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UNUSUAL INCUBATION BEHAVIOR AND EMBRYONIC TOLERANCE OF HYPOTHERMIA BY THE BLOOD PHEASANT (*ITHAGINIS CRUENTUS*)

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ABSTRACT.—Birds with single-sex incubation must resolve tradeoffs in time allocated between incubation and foraging by adopting optimal incubation strategies. We used temperature loggers to study the incubation behavior of the Blood Pheasant (*Ithaginis cruentus*), a uniparental bird of high-elevation forests (3,000 m), at Lianhaushan Nature Reserve in southern Gansu Province, China. The incubation period, 37 days, was 8–10 days longer than for captive birds. Females usually took one recess averaging 6.6 ± 1.2 h day⁻¹, only 6.4% of the days had second recesses, and the latter averaged 28 ± 5 min. Females left the nests near dawn (at 0652 hours, on average) and returned around midday, at 1325 hours; in total, they remained on the nest (i.e., nest attentiveness) for $72.0 \pm 1.4\%$ of the day. Egg predation was not associated with movements of females to and from nests. Egg temperatures dropped rapidly once females left the nest, and eggs often experienced 3.5 h below 10°C for each daily recess. Embryonic hypothermia was thus common, but the hatching rate was >90%. This degree of embryonic hypothermia has rarely been reported. It may be related to the time that Blood Pheasants need to forage on and process their low-quality foods, primarily mosses. Received 7 December 2009, accepted 10 June 2010.

Key words: Blood Pheasant, embryonic hypothermia, high altitude, incubation behavior, *Ithaginis cruentus*, nest predation.

Comportement insolite de couvainon et tolérance embryonnaire de l'hypothermie chez *Ithaginis cruentus*

RÉSUMÉ.—Les oiseaux dont un seul sexe s'occupe de la couvainon doivent faire des compromis entre le temps alloué à la couvainon et celui alloué à l'alimentation en adoptant des stratégies optimales de couvainon. Nous avons utilisé des enregistreurs de température afin d'étudier le comportement de couvainon chez *Ithaginis cruentus*, un oiseau monoparental des forêts en haute altitude (3 000 m), à la réserve naturelle Lianhaushan dans le sud de la province de Gansu, en Chine. La période de couvainon, d'une durée de 37 jours, était 8–10 jours plus longue que pour les oiseaux en captivité. Les femelles prenaient en moyenne une pause de $6,6 \pm 1,2$ h jour⁻¹. Seulement 6,4 % des jours comportaient une seconde pause, laquelle durait en moyenne 28 ± 5 min. Les femelles quittaient leur nid à l'approche de l'aube (à 06:52, en moyenne) et y retournaient à la mi-journée, à 13:25. Au total, elles sont demeurées sur le nid (i.e. soins du nid) pendant $72,0 \pm 1,4$ % de la journée. La prédation des œufs n'était pas associée aux mouvements des femelles hors du nid. La température des œufs a chuté rapidement une fois que les femelles eurent quitté le nid et les œufs ont souvent passé 3,5 h sous les 10°C lors des pauses quotidiennes. L'hypothermie des embryons était alors chose commune mais le taux d'éclosion dépassait 90 %. Ce niveau d'hypothermie des embryons a rarement été rapporté. Ceci peut être lié au temps dont cette espèce a besoin pour s'alimenter et métaboliser ses aliments de faible qualité, principalement des mousses.

INCUBATION IS A stressful period for birds because incubating parents must balance the thermal needs of the developing embryos with their own energetic requirements. The time available for feeding is restricted during incubation in species with unassisted, single-sex incubation, and the effective resolution of the tradeoff between embryos and parent is particularly important in these species (Williams 1991).

