Parental care strategies of grey-headed bulbul, *Pycnonotus priocephalus* in the Western Ghats, South India

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Parental care strategies have important fitness consequences through the trade-offs between costs and benefits associated with providing care. I have studied the patterns of parental care in grey-headed bulbul *Pycnonotus priocephalus*, species endemic to the Western Ghats, for three breeding seasons in Silent Valley National Park, Kerala. Maximum nest attentiveness was recorded in the low ambient temperature periods, viz. morning and evening hours, which may be a strategy to maintain optimum temperature requirements of the embryos. Nest attentiveness and on-bout durations increased by the progress in incubation but decreased towards the end of nestling period which was characterized by higher foraging trips. The parental effort for the nests with larger clutches was significantly higher than the nests with single clutch. Longer on-bout and off-bout durations in general and reduced parental activity at the sites with high predation pressure during the incubation and nestling periods of grey-headed bulbul could be a strategy to reduce the risk of predation.

Keywords: Life history strategies, nest attentiveness, parental care, *Pycnonotus priocephalus*, Western Ghats.

PARENTAL care is an important component of reproductive effort and it influences the evolution of life history strategies. The amount of care given by the parents to dependent offspring is critical to the understanding of a wide range of questions about behaviour, ecology and life history strategies[1–4]. A large number of studies examined the reproductive costs associated with incubation and nestling periods of temperate species[1,5–10], but the parental care strategies of most tropical species remain poorly understood.

In birds, bi-parental care is the most common pattern, although uni-parental care by either male or female parent exists[1,2,11–15]. The differences in parental care patterns among species arise from interspecific differences in the trade-offs between benefits for offspring survival versus parental costs, such as reduced parental survival, fecundity and mating opportunities[2,16–20]. Various environmental conditions can influence this fitness trade-offs and lead to variation among species and populations in the amount or type of parental care provided[2,21]. The optimal division of time is likely to vary with environmental conditions and, indeed, incubation and foraging bout durations have been shown to vary consistently with weather, stage of incubation and time of day[6].

To hatch successfully, avian eggs must be maintained at a temperature that allows embryonic development. The optimal temperature range for development is considered to be about 36–38°C and, as there are few environments in which ambient temperature remains constantly at this level, incubation by the parents is required to prevent embryos from chilling or overheating[22]. In species where only one parent incubates, that parent must divide its time between the mutually exclusive activities of incubating to control clutch temperature and foraging to meet its own energy requirements. Furthermore, in species with uniparental incubation, absences from the nest during foraging bouts can negatively affect egg temperatures and subsequent embryo development, as well as the ability to protect eggs against predators[5–7]. Incubation feeding is common in many species to overcome this constraint, but it increases the male parental visits at the nests. Thus, parents incubating eggs must resolve a number of conflicting demands in response to changing environmental conditions[5]. Consequently, factors that influence reproductive effort during incubation can affect the evolution of other life-history traits (e.g. clutch size, number of broods and probability of renesting). The frequency with which females alternate incubation with other activities varies greatly among passerines. These variations are due to a combination of several proximate and ultimate ecological factors such as variation in body mass, frequency of mate feeding, food availability/foraging success, ambient temperature during incubation, and/or nest predation[6–9,23–29]. Thus an understanding of the parental care strategies from the nest building through the nestling stages provides important insights into the constraints and costs related to these traits.

Here I report the patterns of parental care in grey-headed bulbul *Pycnonotus priocephalus*, one of the

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16 restricted-range bird species of the Western Ghats. Grey-headed bulbul has a very limited range in the heavy rainfall areas from Belgaum along Goa to Kanyakumari[30] and their breeding is restricted to the mid-elevation evergreen forests. Males and females are monomorphic and could not be identified in the field. The breeding activities of the grey-headed bulbul commenced in January (first egg laying dates were 2, 10 and 26 January for 2003, 2004 and 2005 breeding seasons respectively) and ended in May. Peak egg laying was observed in April during 2004 and 2005, while it was in March during 2003 (ref. 31). Of a total of 47 nests examined at Silent Valley National Park and surrounding reserved forests, 25 nests had two eggs, and 22 comprised one egg each (mean = 1.53 ± 0.50). The eggs are incubated for 12–14 days ($n = 9$) and the nestlings spent 11–13 days ($n = 9$) in the nest[31]. The objectives of the study were to quantify the variation in the parental care relative to the nesting phases (incubation and nestling) and clutch size (one versus two eggs) during different daylight hours and days in the nesting cycle using attending time and provisioning rates as estimates of parental care.

