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ORIGINAL PAPER

Temporal variation in the behaviour of a cooperatively breeding bird, Jungle Babbler (*Argya striata*)

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Abstract

Time is an important and limited resource that can drive the trade-off between various essential activities in the lives of animals. Group-living social birds are likely to be constrained for time as they need to perform individual behaviours required for sustenance but also participate in group activities. They must, therefore, partition the available time between these activities which may vary considerably with environmental and ecological conditions, making studies on time-activity budgets of social animals essential in understanding the evolution of sociality. We examined the time-activity budget of a cooperative passerine, Jungle Babbler (*Argya striata*) and temporal variation in their behaviours. A repertoire of 13 behaviours was recorded of which 12 behaviours that occur throughout the year were examined further in detail. This included individual behaviours such as foraging, grooming, rest, shower and group behaviours such as allogrooming, movement, play, sentinel, mobbing and inter-group fight. Our results indicate that most of the time (about 70%) was spent performing individual behaviours and the remaining time (about 30%) was allocated to social behaviours. We also found almost all behaviours varied across diel and seasonal scales with respect to the proportion of time spent performing them. This highlights the impact of environmental factors on how animals partition their time to perform various activities. Our study also lays the foundation for future studies examining the role of ecological factors such as habitat type and predation pressure in driving these patterns of behaviour in Jungle Babblers.

Keywords Activity pattern · Diel activity pattern · Roosting · Seasonal variation · Social behaviour · Time-activity budget

Introduction

Animals carry out different behaviours on a daily basis throughout their lifetime in order to survive and reproduce. Given that time itself is a limited resource, there is often a trade-off between the allocation of time to different behaviours which may depend on the physical state of the animal, environmental and ecological factors (Pollard and Blumstein 2008). For instance, foraging behaviour is crucial for the survival of the animal and helps in acquiring energy to perform other activities. It is, therefore, expected to have a larger proportion of time allocated to it leaving less time for other activities such as resting or grooming (Kramer 2001). However, in social animals, allocation of time becomes more complex since the animals not only need to devote enough time to successfully gather resources and reproduce but also to spend time on activities that help in maintaining social bonds such as allogrooming (Boccia et al. 1982; Dunbar 1991) and play (Pozis-Francois et al. 2004) and in those that aid in group coordination such as movement or sentinel behaviour (Hollén et al. 2008). Activities involved in maintaining or strengthening social bonds correlate with the direct or indirect fitness of the animal (Silk 2007; Dunbar et al. 2009) and are vital for social animals. Failure to manage time between the various activities may have serious consequences on the number of calories consumed and exhaustion (Capellini et al. 2010). In addition, for social animals, it may also impact social bonding and thereby group dynamics (Dunbar 1992; Radford 2011). Thus, different behaviours are allocated differential amounts of time depending on metabolic and energetic constraints as well as the importance of behaviour in the sustenance of life of the animal (Halle and Stenseth 2000). This allocation of time to different activities is called as 'time-activity budget'.

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The behavioural states of an animal are grouped into two broad categories: 'activity' and 'rest'. Activity behaviours such as foraging, territory defence, exploration of novel territory, finding mates etc., require disproportionately more energy while rest behaviours such as sleeping/resting, grooming, playing etc. require less energy. Even though activity behaviours are crucial for survival, one cannot continuously remain in a high activity state. Such behaviours are typically alternated by resting behaviour in order to restore energy. The transition of one behavioural state to another across a 24 h cycle, on a daily basis, leads to the development of a temporal pattern which is generally called diel activity pattern or activity pattern of a species (Halle and Stenseth 2000). Based on the activity patterns at different times of the day, animals can be broadly categorized as nocturnal (active at night), diurnal (active during daytime), crepuscular (active at twilight) and cathemeral (active almost equal proportion of time during day and night). However, these categories are not universal as the activity pattern is flexible and can vary even within the same species with variation in habitat and season (Ikeda et al. 2016). This variation in diel activity patterns across species creates a behavioural niche, allowing the coexistence of different species (Monterroso et al. 2014; Sunarto et al. 2015).

Activity patterns can vary within a species, driven both by abiotic and biotic factors. Biotic factors that may affect the activity pattern in animals include the activity patterns of other species including predators (Lima and Dill 1990), humans (Banerjee and Bhadra 2021) and competitors (Blanchet et al. 2008). Among abiotic factors, the course of seasons and the time of the day are crucial as they significantly impact changes in various environmental parameters such as light intensity and temperature (Steiger et al. 2013). For instance, dark-eyed juncos (*Junco hyemalis*) initiate feeding early in dim light to replenish their low energy reserves and terminate their activity at high light intensity before the risk of predation increases (Lima 1988). European ground squirrels (*Spermophilus citellus*) spend more time resting when the ambient temperature is high during mid-day (Váczi et al. 2006). Emergence and roosting behaviour, in particular, are likely to be strongly influenced by ambient light conditions and are activity patterns which are likely to change across different seasons. Understanding the activity patterns and the extent to which these change with various factors provides insights into the ecology of animals. In social vertebrates, most studies on activity budget and the temporal variation in activity patterns have been carried out on primates (Rasmussen 1985; Isbell and Young 1993; Zhou et al. 2007; Back et al. 2019; Li et al. 2019). While many avian species are social, yet, to our knowledge, similar studies are lacking in social passerines.

