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SPECIALTY SECTION This article was submitted to Conservation and Restoration Ecology, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 19 December 2022 ACCEPTED 16 January 2023 PUBLISHED 10 February 2023

CITATION

Rao X, Li J, He B, Wang H, Wu G, Teng T and Ling Q (2023) Nesting success and potential nest predators of the red Junglefowl (*Gallus gallus jabouillei*) based on camera traps and artificial nest experiments. *Front. Ecol. Evol.* 11:1127139. doi: 10.3389/fevo.2023.1127139

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Nesting success and potential nest predators of the red Junglefowl (*Gallus gallus jabouillei*) based on camera traps and artificial nest experiments

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Breeding success is an important factor determining fecundity with nest predation being the main factor limiting avian breeding success. Understanding of nest predation and its influencing factors are highly significant to explore the dynamics of bird populations and developing appropriate conservation strategies. In two breeding seasons of the year 2020 and 2021, natural nests of the red junglefowl (Gallus gallus jabouillei) were systematically searched and monitored using infrared camera, in two nature reserves (Datian and Bangxi) of tropical Hainan island, China. Results showed that breeding season of the red junglefowl is mainly from March to July, with April being the breeding peak. The clutch size was 5.15 ± 1.28 (n=13), and nesting success of natural nests was 31.2%, with nest predation accounting for 45.4% of nest failure. Artificial nest experiments showed that predation rates of artificial nests were 25% (Datian, 2020), 6.67% (Datian, 2021), and 0% (Bangxi, 2020). Rodents, reptiles, and coucals are the main nest predators of red junglefowls, while activities of Hainan Eld's deers (Panolia siamensis) may interfere with the reproduction of red junglefowls. We suggest that the conservation management policies should consider the impacts on junglefowls' breeding success when reconstructing the suitable habitat of the Hainan Eld's deer.

KEYWORDS

artificial nest, breeding success, Gallus gallus jabouillei, infrared camera, nest predation

Introduction

The study of reproductive biology and the estimation of nest survival rates are critical to understanding avian life history (Martin, 2004; Stutchbury and Morton, 2008, 2023). Life history traits related to reproduction, such as clutch size, parental care, chick development, and survival rate, can provide insights for solving problems related to the assessment of population status and conservation (Martin, 2002, 2008; Martin et al., 2017). Most recent studies on reproductive biology have focused on northern temperate zone birds (Martin, 2004; Lloyd et al., 2014; Xiao et al., 2017), while birds in other regions, especially tropical birds, have been relatively less studied (Xiao et al., 2017). The main reason may be that tropical birds are relatively difficult to monitor (Martin, 1996; Jiang et al., 2017; McCullough and Londoño, 2017). Studies have shown that the reproductive strategies of birds in different regions

are different mainly due to the differences in the breeding habitats of birds and their nest predation rates (Martin, 1996). Compared with temperate birds, tropical birds are characterized by a longer breeding season, smaller clutch size, longer brooding, and hatching periods (Martin, 1996; Lloyd et al., 2014). Therefore, expanding the understanding of the life history of tropical birds can help us better understand the global trend of life history strategies (Ricklefs and Wikelski, 2002; Slevin et al., 2020).

Nest predation is a major factor limiting the success of bird reproduction and affects the life history and population dynamics of birds (Reidy and Thompson, 2012; Thompson and Ribic, 2012; Ibáñez-Álamo et al., 2015; Chen et al., 2020). Especially for ground-nesting birds, nest predation has become one of the most critical factors affecting their reproductive performance and population growth (Sanders and Maloney, 2002; MacDonald and Bolton, 2008; Pedersen et al., 2011; Melville et al., 2014). Based on this, understanding predation on birds and its influencing factors is of great significance for studying bird population dynamics and proposing conservation strategies (Martin, 1993; Chalfoun et al., 2002; Seibold et al., 2013; Chen et al., 2020).