Methods

Study area and field methods

This study was conducted in Silent Valley National Park (11°00′–11°15′N and 76°15′–76°35′E) in the Western Ghats, Kerala, Southern India, between January 2003 and May 2005. This region experiences a typical tropical climate with mean annual temperature ranging between 19°C and 25°C and mean annual rainfall above 5000 mm. Major vegetation types in the study area are west coast tropical evergreen forest which forms extensive dense stands along hills and valleys between 900 and 1400 m; southern subtropical broad-leaved hill forest between 1500 and 2000 m; southern montane wet temperate forest and grasslands restricted mainly to the higher slopes and hill tops in the eastern sector of the valley[32]. All the nests studied were located in the west coast tropical evergreen forests dominated by the *Strobilanthes* and *Ochlandra travancorica* patches between 900 and 1400 m asl. The mean maximum and minimum temperature during the breeding seasons (January–May) were 28.2 ± 0.6°C (range: 21.1–31.1°C) and 19.2 ± 0.4°C (range: 16.8–22.7°C). In general, the temperature was colder in the morning and evening hours and maximum at mid-day. The average rainfall during the three breeding seasons was 219.6 ± 132.1 mm (range: 0–1701.1 mm), more than 85% of which fall during April and May. About 44.7% of the trees encountered in the nest plots (0.04 ha) belonged to the food species of grey-headed bulbul[31]. The abundance of food species and invertebrates was marginally higher in the *Strobilanthes* patches where most of the nests with single eggs were located[31]. The predation pressure of all the potential predators[30,31] quantified through area-search surveys (five 30 min counts of diurnally active predators in an area of 1 ha surrounding the nest)[33,34] indicates that nest sites with smaller clutches had higher predator abundance (3.27 ± 1.50 mean predator per count, $n = 17$ nests) than those with two eggs (1.62 ± 92 mean predator per count, $n = 16$ nests; $t = 3.789$, $P < 0.001$)[31].

Nests of grey-headed bulbuls were located following specific adult behaviour (carrying nest materials or food and frequent visits to certain patches) and by searching individual plants within the breeding habitat[31,35]. The breeding status including the dates of nest construction, egg laying, incubation and nestlings were recorded on every day throughout the breeding season (January–May). A total of 27 nests of grey-headed bulbul (seven nests each during 2003 and 2004 and 13 nests during 2005) were studied to understand the parental care patterns during the incubation and nestling periods using traditional method which involves hourly or day-long watches at nests[36]. As the study population was not colour marked, it is not clear whether the nests of the same individuals were observed in the same year or in subsequent years. Thus each nest was considered as an independent sample. All the observations were made during 06.00–18.00 h from a hide 15–20 m, away from the nest. The total observation period was 1224 hours (range: 3–72 h/nest), which includes 672 hours (for 24 nests) during the incubation stage and the remaining (552 hours for 11 nests) during nestling stage. Nests with two eggs ($n = 21$ nests) were monitored for 930 hours (570 and 360 hours for incubation and nestling periods respectively) and nests with single egg ($n = 6$ nests) were observed for 294 hours (102 and 192 hours for incubation and nestling periods respectively). To describe the incubation patterns, the parameters used were: mean on-bout duration (mean incubation bout duration in minutes), mean off-bout duration (mean time spent away between two incubation visits in minutes), nest attentiveness (as percentage of total daylight hours spent on the nest)[7,37] and nest trips/h (as the number of times the female went to or from the nest per hour). The parameters used for characterizing the parental care patterns during the nestling stage were: nest attentiveness (as percentage of total daylight hours spent on the nest), mean on-bout duration (mean brooding duration in minutes), mean off-bout duration (mean time spent away between two feeding visits in minutes) and feeding trips/h (number of feeding visits/h).

