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Egg laying and incubation rhythm of the Chinese Grouse (*Tetrastes sewerzowi*) at Lianhuashan, Gansu, China

Mei Shi^{1,2}, Yun Fang¹, Jin-ming Zhao³, Siegfried Klaus⁴, Yingxin Jiang¹, Jon E. Swenson⁵ and Yue-Hua Sun^{1*} 

Abstract

Background: Incubating birds must balance the conflict between thermal needs of the developing embryos and their self-maintenance needs for energy. The Chinese Grouse (*Tetrastes sewerzowi*) lives in high mountain conifer forests and faces energy stress, cold environment, and predation pressure. Females might adjust incubation rhythm to adapt to these constraints.

Methods: Two methods were used to investigate egg laying and incubation pattern of the Chinese Grouse; 25 nests were monitored by data loggers and 12 nests by infrared video cameras.

Results: Female Chinese Grouses usually laid an egg every 2 days. The incubation period was 28–31 days. Overall incubation constancy for Chinese Grouse was 93%. The females took 5.0 recesses per day and 34% of all 1696 recesses were taken in the crepuscular period. The average recess duration was 20.3 min. Females took more and shorter recesses in the latter part of incubation. The females who allocated more time to foraging had a higher reproductive success.

Conclusions: Probably due to its high egg/body mass ratio, the Chinese Grouse has a long laying interval of 49 h. We suggest that, due to energy stress, females have relatively more recesses and they increase the number of recesses as incubation progresses. To compensate for the embryos' thermal needs, they extend the incubation period and shorten the recess duration in this cold environment.

Keywords: Body mass, Chinese Grouse, Environment temperature, Incubation pattern, Nest attentiveness

Background

In precocial birds, especially in those where only one sex incubates, egg laying and incubation are important stages of reproductive investment, and may represent critical energy bottlenecks, especially in harsh environments (Wiebe and Martin 1995, 1997, 2000). Incubating individuals must balance the conflict between thermal needs of the developing embryos and their self-maintenance needs by leaving the nest to forage (Wiebe and Martin 2000; Conway and Martin 2000a; Coates and Delehanty 2008). Also, incubating birds have to adjust their

incubation rhythms based on physical conditions and environmental factors.

In smaller species, environmental factors have a greater effect on incubation rhythm and smaller birds are thought to have a greater need for food during incubation (Afton 1980). Large-bodied birds have greater energy reserves and can spend more time on the nest, but in periods of stress, small-bodied birds might not have enough nutrient reserves to complete incubation (Gloutney and Clark 1991) and need more time off nests for foraging (Manlove and Hepp 2000; Camfield et al. 2010). Also, birds living in areas with low temperatures have a higher daily energy expenditure, but foraging away from the nest is almost twice as costly as incubating a four-egg clutch (Piersma et al. 2003). Because low ambient temperatures allow eggs to cool quickly, birds

*Correspondence: sunyh@ioz.ac.cn

¹ Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China
Full list of author information is available at the end of the article



might be required to show higher nest attentiveness in cold climates (Chalfoun and Martin 2007). Martin (2002) has shown that colder ambient temperatures can result in higher attentiveness, such as Anna's (*Calype anna*) and Black-chinned Hummingbirds (*Archilochus alexandri*) nesting in California, which took longer nest attentiveness than Purple-crowned Fairy (*Heliosthryx barroti*) in the warm lowland tropics of Panama (Vleck 1981).

The Chinese Grouse (*Tetrastes sewerzowi*) is an endemic bird distributed in Gansu, Qinghai, Sichuan, Yunnan, and Tibet in western China (Sun 2000), along the high mountain conifer forests at altitudes between 2700 and 4200 m on the eastern edge of the Tibetan Plateau. These birds typically experience a decrease in mass during reproduction, which is usually considered to be an indication of reproductive stress (Cucco and Malacarne 1997). The Chinese Grouse is the smallest grouse in the sub-family of Tetraonidae (Sun et al. 2005). On the other hand, nutritious foods are limited in spring, as willows (*Salix* spp.) are the main food resources for the birds (Zhao et al. 2017), so nutrient constraint possibly exists during the egg-formation and incubation periods (Wang et al. 2010). During the pre-incubation period, the proportion of time allocated for vigilance by male and time for foraging by female Chinese Grouse is the highest recorded among monogamous grouse species (Lou et al. 2017). This probably benefited the female by reducing the danger of predation, increasing her probability of survival, and allowing more time for her to forage for more nutritious food, such as herb leaves and insects, to increase her energy reserves (Lou et al. 2017). Good body condition at the beginning of the breeding season has been associated with large egg volumes and early laying and body mass is positively related to food abundance during the incubation of Wilson's Storm Petrels (*Oceanites oceanicus*) (Quillfeldt et al. 2006).