Jungle Babbler (*Argya striata*) is a cooperatively breeding bird belonging to the order Passeriformes and the family Leiothrichidae (Cai et al. 2019). They are found throughout lowland India, mainly in tropical woodland and scrub vegetation and often close to human habitation (Andrews and Naik 1970; Gaston 1977). They live in groups of 3–20 individuals that engage in many social behaviours (Andrews and Naik 1970) and possess a complex vocal repertoire of calls that mediate various social behaviours such as foraging, movement, sentinel activity and brood care (Yambem et al. 2021). Being social birds, Jungle Babblers engage in many social behaviours such as allogrooming, coordinated vigilance, play behaviour etc., which require proper time budgeting to maintain the balance between sustenance and sociality. Thus, they offer to be a good model system to study the allocation of time in social birds. In this study, we aimed to address the following questions: (1) Do Jungle Babblers differentially allocate time to different behaviours? (2) Does the time spent performing different behaviours change across diel and seasonal scale? (3) Does roosting and emergence from roost vary with ambient light conditions and seasons? We hypothesised that the birds would allocate a higher proportion of time towards behaviours for sustenance as compared to those involved in social bonding. Towards this, we predicted that the highest proportion of their time budget would be allocated to foraging as it is an important behaviour that determines sustenance. We also hypothesized that the fraction of time allocated for a behaviour is likely to be influenced by environmental features. Towards this, we predicted that the activity patterns will vary across different seasons due to changes in ambient temperature and foliage cover across seasons. Following our hypothesis, we also expected both roosting and emergence to vary in relation to ambient light conditions and seasons. Additionally, we examined sentinel duty in detail to understand what proportion of foraging activity had a sentinel on duty and whether this varied with season. Gaston (1977) examined sentinel behaviour in Jungle Babblers during the winter season but did not examine seasonal variation in this behaviour.

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". This study provides insights into the ecology of a tropical social passerine. It also provides novel data on the impact of environmental conditions on activity patterns of a social passerine, thereby furthering our understanding of factors that determine trade-offs in time investment across different behaviours in social animals. Such data are lacking in social avian species and specifically lacking from the tropics which are home to many social animals.

Materials and methods

Study species and study site

The study was conducted in Mohali region, located in the eastern part of Punjab state in India (30° 36′ and 30° 45′ N latitude and 76° 38′ and 76° 46′ E longitude), which covers an area of about 116.50 km^2 (Tur et al. 2011). The climate of Mohali comes under 'Cwa' category. Mohali has a humid subtropical climate with dry winter, hot summer, humid monsoon and a short transitional period of postmonsoon (Kottek et al. 2006). For ease of observation and logistical considerations, all observations were made on institute campuses where a healthy population of Jungle Babblers is known to exist and has been monitored regularly over several years. A total of three locations were selected across two institute campuses: 2 on the IISER (Indian Institute of Science Education and Research) Mohali campus and 1 on the NIPER (National Institute of Pharmaceutical Education and Research) Mohali campus, such that each site was at least 500 m away from each other. These campuses have a mix of gardens, open grasslands, plantations and natural closed-canopy woodlands. The area is dominated by deciduous plants as well as weedy species. The plant species include *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., *Lantana camara, Ricinus communis* and *Cannabis* sp.

Data collection

All the observations were done using 10 × 42 binoculars (Nikon Monarch) at a distance of > 5 m. Ad libitum sampling (Altmann 1974) for 5 months was carried out so that the animals could be habituated to the observers' presence and the observers can understand the patterns of movements, rough territory size and list of observable behaviours. For this study, we observed multiple groups to examine the time-activity budget at the species level. Since several individuals in each group are banded and Jungle Babblers are known to be territorial (Andrew and Naik 1970), we could ensure that we were sampling distinct groups. The repertoire of 13 different behaviours observed in the focal species is summarised for reference in Table 1. Some of the common behaviours are shown in pictures (Fig. 1). This list of behaviours is based on our observations which are validated by previous studies on Jungle Babblers (Andrew and Naik 1970; Gaston 1977; Yambem et al. 2021).

The behavioural data for this study were collected between October 2016 and September 2017. Of the 13 behaviours listed, 12 occurred throughout the year. Parental care was not included in this study as it is limited to

Table 1 Ethogram of Jungle Babbler with 13 behaviours. Shaded rows represent the behaviours that were used in this study for time-activity budget and activity pattern

