for breeding tits and other passerines. Ibis, 145(2), 227-232.

249. Rasmussen, K. L. R. (1985). Changes in the activity budgets of yellow baboons (*Papio cynocephalus*) during sexual consortships. *Behavioral* Ecology and Sociobiology, 17(2), 161-170.

250. Reyes-Arriagada, R., Jiménez, J. E., & Rozzi, R. (2015). Daily patterns of activity of passerine birds in a Magellanic sub-Antarctic Forest at Omora Park (55 S), Cape Horn Biosphere Reserve, Chile. Polar Biology, 38(3), 401-411.

251. Ridley, A. R., Nelson-Flower, M. J., & Thompson, A. M. (2013). Is sentinel behaviour safe? An experimental investigation. Animal Behaviour, 85(1), 137-142.

252. Riehl, C. (2013). Evolutionary routes to non-kin cooperative breeding in birds. Proceedings of the Royal Society B: Biological Sciences, 280(1772), 20132245.

253. Ripley B, Venables B, Bates D, Hornik K, Gebhardt A, Firth D, Ripley MB (2013) Package 'mass'. Cran R 538:113-120

254. Rivers, J. W. (2007). Nest mate size, but not short-term need, influences begging behavior of a generalist brood parasite. Behavioral Ecology, 18(1), 222-230.

255. Robinson CM, Creanza N (2019) Species-level repertoire size predicts a correlation between individual song elaboration and reproductive success. Ecol Evol 9:8362-8377

256. Rodríguez-Gironés, M. A., Zúniga, J. M., & Redondo, T. (2001). Effects of begging on growth rates of nestling chicks. Behavioral Ecology, 12(3), 269-274.

257. Rood, J. P. (1978). Dwarf Mongoose Helpers at the Den 1. Zeitschrift für Tierpsychologie, 48(3), 277-287.

258. Rothstein, S. I. (1990). A model system for coevolution: avian brood parasitism. Annual review of ecology and systematics, 21(1), 481-508.

259. Royle, N., Smiseth, P. & Kölliker, M. 2012. The Evolution of Parental Care. Oxford University Press, Oxford.

260. RStudio Team (2021) RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/

261. Sachs, B. D. (1988). The development of grooming and its expression in adult animals. Annals of the New York Academy of Sciences, 525(1), 1-17.

262. Sanjeeva Raj PJ. 1964. Communal breeding in the white-headed babbler, *Turdoides affinis* (Jerdon) in Tambaram, Madras State. J. Bombay Nat. Hist. Soc. 61: 181- 83

263. Schuetz, J. G. (2005). Reduced growth but not survival of chicks with altered gape patterns: implications for the evolution of nestling similarity in a parasitic finch. Animal Behaviour, 70(4), 839-848.

264. Schwagmeyer, P. L., & Mock, D. W. (2008). Parental provisioning and offspring fitness: size matters. Animal Behaviour, 75(1), 291-298.

265. Searcy WA (1992) Song repertoire and mate choice in birds. Am Zool 32:71-80

266. Seddon N (2002) The structure, context and possible functions of solos, duets and choruses in the Subdesert Mesite (*Monias benschi*). Behaviour 139:645-676

267. Seddon N, Alvarez A, Tobias J (2002) Vocal communication in the Pale-winged Trumpeter (*Psophia leucoptera*): repertoire, context and functional reference. Behaviour 139:1331-1359

268. Seyfarth RM, Cheney DL, Marler P (1980) Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science 210:801-803

269. Sherman, P. W., Lacey, E. A., Reeve, H. K., & Keller, L. (1995). The eusociality continuum. Behavioral Ecology, 6(1), 102-108.

270. Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. Philosophical Transactions of the Royal Society B: Biological Sciences, 362(1480), 539-559.

271. Singh, R., & Jain, M. (2021). Variation in call types, calling activity patterns and relationship between call frequency and body size in a field cricket, *Acanthogryllus asiaticus*. Bioacoustics, 30(3), 284-302.

272. Smiseth, P. T. (2019). Coordination, cooperation, and conflict between caring parents in burying beetles. Frontiers in Ecology and Evolution, 7, 397.

273. Soler, M. (2009). Co-evolutionary arms race between brood parasites and their hosts at the nestling stage. Journal of Avian Biology, 40(3), 237-240.

274. Sommer C (2011) Alarm calling and sentinel behaviour in Arabian Babblers. Bioacoustics 20:357-368

275. Sparks J (1967) Allogrooming in primates: A review. In Morris D (Ed.), Primate Ethology. Weidenfeld and Nicholson, London, pp 148-175

276. Spottiswoode, C. N., & Stevens, M. (2010). Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. Proceedings of the National Academy of Sciences, 107(19), 8672-8676.

277. Sridhar, H., & Guttal, V. (2018). Friendship across species borders: factors that facilitate and constrain heterospecific sociality. Philosophical Transactions of the Royal Society B: Biological Sciences, 373(1746), 20170014.

278. Stacey, P. B., & Koenig, W. D. (Eds.). (1990). Cooperative breeding in birds: long term studies of ecology and behaviour. Cambridge University Press.