How does the Chinese Grouse deal with the cold weather, high altitude, short breeding time, and nutrient stress during the egg-laying and incubation period? In this study, we explored the egg-laying and incubation rhythms of Chinese Grouse and analyzed the strategies Chinese Grouse uses to deal with these disadvantages. We predicted that more feeding during incubation is important for Chinese Grouse reproductive success.

Methods

Study area

We conducted the study during 1999–2016 at the Lianhuashan Nature Reserve (34°45′–35°06′N, 103°27′–103°51′E) in southern Gansu Province, central China. Our research station was at the altitude of 2850 m, surrounded by forest dominated by fir (*Abies fargesii*), spruce (*Picea asperata*), birch (*Betula utilis*), and many

species of willow. The average annual temperature in the reserve is 5.1–6.0 °C, with recorded extremes of 34.0 °C and –27.1 °C at an altitude of 2100 m. For more information, see Sun et al. (2003).

Field methods

The nests of Chinese Grouse are located at the bases of fir, spruce, birch and willow trees. Nesting materials are mainly mosses, leaves and dry twigs. Nests were found by locating radio-tracked females, searching paired males' territories or from reports by local people, who received a reward (Sun et al. 2003; Zhao et al. 2018).

We equipped 25 nests with data loggers (Germin Data Loggers LTD, UK, Tiny Talk II) to record the egg temperatures when the females were on and off their nests, when the temperatures were higher and lower, respectively. In 1999, we equipped 4 nests with thermo-sensors fixed at the bottom of the nests, with a cable (length <3 m) connected to the data loggers. The temperature data recorded in this way were generally lower than the temperature of the egg. However, changes in data logger temperatures should be proportional to those of the eggs, so we could record the nest attendance of the females. In 2000 and 2001, we placed artificial eggs in the center of 16 nests for monitoring both nest attendance and egg temperature. The artificial eggs were from abandoned clutches, and filled with paraffin wax, and thermo-sensors were buried in it (Persson and Göransson 1999). This arrangement did not seem to affect the behaviour of the females, as no females abandoned their nests after we placed the dummy eggs in their nests. We put the thermo-sensors or dummy eggs into the nests as soon as we located them. If the clutch was unfinished, we could record the egg laying intervals. The data loggers were kept dry and covered in plastic boxes. The data loggers were programmed to record temperatures every 6.0 min. In 2010, we monitored 5 nests. The other operations were the same as in 2000, except that the data loggers were programmed to record temperatures every minute. We revisited the nests every 7 days to download the data and restart the logging, mostly without disturbing the hens from the nests. If we disturbed the hens while downloading the data, we excluded the results from that day from the analyses.

The timing and duration of recesses were interpreted from changes in egg ($n=21$) or nest ($n=4$) temperatures associated with the departure and return of the females, as shown on the strip charts. Short temperature drops (lasting only one measurement, 6 min) were likely a result of females repositioning themselves on the nest and moving the eggs; they were not considered to be recesses. Four irregular records from three nests were recorded (two at day time from one nest: 186, 1068 min;

two at night from two nests: 186, 205 min). All three nests hatched successfully. These were most likely associated with predation attempts and all data from these days were excluded from analyses. We defined the overall incubation constancy as the percentage of the time the females spent on the nests during the entire incubation period. Partial incubation was a less regular form of incubation that can occur from the beginning of egg laying to shortly after clutch completion (Wang and Beissinger 2011). Nests were regarded as successful when at least one egg was hatched. We determined nest age by considering that eggs were laid every other day with a mean incubation period of 28 days for successful nests (Sun et al. 2003). For the unsuccessful nests that had been found during incubation, we speculated nest age as Zhao et al. (2019).

In both 2000 and 2001, one data logger was used to record the forest temperature in our study area during the laying and incubating period. All monitored nests were located throughout the study area, so we selected a nest randomly to record the environment temperature. To avoid disturbing the incubating female, thermo-sensors and data logger were hung on a tree 1.5 m high from the ground and 50 m away from the Chinese Grouse nest. Nest site temperatures might differ from our data logger records. However, as the Chinese Grouse made open nests without much concealment, we assumed that there was not a big difference.