Data analysis

For statistical reasons, parameter estimates were averaged across different stages of the nesting cycle (incubation and nestling stages), daylight hours and clutch size variations. Variation in the parental care patterns in terms of nest attentiveness, on- and off-bout durations and nest trips/h or feeding trips/h among the nesting phases (incubation and nestling) and different clutches (single and double eggs), were tested for different daylight hours (06.00–09.00, 09.00–12.00, 12.00–15.00 and 15.00–18.00) and days in the nesting cycle using repeated-measures ANOVA (General Linear Model procedure)[38,39]. Whenever the data did not meet the sphericity criterion (Mauchly's test of sphericity), the F statistics for the within-subject factor and interactions were corrected using the Greenhouse–Geisser adjustment[40–42]. All the statistical analyses were carried out using the statistical package SPSS 10.0.1 for Windows[38]. In all cases, statistical significance was $P \leq 0.05$ and means are presented ± SE, unless otherwise stated.

Results

General patterns

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

Mean on-bout and off-bout periods (attentive and inattentive periods) were 26.39 ± 24.01 min and 17.45 ± 5.25 min respectively, for the entire nesting period (from the start of incubation to the end of nestling period). On-bout durations were longer during 06.00–09.00 h (33.00 ± 29.74 min; range: 0.25–85.50 min) and least during 09.00–12.00 h (20.34 ± 19.30 min; range: 0.24–63.50 min). The mean number of nest visits/h was 2.60 ± 2.23. There was a significant difference in the on-bout durations between the nesting phases across the different daylight hours ($F = 15.72$, $P < 0.0001$; Table 1). However, there was no difference in the off-bout durations between the nesting phases ($F = 1.05$, ns). This indicates that the birds took larger foraging bouts to meet their energy needs during both the phases of nesting. Maximum number of trips was in the evening hours 15.00–18.00 (3.15 ± 2.78; range: 0.33–7.67 trips/h) and minimum during 12.00–15.00 h (2.05 ± 1.82; range: 0.33–5.33 trips/h). Mean number of trips/h was very high during the chick-rearing phase (1.00–7.67 trips/h) compared to the incubation stage (0.33–1.33 trips/h) across different times of the day ($F = 29.89$, $P < 0.0001$; Table 1).

Parental care in nests with different clutch sizes

Incubation stage: During the incubation, birds were most attentive (80.32 ± 6.28%) during 06.00–09.00 h and least attentive (66.00 ± 7.56%) during 09.00–12.00 h, when the data were clubbed for all nests. During the daytime, incubation was intermittent with relatively longer bouts of incubation being interspersed with bouts of foraging during which the clutch was left unattended. Comparison of the parental care patterns between the nests with different clutches revealed a significant difference (repeated-measures ANOVA, $P < 0.01$; Table 2) in all the parameters, except off-bout duration across daylight hours (Figure 1). Mean attentive periods (on-bout durations) for the nests with two eggs were significantly higher (53.33 ± 11.84 min; range: 25.25–87.00 min) than the nests with single egg (39.69 ± 7.91 min; range: 21.50–84; Figure 1). The mean off-bout durations were 21.34 min for nests with two eggs and 20.81 min for nests with single egg. The birds with single egg made more trips (0.79 ± 0.23 trips/h) than the birds incubating two eggs (0.66 ± 0.11 trips/h; Figure 1) across different daylight hours.

Almost similar parental behaviour was seen in different days of the incubation period (repeated-measures ANOVA, $P < 0.01$; Table 2). The nest attentiveness increased with the progress of incubation for both type of nests (Figure 2; linear regression: $R^2 = 0.81$, $F_{1,12} = 47.33$, $P < 0.001$ and $R^2 = 0.98$, $F_{1,11} = 490.21$, $P < 0.001$ for nests with two eggs and single eggs respectively). Mean nest attentiveness was marginally higher in nests with single egg than in nest with two eggs (range: two eggs = 54.53–75.84%; one egg = 60.28–86.39%). However, the average attentive periods (on-bout duration) were significantly higher in nests with two eggs (range: two eggs = 39.17–82.63 min; one egg = 28.13–63.25 min, $F = 0.98$, $P < 0.01$; Figure 2). The on-bout durations also increased with the

Table 1. Comparison of the parental care patterns between the nesting phases across different daylight hours

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

*F statistics after Greenhouse–Geisser adjustment.

