The clutch size, incubation rhythm of Reeves's Pheasant (Syrmaticus reevesii) and their responses to ambient temperature and precipitation

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June 7, 2023

Abstract

Clutch size and incubation rhythm are critical components of avian life history. Incubating birds must balance the trade-offs between their energy requirements and the thermal needs of the developing embryos. Reeves's Pheasant (Syrmaticus reevesii) is a uniparental bird endemic to China that lives in mountain forests, and female Reeves's Pheasants may adjust their incubation behavior to cope with cold environments and energy stress. Using satellite tracking, we tracked 21 wild female Reeves's Pheasants in northern Hubei Province, China from 2020 to 2022, and explored the birds' clutch size, incubation rhythm and their responses to ambient temperature and precipitation. The average clutch size of Reeves's Pheasant was 7.72 ± 1.51, showing strong seasonal declines, and was markedly affected by the average temperature during the spawning period. During the incubation period, the females took 0.74 ± 0.46 recesses per day with an average recess duration of 99.23 ± 72.93 mins and an average nest attendance of 93.11 ± 5.06%. There was a peak of nest departures at around 13:00, and the recess duration was significantly negatively correlated with both daily mean temperature and daily precipitation. Our findings demonstrated that female Reeves's Pheasants adjusted their behavior in response to the changing ambient temperature and precipitation, and the unimodal pattern of recess timing may not be driven primarily by the physiological needs of incubating females, but by the thermal needs of their developing embryos.

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females, but by the thermal needs of their developing embryos.

Keywords: clutch size; incubation rhythm; response; ambient temperature and precipitation; Reeves's Pheasant

1. Introduction

Clutch size and incubation are crucial components of avian reproduction and may represent critical energy bottlenecks (Wiebe and Martin 1995, 2000). Incubating birds must balance the trade-offs between their own physiological needs and the thermal needs of embryos (Cresswell et al. 2003, Amininasab et al. 2017). In avians, differences in clutch size represent different reproductive strategies chosen by females (Martin et al. 2000, Christians 2002). Incubation rhythm affects the reproductive fate and survival of incubating birds, reflecting their survival strategies and adaptation to the environment (Spiegel et al. 2012). Thus, knowledge of clutch size and incubation rhythm can help us understand the life-history strategies of avians (Conway and Martin 2000, Evans et al. 2009, Mougeot et al. 2014).

Incubation behaviors of avians may be influenced by a variety of factors, including internal factors such as the weight (Tombre et al. 2012), age and experience of incubating birds (Amininasab et al. 2016), as well as external factors such as predation risks (Cervencl et al. 2011, Brynychová et al. 2020), human disturbance (Spiegel et al. 2012) and food availability (Boulton et al. 2010, Vafidis et al. 2018). In species that incubate uniparentally, incubating birds are constrained by their physiological conditions and ability to store nutrients, and must balance the time spent in foraging and incubating (Cresswell et al. 2004, Setash et al. 2021). When they forage outside the nest, the eggs in the nest may face a risk of cooling or overheating (Brown and Downs 2003, Mougeot et al. 2014), since the changing ambient temperature is usually outside the optimal temperature range for embryonic development (DuRant et al. 2013). Therefore, ambient temperature strongly influences the behavioral decision of incubating birds. If the ambient temperature is low, the incubating birds may tend to reduce recess frequency and recess duration to avoid egg cooling (Bueno-Enciso et al. 2017). However, to cope with high energy demands in cold weather, incubating birds have to take off-bouts to forage (Moiron et al. 2018). Precipitation is also assumed to affect the incubation behavior of birds, as incubating birds may choose to stay at nests to protect embryos from precipitation, especially in species that build open nests and ground nests and whose nests are more prone to be soaked by precipitation (Martin et al. 2017). Coe et al. (2015) have found that female Tree Swallows (*Tachycineta bicolor*) tend to spend less time outside their nests when precipitation occurs. In contrast, Schöll et al. (2020) have found that precipitation has no effect on the recess behavior of female Great Tit (*Parus major*). Thus, the effect of precipitation on incubation rhythm is not yet clear.