The red junglefowl (*Gallus gallus*) belong to the genus *Gallus* of the pheasant family (Phasianidae) in the order Galliformes and is a ground-active bird (Zheng, 2022). According to the differences in their distribution range and morphological characteristics, the world's red junglefowl can be divided into five subspecies, all of which are distributed in southern Asia (Johnsgard, 1999; del Hoyo et al., 2001). There are two subspecies in China, the southern Yunnan subspecies (*G. g. spadiceus*) and the Hainan subspecies (*Gallus gallus jabouillei*; Zheng, 2022).

In this study, we searched and monitored the natural nests of red junglefowls, the Hainan subspecies, in Datian and Bangxi Nature Reserves, tropical Hainan Island, China, using infrared cameras. Considering that the number of natural nests of Galliformes birds is limited and nest sites are relatively difficult to find (Luo et al., 2017), the use of artificial nests for simulation studies can not only reduce human interference on hatching in the wild but also has the advantage of ease of use, and can provide sufficient samples for research (Martin, 1987; Major and Kendal, 1996; Wilson et al., 1998; Zanette and Jenkins, 2000; McDonald et al., 2009; Melville et al., 2014; Luo et al., 2017), we carried out artificial nest experiments in the study area to compare the survival rates and potential predators of natural nests and artificial nests.

Materials and methods

Study area

This study was conducted in Datian and Bangxi Nature Reserves. The Hainan Datian National Nature Reserve (19°05′-17′ N, 108°47′-49′ E, with 30–80 m in elevation and 1,310 ha in total area) is located in Dongfang city, Hainan Province, with the Hainan Eld's deer and its habitat being the main target for protection. Bangxi Provincial Nature Reserve (19°22′-24′ N, 109°05′-06′ E, with an elevation of 17–80 m and a total area of 361.8 ha) is located in Bangxi town, northwest of Baisha County, Hainan Province, with the Hainan Eld's deer and its habitat also being the main target for protection.

Monitoring of natural nests

In 2020 and 2021, we carried out a search for the natural nests of red junglefowls following Conkling et al. (2012). The search was divided

between two groups. The first group consisted of forest rangers in the reserve, who searched for nests during daily routine patrols; the second group consisted of researchers who used the behavioral observation and systematic search technology of adult birds and monitored them at 06:00 ~ 09:00 and 16:00 ~ 19:00 every day. Once the nest was found, we used a GPS device (eTrex 32x, Garmin) to mark its location and recorded the status of the female (brooding or flew away) and of the nest (building, hatched, brooded, or abandoned). To avoid interference, we used a telescope to observe the nest every 3–5 days. If at least one egg in the nest successfully hatched, we considered the reproduction to be successful; if all the eggs were not hatched or were destroyed, we considered the reproduction to be a failure (Visco and Sherry, 2015).

In addition, an infrared camera was also aimed at each breeding nest to accurately identify predators and assess the fate of the nests. To avoid abandonment by parent birds due to human interference, the infrared cameras were installed in the incubation period (DeGregorio et al., 2016). We usually adopted the method of using local materials to fix the camera to the tree trunk at 1-1.5 m away from the nest; for situations in which we were unable to fix the camera to a tree trunk, we used the method of piling objects to set up the camera and disguise it appropriately. The infrared camera was set to record continuously throughout the day, and the shooting mode was set to "photograph + video." Each time the camera was triggered, it shot three photos and 15s of video, and the trigger sensitivity was set to "medium" (Xiao et al., 2014). After the nest was preyed upon, we reviewed the camera records to identify the type of predator and recorded the time of predation. For predation events in which the predators were not recorded due to camera failure or other reasons, we speculated on the identity of the predators based on the status of the nests after the predation event occurred because some predators will leave evidence behind. For example, rodents usually leave behind eggshell fragments, while some reptiles prey on nests without leaving any traces (Klug et al., 2010).