During 2013 to 2016, we monitored 12 nests with infrared video cameras (The Ltl Acorn Ltl-6210 M). With its highly sensitive passive Infra-Red sensor, the camera detects the sudden change of ambient temperature caused by moving animals in a region of interest, triggering the camera to take pictures/videos. Thus when a female moved, we obtained videos. By this means, we knew the exact time that a female left and arrived at a nest. We mounted cameras on trunks about 0.5 m away from the nests. The video lasted 10 s for every triggering and 3 pictures for confirmation. We recorded date, time, and frame number on video images electronically.

Data analysis

Data from nests monitored less than 7 days were not included in calculating the recess rates and incubation constancy. We excluded video footages that were interrupted by camera malfunction, loss of power, or disturbance from changing batteries, memory cards, and long-time recess because of predation. Nineteen samples using the data logger and nine from the video camera were included in our analyses. All recesses occurred from 05:30 to 20:30. Nest constancy was calculated in days, and the average was taken.

We conducted a mixed effects linear model, the daily number of recesses as the dependent variable and year, method, nest age, recess duration as fixed factors, with individual as a random factor. And we used a mixed effects linear model to test how the fixed factors year, method, nest age, hour and number of recesses affected recess duration, with individual as a random factor. There was a correlation between year and method. To exclude the effect of method on year, we separated all data to three groups: datalog6, datalog1 and camera, then reanalyzed. To examine how incubating females adjusted recess timing, we grouped all individuals into these groups: reproduction successful and failed, tracked and untracked. We used *t* tests to test the difference in incubation patterns between groups. The data were analyzed using the program R. All values were expressed as mean \pm SD.

Results

We monitored the egg laying of 8 females. Females laid eggs at midday, between 10:59 and 15:45 (time arriving at nest, $n=16$), except for one female that arrived at the nest at 07:27 and spent 6 h there when laying its sixth egg. The laying time of all six of one female's eggs occurred within two and half hours (12:32–15:11). Females usually laid one egg every 2 days, except for one instance of 3 days. The laying intervals of five females were 49.0 ± 1.3 h ($n=18$). Females spent variable amounts of time on the nests when laying eggs. Less time was spent when laying the first four eggs (71.3 ± 19.8 min, $n=9$) than for laying the fifth and sixth eggs (162.8 ± 89.0 min, $n=8$). Full incubation started in the early morning (6:30–8:30, $n=8$). Two females started right after laying the sixth egg, five on the next day, and one on the third day.

We included 28 nests of data in our analyses of nest attendance of Chinese Grouse, for a total of 201 days during 1999 to 2001, 62 days in 2010, and 108 days during 2013 to 2016 (Table 1). Based on the 14 females for which we had documented when they started incubating and hatching of the eggs, the incubation period of Chinese Grouse was around 29.8 (28–31) days.

The overall incubation constancy was $92.8 \pm 2.0\%$ ($n=376$ days). The females took 5.0 ± 1.0 ($n=376$) recesses per day with the average recess length of 20.3 ± 7.7 min ($n=1696$). Three methods (data log-6 min, data log-1 min and camera) affected neither number of recesses nor recess duration. Recess number and recess duration had a significantly negative relationship ($df=367.018$, $t=-6.016$, $p<0.001$, Fig. 1b). Time of day significantly affected recess duration ($df=1658.666$, $t=9.948$, $p<0.001$, Fig. 1a). Recess number increased significantly ($df=370.879$, $t=3.397$, $p<0.001$, Fig. 1c), but recess duration decreased ($df=1391.690$, $t=-1.781$,

Table 1 The number of daily recesses and nest constancy of Chinese Grouse females during the incubation period at Lianhuashan Nature Reserve, Gansu, China