Behaviour	Description
Foraging +	Process of finding and obtaining food by hopping and pecking on the leaf litter, foliage, bark crevices and ground
Grooming	The activity of cleaning or maintaining one's own body with its beak
Rest	One or more individual(s) perch on a branch next to each other with eyes open or closed, not partaking in other activities
Shower*	Quickly dipping body in a shallow pool of water and subsequently shaking off water from feathers
Allogrooming	Two or more individuals groom each other by pecking lightly
Movement +	Flying as a group, with or without vocalizations, from one spot to another within a distance of 10–20 m by making quick stops in between
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 trees (Gaston 1977)
Sentinel +	One, sometimes two, individual(s) perch on an elevated platform exhibiting vigilance, while other group members forage on the ground
Mobbing* +	Attacking or chasing a predator, by some individuals or all group members
Inter-group fight* +	Aggressive interactions between members of two groups that encounter each other. Interactions are mainly mediated through vocalizations and sometimes followed by physical combat
Emergence	All members of a group emerge from the roost one by one
Roosting	Group members perched on one or two branches in a clumped manner, either facing in the same or opposite direction
Parental care +	Involves behaviours such as nest building, incubation, brooding, feeding, grooming and guarding the nestling/fledgling, or prompting the fledglings to fly

*Indicates the behaviours which were grouped into 'other' behaviour and + represents those behaviours which are associated with vocalization (Yambem et al. 2021)

Fig. 1 Jungle Babbler showing various behaviours. From top left to bottom right: foraging, grooming, allogrooming and rest

breeding time which generally lies between March to October (Andrew and Naik 1970). To record the activity pattern between 5:00 and 20:00, 6 h of observations were carried out in 2 sessions in a day with a break of at least 3 h in between. Each session included 3 sampling hours of observations and a sampling hour was divided into a sequence of alternating 5-min periods of observation and rest each to avoid exhaustion of the observer. Timings of the observations were alternated across days such that all time slots between 5:00 and 20:00 were covered at least once a week. Every 1-h time slot was sampled for at least 20 days, spread across the year, in the study period (Table S1). However, due to adverse weather conditions and poor visibility, only 9 days of sampling could be carried out in January (Table S2). The frequency of visiting the three different locations was kept the same. The sampling technique used was instantaneous scan sampling (Altmann 1974) in which all the behavioural activities performed by observable group members as well as the durations of the activities were noted using a digital stopwatch (Marathon Adanac 3000). If all the birds being observed went out of sight before completing the 5 min, then the observation was truncated and data from that sampling period was discarded to maintain uniformity across sampling times.

Observations on emergence from and return to the roost sites of Jungle Babblers were done from October 2016 to February 2018, one hour before predicted sunrise (5:19–7:21) and sunset (17:32–19:30), respectively. The time of the return to roost and emergence was noted down only when all the group members settled down and clumped together on a branch of a tree and when all the group members flew out from the roosting tree respectively. The light intensity at the time of roosting and emergence was also noted down using the light meter (Lutron 1102).

Data analyses

The time-activity budget was calculated for 10 out of the 13 observed behaviours (highlighted in colour in Table 1). Emergence and roosting behaviour were analysed separately since emergence is an event behaviour and roosting occurred at the end of the day and through the night time. The time-activity budget was calculated as the proportion of time spent performing each behaviour by dividing the number of scans in which a particular behaviour was exhibited by the total number of scans summed across all behaviours. This was then converted into percentage values representing the percentage of time spent for each of the different behaviours. In addition, we calculated the proportion of time spent for each behaviour in each of the 15 sampling hours (5:00–20:00), averaged across all months, to examine the diel pattern of the behaviour and for each month of the year, averaged across all sampling hours, to examine seasonal variations in activity patterns. To compare time spent on individual versus social behaviours, the 10 behaviours were grouped into two categories: individual and social behaviour. Those behaviours that do not require the participation of other members of the group were designated as individual behaviour (foraging, grooming, rest and shower), whereas those that require the participation of others in the group were labelled as social behaviour (allogrooming, movement, play, sentinel, mobbing and inter-group fight). For ease of analyses, rarely observed behaviours (that occurred in < 1% of all observations) were grouped into a single behavioural category called 'other' (Table 1). To examine seasonal variation in activity patterns, data were arranged into four seasons: winter (December–February), summer (March–June), monsoon (July–September) and postmonsoon (November–December). This grouping resulted in fewer days in some seasons and more in others, however, it represents the most relevant categorization given the meteorological conditions experienced in Mohali. Since the data for seasonal variation were calculated as averages, this inequality should not matter.

Statistical analyses

All the statistical analyses were carried out in R version 4.1.0 (R Core Team 2021). To check the influence of factors such as time of the day (diel pattern) and length of the day on different behavioural activities, Generalised Linear Model (GLM) was run for each behavioural activity. Response variable for the model was the proportion of time allocated to each behaviour: foraging, grooming, rest, allogrooming, movement, sentinel and 'other'. Since the response variable was the proportion data, family "quasibinomial" with link "logit" was applied in the model. Kruskal–Wallis test was carried out to examine seasonal variation in the proportion of time spent on behavioural activities as well as on the timing of emergence and roosting. Mann–Whitney *U* test was further carried out to make pairwise comparisons between seasons. Mann–Whitney *U* test was carried out to examine the difference between the light intensity at the time of emergence and roosting.