Reeves's Pheasant (*Syrmaticus reevesii*) is a bird endemic to China that lives in mountainous forests. As a uniparental incubator, female Reeves's Pheasants build nests, incubate eggs, and raise pre-fledged young alone (Zhang et al. 2004). Female Reeves's Pheasants usually build open nests on the ground. Compared with closed nests, open nests do not provide higher thermal benefits for eggs, nor do they offer shelter from precipitation (Fast et al. 2007, Martin et al. 2017). During the incubation period of up to 26-27 days (Zhang et al. 2004), nests may face adverse conditions such as low temperature and precipitation. Therefore, the females may adjust their incubation behavior according to the changes in environmental factors to meet their physiological needs and the thermal needs of embryonic development. Previous studies on incubation rhythm of Reeves's Pheasant mostly relied on cage conditions, while exploring the incubation rhythm of wild Reeves's Pheasant based on nest temperature changes may attract natural predators or make breeding females abandon their nests, and can not address the issues of small sample size and technical limitations for measuring weather conditions. Our study is the first to investigate the effects of environmental factors on the clutch size and incubation behavior of wild Reeves's Pheasants.

In conclusion, the purpose of this study was to explore the clutch size and incubation rhythm of Reeves's Pheasant, as well as their responses to the ambient temperature and precipitation, so as to better understand the reproductive strategy of Reeves's Pheasant and provide useful information concerning the conservation of this specie and related endangered pheasants.

2. Methods

2.1. Study areas

We conducted this study in Pingjingguan Village (31°51'-31°52'N, 113°54'-113°55'E, hereafter 'PJG') and Zhonghuashan Bird Provincial Nature Reserve (31°37'-31°44'N, 113°54'-113°59'E, hereafter 'ZHS') in Hubei Province, China (Figure 1). PJG contains coniferous forests, deciduous broad-leaved forests and coniferous broad-leaved mixed forests at elevations of 130 to 850 m, and ZHS contains evergreen broad-leaved forests and coniferous broad-leaved mixed forests at elevations of 150 to 810 m. The two sites with similar climates are about 40 km apart, and both are the main distribution areas of Reeves's Pheasant (Zhao et al. 2013, Zhou et al. 2015).

2.2. Data collection

Individual tracking

From 2020 to 2022, we captured 21 adult female Reeves's Pheasants (17 in PJG; 4 in ZHS) using non-injury rope techniques and attached satellite trackers (LEGO, Chengdu, China) to them (Lu et al. 2022). All field procedures were reviewed and approved by the Forestry Department of Hubei Provinces. Each satellite tracker weighs about 20g, less than 3% of the body mass of an adult female Reeves's Pheasant. They were set to locate targeted individuals once an hour and record the overall dynamic body acceleration (ODBA) of each individual every 30 min or 10 min. ODBA can be used as a measure of the energy consumption of wild animals to help us determine whether an individual is in a state of movement (Wilson et al. 2006, Stothart et al. 2016, Pagano and Williams 2019).

Determination of incubation behavior

The ODBA of female Reeves's Pheasants was low and stable during incubation but changed rapidly when incubation was interrupted. Thus, the beginning of incubation was determined from a sharp decline in ODBA, the interruption of incubation was determined from a sharp increase in ODBA, and constant ODBA was interpreted as continuous incubation (Figure 2). Based on the changes in ODBA, we determined whether the females started to incubate, then searched for their nests according to the location information, and recorded clutch size and related nest site information.

The first day of incubation was determined based on changes in ODBA, and the first egg-laying date was determined by clutch size and the number of periodic visits by females to the nest before incubation started. Due to this remote monitoring system, there was no need to visit targeted nests frequently during the incubation period, which minimized human disturbance and the possible risk of nest predation.