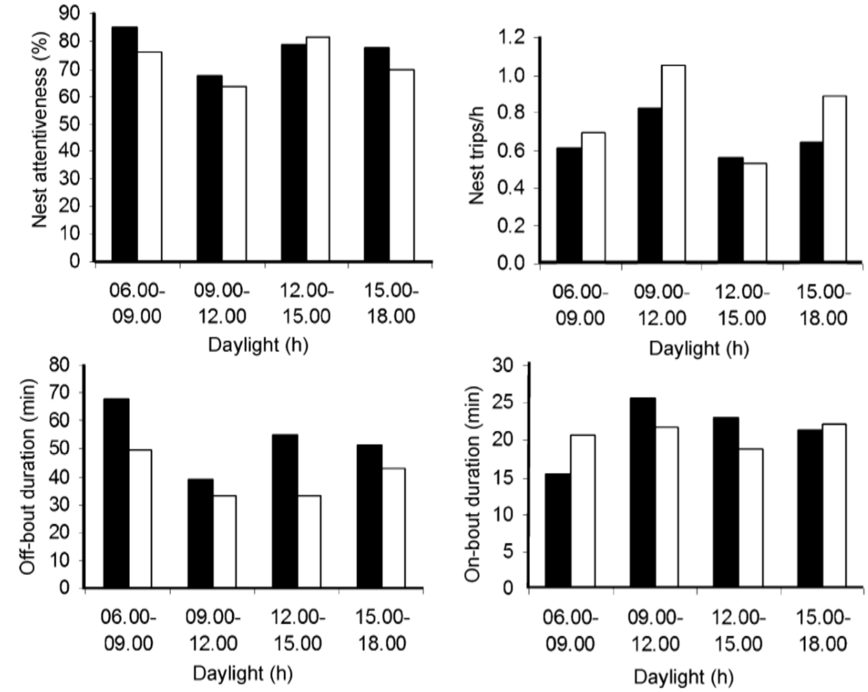

Figure 1. Nest attentiveness, mean nest trips/h, and mean on-bout and off-bout durations of grey-headed bulbul during incubation across daylight hours (■, nest with two eggs; □, nest with one egg).

Table 2. Comparison of the parental care patterns of grey-headed bulbuls with different clutch sizes across daylight hours and different days during incubation period

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

**F* statistics after Greenhouse–Geisser adjustment.

progress of incubation for both types of nests (linear regression: $R^2 = 0.52$, $F_{1,12} = 11.71$, $P < 0.01$ and $R^2 = 0.81$, $F_{1,11} = 42.01$, $P < 0.001$ for nests with two eggs and single egg respectively). The number of nest trips/h was significantly decreased with the progress of incubation for both nests with two eggs ($R^2 = 0.55$, $F_{1,12} = 13.65$, $P < 0.01$) and single egg ($R^2 = 0.91$, $F_{1,12} = 95.35$, $P < 0.001$). The nest trips/h (range: two eggs = 0.33–0.83 trips/h; one egg = 0.42–1.17 trips/h) and off-bout durations (range: two eggs = 14.75–26.92 min; one egg = 17.08–23.00 min) were not different among the nests with different clutch sizes (Table 2, Figure 2). This shows that the time devoted for foraging was independent of the progress in incubation, although foraging bouts varied significantly within the day.

Nestling stage: There were no significant differences in the mean attentiveness (17.88 ± 1.96% versus 16.37 ± 1.12%) and on-bout durations (7.75 ± 1.97 min versus 4.71 ± 1.30 min) between the nests with single egg and those with two eggs across the daylight hours (Table 3, Figure 3). During the initial phase of brooding, attentiveness was higher in both types of nests (two eggs: 65.97% versus one egg: 73.19%), however, it reduced to about 3.33% (two eggs) and 2.36% (one egg) at the end of the chick-rearing period. The mean off-bout durations were significantly higher for the nest with single nestling than the nest with two chicks. In both nest types, birds took larger foraging bouts in the morning 06.00–09.00 h ($F = 8.13$, $P < 0.001$; Figure 3). Feeding trips varied significantly ($F = 21.00$, $P < 0.001$) among the nest types