Results

Time-activity budget

In one year, a total of 18,178 behavioural records (pooled across all behaviours) were obtained by combining all the observations from the three locations. These behavioural records were collected from 12,330 scan samples recorded across 192 days of observations. Detailed sample size for every sampling hour and month are given in Tables S1 and S2. Time-activity budget is represented in percentages in Fig. 2. Our findings suggested that Jungle Babblers spent around 69% of their time on individual behaviours and the remaining 31% was allocated to social behaviours (Fig. 2). Individual behaviours such as foraging, grooming, rest and shower are necessary for sustenance and maintenance, whereas, social behaviours such as allogrooming, movement, play, sentinel, mobbing and inter-group fight are required to

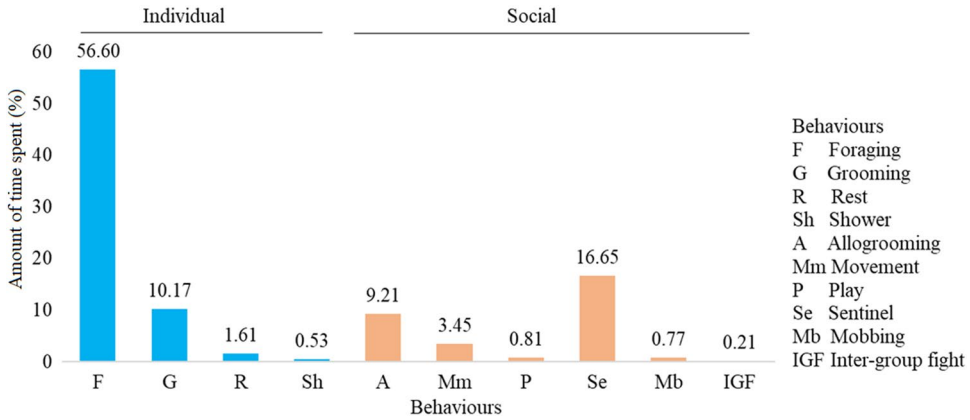

Fig. 2 Amount of time spent (represented in percentage) on each behavioural activity calculated from 18,178 scans of all behaviours collected from 192 days between October 2016 and September 2017

maintain group stability. Amongst different behaviours, the highest amount of time was devoted to foraging (56.6%) followed by sentinel (16.65%). Further, we found that on average, a sentinel was present only about 32% of the time while Jungle Babblers foraged. For the remaining time, no sentinel was found to be on duty. Furthermore, we found that Jungle Babblers spent almost equal amount of time ($\chi^2 = 0.047$, $df = 1$, $p = 0.82$) on grooming (10.17%) and allogrooming (9.21%) and the least amount of time was devoted to movement (3.45%) and resting (1.61%). The remaining amount of time was allocated to several behaviours that were pooled as 'other' (1.79%) (Fig. 2).

Diurnal and seasonal variation in activity pattern

The outputs of GLM showed that foraging, grooming, rest, sentinel and movement behaviour exhibited diurnal activity patterns whereas, allogrooming and 'other' behaviour did not show any diurnal pattern (Fig. 3 and Table 2). Sentinel, rest and movement behaviour increased with the time of the day (Table 2) while foraging and grooming decreased with the time of the day (Table 2). Diurnal activity pattern of allogrooming, rest and sentinel varied with the length of the day wherein, allogrooming and rest increased but sentinel activity decreased with the length of the day (Table 2). Results of the Kruskal–Wallis test showed that all behaviours varied across seasons (Fig. 4 and Table 3a). The proportion of time spent foraging was highest during postmonsoon and lowest during winter (Fig. 4). Pairwise comparisons across seasons revealed a significant difference in time spent foraging across most seasons (Table 3b). Grooming and allogrooming were high during monsoon, rest and movement activities were found to be high during summer and 'other' activity was high during monsoon (Fig. 4). The percentage of time that a sentinel was present during foraging activity varied significantly across seasons wherein, in winters a sentinel was found to be on duty 48% of time but only 14% of time during the monsoon (Fig. 5 and Table 3c).

Emergence and roosting

Results of Kruskal–Wallis test showed that the timing of emergence and roosting varied with seasons (Fig. 6a and Table 3a). Pairwise comparisons showed that Jungle Babblers emerged from their roosts earliest during summer (Fig. 6a and Table 3b). Pairwise comparisons also revealed that Jungle Babblers returned to their roosts significantly earlier during winter and monsoon, which did not differ significantly from each other (Fig. 6a and Table 3b). Light intensity at the time of roosting was significantly higher than at the time of emergence (Mann–Whitney U: $p < 0.001$, Fig. 6b.).

Discussion

Time-activity budget

Time is an important resource and its availability to animals is limited. Examining how animals partition their time between various activities can reveal much about their ecology. Gadagkar and Joshi (1983), in their study on the social wasps, *Ropalidia marginata* used time-activity budget data to reveal behavioural castes in the species that lacks morphological differences between individuals, unlike other social insects. Dunbar (1992) showed that spending a lot of time on activities that are simply required for sustenance comes at the cost of time spent on social behaviour and may result in group instability and thereby limit group size. This makes the studies on time-activity budgets of social animals essential to understand the evolution of sociality. We found that Jungle Babblers devoted around 70% of their time on individual behaviours which are required for one's sustenance and maintenance and the remaining 30% for social behaviours. The relatively high proportion of time spent on individual behaviours is mainly dominated by foraging behaviour. This is unsurprising, given that foraging helps in gaining energy, which is required for survival, growth as well as reproduction (Kramer 2001). Similar findings have been reported in urban Capuchin monkeys (*Sapajus* sp.) (80%) and Shelducks (*Tadorna tadorna*) (60%) in which most of their time is allocated to foraging (Back et al. 2019; Bensizerara and Chenchouni 2019). However, Vervet monkeys (*Chlorocebus pygerythrus*) have been reported to spend much less time in foraging (30–40%, Isbell and Young 1993) in comparison.