Definition of incubation parameters

Observations and records for this study were made over a 24-hour period starting at 0:00 and ending at 24:00 every day. Since the first and last incubation days were not complete (0:00-24:00) monitoring days, they were not included in the analysis. For each complete monitoring day of each nest, we calculated: (1) recess frequency, estimated as the number of times a female left the nest per day; (2) recess duration, estimated as the total recess length (in minutes) per day; (3) nest attendance, estimated as the proportion of 24 hours a female devoted to incubation per day.

Temperature and precipitation data collection

We cannot place temperature data loggers around each nest to finely measure ambient temperature as such human disturbance may attract natural predators or cause the timid and sensitive females to abandon their nests. We had to obtain ambient temperature and precipitation data for the two study areas from*https://www.ventusky.com/*, and the meteorological data of the website were mainly from the Deutscher Wetterdienst (DWD) and National Oceanic and Atmospheric Administration (NOAA). We calculated the daily mean temperature and daily precipitation for each female from the day she laid her first egg to the day she laid her last egg, and used their mean to measure the average temperature and the average precipitation during each spawning period. We also calculated the daily mean temperature and daily precipitation during the incubation period.

2.3. Statistical analyses

The relationships of recess frequency, recess duration and nest attendance with the day of incubation were examined using nonlinear regression in R (version 4.1.2), and the differences in recess frequency, recess duration and nest attendance between successful and unsuccessful incubators were tested by Mann–Whitney *U* test in SPSS (version 26.0). All values were reported as mean +- SD.

We used Spearman's correlation to assess whether clutch size was associated with the first egg-laying month in SPSS (version 26.0). The general linear model (package *lme4* , Bates et al. 2015) was used to analyze the effects of ambient temperature and precipitation on clutch size. We took the average temperature and average precipitation during each spawning period as fixed effects and year as a random effect. And we did not include female identity as a random factor as most females in our study bred once and only four females had two breeding records, and the multiple records for these four females were assumed as independent observations.

Based on the timing of nest departure and return, we used the kernel density estimation method (package *overlap* , Ridout and Linkie 2009) to analyze the diurnal activity rhythm of females during the incubation period, and explore the relationship between the recess behavior of females and the changing ambient temperature on one day. We explored the responses of recess frequency, recess duration, and nest attendance to ambient temperature and precipitation with generalized linear mixed models (package *lme4* , Bates et al. 2015) in which daily mean temperature, daily precipitation, and their interactions were included as fixed effects and year was included as a random effect.

3. Results

3.1. Clutch size and incubation rhythm of Reeves's Pheasant

A total of 252 incubation days (2020: n = 132; 2021: n = 80; 2022: n = 40) for Reeves's Pheasant were monitored in 25 nests. The average clutch size of Reeves's Pheasant was 7.72 +- 1.51 (range 5-11). Based on the three successfully hatched nests, the incubation period of Reeves's Pheasant lasted for 26-27 days, and the successful hatching rate was only 12%. During incubation, the females took 0.74 +- 0.46 recesses per day (range 0-2), with an average recess duration of 99.23 +- 72.93 mins (range 0-516 mins) and an average nest attendance of 93.11 +- 5.06% (range 64.17-100%) (Table 1).

Table 1.The recess frequency, recess duration and nest attendance of Reeves's Pheasant in each nest