279. Starck, J. M., & Ricklefs, R. E. (Eds.). (1998). Avian growth and development: evolution within the altricial-precocial spectrum (No. 8). Oxford University Press on Demand.

280. Steiger SS, Valcu M, Spoelstra K, Helm B, Wikelski M, Kempenaers B (2013) When the sun never sets: diverse activity rhythms under continuous daylight in free-living arctic-breeding birds. Proc Royal Soc B 280(1764): 2013-1016

281. Stephenson, S., Hannon, S., & Proctor, H. (2009). The function of feathers in tree swallow nests: insulation or ectoparasite barrier? The Condor, 111(3), 479-487.

282. Stoddard, M. C., & Hauber, M. E. (2017). Colour, vision and coevolution in avian brood parasitism. Philosophical Transactions of the Royal Society B: Biological Sciences, 372(1724), 20160339.

283. Stoddard, M. C., & Stevens, M. (2010). Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. Proceedings of the Royal Society B: Biological Sciences, 277(1686), 1387-1393.

284. Stoddard, M. C., Kilner, R. M., & Town, C. (2014). Pattern recognition algorithm reveals how birds evolve individual egg pattern signatures. Nature communications, 5(1), 1-10.

285. Strickland, D., & Waite, T. A. (2001). Does initial suppression of allofeeding in small jays help to conceal their nests? Canadian Journal of Zoology, 79(12), 2128-2146.

286. Stynoski, J. L., & Noble, V. R. (2012). To beg or to freeze: multimodal sensory integration directs behavior in a tadpole. Behavioral Ecology and Sociobiology, 66(2), 191-199.

287. Sullivan, K. A. (1989). Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). The Journal of Animal Ecology, 275-286.

288. Sunarto, S., M. J. Kelly, K. Parakkasi, and M. B. Hutajulu. (2015). Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. J. Zool. 296, 104– 115.

289. Sussman, R. W., Garber, P. A., & Cheverud, J. M. (2005). Importance of cooperation and affiliation in the evolution of primate sociality. American journal of physical anthropology, 128(1), 84-97.

290. Batra, S. W. (1966). Nests and social behavior of halictine bees of India (Hymenoptera: Halictidae). The Indian Journal of Entomology, 28, 375.

291. Suzuki, T. N. (2014). Communication about predator type by a bird using discrete, graded and combinatorial variation in alarm calls. *Animal Behaviour*, *87*, 59-65.

292. Swingland IR (1976) The influence of light intensity on the roosting times of the Rook (*Corvus frugilegus*). Anim Behav 24(1):154-8

293. Tanaka KD, Morimoto G, Stevens M, Ueda K. 2011. Rethinking visual supernormal stimuli in cuckoos: visual modeling of host and parasite signals. Behav. Ecol. 22:1012–19

294. Tinbergen, N (1955). The Study of Instinct. Clarendon Press; Oxford.

295. Tinbergen, N. (1963) On aims and methods in ethology. Zeitschrift für Tierpsychologie 20: 410–33.

296. Tokue K, Ueda K. 2010. Mangrove gerygones *Gerygone laevigaster* eject little bronze-cuckoo *Chalcites minutillus* hatchlings from parasitized nests. Ibis 152:835–39

297. Trnka, A., & Grim, T. (2013). Color plumage polymorphism and predator mimicry in brood parasites. Frontiers in zoology, 10(1), 1-10.

298. Troisi, A., & Schino, G. (1986). Diurnal and climatic influences on allogrooming behaviour in a captive group of Java monkeys. Animal behaviour, 34(5), 1420-1426.

299. Tuero, D. T., Gloag, R., & Reboreda, J. C. (2016). Nest environment modulates begging behavior of a generalist brood parasite. Behavioral Ecology, 27(1), 204-210.

300. Ursino, C. A., De Mársico, M. C., Sued, M., Farall, A., & Reboreda, J. C. (2011). Brood parasitism disproportionately increases nest provisioning and helper recruitment in a cooperatively breeding bird. Behavioral Ecology and Sociobiology, 65(12), 2279-2286.

301. Váczi, O., Koósz, B., & Altbäcker, V. (2006). Modified ambient temperature perception affects daily activity patterns in the European ground squirrel (*Spermophilus citellus*). Journal of Mammalogy, 87(1), 54-59

302. Valencia, J., De La Cruz, C., Carranza, J., & Mateos, C. (2006). Parents increase their parental effort when aided by helpers in a cooperatively breeding bird. Animal Behaviour, 71(5), 1021-1028.

303. Van Lawick-Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Animal behaviour monographs, 1, 161-IN12.

304. Vijayan, S., Warrant, E. J., & Somanathan, H. (2022). Defensive shimmering responses in Apis dorsata are triggered by dark stimuli moving against a bright background. Journal of Experimental Biology, 225(17).

305. Walters, J. R. (1984). The evolution of parental behavior and clutch size in shorebirds. In Shorebirds (pp. 243-287). Springer, Boston, MA.