Grooming and shower behaviour come under the same category of maintenance which involves removing dirt, parasite and maintaining hygiene (Clayton and Cotgreave 1994). Clayton and Cotgreave (1994) stated that grooming is a time-consuming activity and in a comparative study across 62 species of birds, they showed that on an average 9.2% of time was devoted to grooming which is similar to the amount of time Jungle Babblers allocated to grooming (10.17%). Jungle babblers spent only a small percent of the time in resting (1.61%) during the day. However, it must be noted that the time between roosting and emergence is devoted exclusively to resting and has not been included in the analyses. Further, during the daytime, the time spent grooming may also serve similar function as rest behaviour, providing a break from high activity and thereby avoiding exhaustion. Resting is important for physiological processes such as digestion and thermoregulation, however, the time spent during resting is considered to be free and can be utilized for other

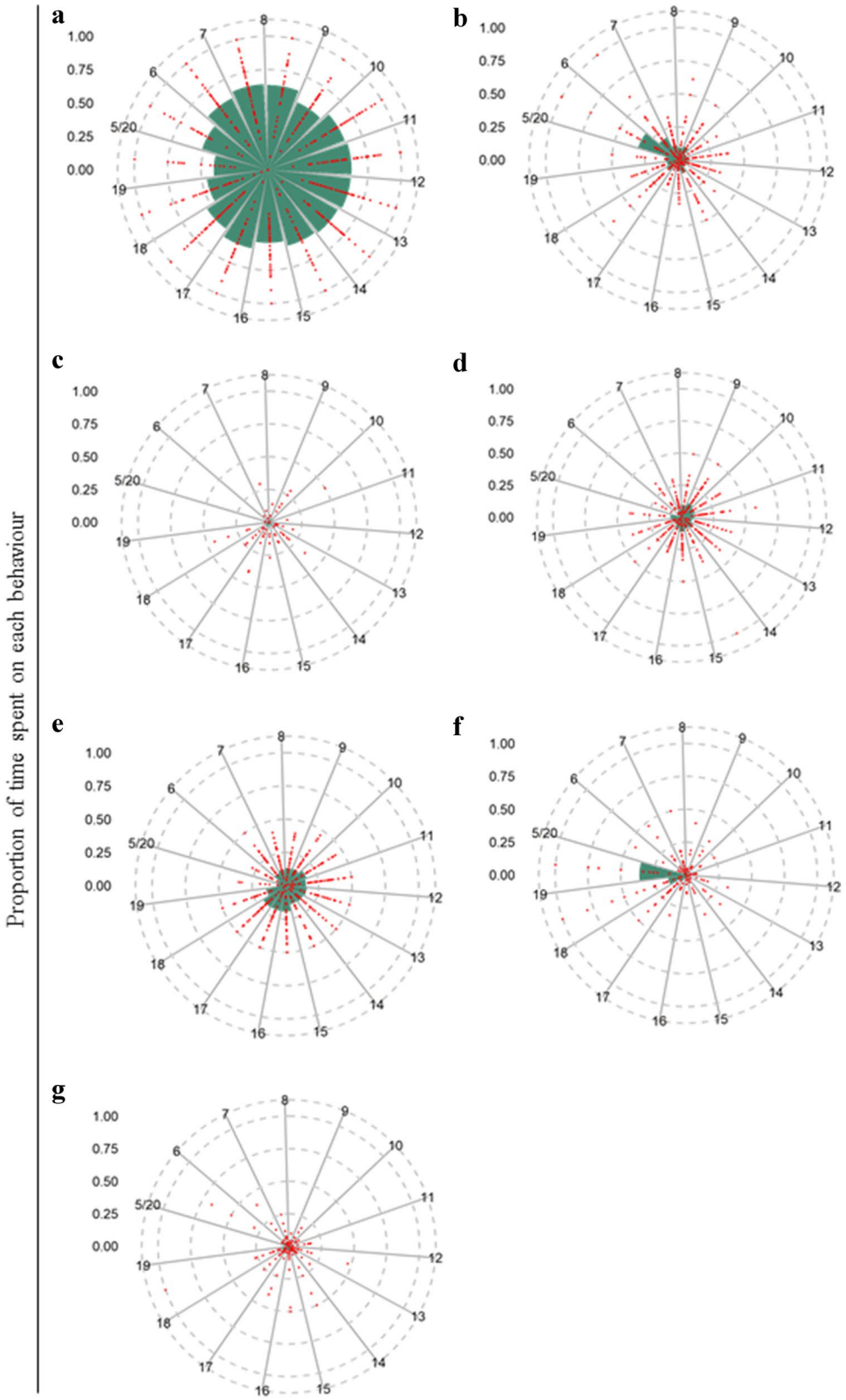

Fig. 3 Polar plots showing the proportion of time spent on each behavioural activity across 15 h (5:00–20:00): **a** foraging, **b** grooming, **c** rest, **d** allogrooming, **e** sentinel, **f** movement and **g** 'other' at different times of the day. Each point represents the proportion of time spent on each behaviour in each sampling hour of a day and the bar represents the average proportion of time spent on each behaviour in each sampling hour across one year

activities when required (Herbers 1981; Dunbar 1992). Thus, in social animals, it is expected that most of the resting time will be devoted to social activities (Dunbar and Dunbar 1988). In fact, Jungle Babblers also devote nearly 10% of their time in allogrooming, which too is a less energy-intensive activity but is crucial for social bonding.

