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In some monogamous birds, males invest more time in vigilance than females, especially during the pre-incubation period. As behaviors are time costly, there is a tradeoff between vigilance and feeding behavior. Male vigilance can be regarded as a male investment in their mates and may benefit the female by reducing the danger of predation, increasing her probability of survival, and allowing more time for her to forage to obtain more resources for egg production and incubation. In this study, we documented the proportion of time spent in vigilance and feeding by Chinese grouse *Tetrastes sewerzowi* with their mates and alone during the pre-incubation period, and then estimated male vigilance under more severe predation pressures through predator call playback. Our results indicated that paired male Chinese grouse spend more time in vigilance than unpaired males and paired females and could alter their activity budgets in response to the social context (i.e. with and without their mate) and an experimental encounter with an important predator. Male vigilance behavior and presence allowed females to spend more time foraging. We therefore conclude that vigilance behavior by their male partners by may play an important role in promoting the females' survival and probably the reproductive success. The proportion of time allocated for vigilance by males and foraging by females of Chinese grouse during the pre-incubation period was the highest recorded among monogamous grouse species, perhaps because the Chinese grouse is the smallest grouse species and has the highest relative reproductive investment.

Social monogamy is the most common mating system in birds (Lack 1968), among monogamous species, both parents normally contribute to parental investment (Bart and Tornes 1989, Ligon 1999), which is important to increase the survival rate of offspring (Whittingham and Robertson 1994). Grouse species have a diversity of mating systems, ranging from monogamy to polygamy (Johnsgard 1983). Swenson (1991) hypothesized that mating systems were influenced by the nutritional status of females before egg laying, which was related to female body sizes. Unlike large species, small species face more challenges in acquiring nutrition. Therefore, they need the protection of their partners during the pre-incubation period, because they invest proportionally more in their clutches than females of large species (Sæther and Andersen 1988). Therefore, the mating system should influence the activity budgets of both sexes during the pre-incubation period. In lekking and polygamous

species, the female leaves the male after copulation and raises the young without assistance from the father (Wiley 1974), whereas in monogamous species, paternal care is variable. In the willow ptarmigan *Lagopus lagopus*, the pairs stay together during the entire breeding period and males participate in offspring care. However, in the white-tailed ptarmigan *L. leucurus* male investment occurs only during the pre-incubation period, and males leave the females after they begin to incubate and do not participate in parental care (Artiss et al. 1999).

Vigilance behavior is defined as a behavior to scan the environment, and could be influenced by group size, sex (Li et al. 2009), social status (Krams 1998), and reproductive status (Rieucau and Martin 2008). The levels of vigilance are often sex-related in pairs (Dahlgren 1990). We consider the main functions of a male's vigilance behavior is to be mate guarding and predator detection vigilance behavior (Squires et al. 2007). Vigilance behavior is a time cost by reducing the time a male can spend on feeding or resting behaviors (Bertram 1980, Dukas 1998, Elias et al. 2014). Even so, in some species paired males have been found to show higher levels of vigilance (Gauthier and Tardif 1991, Artiss and Martin 1995, Squires et al. 2007). Male vigilance could prevent extra-pair paternity, thus guaranteeing that the male has

fathered its mate's offspring. It could also allow females to devote more time to feeding, enhancing their nutritional status (Artiss et al. 1999, Christensen 2000), which may relate in higher quality eggs. However, vigilant behaviors of some paired males may also have been for self-protection, because bright or colorful feather may attract predators (Huhta et al. 2003). So their vigilance behavior would also increase their survival rate. Although previous studies have shown a relationship between male vigilance and female foraging, there are few studies addressing the influence of different social contexts within pairs in areas with difficult climatic environments, such as the edge of the Tibetan Plateau.

We studied the feeding and vigilance behaviors of the monogamous Chinese grouse *Tetrastes sewerzowi* during the pre-incubation period. It is the southernmost and smallest grouse species in the world (Sun et al. 2003, 2005), inhabiting subalpine coniferous forests between 2600 and 3600 m (Sun 2000). Most Chinese grouse live in flocks during winter. The flocks dissolve in late March to April, when the males establish territories and pairs form (Sun and Fang 2010). The pairs were relatively stable pair bonding, and they spend most of their time together, staying close while foraging and moving until the beginning of incubation (Sun and Fang 2010). Female grouse have the greatest nutritional investment in clutches among tetraonids (Sun et al. 2005) and longer egg laying intervals (48 h) than other grouse (Sun et al. 2002). The females start incubation in late May and are alone in caring for offspring (Sun 2004). Chinese grouse have both avian and mammalian predators, but avian are predators are more important in the Lianhuashan Nature Reserve (Sun 2004).