Nest number	Nest number	Clutch size	Recess frequency (times)[a]	Recess duration (min)[a]	nest attendance (%)[a]
PJG1	8	8	0.80±0.52	115.20±112.36	92.00±7.80
PJG2	7	7	0.68±0.48	100.00±79.19	93.06±5.50
PJG3	8	8	0.63±0.51	77.63±66.09	94.61±4.59
PJG4	7	7	0.88±0.33	100.28±48.74	93.04±3.39
PJG5	10	10	1.00±0.00	169.82±46.35	88.21±3.22
PJG6	9	9	1.14±0.38	129.29±39.45	91.02±2.74
PJG7	6	6	0.86±0.38	112.43±57.22	92.19±3.97
PJG8	6	6	0.63±0.52	87.75±79.06	93.91±5.49
PJG9	5	5	0.40±0.51	59.47±80.09	95.87±5.56
PJG10	8	8	1.00±0.00	148.00±0.00	89.72±0.00
PJG11	9	9	1.00±0.00	167.80±25.64	88.35±1.78
PJG12	6	6	1.00±0.00	117.50±13.44	91.84±0.93
PJG13	6	6	0.75±0.50	75.00±60.94	94.79±4.23

Nest number	Nest number	Clutch size	Recess frequency (times)[a]	Recess duration (min)[a]	nest attendance (%)[a]	I
PJG14	9	9	0.45±0.51	69.40±83.45	95.18±5.80	I
PJG15	8	8	0.83±0.41	95.33±52.60	93.38±3.65	I
PJG16	7	7	1.00±0.00	130.50±23.33	90.94±1.62	I
PJG17	10	10	0.93±0.26	117.93±42.73	91.81±2.97	I
PJG18	11	11	0.78±0.44	97.89±60.41	93.20±4.20	I
PJG19	8	8	1.00±0.00	120.00±55.15	91.67±3.83	I
PJG20	7	7	0.67±0.49	81.92±62.67	94.31±4.35	I
PJG21	9	9	1.00±0.00	187.55±108.19	86.98±7.51	I
ZHS22	7	7	0.58±0.50	66.29±60.78	95.40±4.22	I
ZHS23	9	9	0.57±0.53	97.14±93.58	93.25±6.50	I
ZHS24	7	7	0.75±0.46	68.75±47.34	95.23±3.29	I
ZHS25	6	6	1.00±0.00	90.00±0.00	93.75±0.00	I
Mean ± SD	7.72±1.51	7.72±1.51	0.74±0.46	99.23±72.93	93.11±5.06	

[a]Mean ± SD

Mann-Whitney U test showed that there were no significant differences in recess frequency, recess duration, and nest attendance between hatched and failed nests ($P > 0.05$). As incubation progressed, recess frequency and recess duration tended to decrease ($R^2 = 0.03$, $P < 0.01$, Figure 3a; $R^2 = 0.09$, $P < 0.0001$, Figure 3b), while nest attendance showed an increasing trend ($R^2 = 0.09$, $P < 0.0001$, Figure 3c).

3.2. Effects of ambient temperature and precipitation on the clutch size of Reeves's Pheasant

Spearman correlation analysis showed that there was a significant negative correlation between the first egg-laying month and clutch size (R = -0.64, $P < 0.01$, Figure 4a). Clutch size was significantly negatively correlated with the average temperature during the spawning period ($P < 0.01$, Table 2, Figure 4b), and insignificantly positively correlated with the average precipitation during the spawning period ($P = 0.079$, Table 2, Figure 4c).

Table 2. The results of general linear model analyzing the effects of average temperature and average precipitation during the spawning period on clutch size

Fixed effects	Estimate ± SE	t	P
(Intercept)	11.645 ± 1.331	8.748	< 0.001
Average temperature	-0.280± 0.083	-3.353	0.003
Average precipitation	0.190 ± 0.103	1.844	0.079

3.3. Effects of ambient temperature and precipitation on the incubation rhythm of Reeves's Pheasant

For female Reeves's Pheasants, their nest departures peaked at around 13:00 and nest returning peaked at around 15:00 when the ambient temperature was relatively high during the day (Figure 5a, 5b). Both daily mean temperature and daily precipitation were significantly negatively correlated with recess duration ($P < 0.05$, Table 3, Figure 5c, 5d), but had no significant effect on recess frequency and nest attendance ($P > 0.05$, Table 3).