After breeding, we recorded and measured the following nest site parameters: (1) nest size (long and short diameters); (2) nest depth; (3) nest materials; (4) distance from nest to the nearest water source; and (5) shortest distance from the nest to the road. For the natural nests in which reproduction failed, the following parameters were recorded and measured: (1) clutch size; (2) egg size; and (3) weight of the eggs. We used a tape measure which ranging from 0 to 500 cm to measure the nest size, nest depth, distance from the nest to the nearest water source, and shortest distance from the nest to the road. For indicators that exceeded the measuring range of the tape measure, we used the method of walking estimation. Eggs were measured using a digital Vernier caliper; the egg size measurement was accurate to 0.01 mm. The egg weight measurement was accurate to 0.01 g.

Artificial nest experiments

During the breeding season in 2020, we conducted artificial nest experiments in Datian (6–25 May 2020) and Bangxi (7–25 May 2020). The location for setting up the artificial nests was selected in the same area where natural nests of red junglefowl were found in a previous study (Yuan, 2009) or was determined according to the characteristics of the site of the natural nests (Yuan et al., 2009a). Artificial nests were constructed by imitating the structure of natural nests, which are shallow pits, and using dry leaves, twigs, and feathers as nest materials. Two eggs of domesticated chickens that were similar in size and color to those of wild red junglefowl were placed in each artificial nest. Two

groups of experiments were set up at each study site (the distribution of artificial nests is shown in Figures 1, 2). The first group consisted of 10 nests for the non-covered group (infrared camera), and the second group consisted of 10 nests, with dry leaves used to cover the experimental eggs. The artificial nest incubation period was set as 19 days, which similar to its natural incubation period (Yuan, 2009). The artificial nests were inspected every 6 days for a total of three times, on the 7th day, 13th day, and 19th day after nest set up (Dinsmore et al., 2002). In each inspection, the artificial nest was photographed, and the nest number was recorded. If there were two eggs or one egg in the artificial nest, the nest was inspected again the next time (fully covered nests were covered with leaves again after the inspection); if the two eggs were preyed on or disappeared, the results were recorded immediately after taking pictures, and this signified the end of the experiment. The inspection results were divided into: (1) two eggs intact; (2) one egg intact, one egg preyed on (with eggshell or predation traces); (3) one egg intact, one egg missing (no traces); (4) two eggs preyed on (with eggshell or predation traces); (5) two eggs missing; and (6) experimental eggs were moved by unknown animals.

During the breeding season in 2021, we conducted artificial nest experiments in Datian (11–29 March 2021). Similarly, we set up two sets of experiments, with 15 nests in each group (the distribution of artificial nests is shown in Figure 3). In the non-covered group, every nest was deployed together with an infrared camera, and only some of the nests (three totals) in the fully covered group were deployed together with a camera. The specific operations and methods were the same as described above.

To reduce the influence of researchers on the experiment, human interference should be minimized during artificial nest inspection, for example, to leave as little footprint as possible around the artificial nest and to avoid the behavior that may affect the nest, such as touching the experimental eggs (Driscoll et al., 2005). In the wild, if the nest is disturbed or the eggs in the nest are preyed upon, the female chickens will abandon the nest (Yuan, 2009). Therefore, if the eggs in the artificial nest are damaged, removed or disappeared, we will not replace the new experimental eggs (Nour et al., 1993) and define the nest as a reproductive failure (Noske et al., 2008). Otherwise, the nest is considered a successful breeding nest.

Species identification was performed based on photos or videos taken by the infrared cameras. When identifying species, we mainly referred to the "Chinese Wildlife Manual of Mammals" (Smith and Xie, 2009), "A Checklist on the Classification and Distribution of the Birds of China (third Edition)" (Zheng, 2022) and the "The CNG field guide to the birds of China" (Liu and Chen, 2021). To calculate the number of animals captured by the cameras, when an animal was photographed by the same camera more than 30-min apart, this was considered an independent capture and an individual animal (O'Brien et al., 2003; Rovero et al., 2014).