In most birds, the optimal temperature for embryonic development is 35–40°C, and no embryonic development occurs below 26°C (the physiological zero temperature) (Drent 1975, Webb 1987,

Olson et al. 2006). Ambient temperature is commonly thought to influence avian incubation behavior (Conway and Martin 2000a). In cold environments, like high-altitude mountains, average ambient temperatures during incubation can be well below the optimal values for embryonic development, creating harsh conditions for uniparental incubators. Thus, because short-term declines in egg temperature apparently have little effect on hatching success (Olson et al. 2006), uniparental-incubating species that breed in colder environments tend to take shorter bouts off the nest (Turner 1994), which prevents eggs from cooling below the physiological

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zero temperature. These species must compensate for shorter bouts off the nest by taking more of them (and, thus, shorter on-bouts) to obtain the energy needed to sustain the adult through incubation (Conway and Martin 2000b). Some Arctic-nesting birds take more and longer recesses during the warmest part of the day to prevent heat loss from the clutch (Cantar and Montgomerie 1985, Poussart et al. 2001). In other species, however, embryonic hypothermia has been documented after long parental absences that are related to the exploitation of undependable food (Boersma and Wheelwright 1979), inclement weather (Haftorn 1988), or disturbance (Sockman and Schwabl 1998).

Nest predation should also affect incubation patterns, especially in species with a high risk of nest predation. If the common nest predators locate nests by observing adult activity (most avian predators), selection should favor few feeding trips to and from the nest. The risk of nest predation appears to be generally high for ground-nesting galliform birds (Johnsgard 1983), with up to 50% of grouse nests being lost to predators (Bergerud and Gratson 1988). Higher nest predation was significantly related to more frequent recesses in the Ring-necked Pheasant (*Phasianus colchicus*; Persson 2000).

The Blood Pheasant (*Ithaginis cruentus*) is a monogamous galliform (mean female body mass = 621 g; C. X. Jia unpubl. data) that inhabits coniferous and mixed coniferous–deciduous forests on the Qinghai-Tibet Plateau and surrounding high mountains (2,135–4,575 m; Johnsgard 1999). Females incubate alone, and during the incubation period males guard their mates while females forage away from the nest (Jia and Zheng 2001). Their nests are always placed on the ground and generally in a depression at the bases of trees, rocks, or fallen trees. Most eggs are laid at 2-day intervals, although the clutch's last egg is laid 1 day after the penultimate egg. The female begins incubation when the last egg is laid and incubates for about 27–29 days in captivity when given abundant high-quality food (Grahame 1971). Here, we report much longer incubation periods in the wild (~37 days) and examine the reasons for this difference by (1) describing the incubation pattern of this uniparental incubator that eats low-quality food (Liu 2000) and (2) determining whether predation was associated with incubation recesses.

METHODS

We conducted our study during the breeding season (April–July) of 2001 and 2002 at Lianhaushan Nature Reserve in southern Gansu Province, China (34°45′–35°06′N, 103°27′–103°51′E). The forest is dominated by fir (*Abies fargesii*) and spruce (*Picea asperata*) and occurs on north-facing slopes between 2,700 and 3,400 m above sea level. The area has been described in detail by Sun et al. (2003).

Radiotelemetry was used to locate birds and their nests. Nine (4 males and 5 females) and eight (3 males and 5 females) birds were captured by snares during April and May in 2001 and 2002, respectively. Each bird was fitted with a necklace-type radiotransmitter that weighed ≤16 g, which represented <3% of the bird's body mass. The birds were released at the capture site after they were banded and standard measurements were taken (<1 h), and they were tracked daily between 0600 and 2000 hours (Beijing time) from the end of April to July.

Thirteen Blood Pheasant nests (7 in 2001 and 6 in 2002) were found by following radiotracked birds (12 nests) or reported by local people (1 nest). Nine nests were found during the egg-laying stage and four during the incubation stage. Date of egg laying, hatching, or predation was known precisely for nests that were monitored with data loggers. The first egg-laying date was estimated by back-dating from the hatching date (incubation period = 37 days; see below) and the egg-laying interval (2 days). Gemini data loggers (Tiny Talk II, Gemini Data Loggers, Chichester, United Kingdom) were fixed into one artificial egg filled with paraffin wax to monitor incubation rhythms. The paraffin wax has similar specific-heat properties to egg albumen (Varney and Ellis 1974), but the heating and cooling rate of the dummy egg was ~18% faster than that of a real egg of similar size. The sensor wire between the paraffin egg and the data logger was reinforced with a fine metal wire that was buried in the soil under the nest. This wire restricted movement of the paraffin egg in the nest somewhat, although they could still be turned to a certain extent. The data loggers were packed with waterproof plastic materials outside the paraffin eggs and fastened to a metal stake driven into the ground 0.2–0.8 m from the nest. Temperatures were logged at 6-min intervals with an accuracy of 0.1°C. The nests were revisited every 7 days to download data when females were feeding and off the nests. The attentiveness of the incubating female was determined from inspection of the temperature recordings, because sudden temperature changes usually indicated departure or arrival of the incubating female. One temperature logger was placed in the forest no more than 2 km from any nest studied to record the ambient temperature at 1-h intervals throughout the breeding season in 2001 and 2002.