Year-female number	Nest age	Number of daily recesses ^a	Recess duration (min) ^b	Nest constancy (%) ^c	Hatched/Failed	Radio-tracked
99-01	2–26	5.36 ± 1.16 (23)	28.93 ± 7.59 (129)	89.16 ± 1.96	H	Y
99-02	5–16	4.83 ± 0.79 (12)	22.84 ± 5.49 (57)	92.31 ± 1.17	F	Y
99-03	18–24	5.57 ± 0.82 (7)	22.76 ± 10.23 (39)	91.19 ± 1.62	H	Y
00-01	22–30	3.56 ± 0.53 (9)	21.48 ± 7.06 (31)	94.72 ± 1.18	H	N
00-02	6–29	5.25 ± 0.61 (24)	18.87 ± 6.66 (126)	93.12 ± 1.16	H	Y
00-03	7–25	4.84 ± 0.96 (19)	20.66 ± 6.67 (92)	93.05 ± 1.22	F	N
00-04	5–28	4.67 ± 0.87 (24)	23.52 ± 7.93 (113)	92.40 ± 1.29	H	Y
00-05	8–21	4.69 ± 0.63 (13)	22.78 ± 7.42 (64)	92.66 ± 1.07	H	Y
00-06	13–25	6.15 ± 0.81 (13)	21.19 ± 6.31 (78)	91.30 ± 1.69	F	Y
00-07	12–19	4.50 ± 0.53 (8)	18.83 ± 4.34 (36)	94.11 ± 0.75	F	N
01-01	8–18	4.36 ± 0.67 (11)	19.38 ± 6.69 (48)	94.13 ± 1.09	F	Y
01-02	15–29	6.07 ± 0.70 (15)	15.9 ± 5.06 (92)	93.39 ± 1.08	H	Y
01-03	10–26	5.19 ± 0.75 (16)	16.36 ± 6.48 (84)	94.11 ± 1.20	F	N
01-04	13–20	4.29 ± 0.49 (7)	22.32 ± 5.06 (25)	93.54 ± 0.57	F	Y
10-01	1–13	4.54 ± 0.66 (13)	21.97 ± 5.48 (59)	93.08 ± 1.26	F	N
10-02	2–23	4.64 ± 0.58 (22)	14.38 ± 4.09 (101)	95.42 ± 0.73	F	Y
10-03	13–20	4.75 ± 0.71 (8)	23.56 ± 8.94 (36)	92.27 ± 1.60	F	Y
10-04	19–27	4.89 ± 0.78 (9)	22.37 ± 7.4 (43)	92.42 ± 0.91	H	Y
10-05	17–26	5.30 ± 0.82 (10)	20.55 ± 5.71 (52)	92.58 ± 1.17	H	N
13-01	2–16	4.41 ± 0.79 (15)	21.09 ± 7.38 (52)	93.29 ± 1.91	H	Y
13-02	7–18	4.45 ± 0.52 (11)	23.6 ± 9.36 (10)	93.08 ± 2.65	F	Y
13-03	15–24	5.18 ± 0.60 (11)	19.86 ± 8.8 (43)	93.02 ± 1.68	H	N
14-01	10–20	4.15 ± 0.69 (11)	18.28 ± 5.78 (39)	94.56 ± 1.48	H	Y
14-02	3–12	5.90 ± 0.88 (10)	18.71 ± 9.61 (45)	92.32 ± 1.76	H	Y
15-01	2–8	4.29 ± 0.49 (7)	17.64 ± 4.93 (28)	94.85 ± 0.86	H	Y
16-01	19–25	6.00 ± 0.76 (7)	18.21 ± 7.56 (29)	92.96 ± 1.29	H	Y
16-02	2–25	6.13 ± 0.85 (24)	16.24 ± 7.51 (109)	93.53 ± 1.81	H	N
16-03	14–25	4.33 ± 0.49 (12)	16.28 ± 4.22 (36)	95.21 ± 0.71	H	Y

^a Mean ± SD (*n*), *n* was days excluding those disturbed by research action and irregular recesses

^b Mean ± SD (*n*), *n* was recesses excluding those missing record of female going out or coming back

^c Mean ± SD, *n* (constancy) = *n* (number of daily recesses), nest constancy = (1440 min – *t* (female staying out of nest)/1440 min) × 100%