306. Wang, J., Li, Q., & Yang, C. (2020). Coevolution of acoustical communication between obligate avian brood parasites and their hosts. Avian Research, 11(1), 1-13.

307. Warrington MH, McDonald PG, Sager AK, Griffith SC (2014) The vocal repertoire of the cooperatively breeding Apostlebird (*Struthidea cinerea*). Emu 114:206-221

308. Weathers, W. W. (1992). Scaling nestling energy requirements. Ibis, 134(2), 142-153.

309. Welbergen, J. A., & Davies, N. B. (2009). Strategic variation in mobbing as a front line of defense against brood parasitism. Current biology, 19(3), 235-240.

310. West, S. A., Griffin, A. S., & Gardner, A. (2007). Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. Journal of evolutionary biology, 20(2), 415-432.

311. Whistler, H. (1949). Popular handbook of Indian birds. Gurney and Jackson, London.

312. Whittow, G. C., & Tazawa, H. (1991). The early development of thermoregulation in birds. Physiological Zoology, 64(6), 1371-1390.

313. Wickler W (1985) Coordination of vigilance in bird groups: The “Watchman’s song” hypothesis. Z. Tierpsychol 69: 250-253

314. Wiley, E. M., & Ridley, A. R. (2016). The effects of temperature on offspring provisioning in a cooperative breeder. Animal Behaviour, 117, 187-195.

315. Wilkin, T. A., King, L. E., & Sheldon, B. C. (2009). Habitat quality, nestling diet, and provisioning behaviour in great tits *Parus major*. Journal of Avian Biology, 40(2), 135-145.

316. Wilson, E. O. (1970). Competitive and aggressive behavior. Social Science Information, 9(6), 123-154.

317. Winkler, D. W. (1987). A general model for parental care. The American Naturalist, 130(4), 526-543.

318. Wong, M. Y., Jordan, L. A., Marsh-Rollo, S., St-Cyr, S., Reynolds, J. O., Stiver, K. A., ... & Balshine, S. (2012). Mating systems in cooperative breeders: the roles of resource dispersion and conflict mitigation. Behavioral Ecology, 23(3), 521-530.

319. Wong, M. Y., Munday, P. L., & Jones, G. P. (2005). Habitat patch size, facultative monogamy and sex change in a coral-dwelling fish, *Caracanthus unipinna*. Environmental Biology of Fishes, 74, 141-150.

320. Wright, J. (1998). Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. Behavioral Ecology and Sociobiology, 42(6), 423-429.

321. Wright, J., Maklakov, A. A., & Khazin, V. (2001). State-dependent sentinels: an experimental study in the Arabian babbler. Proceedings of the Royal Society of London B: Biological Sciences, 268(1469), 821-826.

322. Yambem, S. D., Chorol, S., & Jain, M. (2021). More than just babble: functional and structural complexity of vocalizations of Jungle Babbler. *Behavioral Ecology and Sociobiology, 75*(8), 1-14.

323. Yambem, S. D., & Jain, M. (2022). Temporal variation in the behaviour of a cooperatively breeding bird, Jungle Babbler (*Argya striata*). *Tropical Ecology*, 1-13.

324. Yang, C., Wang, L., Cheng, S. J., Hsu, Y. C., Liang, W., & Møller, A. P. (2014). Nest defenses and egg recognition of yellow-bellied prinia against cuckoo parasitism. Naturwissenschaften, 101(9), 727-734.

325. Young, C. (2019). Agonistic Behavior. In: Vonk, J., Shackelford, T. (eds) Encyclopedia of Animal Cognition and Behavior. Springer, Cham. https://doi.org/10.1007/978-3-319-47829-6_320-1

326. Zacharias, V. J., & Mathew, D. N. (1988). Ecology of Babblers (*Turdoides* spp.). Journal of the Bombay Natural History Society, 85(1), 50-63.

327. Zahavi, A. (1995). Altruism as a handicap: the limitations of kin selection and reciprocity. Journal of Avian Biology, 26(1), 1-3.

328. Zeileis A, Hothorn T (2002) Diagnostic checking in regression relationships. R News 2:7-10

329. Zhou, Q., Wei, F., Huang, C., Li, M., Ren, B., & Luo, B. (2007). Seasonal variation in the activity patterns and time budgets of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China. International Journal of Primatology, 28(3), 657-671.

330. Zöttl, M., Heg, D., Chervet, N., & Taborsky, M. (2013). Kinship reduces alloparental care in cooperative cichlids where helpers pay-to-stay. Nature communications, 4(1), 1-9.

List of Awards

- Association for Tropical Biology and Conservation (ATBC) **Travel Grant** 2023
- International Society for Behavioural Ecology (ISBE) 2022 **Travel Award** 2022
- Association for the Study of Animal Behaviour (ASAB) Summer 2019 **Diversity Travel Grant** 2019
- **2nd Best Oral Presentation Award in** 42nd Annual Conference of Ethological Society of India (ESI) and National Symposium on Animal Behaviour, Biodiversity and Human Future at University of Calicut, Kerala, India 2018