The incubation period was defined as the number of days between the start of incubation and hatching of eggs. Nest attentiveness and recess duration were calculated from the departure time and return time from and to the nest. Nest attentiveness was defined as the total time spent on the nest each day (expressed as a percentage of 24 h) and recess duration as the length of each feeding trip off the nest.

The type of predator was identified by nest remains. Mammalian predators usually either leave tooth marks on the dummy eggs and crush the eggshells into small fragments or eat the eggs entirely, leaving no eggshells. Avian predators left holes in the sides of eggs and left the rest of the eggshell intact. Few snakes were found in the study area.

Only data from complete daily records were used to calculate nest attentiveness and recess duration. The incubation-rhythm data on the day before hatching were very different from those on other days and were excluded from all analyses. We used general linear mixed models (GLMM) to explore the effects of incubation day (fixed factors) on incubation-rhythm components (nest attentiveness, recess duration, departure time, and return time) for the complete data set, with individual bird as a random factor, to account for the repeated measurements made on the same individual birds. Values presented are means ± SD.

RESULTS

A total of 267 incubation days were monitored in 13 nests from 9 May to 30 June in 2001 and 2002. Nest initiation dates ranged from 27 April to 13 May, with an average initiation date of 3 May,

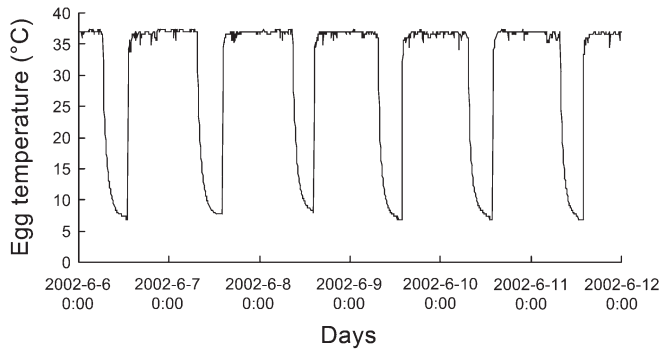


FIG. 1. Egg temperature and pattern of nest attendance of a female Blood Pheasant during 6 consecutive days (6–12 June 2002) at the Lianhuashan Nature Reserve, China.

and clutch sizes ranged from 6 to 10 eggs per nest (mean = 7.8 ± 1.2 eggs). Three complete incubation periods lasted 35, 38, and 39 days, for an average of 37.3 days. Female Blood Pheasants typically take one incubation recess each day to feed (Fig. 1). Females normally left the nests at 0652 hours (± 41 min; $n = 244$) following nocturnal incubation and returned at 1325 hours (± 62 min; $n = 244$) to incubate continuously through the remainder of the day and night. Recess length thus averaged 6.6 h ± 71 min ($n = 244$). They seemed to leave the nest punctually. Most departures (68%) were concentrated near dawn between 0600 and 0700 hours, but return times, around midday, were more variable (87% between 1200 and 1500 hours; Fig. 2). Female nest attendance averaged $72.0 \pm 1.4\%$ ($n = 13$). Female behavior changed during the incubation period. As incubation proceeded, females gradually delayed leaving the nests (GLMM, $F = 25.58$, $df = 1$ and 10, $P < 0.001$) and returned to the nests earlier (GLMM, $F = 15.86$, $df = 1$ and 9, $P < 0.01$). Accordingly, the recess duration declined significantly over the incubation period (GLMM, $F = 78.85$, $df = 1$ and 8, $P < 0.001$). The net effect of these changes was that nest attentiveness increased from 67% on the first day of incubation to a high of 82% before hatching.