Table 2 Summary of GLM results examining the effect of time and length of the day on the proportion of time spent on 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	0.72
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	0.256
	Length	0.19	0.05	<0.001
Sentinel	Intercept	0.84	0.41	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	0.04

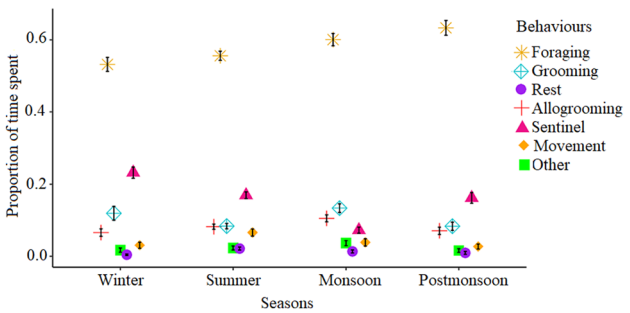

Fig. 4 Proportion of time spent on each behavioural activity across different months representing different seasons. Values represent mean ± SE

Besides maintaining social bonds (Isbell and Young 1993; Cox 2012; Picard et al. 2020), allogrooming also serves a similar role as grooming behaviour in removing dirt, parasites and maintaining hygiene (Sparks 1967; Sachs 1988) suggesting that both the behaviours share somewhat similar kind of ecological function. In fact, our finding suggests that the proportion of time dedicated to grooming and allogrooming are almost equal. Among all social behaviours in Jungle Babblers, most of the time was allocated to sentinel behaviour (16.65%, averaged across all months of the year) with respect to time-activity budget. This activity was carried out by 1 individual and rarely by 2 individuals by taking turns. Sentinel activity in Jungle Babblers is associated with a soft vocalization (Gaston 1977; Yambem et al. 2021). Even though there is no visible response from group members towards this vocalization (Yambem et al. 2021), Wickler (1985) suggested that this vocalization might mediate the coordination between the foragers and the sentinel in Jungle Babblers. Further, during foraging bouts, we found a sentinel to be present about 32% of the time on an average. This is similar to the findings in Pied Babblers (*Turdoides bicolor*), where too sentinel was found to be present only 30% of the time during foraging bouts (Hollén et al. 2008). Play behaviour has been proposed to help in maintaining social bonds, yet Jungle Babblers allocated only 0.81% of their time to play. Since play is physically and socially demanding behaviour (Pozis-Francois 2004), we speculated that for maintaining social bonds Jungle Babblers spent more time in allogrooming which is likely to be less energy demanding. Studies in chimpanzees have shown that the time allocated to play decreases when allogrooming time increases (Lawick-Goodall 1968). Our finding that Jungle Babblers devoted only 3.45% of time on movement can be partly explained by the fact that we only included flight as part of movement. Locomotion would include walking as well but we were particularly interested in displacement behaviour and not locomotion per se, which is included in foraging implicitly. Further, Jungle Babblers typically have small territory sizes (Andrews and Naik 1970) which limit the opportunity for movement and corroborates our findings. Four behaviours (shower, play, mobbing and inter-group fight) were grouped as 'other', yet, put together, they consumed only 2.32% of the total time-activity budget. This might be because shower and play behaviours are functionally similar to grooming and allogrooming, respectively, by virtue of their similar role in maintaining hygiene and social bonding respectively (Lawick-Goodall 1968; Clayton and Cotgreave 1994; Cox 2012). Besides, mobbing and inter-group fight are aggressive behaviours which are likely to be infrequent anyway.

Diurnal and seasonal variation in activity pattern

The variation in the activity pattern of an animal depends upon many factors, including 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). From our results, it was found that most of the behaviours of Jungle Babblers showed both diurnal and seasonal variation except for allogrooming and 'other' behaviour that did not show diurnal pattern. We found that the time spent on foraging varied with the time of the day and season irrespective of

Table 3 Summary of (a) Kruskal–Wallis test 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 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	0.04
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)