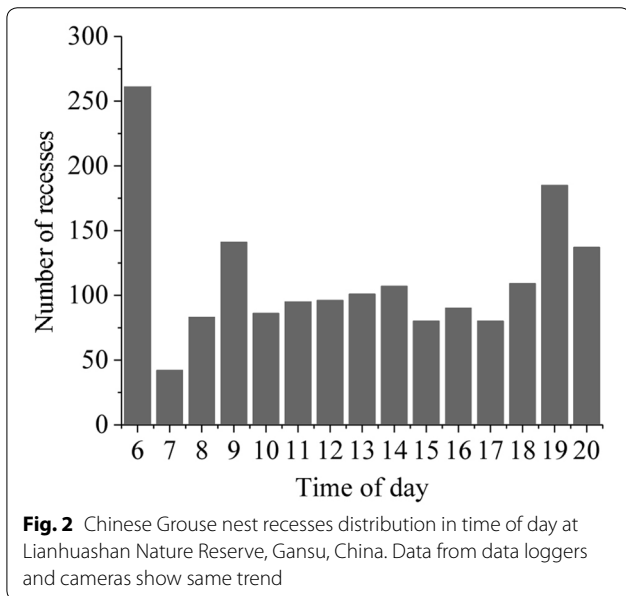
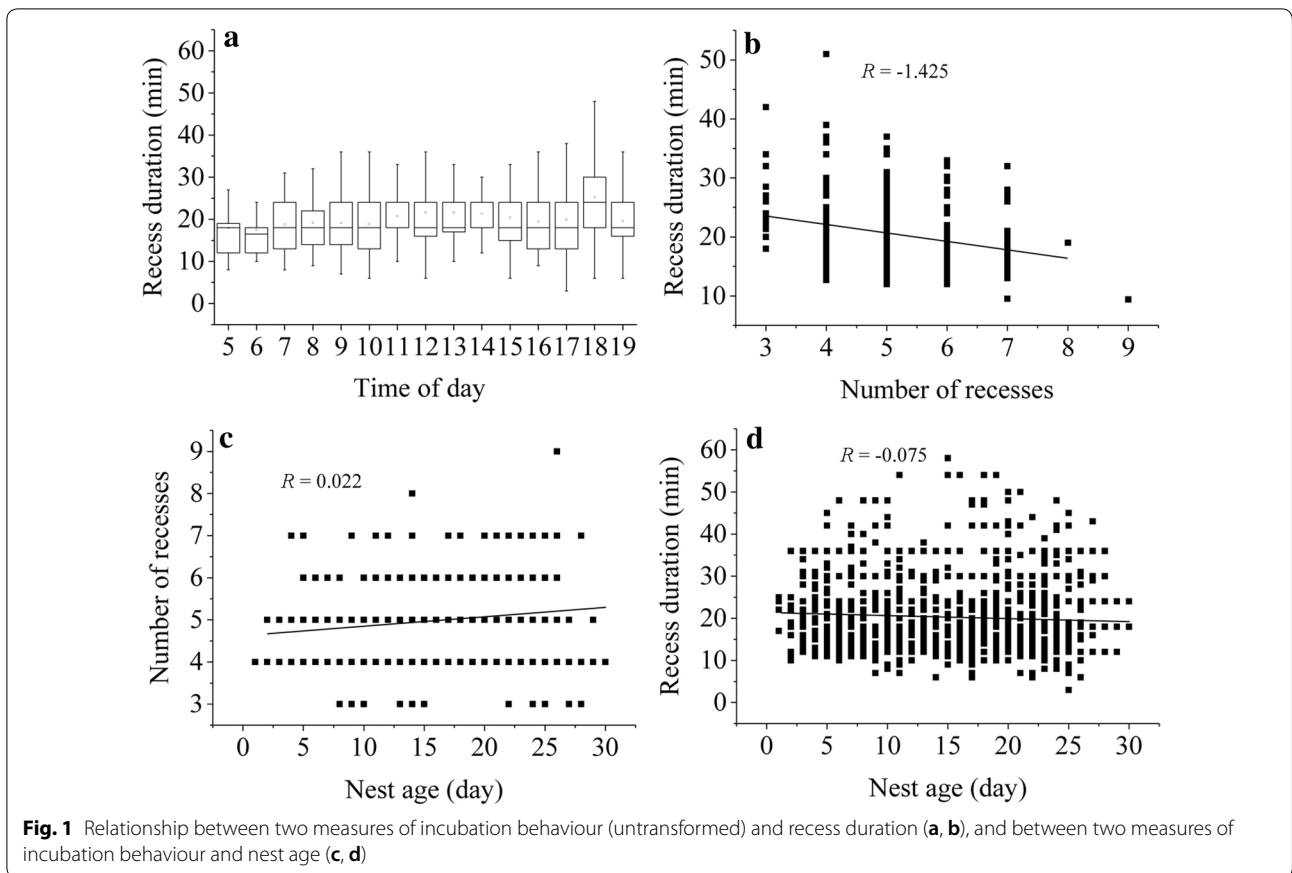
$p = 0.075$, Fig. 1d) as nest age progressed. Recess duration was also affected by year (data logger-6 min, $t = -3.820$, $p < 0.001$; camera, $t = -3.426$, $p < 0.001$). Of the 1696 recesses, 34.4% were taken in the crepuscular periods (before 6:30 and after 18:30, Fig. 2). In all 376 monitored days, we recorded 262 (69.7%) dawn recesses and 321 (85.4%) dusk recesses (Fig. 2). Dawn recess duration was shortest (17.9 ± 6.4 min, $n = 261$) and dusk recess duration was longest (25.3 ± 8.3 min, $n = 185$, Fig. 1a).