We specifically aimed to test four hypotheses regarding male vigilance in the Chinese grouse. (H1) The vigilance of paired males is higher than unpaired males and paired females. (H2) Male vigilance enables the females to spend more time in foraging. (H3) Chinese grouse have the ability to adjust activity budgets according to social context (with or without its mate) and potential predation risk. (H4) The proportions of time spent in male vigilance and female feeding by Chinese grouse should be the highest among the monogamous grouse species. To test these hypotheses, we gathered data on foraging and vigilance behavior of Chinese grouse, conducted call playback experiments, and reviewed the literature about the vigilant and foraging behaviors of white-tailed ptarmigan and willow ptarmigan.

Methods

Study area

Our study area was located in the Lianhuashan Natural Reserve, southern Gansu Province, China. The climate and vegetation of study area has been described in detail previously (Sun et al. 2003).

Data collection

Pre-incubation behaviors were defined as the time Chinese grouse devoted to living-related activities from their arrival on the breeding area to the beginning of incubation. In our study area, the pre-incubation period lasts about 1.5 months from early April to late May (Sun 2004), and we obtained activity budgets from 4 April to 21 May in 2014. Chinese grouse always forage on willow during this period and the feeding areas are relatively stable. We found them by radio-tracking or direct observation. We used focal sampling (Altmann 1974) during 5-s intervals to record the proportions of vigilance and foraging behavior from 06:30 to 20:00, using the following methods. Observations were made by using binoculars and a stopwatch. We distinguished the sexes and their reproductive status based on Bergmann et al. (1996), Yang et al. (2013), and prior field experience. We considered all females we encountered to be paired, due to the heavily male-biased sex ratio in the study area (Sun et al. 2003). Although not all the males we encountered were individually marked, their strong degree of territoriality helped us to identify all of them (Sun and Fang 2010).

We considered vigilance behavior to be when the bird's head was up or scanning the surroundings. Foraging was when the bird was pecking for food. When we encountered grouse in the field, we stayed about 25 m away from them and observed them for several minutes before recording their behaviors. For each observation, we recorded the sex, reproductive status and social context (with or without a mate) (Cezilly and Keddar 2012), and recorded proportion of time spent on vigilance and foraging for at least 2 min when we met single or paired grouse. If the observation lasted more than 10 min, we played tone vocalization of a goshawk *Accipiter gentilis*, a common predator in the Lianhuashan Nature Reserve. We used the same method to record the proportions of time spent foraging and vigilant during the following 5 min (see Supplementary material Appendix 1 for details). We stopped observations when the grouse were out of sight or disturbed. Though our call playback experiment may reflect the behavior of Chinese grouse to the vocalization of a common predator, it still has some limitations, such as the lack of a control recording and the use of only one goshawk vocalization. All field observations and recordings were taken by the same person (Y. Lou). Finally, we reviewed the previous literature by searching for vigilance/alert of white-tailed ptarmigan, vigilance/alert of willow ptarmigan, foraging/feeding of white-tailed ptarmigan, and foraging/feeding of willow ptarmigan in Google Scholar to compare these parameters among monogamous grouse species.

We recorded 386 observations totaling 2493 min, each observation ranged from 2.0 to 27.0 min, with an average of 6.0 min. We obtained 112 observations of males and females together in 11 pairs, 16 individuals (9 males and 7 females) in 11 pairs observed while their partners were absent (87 and 25 observations, respectively), and 4 unpaired males (37 observations). Playback experiments were conducted on eight pairs, three unpaired males, and two lone females. Three paired males (3 of 11), all radio-tracked grouse, were killed by predators during our study, but no paired females were. We were unable to determine whether an unmarked, unpaired male that lost track off had died or moved away. Seven papers satisfied the selection criteria and we extract the available data in Table 4.

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Table 1. Linear mixed-effect model outputs for the factors which influence the proportion of time foraging and vigilance in Chinese grouse during the preincubation period in Lianshanhua Natural Reserve, Gansu Province, China.

Model	Variable	F	p
Foraging	sex (n = 11)	48.373	< 0.001**
	social context (n = 11)	0.211	0.649
	sex and social context (n = 11)	7.597	0.009*
Vigilance	sex (n = 11)	92.316	< 0.001**
	social context (n = 11)	0.328	0.571
	sex and social context (n = 11)	16.820	< 0.001**

$*p < 0.05$; $**p < 0.01$.