Seasons	Foraging	Grooming	Rest	Allogrooming	Movement	Sentinel	Other	Emergence	Roosting
Postmonsoon–Winter	< 0.01	0.46	0.61	0.40	0.65	< 0.01	0.91	0.12	0.26
Postmonsoon–Summer	< 0.01	0.99	0.06	0.40	< 0.01	0.71	0.87	0.03	0.09
Postmonsoon–Monsoon	0.40	0.03	0.99	0.07	0.29	< 0.001	0.06	0.64	< 0.01
Winter–Summer	0.31	0.4	0.01	0.06	0.03	< 0.001	0.77	< 0.001	0.02
Winter–Monsoon	0.01	0.17	0.58	< 0.01	0.09	< 0.0001	0.04	0.39	0.05
Summer–Monsoon	0.03	< 0.01	0.01	0.21	< 0.0001	< 0.0001	0.02	< 0.001	< 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

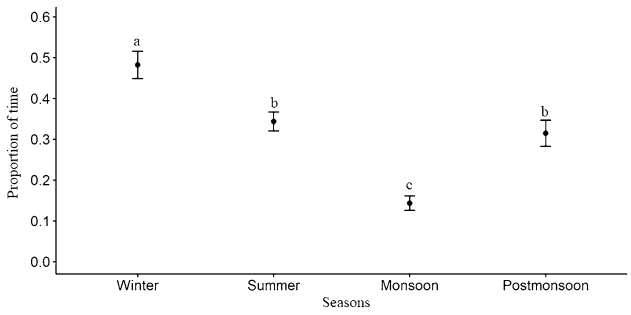

Fig. 5 Proportion of foraging time spent on sentinel duty across different months representing different seasons. Values represent mean ± SE. Different letters indicate the significant difference with $p < 0.05$

the length of the day. Reyes-Arriagada (2015) examined diel patterns of activity in three species of forest-dwelling passerines and reported that foraging patterns were nonuniform throughout the day and also varied with season and habitat type. In Jungle Babblers, foraging time decreased with the time of the day. Higher foraging activity early in the day ensures rapid energy gain after an extended period of starvation through the night and also reduces the risk of starvation due to lost foraging opportunities later in the day (Bednekoff and Houston 1994). With respect to seasonal variation, Jungle Babblers had highest foraging activity during postmonsoon (63%) and lowest during winters (53%). Yet, the proportion of time spent foraging never dropped below 50% at any given time of the year. This is not surprising given that foraging is an essential sustenance activity. Grooming behaviour in Jungle Babblers was highest in the morning and peaked during the monsoon. This is similar to findings

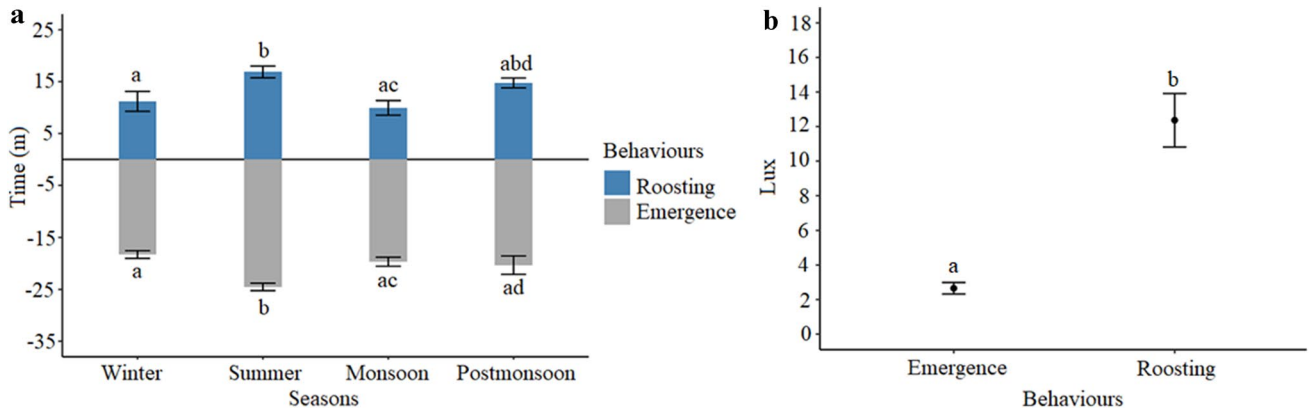

Fig. 6 **a** Emergence and roosting time (mean ± SE) in relation to sunrise and sunset, respectively, during different months representing different seasons. The number of days of observation of emergence and roosting in winter, summer, monsoon and postmonsoon months are 25, 17, 15, 12 and 26, 23, 15, 21, respectively. **b** Light intensity in lux unit (mean ± SE) at the time of emergence and roosting. The number of days of observation (light intensity) for the emergence and roosting are 50 and 53, respectively. Different letters indicate the significant difference with $p < 0.05$

in Java monkeys (*Macaca fascicularis*) in which grooming was higher during morning as compared to evening (Troisi and Schino 1986). Further, the presence of ectoparasite load in White Shifakas (*Verreaux's sifaka*) has been shown to be higher in monsoon which elicits an increase in grooming to maintain self-hygiene (Lewis 2010). Whether parasite load in Jungle Babblers varies with seasons remains to be examined. Allogrooming did not show any pattern across the day. However, day length had a significant effect on allogrooming (increases with an increase in day length). This may be because allogrooming mainly aids in social bonding (Picard et al. 2020), and can be carried out at any time of the day (Dunbar 1992). Further, allogrooming was found to increase during monsoon which might be explained by its shared ecological role with grooming behaviour in maintaining hygiene. However, this is in contrast to the findings of Gaston (1977), who found that allogrooming in Jungle Babblers increased during the postmonsoon and winter and was lower during summer and monsoon.