During 267 days of observation, only 17 second recesses (6.4% of the days) were recorded from 5 birds, and these occurred between 1349 and 1918 hours. They were shorter than normal

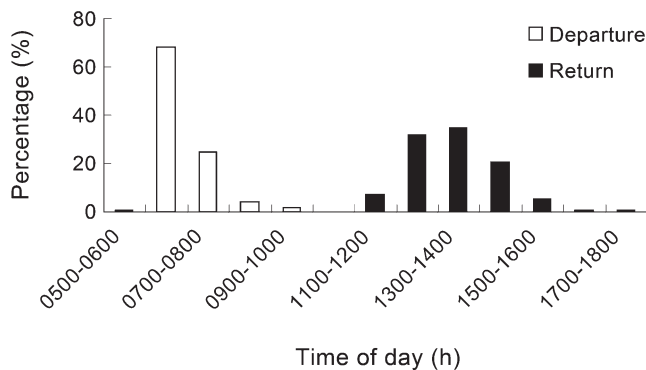


FIG. 2. Hourly variations in departure and return times of incubating female Blood Pheasants at the Lianhuashan Nature Reserve, China, in 2001 and 2002.

recesses and averaged 28 ± 5 min. Most second recesses (11 of 17) occurred late in incubation, although the frequency of second recesses did not differ between days 1–20 of incubation and later ($\chi^2 = 1.47$, $df = 1$, $P > 0.05$). Female 02-16 was possibly flushed from its nest by predators on two occasions at 2317 and 2006 hours and left the nest unattended for 8.2 h and 11.9 h, respectively. Five and four more recesses were taken the following day. These extra recesses were excluded from all analyses.

The hourly mean ambient temperature was 3.4°C (range: -5.8 to 19.8°C) and 4.2°C (range: -5.8 to 16.0°C) during the monitoring period in the 2 years, respectively, with no difference between years ($F = 0.091$, $df = 1$ and 120, $P = 0.764$). During the incubation period, the average on-nest and off-nest egg temperatures were $33.6 \pm 2.1^\circ\text{C}$ (13 birds, 4,366 h) and $11.1 \pm 2.6^\circ\text{C}$ (13 birds, 1,634 h). The mean ambient temperature during the day rose gradually from the low at 0600 hours ($-1.0 \pm 2.9^\circ\text{C}$ in 2001 and $-0.2 \pm 3.4^\circ\text{C}$ in 2002) to the high at 1600 hours ($8.8 \pm 5.6^\circ\text{C}$ in 2001 and $7.7 \pm 4.9^\circ\text{C}$ in 2002) during the incubation period. Almost invariably, the females left the nests between 0600 and 0800 hours each day, the period with the lowest daily ambient temperature, and returned to the nests during the warmest period, between 1200 and 1500 hours each day. Egg temperatures declined dramatically after females left their nests. For each daily recess, the eggs experienced ~ 3.5 h below 10°C (2001: 3.7 h; 2002: 3.4 h; Fig. 3) and ~ 6.5 h below 26°C (the physiological zero temperature; 2001: 6.6 h; 2002: 6.3 h). The lowest egg temperature recorded was 1.5°C , on 15 May 2001. In spite of low incubation temperatures, the hatching rate was high, 97% ($n = 30$ eggs) for data-logged nests and 92% ($n = 71$) for all eggs in data-logged and nonlogged nests.

All nest predation events were caused by mammalian predators while the females incubated. Six of eight predation events recorded by data loggers occurred during the night between 2030 and 0600 hours and without any relationship with recesses (Table 1). One of two predation events during the day was certainly associated with a nest recess, given that it occurred immediately after the female returned to the nest. In the other loss of a nest to a predator during daylight, the female was flushed from the nest 3.5 h after a normal recess, and therefore the loss of the nest seemed to be unrelated to its recess behavior.