Statistical analyses

Because we recorded the vigilance and foraging data as proportions, we arcsin square-root transformed them to meet the assumptions of normality. A multi-factor analysis of variance was used to test whether the proportion of male vigilance and foraging were significantly different from that of its partner. We used a linear mixed-effect model, with pair as a random factor, for the analysis of whether sex, social context, or an interaction between the two influenced the proportion of time that paired grouse spent vigilant or foraging, using the lme4 package in R ver. 3.1.2 (< www.r-project.org >). We used the paired t-test to examine for differences between the pre- and post-playback experiments. A linear regression model was used to test whether the proportion of time spent vigilant by a male was related to the proportion of time spent foraging by its partner (Cézilly and Keddar 2012). Using an ANOVA test, we tested for possible differences in feeding and vigilance behavior among the following groups: paired males and females encountered alone, paired males and females encountered with their partners, and unpaired males. All statistical analyses were carried out in R ver. 3.1.2 and all values are presented as means ± SE. Tests were considered statistically significant if $p < 0.05$.

Results

The result of multi-factor analysis of variance showed that the percentage of time spend vigilant and foraging were both significantly different between males and females in all sampled pairs ($F_{1,10} = 144.744$, $p < 0.001$, vigilance of male and female (mean ± SE): 0.441 ± 0.062 and 0.175 ± 0.037; $F_{1,10} = 92.297$, $p < 0.001$, foraging of male and female (mean ± SE): 0.296 ± 0.093 and 0.585 ± 0.111, respectively), but they were no significant difference among pairs ($F_{1,10} = 0.942$, $p = 0.536$, $F_{1,10} = 1.596$, $p = 0.237$,

respectively). Males were more vigilance than females in all sample pairs. The proportion of time spent vigilant by males was significantly and positively related to the proportion of time spent foraging by female ($R^2 = 0.588$, $n = 11$, $p = 0.006$). The linear mixed-effect model revealed that time spent foraging was significantly influenced by the interaction between sex and social context and by sex ($F_{1,10} = 48.373$, $p < 0.001$, $F_{1,10} = 7.597$, $p = 0.009$, respectively), but not by social context alone ($F_{1,10} = 0.211$, $p = 0.649$). Similarly, sex and the interaction between sex and social context also significantly influenced the proportion of time invested in vigilance ($F_{1,10} = 92.316$, $p < 0.001$, $F_{1,10} = 16.820$, $p < 0.001$, respectively), but social context alone did not ($F_{1,10} = 0.328$, $p = 0.571$, Table 1).

After the playback experiments, paired males with their mates, unpaired males, and paired females with their mates were all significantly more vigilant than before the playback ($t = -3.300$, $p = 0.013$, $t = -7.27$, $p = 0.018$, and $t = -3.352$, $p = 0.012$, respectively, Table 3). Lone females were also more vigilant and foraged less, but the difference was not significant ($t = -0.325$, $p = 0.800$, $t = -1.748$, $p = 0.331$, respectively), perhaps due to the small sample size ($n = 2$, Table 3). The proportion of time spent foraging after the playback was significantly lower than before the playback for paired male with their female and unpaired males ($t = 2.642$, $p = 0.033$; $t = 6.144$, $p = 0.025$, respectively), but there was no significant different for females with their mates ($t = 2.079$, $p = 0.076$, Table 3).

Foraging patterns were significantly different between unpaired males and paired males when alone ($F_{1,11} = 8.180$, $p = 0.016$), but there was no significant difference in vigilance pattern ($F_{1,11} = 2.733$, $p = 0.127$). Also, the foraging and vigilance patterns were significantly different between unpaired males and paired males with their partners ($F_{1,13} = 18.318$, $p = 0.001$ and $F_{1,13} = 27.711$, $p < 0.001$, respectively, Table 2). Paired males were significantly more vigilant and foraged significantly less when with their mates than when alone ($F_{1,18} = 9.522$, $p = 0.006$, $F_{1,18} = 10.195$, $p = 0.005$, respectively, Table 2). Paired females spent significantly more time foraging and less time vigilant when they were with their mates than when alone ($F_{1,16} = 6.583$, $p = 0.021$; $F_{1,16} = 7.775$, $p = 0.013$, Table 2).