Table 3. The results of generalized linear mixed model analyzing the effects of daily mean temperature and daily precipitation on recess frequency, recess duration and nest attendance

Response variable	Fixed effects	Estimate ± SE	z	P
Recess frequency	(Intercept)	0.279±0.379	0.735	0.462
	Daily mean temperature	-0.029± 0.020	-1.484	0.138
	Daily precipitation	-0.039±0.497	-0.078	0.938
	Daily mean temperature*Daily precipitation	-0.004± 0.029	-0.152	0.879
Recess duration	(Intercept)	5.317± 0.081	66.011	< 0.001
	Daily mean temperature	-0.040±0.002	-22.673	< 0.001
	Daily precipitation	-0.087± 0.040	-2.173	0.030
	Daily mean temperature*Daily precipitation	0.001± 0.002	0.308	0.759
Nest attendance	(Intercept)	4.474± 0.034	130.629	< 0.001
	Daily mean temperature	0.003± 0.002	1.774	0.076
	Daily precipitation	0.008± 0.034	0.233	0.816
	Daily mean temperature*Daily precipitation	-0.000± 0.002	-0.078	0.938

4. Discussion

The clutch size of Reeves's Pheasant ranged from 5 to 11, and tended to decrease as the nesting season progressed, which is consistent with the studies on other uniparental species (Murphy 1986, Hochachka 1990). Previous studies have explained the seasonal variation in clutch size from a variety of perspectives, including food restriction (Aparicio 1994), weather variation (Grudinskaya et al. 2022) and predation risk (Travers et al. 2010). Collectively, these studies suggest that females need to strike a balance between the acquisition and allocation of energy, predation risk, and the reproductive value of offspring to optimize reproductive investment.

Female Reeves's Pheasant laid more eggs when ambient temperature was lower, which is consistent with the egg viability hypothesis put forward by Stoleson and Beissinger (1999) and the clutch cooling hypothesis put forward by Reid et al. (2000a). That is, when ambient temperature is higher than the physiological zero (24-26), embryos will experience unsynchronized growth and development accompanied by a risk of abnormal death, so the clutch size in a warmer environment should be smaller (Webb 1987, Veiga 1992). In addition, compared with small clutches, large clutches cool much more slowly and therefore are favored in cooler weather (Reid et al. 2000b, Reid et al. 2002). The positive relationship between clutch size and average precipitation during the spawning period may be due to the promoting effect of precipitation on primary productivity as well as secondary productivity (e.g., the biomass of protein-rich prey), and increased food abundance may drive females to lay more eggs (Skagen and Adams 2012). In addition, precipitation may inhibit the activity of nest predators of ground-nesting birds such as snakes (Cox et al. 2013). Meanwhile, visually hunting corvids mainly attack nests with poor concealability (Weidinger 2002), while the rapid vegetation development after precipitation helps hide ground-open nests from the eyes of predators (Ringelman and Skaggs 2019, Laidlaw et al. 2020). Thus, clutch size may increase due to low predator activity during precipitation and high nest concealment after precipitation (Grudinskaya et al. 2022).

Female Reeves's Pheasant maintained a high nest attendance (93.11%) with a low recess frequency (0.74 times). A high incubation constancy can ensure rapid and stable development of embryos and shorten the incubation period (Thompson and Raveling 1987, Hepp et al. 2006, Carter et al. 2014), and a low frequency of nest activity may reduce the attraction to visually oriented predators, thereby reducing the risk of predation (Fontaine and Martin 2006, Cervencl et al. 2011). Previous studies on artificial nests of Reeves's Pheasant have shown that the predation rate reaches more than 50.00% (Wang et al. 2016). Therefore, the incubation pattern with a high nest attendance and a low recess frequency can relieve predation pressure while minimizing physiological costs of female Reeves's Pheasant. As incubation progresses, embryos become more sensitive to temperature variations and less tolerant to low temperatures (Batt and Cornwell 1972, Webb 1987). In addition, the heat loss rate of eggs increases gradually as embryos develop (Cooper and Voss 2013). In this study, as incubation progressed, the nest attendance of Reeves's Pheasant gradually increased, while the recess frequency and recess duration gradually decreased, indicating that the females adjusted their incubation behavior as well as time and energy investment in brooding according to the development of embryos. A similar pattern has been recorded in Redshanks (*Tringa tetanus*), with nest attendance being about 60% at the beginning of incubation and increasing to 94% at the later stage of incubation (Cervencl et al. 2011).