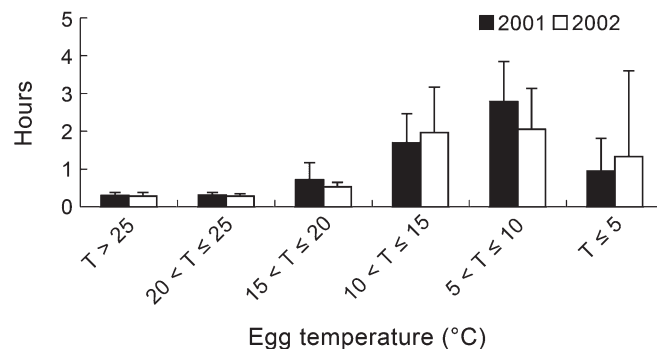


FIG. 3. The length of time that Blood Pheasant eggs experienced different temperatures (5° intervals) while females were off the nest at the Lianhuashan Nature Reserve, China (years 2001 and 2002 calculated separately). The data are from 7 females in 2001 and 6 females in 2002. Columns and error bars show the mean length and the SD for the females.

TABLE 1. Timing of recess behavior and predation events on eggs of Blood Pheasants at the Lianhuashan Nature Reserve, China, during incubation in 2001 and 2002.

Female	Date	Normal recess		Supplementary recess		Time of predation
		Departure time	Return time	Departure time	Return time	
01-76	2001-5-25	0630	1530			1536
01-83	2001-5-30	0711	1400			2130
01-84	2001-6-5	0659	1224			2224
01-86	2001-6-16	0642	1148	1618	1648	2118
01-88	2001-6-8	0648	1224			2048
02-69	2002-5-25	0606	1418			1748
02-76	2002-6-5	0624	1213	1349	1419	
02-88	2002-6-6					0549
	2002-6-8	0730	1312			
	2002-6-9					0112

DISCUSSION

Blood Pheasants exhibited an unexpectedly long incubation period, a low attendance rate at the nest, and, usually, a single long daily recess that started at the coldest part of the day and during which the egg temperature normally dropped below 10° for 3 h without affecting hatching success negatively. Most studies of incubation behavior have been conducted on passerine and precocial species (mainly on waterfowl and grouse). More and shorter recesses are usually taken by passerines, whereas waterfowl and grouse take fewer and longer recesses (e.g., recess length: 10.2 min for passerines and 61.2 min for waterfowl; Deeming 2002). A relatively small number (2–7) of recesses per day seems typical for most galliforms (Johnsgard 1983). Chinese Grouse (*Bonasa sewerzowi*), which are sympatric with Blood Pheasants in the Lianhuashan Nature Reserve, take five recesses per day, with a total recess duration of 94 min and a nest attentiveness of 93.5% (Sun 2004). Thus, compared with most other birds, the incubation pattern of female Blood Pheasants was unusual, with one long recess of 6.6 h per day between early morning and afternoon. The incubation rhythm was modified simply by scheduling the departure time and, especially, the return time, for each recess per day throughout the incubation period. Nest attendance (72%) was much less than the >90% reported for eight other species of galliform birds (Deeming 2002).

Wild Blood Pheasants also had a surprisingly long incubation period (37 days). It was much longer than the expected period of 23.8 days that was predicted from the relationship between initial egg mass (IEM) and incubation period (Ip) for Galliformes ($Ip = 17.14IEM^{0.096}$; Deeming et al. 2006). Grahame (1971) found much shorter incubation periods (27–29 days) in captive Blood Pheasants given high-quality food (Grahame 1971), although longer than the expected incubation period. We suggest that captive incubating females could feed more efficiently and spend more time on the nest. Thus, the duration and rhythm of incubation in wild Blood Pheasants may be influenced by their low-energy diet. In spring, Blood Pheasants feed mainly on mosses (Liu 2000), which are low-quality food with a high concentration of lignin-like compounds that result in low digestibility (Prins 1982, Prop and Vulink 1992). Many bird species modify activity patterns during incubation in

response to variation in food availability, and most food supplementation experiments have shown that supplemental food increases nest attentiveness (Chalfoun and Martin 2007). Leaving the nest at dawn for long feeding recesses may be associated with foraging constraints and the physiology of hunger and digestion (Wiebe and Martin 1997). Females should be most hungry in the morning after nearly 18 h of continuous incubation. Therefore, female Blood Pheasants may be forced to take long recesses, starting as soon as light levels allow, to obtain adequate energy for survival and incubation, even though this entails leaving the nest when air temperatures are coldest.