Results

Natural nests

In the breeding season of 2020 and 2021, we found 16 natural nests of red junglefowl at the two study sites (Table 1; Figure 4). There were 12 nests in Datian and four nests in Bangxi (Figures 5A–D). Among the 16 nests found, infrared cameras were installed in 13 nests for







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TABLE 1 Active nests of red junglefowls (Gallus gallus jabouillei) in Datian and Bangxi Nature Reserves in 2020 and 2021.

Nest	Site	Date found	Content	Observation and nest fate
001	DT	2 April 2020	Two eggs	Adult flew away, Nest abandoned
002*	DT	8 April 2020	Five eggs	Adult flew away, Nest abandoned, Predated
003*	BX	13 April 2020	Four eggs	Adult incubating, Four Nestlings hatched
004*	BX	15 April 2020	Five eggs	Adult flew away, Nest abandoned
005*	DT	16 April 2020	One egg	No adult, Nest abandoned, Predated
006*	DT	21 April 2020	Four eggs	Adult flew away, Nest abandoned
007*	DT	22 April 2020	Two eggs	No adult, Nest abandoned, Predated
008*	DT	26 April 2020	Six eggs	Adult incubating, One Nestling hatched
009**	DT	26 April 2020	Four eggs	No adult, Two Nestlings hatched
010*	BX	7 May 2020	Eight eggs	No adult, Nest abandoned, Predated
011*	BX	18 May 2020	Five eggs	Adult flew away, Nest abandoned
012*	DT	14 June 2020	Six eggs	Adult flew away, Five Nestlings hatched
013*	DT	2 July 2020	Four eggs	Adult flew away, Nest abandoned, Predated
014*	DT	26 March 2021	Seven eggs	Adult flew away, Nest abandoned
015*	DT	10 April 2021	Five eggs	Adult flew away, Nest abandoned
016**	DT	24 April 2021	Four eggs	No adult, Four Nestlings hatched

DT, Datian National Nature Reserve; BX, Bangxi Nature Reserve.

*The nest was monitored by infrared camera; **The nest had finished breeding when discovered.



Distribution of natural nests of red junglefowls (Gallus gallus jabouillei).

monitoring (Figure 6). In total, five out of the 16 nests reproduced successfully (Figures 7A–C), and the reproductive success rate was 31.25%. Among them, five nests were preyed upon and nest predation accounted for 45.45% of nest failures. Nests 008 and 013 were both visited by the Hainan Eld's deer during the hatching period (Supplementary Videos S1, S2; Figure 8); the female bird in nest 008 abandoned it (one chick hatched successfully), and the eggs were preyed upon after the female bird abandoned nest 013.



FIGURE 5

(A,B) Natural nests of red junglefowl (*Gallus gallus jabouillei*) found in the study sites (females brooding), (C,D) Natural nests of red junglefowl (*Gallus gallus jabouillei*) found in the study sites (female birds flew away).



FIGURE 6 Infrared camera monitoring of a natural nest of red junglefowl (Gallus gallus jabouillei).

The clutch size of red junglefowls was 4.50 ± 1.83 (n = 16). The egg parameters were showed as follows: weight: 24.26 ± 0.60 g, long diameter: 43.88 ± 1.18 mm, and short diameter: 33.45 ± 0.52 mm, n = 9. The nest parameters were showed as follows: long diameter: 15.51 ± 4.21 cm, short diameter: 13.00 ± 4.23 cm, and depth: 3.55 ± 0.80 cm, n = 8. The distance between the natural nest and the nearest water source was 56.18 ± 57.58 m (n = 11), and the closest distance between the natural nest and the road was 12.65 ± 27.40 m (n = 13). The number of nests found was the highest in April, with 11 nests, accounting for 68.75% of the total number of nests, followed by May, with two nests, accounting for 15.38%. Only one nest was found in July.