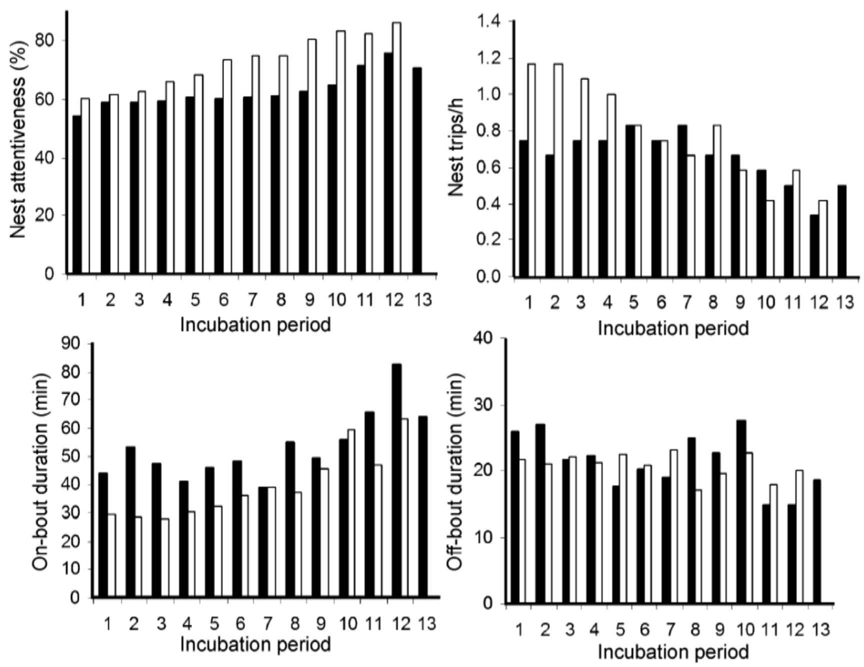

Figure 2. Nest attentiveness, mean nest trips/h, and mean on-bout and off-bout durations of grey-headed bulbul across different incubation days (■, nest with two eggs; □, nest with one egg).

Table 3. Comparison of the parental care patterns of grey-headed bulbuls with different clutch sizes across daylight hours and different days during nestling period

Source	Dependent variable	Type III sum of squares	*df*	Mean square	*F*	*p*
Daylight hours	Attentiveness	48.00	3	29.39	0.29*	0.700
	On-bout duration	129.60	3	43.20	1.59	0.200
	Off-bout duration	638.88	3	304.25	8.13*	0.001
	Nest trips	59.13	3	28.58	21.00*	0.001
Nestling period	Attentiveness	55,047.86	11	5004.35	92.85	0.001
	On-bout duration	14,480.28	11	1316.39	48.49	0.001
	Off-bout duration	2,585.23	11	235.02	8.98	0.001
	Nest trips	234.56	11	21.32	22.72	0.001

*F statistics after Greenhouse–Geisser adjustment.

across the daylight hours with maximum trips during the evening 15.00–18.00 h (Table 3, Figure 3).

All the behavioural attributes measured to assess the parental care across the nestling period (12 days) varied significantly between pairs with two and single chicks (repeated measures-ANOVA, $P < 0.001$, Table 3). The attentiveness varied significantly between nests with single nestling ($F = 92.85$, $P < 0.001$; range: 2.50–73.19%) and with two nestlings (range: 3.33–65.97%; Figure 4). On-bout (range: 0.29–55.59 min versus 0.31–32.17 min) and off-bout durations [16.36 ± 7.07 (range: 11.08–35.13 min) versus 11.61 ± 3.83 (range: 8.24–21.71 min)] were significantly higher in the nest with single nestling than with two nestlings (Table 3, Figure 4). Parental visiting rate increased by the progress in nestling stage and was significantly higher at nest with two chicks (4.95 ± 1.78, range: 1.17 ± 7.08) than the nests with single chick (3.85 ± 1.50, range: 0.50–5.75 visits/h; Figure 4). In each trip, the birds brought food to the young ones, thus it can be considered as the feeding rate/h. The identification of the prey-item was extremely difficult because of poor visibility. However, the birds were found carrying caterpillars to the nest. Furthermore, the birds were found feeding both the chicks in a single visit. Thus, estimation of feeding rates/nestling was not attempted in this study.