Of the 28 females yielding data on incubation rhythm, 18 females were successful in hatching. Recess duration and number of recesses were significantly different between the successful and unsuccessful females ($df = 1512$, $t = 3.131$, $p = 0.002$ and $df = 338.771$, $t = 2.863$, $p = 0.005$ respectively, $T_{\text{successful}} = 20.7 \pm 8.2$ min,

$T_{\text{unsuccessful}} = 19.5 \pm 6.7$ min, $N_{\text{successful}} = 5.1$, $N_{\text{unsuccessful}} = 4.8$). Successful females took more and longer recesses. Twenty of 28 females were followed with transmitters. There was no difference in number of recesses between those that were tracked and those that were not ($N_{\text{tracked}} = 5.0$, $N_{\text{untracked}} = 5.1$, $df = 188.791$, $t = -1.024$, $p = 0.299$), however, tracked individuals had longer recess durations ($T_{\text{tracked}} = 20.8$, $T_{\text{untracked}} = 19.0$, $df = 1063.200$, $t = 4.591$, $p < 0.001$).

Discussion

In Willow Ptarmigan (*Lagopus lagopus*), as in many other ground-nesting precocial birds, the greatest attrition in fecundity is the loss of eggs to predators (Martin et al. 1989). Shorter laying period would reduce the



chances of egg predation (Clark and Wilson 1981); however, birds have limited energy reserve in their body and must gain additional energy by feeding, especially for

precocial birds, because they produce eggs with more yolk (Carey et al. 1980) and might need more time for egg production. Egg-laying interval is thought to be a balance between egg size, clutch size, and time for laying the eggs (Schubert and Cooke 1993). The Chinese Grouse has the smallest body mass in the grouse sub-family (Tetraoniinae). The average mass for the females is 327.4 ± 26.3 g ($n=55$, Sun et al. 2005). The mass of Chinese Grouse eggs averages 20.5 ± 1.6 ($n=165$, Sun et al. 2005), yielding egg/body mass ratio of 6.1–6.9%, which is the highest among the grouse (Johnsgard 1983). Thus, Chinese Grouse should be physiologically stressed by egg production. The laying interval we documented was 49 h for the Chinese Grouse, longer than other grouse species, such as Willow Ptarmigan (24 h, Wiebe and Martin 1995), White-tailed Ptarmigan (*Lagopus leucurus*) (26 and 44 h, Wiebe and Martin 1995), Rock Ptarmigan (*Lagopus mutus*) (36 h, Watson 1972), Ruffed Grouse (*Tetrastes umbellus*) (36 h, Bump et al. 1947), and Hazel Grouse (*T. bonasia*) (31 h, Pynnönen 1954; Semenov-Tyan-Shanskii 1960) (Table 2). The average clutch size of the Chinese Grouse is 6.19 (Sun et al. 2003, first clutch), so the bird needs more than 12 days to lay a clutch. We suggest that

Table 2 Reported reproductive parameters between grouse species

Species	Body weight (g)	Egg laying interval (h)	Clutch size	Egg weight (g)	Incubation (days)	Incubation constancy (%)	Number of daily recesses	Recess duration (min)	References ^a
Chinese Grouse (<i>Tetrastes sewerzowi</i>)	327.4	49	6.19	20.5	28–31	92.8	5.0	20.25	1
Willow Ptarmigan (<i>Lagopus lagopus</i>)	525–652	24	7.1, 10.2	23	21–22				2, 3
White-tailed Ptarmigan (<i>Lagopus leucurus</i>)	329	26–44	5.9	21	22–23	95.7, 93.9	3.07		2, 3, 4
Rock Ptarmigan (<i>Lagopus mutus</i>)	427–701	36	6.6	21	21				2, 5
Ruffed Grouse (<i>Bonasa umbellus</i>)	500–586	36	11.5	19	24	96	2.0	20–40	2, 6, 7
Hazel Grouse (<i>Tetrastes bonasia</i>)	370–422	31	8.3	19	23–27	95	2.0	33	2, 8, 9
Blue Grouse (<i>Dendragapus obscurus</i>)	813–867		6.37	33	26				2
Greater Sage-grouse (<i>Centrocercus urophasianus</i>)	770		12	24	26.5	96.1	2.2	26.5	2, 10
Spruce Grouse (<i>Dendragapus canadensis</i>)	456–620		5.8, 7.54	23	21–25			26.4	2, 11
Capercaillie (<i>Tetrao urogallus</i>)	1755–2004		7.07	48	24–28			35	2