Sentinel activity varied through the day, wherein it increased in the evening. Our results are similar to the findings of Gaston (1977) where it was shown that sentinel behaviour increased with the time of the day, which might be related to achieving satiation later in the day. An experimental study in Arabian babblers (*Argya squamiceps*) showed that well-fed individuals performed more sentinel duty suggesting that sentinel is a state-dependent behaviour (Wright et al. 2001). The proportion of time allocated to sentinel duty varied significantly with season in Jungle Babblers and peaked during the winters. Gaston (1977) observed sentinel behaviour in Jungle Babbler in the winters and found that the sentinel was on duty 82% of the time. We further inspected sentinel duty as a proportion of foraging time during which sentinel was present and how that varied with season. Our results indicate a peak in sentinel duty during winter, with a sentinel being present 48% of foraging time, that drops to 14% during monsoon. This trend is similar to what was found in Florida scrub jays (*Aphelocoma coerulescens)*, where sentinel duty during foraging peaked in winters (75% of total foraging time) and dropped during summer to about 33% (Mcgowan and Woolfenden 1989). The difference in sentinel activity can be attributed to various factors such as canopy cover, predation risk and even group size. In our study, the increase in sentinel activity during winters and summer can be attributed to poor canopy cover during this time of the year. We speculate this trend could be because the study sites were dominated by winter deciduous trees that shed their leaves during winter and early summer, thereby possibly increasing predation risk. Given that time must first be allocated for crucial activities like foraging, time for resting is likely to become available only when other activities are fulfilled (Altmann and Muruthi 1988; Dunbar 1992). Our results agree with this prediction and we found that the time spent resting increased with the time of the day as foraging activity decreased. Besides, we also found that resting increased with the day length. Movement behaviour also showed variation with time of the day and season. It increased during the summer which coincides with the starting of breeding season (Andrew and Naik 1970). During this time the birds may spend more time searching for the nest site, building nests etc. that may require frequent displacement.

Emergence and roosting

The timing of emergence and roosting in Jungle Babblers in relation to time of sunrise and sunset, respectively, was different in different seasons. Similar findings have also been

reported in Indian myna (*Acridotheres tristis*) that showed diurnal and seasonal variation in the emergence and roosting behaviour under the influence of environmental, physiological and behavioural factors (Mahabal and Vaidya 1989). Jungle Babblers emerged earlier and returned to roost later during summer which coincides with their breeding time. In the study sites, light intensity at the time of roosting was found to be significantly higher than the light intensity at the time of emergence. Similar findings have also been reported in Rook (*Corvus frugilegus*) by Swingland (1976) where it was shown that Rooks departed from their roost at a low light intensity and arrive at the roost at high light intensity. It may be possible that it is easier to find the roost site when it is brighter than under low-light conditions.

Conclusion and future directions

Andrews and Naik (1970) and then Gaston (1977), carried out foundational work on the biology and social behaviour of Jungle Babbler, thereby presenting an excellent model system, to study sociality in a common backyard bird in the paleotropics. Yet, even three decades later, no serious attempt to follow on their seminal work was taken up in the form of a rigorous scientific study of these cooperatively breeding passerines. In so, our study provides detailed information on their behavioural ecology with a quantified time-activity budget, diurnal and seasonal variation in activity patterns of the individual and social behaviours of Jungle Babblers. Several findings in Jungle Babblers with respect to time-activity budget were similar to social primates and were in contrast to what was found in similar studies on birds. This is likely due to the general paucity of time-activity budget studies on social birds and most similar studies on birds were carried out on solitary species, especially water birds. The similarity of our findings in Jungle Babblers to social primates highlights the importance of sociality in determining patterns of behaviour. Further, constraints on time allocation have been shown to impact aspects of social behaviour such as group size and it has been argued that activity budget needs to be included in models examining drivers of sociality (Pollard and Blumstein 2008). Studies on how animals allocate time to different activities according to their current status and surrounding environment will also be useful in providing valuable insights into how animals trade-off between different fitness-enhancing behaviours and inform conservation policy making. Our study opens avenues for future studies examining the effect of ecological factors such as resource availability (abundant vs limited), habitat type (open vs closed), sociality (group size and composition) and predation pressure on the behaviour of Jungle Babblers in particular, but also of other social passerines in general.

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Author contributions MJ conceived and designed the study and secured funding for the work. SDY carried out the field work for data collection. SDY and MJ carried out all statistical analyses and wrote the manuscript.

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Data availability The datasets generated are available as supplementary material.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Jungle Babblers are listed in Schedule IV under the Indian Wildlife Protection Act (1972) and designated as 'Least Concern' by IUCN's Red List of Threatened Species. This study was conducted with necessary permits (No. 3625) from the Department of Forest and Wildlife Preservation, Government of Punjab, India, and with the approval of the Institute Animal Ethical Committee (IISER/SAFE/PRT/2018/003), IISER Mohali, India. No animals were harmed or kept in captivity for this study.

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