Discussion

Biparental care is almost a norm in birds, as it occurs in more than 80% of the living species[1,13,14,43]. Grey-headed bulbul is no exception. As seen in majority of bulbuls[44],

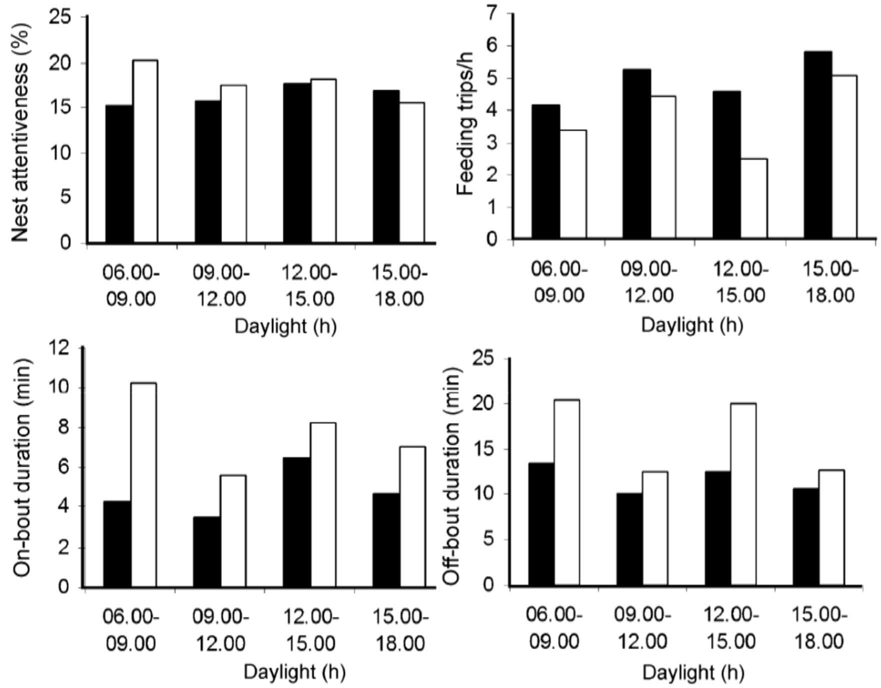

Figure 3. Nest attentiveness, mean feeding trips/h, and mean on-bout and off-bout durations of grey-headed bulbul during nestling period across daylight hours (■, nest with two eggs; □, nest with one egg).

the incubation is assumed to be undertaken by female alone as the nest remains unattended till the same incubating individual returns to the nest after foraging. However, the demand of high degree of parental care for the altricial chicks was ensured by the participation of male during the nestling stage. Although the roles of male and female birds may vary in parental care, in the present case this could not be explored due to lack of sexual dimorphism. However, the effort of male in feeding the nestlings seems almost equal to that of the female. Moreover, the birds were found making alternative feeding trips continuously, especially towards the end of nestling period. Thus, the patterns presented for the nestling periods are combined parental investment of male and female birds.

The temporal variation in the nest attentiveness was prominent during the incubation period. Maximum nest attentiveness was recorded in the morning and evening hours. On-bout and off-bout durations are often assumed to reflect a tradeoff between energy needs of the adult (food limitation) and thermal needs of the developing embryos (temperature)[7,37]. The reproductive investment in the food rich *Strobilanthes* patches was reported to be significantly lower than the *Ochlandra* patches which host nests with larger clutch sizes[31]. Thus food limitation did not appear to be a constraint to the breeding grey-headed bulbuls. On the other hand, thermal requirements of the eggs seem to have a significant role in the on-bout and off-bout durations of incubation. Although temporal variations in the weather conditions were not recorded, in general, the early morning and late afternoon hours had lower temperatures in the study area. Thus, the higher attentiveness in the morning and evening hours could be a strategy to ensure the thermal needs of the eggs. Moreover, off-bouts for foraging were significantly higher during 09.00–12.00 h which coincides with an increase in the air temperature at the study site, and therefore maintaining the optimum temperature requirements of the embryos. Similar patterns were observed during the brooding stage, however, nest attentiveness and durations of on- and off-bouts decreased and number of trips/h increased during the nestling phase. The evening hours during the nestling period was characterized by low on-bouts and maximum foraging trips, hence allowing the incubating bird to obtain more food for itself and the chicks before roosting.