We conducted a literature review of the proportion of time spent in vigilance and foraging behavior during the pre-incubation period among the monogamous grouses. We found that proportion of time spent vigilant between male Chinese grouse and white-tailed ptarmigan overlapped partially, but the percent of vigilance was higher in Chinese grouse. Comparing to other two monogamous grouse, percent of time on foraging in female Chinese grouse is higher during the pre-incubation period (Table 4).

Table 2. Summary of focal observation samples with different social status in Chinese grouse during the pre-incubation period in Lianshanhua Natural Reserve, Gansu Province, China. The data on vigilance and feeding were presented as means ± SE.

Sex	Condition	Social context	Vigilance	Feeding
Male	paired (n = 11)	together (n = 11)	0.451 ± 0.065	0.296 ± 0.093
		alone (n = 9)	0.343 ± 0.085	0.432 ± 0.105
Female	paired (n = 11)	together (n = 11)	0.175 ± 0.037	0.604 ± 0.078
		alone (n = 7)	0.230 ± 0.053	0.507 ± 0.060
Male	unpaired (n = 4)		0.270 ± 0.033	0.523 ± 0.083

Table 3. Proportion of the time Chinese grouse spent vigilant and foraging before and after an experimental exposure to a goshawk call during the preincubation period in Lianshanhua Natural Reserve, Gansu Province, China.

Sex	Context	Behavior	Before playback	After playback	t	p
Male (n = 8)	pair	feeding	0.370 ± 0.287	0.170 ± 0.57	2.642	0.033*
	together	vigilance	0.440 ± 0.238	0.670 ± 0.182	−3.300	0.013*
Female (n = 8)	pair	feeding	0.612 ± 0.173	0.404 ± 0.255	2.079	0.076
	together	vigilance	0.168 ± 0.066	0.512 ± 0.305	−3.352	0.012*
Male (n = 3)	unpaired	feeding	0.688 ± 0.161	0.289 ± 0.051	6.144	0.025*
		vigilance	0.202 ± 0.062	0.629 ± 0.054	−7.270	0.018*
Female (n = 2)	paired	feeding	0.374 ± 0.201	0.272 ± 0.023	−1.748	0.331
	alone	vigilance	0.388 ± 0.142	0.473 ± 0.186	−0.325	0.800

*$p < 0.05$; **$p < 0.01$.

Discussion

We found support for all of our four hypotheses. Our results showed that the proportion of time spent vigilant was sex-related; males spent a greater percentage of time vigilant than females and the proportion of time females spent foraging was positively correlated with the percent of time their mates were vigilant, which was similar to that reported for two ptarmigan species (Hannon and Martin 1992, Artiss and Martin 1995). When with their partners, males and females showed different behavioral patterns; males spent more time on vigilance than when alone, which suggested that the benefits of vigilance outweighed the costs. Females of other monogamous grouse species have been found to spend more time on foraging when with their males than when alone (Ridley and Hill 1987, Swenson 1993, Artiss and Martin 1995, Artiss et al. 1999). The presence of mates may be similar to the group size effect, where the degree of vigilance behavior decreases with increasing group size (Li and Jiang 2009). By providing vigilance, a paired male may reduce the mortality risk of its female and may allow her to spend more time on other behaviors (e.g. foraging, preening). During our observations, we found that paired males with their partners detected predators or were disturbed by humans, they would fly or walk while giving warning calls to attract the predator's attention, meanwhile, the females kept feeding. By doing so, the female would be able to forage more and attract less attention, increasing the amount of time she could devote to foraging, perhaps enhancing her fecundity, and in turn potentially increasing the breeding output of both members of the pair (Teunissen et al. 1985, Artiss et al. 1999). Though our study showed that male vigilance and presence were very important to females

(Gauthier and Tardif 1991), we did not demonstrate a causal link between male vigilance and female foraging. More research on this subject is required.