Tradeoffs in the time allocated to foraging and incubation by uniparental-incubating birds might be resolved by optimizing the daily recess frequency and recess length to maximize hatching success and minimize the probability of nest loss to predators or death of a parent (Conway and Martin 2000b). Taking fewer but longer foraging bouts, rather than many short ones, can reduce the energy cost of incubation to the adult, because such a strategy reduces the number of times that females must rewarm the clutch. However, taking long foraging bouts may slow embryonic development because of lower egg temperatures during recesses (Drent 1975, Williams 1996, Olson et al. 2006). Avian embryo development usually has a narrow range of optimal temperatures (35–40°C in most birds; Webb 1987). Most birds normally return to their nests quickly to warm their eggs, and the egg temperature is little affected by the recesses. However, embryonic hypothermia due to egg neglect or lower nest attentiveness has been found in some birds. Most species that breed at low temperatures maintain fairly constant egg temperatures through a high level of nest attentiveness, even when incubation is by one parent (White and Kinney 1974). For example, minimum egg temperatures in the Capercaillie (*Tetrao urogallus*) averaged 27.7°C during absence, compared with incubation temperatures of 34–35°C (Lennerstedt 1966). Egg temperature of the Arctic-nesting Greater Snow Goose (*Chen caerulescens atlantica*) dropped only 2.8°C, on average, during recesses (Poussart et al. 2000). However, some procellariiform birds neglected their eggs continuously for several days (with great variation between individuals) when their incubating partner was delayed from returning to relieve them because of undependable food or storms (Boersma and

Wheelwright 1979). Embryonic tolerance of chilling thus varies greatly among birds.

The Superb Lyrebird (*Menura superba*), a pheasant-sized songbird in southeastern Australia, has an incubation pattern similar to that of the Blood Pheasant. Females usually take two recesses per day, with a long morning recess of 3–6 h (Lill 1979), and egg temperatures fall and stabilize near ambient levels (~10°C) for several hours daily during morning recesses (Lill 1979). In Blood Pheasants, females typically left the eggs unattended for nearly 7 h at low air temperatures in the morning. As a result, the eggs experienced more than 3 h below 10°C during each daily recess throughout the 37-day incubation period, and large differences in temperature between incubation and recesses. Therefore, embryonic hypothermia occurred daily, in contrast to the unpredictable pattern observed in the procellariiforms and similar to that observed in the Superb Lyrebird. The ability to withstand temporary embryonic hypothermia would have adaptive value for Blood Pheasants that breed at high altitudes and cold regions, possibly allowing females sufficient time to feed on low-energy food. This would reduce the conflict between attentiveness and foraging time.

Nest predation was high in our study area, and only 41% of 27 Blood Pheasant nests hatched eggs (C. X. Jia unpubl. data). However, only one of eight nest-predation events was associated with recess behavior. Six of eight nest-predation events occurred at night and all were caused by mammals, which suggests that predators detected the nests by olfactory rather than visual cues. Therefore, factors other than predation risk may be most important in determining the patterns of incubation recesses observed in the Blood Pheasant, which is consistent with observations of forest-dwelling grouse (Storaas and Wegge 1997).

Our findings raise questions regarding the physiological basis underlying hypothermic tolerance in avian embryos and its adaptive and evolutionary significance. Revealing this mechanism would have great significance for understanding the evolution of hypothermia during avian incubation. The existence of embryonic hypothermia in such unrelated taxa as the Blood Pheasant and Superb Lyrebird suggests that the evolution of embryonic hypothermia is not constrained phylogenetically and raises the question of why so few species, especially those that breed in cold environments, have failed to do so.

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