^a The references refer to as follows: 1. Sun (2000), 2. Johnsgard (1983), 3. Wiebe and Martin (1995), 4. Wiebe and Martin (1997), 5. Watson (1972), 6. Bump et al. (1947), 7. Maxson (1977), 8. Semenov-Tyan-Shanskii (1960), 9. Müller (1992), 10. Coates and Delehanty (2008), 11. Naylor et al. (1988)

the relatively long egg interval in Chinese Grouse is due to relatively high physiological costs of egg production.

The laying time of Chinese Grouse was concentrated around noon. It is different from Hazel Grouse, which lays their eggs during 04:00–20:00 (Semenov-Tyan-Shanskii 1960) and the ptarmigans, which lay eggs during 07:00–19:00 (Wiebe and Martin 1995). In 11% failed nests, we identified three nest predator species using infrared video cameras: Asian Badger (*Meles leucurus*) accounting for three nest failures, Hog Badger (*Arctonyx collaris*) for one nest failure, and Blue-eared Pheasant (*Crossoptilon auritum*) for one nest failure. Badgers, the main nest predators in our study area were active in the evening-night period, so around noon might be the

safest time for the Chinese Grouse to visit their nests. The length of the egg-laying interval (around 48 h) also permitted all eggs to be laid around noon. Partial incubation existed especially in the late period of egg laying. White-tailed Ptarmigan and Spruce Grouse (*Dendragapus canadensis*) also showed this pattern (McCourt et al. 1973; Giesen and Braun 1979). In anseriforms and galliforms species, incubation starts during the laying period without causing hatching asynchrony (Wang and Beissinger 2011). Partial incubation thus shortens the incubation period and benefits incubating females (Wang and Beissinger 2011).

The incubation period of Chinese Grouse (around 28–31 days) was relatively long compared to Blue Grouse

(*Dendragapus obscurus*, 26 days) Greater Sage-grouse (*Centrocercus urophasianus*, 26.5 days) Hazel Grouse (23–27 days) and Spruce Grouse (21–25 days) (Johnsgard 1983) (Table 2). During incubation period, female Chinese Grouse spent on average 92.8% of their time per day on nest, which was lowest in grouse species: Ruffed Grouse (96%, Maxson 1977), White-tailed Ptarmigan (95.7% and 93.9%, Wiebe and Martin 1997), Greater Sage-grouse (96.1%, Coates and Delehanty 2008) and Hazel Grouse (95%, Semenov-Tyan-Shanskii 1960) (Table 2). The number of daily recesses taken by Chinese Grouse females averaged 5.0, much higher than that of the Hazel Grouse (2.0, Müller 1992), and White-tailed Ptarmigan (3.07, Wiebe and Martin 1997). The average recess duration of Chinese Grouse was 20.25 min, shorter than that of Spruce Grouse (26.4 min, Naylor et al. 1988), Hazel Grouse (33 min, Müller 1992), Capercaillie (*Tetrao urogallus*) (35 min), and Ruffed Grouse (20–40 min, Johnsgard 1983) (Table 2). And our result showed the number of recesses was negatively related to recess duration. The incubating females might adjust recess duration to guarantee incubation attendance. Chinese Grouse therefore showed a pattern of a long incubation period with low incubation constancy, and more and shorter recesses.

Theory predicts shorter embryonic periods in species with smaller body size (Martin et al. 2007). However, Martin (2002) found no relationship between body mass and incubation period, and proposed that longer incubation periods were associated with lower attentiveness. Deeming et al. (2006) also believed that nest attentiveness affected egg temperature maintenance, and resulted in incubation period variation. Cartar and Montgomerie (1985) suggested that small-bodied incubators have a low fasting endurance and modified nest attentiveness by adjusting the frequency of recesses. Our results support their proposals. With small body mass, females have less endogenous reserves and more nutritional requirements (Demment and Vansoest 1985; Swenson et al. 1994). Limited by energy reserve, they have to leave their nests more often for foraging. Studies have documented that parents compensate for energy demands by reducing nest attentiveness (MacDonald et al. 2014). These might be the reasons why breeding success was related to more and longer recesses in Chinese Grouse females.