The nest attentiveness and on-bout durations increased by the progress in incubation which could be explained by increasing thermal needs of the embryo[6]. Nest attentiveness during incubation and brooding represents a parent–offspring conflict; incubating birds must balance a trade-off between caring for embryos or chicks by staying on the nest versus self-maintenance by getting off the nest to forage. For species in which females are the sole incubators, males can potentially affect this trade-off and increase nest attentiveness by feeding incubating females on the nest[24,25,45]. However, no mate feeding was recorded in the case of grey-headed bulbul, thus they avoided risk

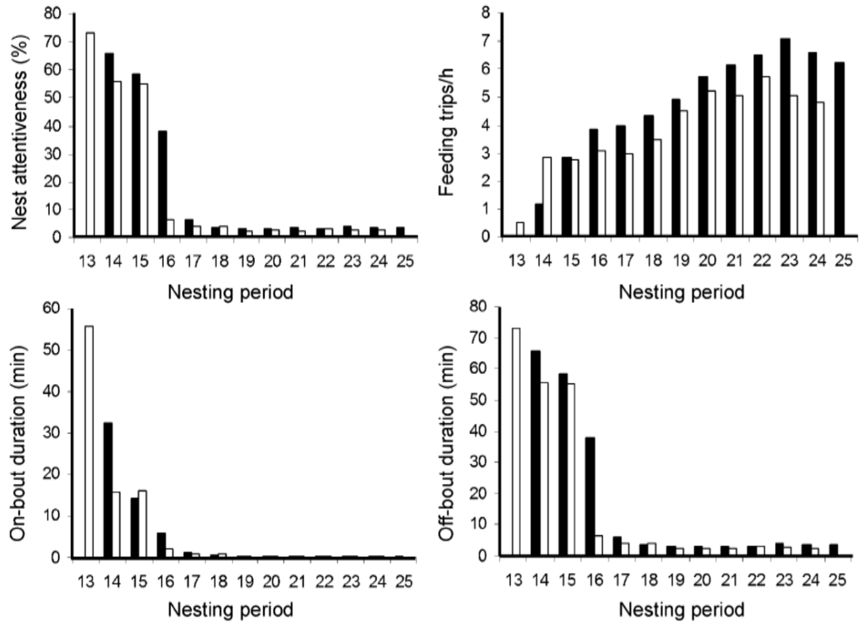

Figure 4. Nest attentiveness, mean feeding trips/h, and mean on-bout and off-bout durations of grey-headed bulbul across different days of nestling period (■, nest with two eggs; □, nest with one egg).

of predation by increased parental activity at the nest site. The initial stages of brooding are characterized by higher nest attentiveness, and larger on-bout and off-bout durations. Since increase in the age of chicks leads to higher food demands, the number of trips increased significantly towards the end of the nestling period. During this phase, both birds were found feeding the young.

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

Predation was the major factor limiting nesting success in grey-headed bulbul[31]. The abundance of potential predators was significantly higher in the sites with single eggs than the sites with two eggs[31]. Thus, longer on-bout and off-bout durations in general and reduced parental activity at the sites with high predation pressure (sites with single eggs) during the incubation and nestling periods of grey-headed bulbul could be a strategy to reduce the risk of predation. Similarly, several other experimental and comparative studies on passerine incubation behaviour have demonstrated that the species with high nest predation take longer on-bout and off-bout durations, despite increased time off the nest may lengthen the incubation period, which would increase the exposure to nest predation[7–10,46]. However, such a strategy may prevent frequent feeding by adults and thus compromise future reproductive attempts[7]. In conclusion, although the differential parental care strategies for nests with different clutch sizes seem to be an adaptive behaviour, further research is needed to understand the role of predation and other factors influencing the parental effort in grey-headed bulbul.

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