The timing of recesses is involved in the survival of incubating birds and offspring, and may be related to ambient temperature (Winder et al. 2016). It is reported that low temperatures at night may make females that fast overnight have greater energy demands at dawn and forage at dusk for overnight energy reserves (Wiebe and Martin 1997, Moiron et al. 2018, Schöll et al. 2020). If incubating females adjust recess timing to meet their own physiological needs first, recesses may occur more often at dawn and dusk. In contrast, we observed that the females usually chose to leave the nest in the afternoon when temperature was relatively high, and the timing of recesses showed a unimodal pattern in response to the changing ambient temperature. Such behavior appears to be adaptive: the females chose to leave the nest to forage at a higher ambient temperature so as to make their eggs cool relatively slowly, avoid the adverse effect of low temperature on embryonic development, and minimize the time and efforts required to reheat the eggs. The unimodal pattern of recess timing may be driven primarily by embryonic thermal needs rather than by the physiological needs of incubating females, which is different from the bimodal activity pattern observed in species like Chinese Grouse (*Tetrastes sewerzowi*) (Shi et al. 2019), Greater Prairie-Chickens (*Tympanuchus cupido*) (Winder et al. 2016) and Greater Sage-Grouse (*Centrocercus urophasianus*) (Coates and Delehanty 2008).

Ambient temperature and precipitation had significant effects on the recess duration of female Reeves's Pheasant. In cold weather, females are more susceptible to energy constraints due to increased basal metabolism and incubation costs (Bryan and Bryant 1999), and need to spend more time foraging to cope with high energy expenditure (Tulp and Schekkerman 2006, Diez-Méndez et al. 2021). In contrast, warm weather may be associated with higher food availability (Avery and Krebs 1984), which improves foraging efficiency and thus relatively reduces recess duration. The recess duration decreases gradually with an increase in daily precipitation, and in birds like Reeves's Pheasant that build open nests on the ground, the presence of parents in the nest during precipitation can protect the eggs from rain and cold (Kovařík et al. 2009).

Reeves's Pheasants nest under dead woods, shrubs and grass, and their nests are characterised by high nest concealment, which makes it difficult to conduct nest searches (Wang et al. 2016). Although only 25 nests were monitored in this study, they were quite important in helping us better understand the life history strategies of Reeves's Pheasant. Future studies should continue to investigate the influence of environmental factors such as food restriction and predation risk on the breeding behavior of Reeves's Pheasant, so as to better understand the reproductive strategies of Reeves's Pheasant, and to enable wildlife conservationists to better manage the habitat in a way that reduces disturbance to the breeding of Reeves's Pheasant.