Potential predation risk can influence animals' behaviors (Swenson 1993, Lima and Bednekoff 1999, Altendorf et al. 2001, Li et al. 2009) and animals in nature should behave according to the tradeoff between costs and benefits. In our study, all social categories of Chinese grouse increased their level of vigilance following an experimental playback of a goshawk call, except the paired females that were alone, for which we had a very small sample size (n = 2). Also, time spent foraging decreased significantly for all categories, except for paired females with their mates. These results are consistent with the hypothesis that Chinese grouse adjust their activity budgets according to potential predation risk, though we cannot rule out the possibility that they would respond similarly to playback of non-threatening calls nor that our presence affected their vigilance behavior. Paired males have often been reported to be flexible in their activity budgets and invest more energy into vigilance when potential predators are present (Lima 2009). Yet, if males could detect predators early, escaping from predators or alarming for their female mates when attacked by predators would have a great probability of surviving (Lind and Cresswell 2005) and save large energy from fleeing or fighting with predators (Ruxton et al. 2004). After the playback, paired females with their mates increased their proportion of time spent vigilant, but they still maintained a relatively stable proportion of foraging comparing to before the playback. Therefore, we conclude that females could benefit from the vigilance or presence of their mates, which allowed the females to forage more, probably detect predators earlier, or escape more easily from them (Bertram 1980, Michael 2007).

Table 4. Reported clutch size, duration of the incubation periods and percentage of time used for vigilance by males and foraging by females during the preincubation period by monogamous grouse.

Species	Male vigilance (%)	Female foraging (%)	Body size in breeding season (mean: g)	Cluth size	Duration of the incubation period (days)	Source
Chinese grouse	22–54	39–77	male: 322.4 ± 28.6 female: 327.4 ± 26.3	6–8	28	1
White-tailed ptarmigan	22–30	25–30	male: 348.7 ± 19.8 female: 455 ± 43.1	2–8	23	2
Willow ptarmigan	no data	25–35	male: 538 ± 65.0 female: 542.3 ± 6.2	6–7	22	3

1. Sun et al. 2005.
2. Artiss and Martin 1995, Wiebe and Martin 1998, Thomas et al. 1994, Johnsgard 1983.
3. Hannon and Martin 1992, Mortensen and Blix 1986, Johnsgard 1983.

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Our study generally indicated that the proportion of time vigilant and foraging by paired males with partners was higher than unpaired males during the pre-incubation period. Males normally synchronize their behaviors with their mates and whether vigilance evolved for predator detection, mate guarding (Brodsky 1988), territory defense (Black 2001), or all three functions, it could increase the foraging time and survival of their partners when females were most vulnerable (Gauthier and Tardif 1991). The level of vigilance exhibited by unpaired males can be regarded as the basic vigilance level in Chinese grouse. Compared to unpaired male grouse (27%), the paired males with partners spent 45% of their time on vigilance, which may also have included predator detection for their female mates and mate guarding (Brodsky 1988) to protect their own paternity (Chuang-Dobbs et al. 2001, Guillemain et al. 2003). During the field observations, we found that paired males would drive intruder males out of his territory, which indicated that vigilance behavior also contains elements of mate guarding (Fusani et al. 1997). However, we did not test how vigilance related to mate guarding in Chinese grouse, more research is required to be examined.

We found references to the percent of vigilance and foraging behavior of three species of monogamous grouse (Table 4). The proportion of time spent vigilant by male Chinese grouse and white-tailed ptarmigan partially overlapped, but the percent of vigilance was higher in Chinese grouse. This could be affected by the abundance of predators (Forslund 1993) or different degrees of extra-pair paternity. Female Chinese grouse spend a larger percent of their time foraging than the other two monogamous grouse during the pre-incubation period. These differences may be influenced by different methods of data collection (Hannon and Martin 1992, Artiss and Martin1995). However, Chinese grouse have the highest relative reproductive investment among the grouse (Sun et al. 2005). Small females face more pressure to obtain the energy and nutrients for egg formation (Swenson et al. 1994, Nager 2006) and thus small females may benefit from increased male vigilance as they forage to obtain these resources for laying and incubating eggs. We predicted that birds with small body size species are dependent on their partners spending more time vigilant than birds with large body size. Our results are consistent with this hypothesis, though a larger sample of species and individuals is needed to test this possibility statistically.

Conclusions

Our results were consistent with our four hypotheses about vigilance and foraging behavior, though further research is needed to address the causal links between male vigilance and female foraging, and between body size and vigilance among grouse species. Our results also suggest that the patterns of male vigilance and female feeding in pairs in Chinese grouse are similar to those previously detected in other monogamous bird and mammal species (Burger and Gochfeld 1994, Dahlgren 1990, Squires et al. 2007), with males spending more time vigilant and less time foraging than their partner females. These behaviors may enhance the survival and reproduction of both sexes.

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Supplementary material (available online as Appendix wlb-00257 at <www.wildlifebiology.org/appendix/wlb-00257>). Appendix 1.