Females who were tracked by transmitters (weighing about 12 g, or 3–4% of their body weights, Sun et al. 2003) required longer recesses, presumably for more foraging. However, low attentiveness can decrease reproductive success (Mallory 2009; Shoji et al. 2011). Although we found no significant difference on reproductive success between tracked and untracked females, we believe that the additional burden of the transmitters

might have adverse effects on the tracked females during incubation.

Our results showed differences in recess duration between years, which might be affected by environment temperatures and different monitoring methods. Method does affect recess duration (one-way ANOVA, $F=16.37$, $p<0.001$, $T_{\text{datalog6}}=21.32$, $T_{\text{datalog1}}=19.34$, $T_{\text{camera}}=18.21$). Data logger could overestimate the recess duration because of delayed temperature recording. But recess duration still has significant difference among years, when we excluded the effect of method. Many studies have shown that females take more and shorter recesses in cold environments (Conway and Martin 2000b; Londono et al. 2008; Reneerkens et al. 2011; MacDonald et al. 2014). The recess length of Chinese Grouse in 2001 (17.37 ± 6.23 min) was shorter than that in 2000 (21.06 ± 7.06 min) (t test, both $p<0.001$). We recorded the air temperature in 2000 and 2001. The daily average air temperature during incubation was significantly lower in 2001 (5.4 ± 1.6 °C) than in 2000 (8.5 ± 2.1 °C) (t test, $p<0.001$). As the daily number of recesses was higher in 2001 (5.37 ± 0.96 , $n=249$) than in 2000 (5.09 ± 0.95 , $n=540$) (t test, $p=0.093$), we suggest that the Chinese grouse females adjust incubation rhythm to adapt environment constraints. This correlation has also been found in other grouse species, such as the Spruce Grouse (Naylor et al. 1988). However, studies on the Capercaillie showed that cold weather did not affect the number and length of recesses for this largest grouse (Semenov-Tyan-Shanskii 1960).

Fluctuations in temperature are more detrimental to eggs as incubation progresses (Webb 1987). Meanwhile, the rate of heat loss from eggs increases with embryo age (Cooper and Voss 2013). Female Black-capped Chickadee (*Poecile atricapillus*) responds to increased egg cooling rates by altering incubation rhythms (with more frequent and shorter on- and off-bouts) (Cooper and Voss 2013). The Chinese Grouse females also reduced the recess length as the incubation progressed. However, the daily inattentive period did not differ. For incubating females, body mass has been associated with food abundance (Quillfeldt et al. 2006), and positively related to reproductive success (Gloutney and Clark 1991). In the latter period of incubation, their foraging requirement might be more urgent, as adequate feeding is essential for reproductive success. So, female Chinese Grouse might increase the frequency of recesses and shorten recess duration. Similar results were also found in the Wood Duck (*Aix sponsa*) (Hepp et al. 1990).

A bimodal pattern of recess timing may not be driven primarily by predation pressure, but by physiological needs of the incubating female (Winder et al. 2016). Female grouse may have a greater energy demand at

dawn after fasting overnight, and take recesses at dusk to obtain energy reserves for overnight hours (Wiebe and Martin 1997). Successful females took more and longer recesses, which is at odds with the view that fewer trips to and from the nest may attract fewer predators to the eggs (Ghalambor and Martin 2002). In addition, radio-tracked females increased food intake to cover the additional burden of carrying the transmitter. We suggest that the energy needs of the incubating female are more important than egg chilling and predation risk. We conclude that the egg laying and incubation rhythm of the Chinese Grouse is an adaptation mainly to deal with energy stress, with predation risk being of less importance.

Conclusion

We conclude that the egg laying and incubation rhythms of Chinese Grouse are driven by energy constraints. Compared with other grouse, female Chinese Grouse take longer egg laying intervals, leave nests more times per day with lower incubation attentiveness and longer incubation period to balance the thermal needs of the developing embryos and their self-maintenance needs.

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Authors' contributions

MS and YHS conceived and designed the idea. YF, JMZ, YXJ and MS performed the field work. MS, JS and SK analyzed the data. MS and YHS wrote the paper. All authors contributed critically to the manuscript and gave final approval for publication. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

All capture, radio-tag and tracking procedures on Chinese Grouse used in the present study had been given prior approval and were supervised by the Animal Care and Use Committee of the Institute of Zoology, the Chinese Academy of Sciences (Project No. 2008/73).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

¹ Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China. ² University of Chinese Academy of Sciences, Beijing 100049, China. ³ School of Life

Science, Huaibei Normal University, Huaibei 235000, China. ⁴ Jena, Germany. ⁵ Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Box 5003, 1432 Ås, Norway.

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