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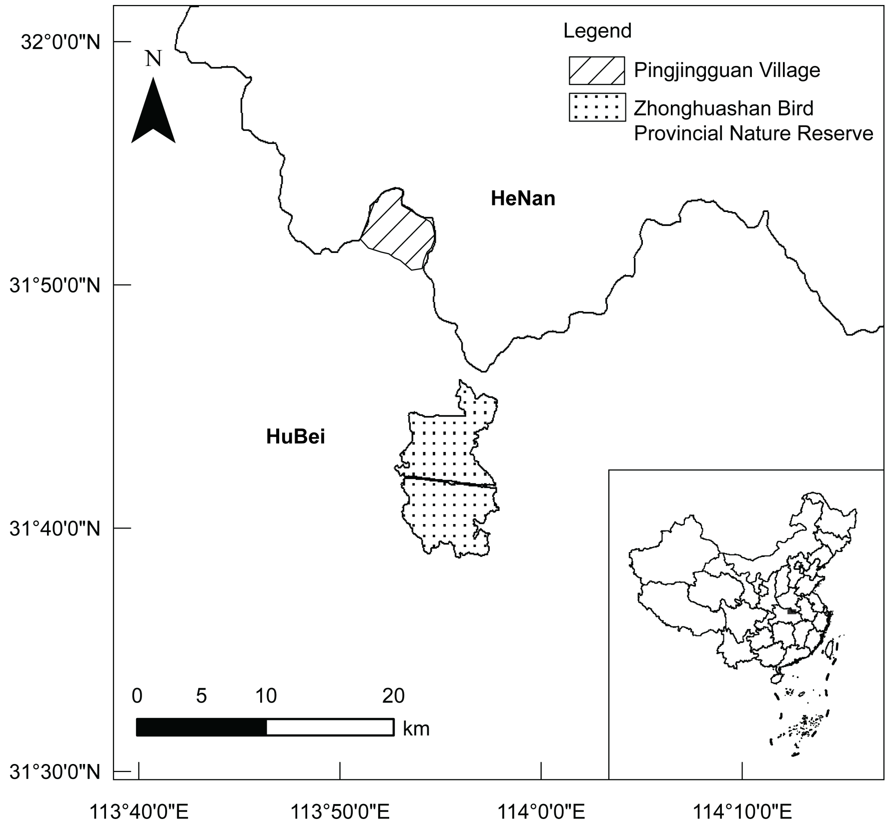
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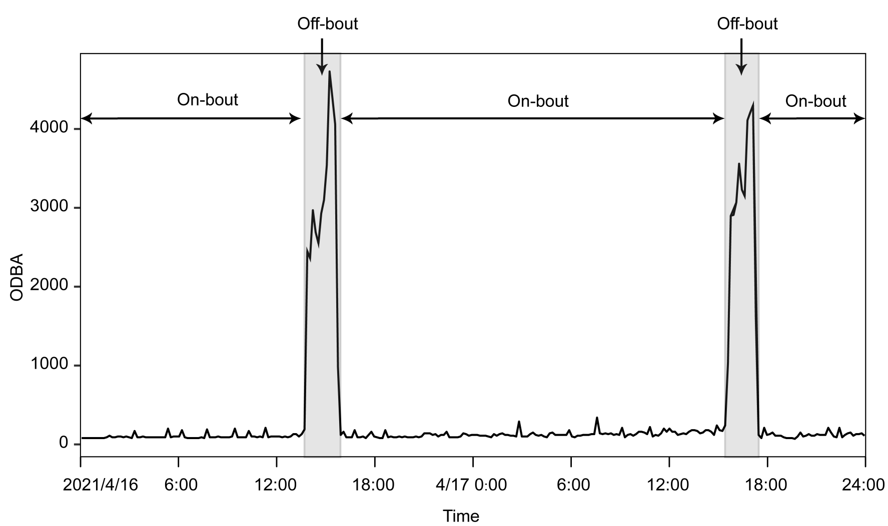
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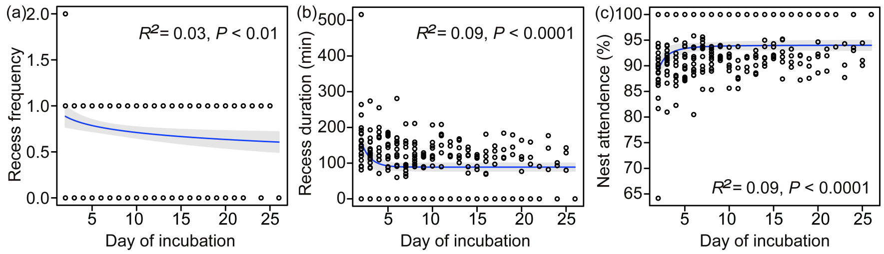
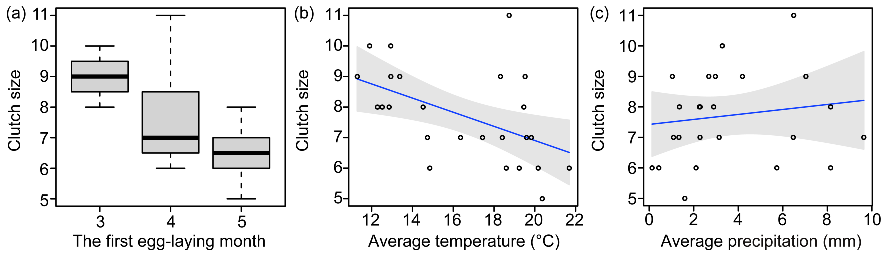
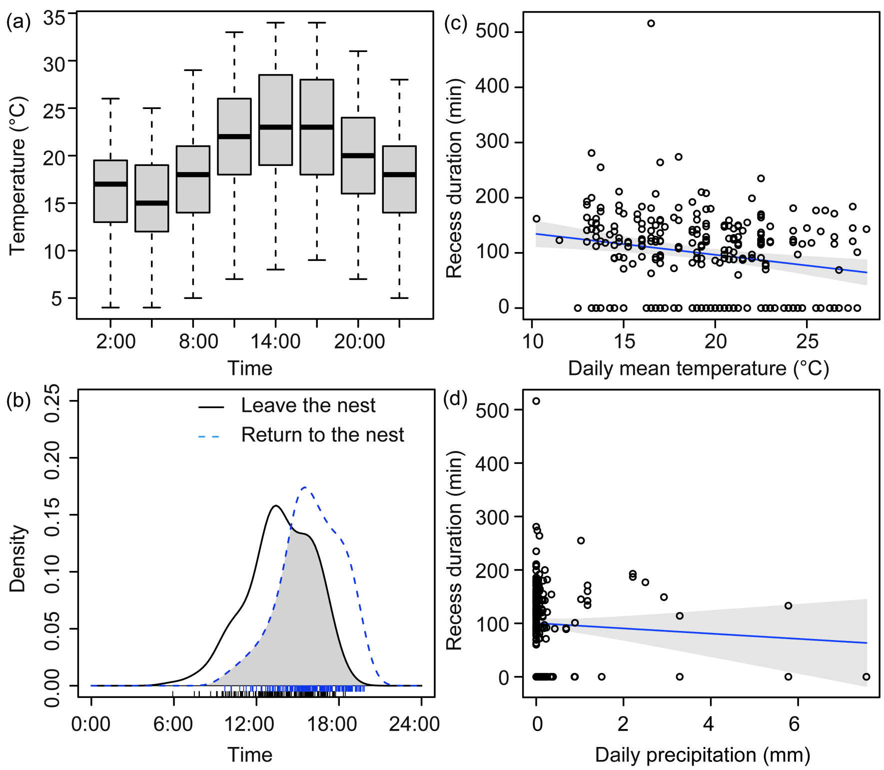

(a)
Recess frequency
R^2= 0.03, P < 0.01
Day of incubation
(b)
Recess duration (min)
R^2= 0.09, P < 0.0001
Day of incubation
(c)
Nest attendence (%)
R^2= 0.09, P < 0.0001
Day of incubation


(a)
Clutch size
The first egg-laying month
(b)
Clutch size
Average temperature (°C)
(c)
Clutch size
Average precipitation (mm)


(a)
Temperature (°C)
Time
(b)
Density
Leave the nest
Return to the nest
Time
(c)
Recess duration (min)
Daily mean temperature (°C)
(d)
Recess duration (min)
Daily precipitation (mm)