Artificial nest experiments and potential nest predators

Among the 20 nests in Datian, five nests were preyed upon, and the predation rate was 25%. In one of the nests, the experimental eggs were moved (Figure 9A). However, no predation occurred in the Bangxi. Vertebrates were the main cause of nest predation in the experiments, including two bird incidents (coucals) and two rodent incidents (Figure 9B). There were similarities in the types and numbers of animals that visited the artificial nests at the two study sites. Among them, Hainan Eld's deers (Figure 10A) and several small rodents (*Rattus* spp.; Figure 10B) were photographed at the two experimental sites. Wild boars (*Sus scrofa*; Figure 11A), greater coucals (*Centropus sinensis*; Figure 11B), and lesser coucals (*Centropus bengalensis*; Figure 11C) were only photographed in Datian, while red-bellied squirrels (*Callosciurus erythraeus*; Figure 11D) and domestic chicken (*Gallus gallus domesticus*; Figure 12) were only photographed in Bangxi.

Among 30 artificial nests set up in Datian in March 2021, two nests that were preyed on (Figure 9B), and experimental eggs in two nests were moved by unknown animals. However, they were not preyed upon. The predation event was not captured by the infrared camera, but animals that appeared near the artificial nests were recorded. These animals were the red junglefowl (Figure 13), black-throated laughingthrush (*Garrulax chinensis monachus*), wild boar, Hainan muntjac (*Muntiacus nigripes*; Figure 14), leopard (*Prionailurus bengalensis alleni*; Figure 15), and several small rodents.

Discussion

In the two breeding seasons of 2020 and 2021, we found a total of 16 natural nests and nesting success of the red junglefowl was 31.25%,



FIGURE 7

(A,B) Natural nests with successful reproduction; (C) Natural nests that failed to reproduce.



FIGURE 8

A Hainan Eld's deer visited the natural nest (the date was set incorrectly).



(A) Experimental eggs were moved by unknown animals; (B) Rodent predation of experimental eggs.

which was higher than the result observed by Yuan (2009) in the same area (18.2%). However, the rate of nest abandonment was as high as 68.75%, higher than the results of previous studies (55.6%; Yuan, 2009).

In a study of the Indian subspecies, it was found that after the first reproductive failure, red junglefowls would choose to reproduce a second time (Collias and Collias, 1967). Similarly, the reproduction record of the southern Yunnan subspecies also mentions that it may reproduce twice a year (Zheng et al., 1978). It is likely that the Hainan subspecies may reproduce multiple times to improve the reproductive success, which needs further confirmation in the wild. The clutch size in our study areas was similar to that of the Indian subspecies (Anwar et al., 2016) but was significantly lower than that of the southern Yunnan subspecies (Zheng et al., 1978). In southern Yunnan, female and male birds brood and hatch eggs together (Zheng et al., 1978). Yuan (2009) observed that in the field, both male and female birds brood nestlings, while we found that only female birds were responsible for brooding in the wild.

We found that the Hainan subspecies was breeding from March to July, and that the number of broods was highest in April. It is thus speculated that the breeding peak in the Hainan subspecies is April. This is consistent with the results of Yuan (2009), but there are differences between the Indian subspecies from different areas and the southern Yunnan subspecies. For example, in India, broiler flocks were found to breed in January–October, and the breeding peak period was March– May (Ali and Ripley, 1987; Anwar et al., 2016); in the Malay Peninsula region, the breeding time is from December to May of the following year, and the breeding peak is from January to February



FIGURE 10 (A) Hainan Eld's deer near the artificial nest; (B) Small rodent near the artificial nest.



FIGURE 11

(A) Wild boar near the artificial nest, (B) Greater coucal near the artificial nest, (C) Lesser coucal near the artificial nest, and (D) Red-bellied squirrel near the artificial nest.

(del Hoyo et al., 2001). In areas with sufficient food, red junglefowl can even breed year-round (Arshad and Zakaria, 1999). In southern Yunnan, the breeding time is from February to October (Zheng et al., 1978). Tropical birds have different life history traits (Stutchbury and Morton, 2023). Anyway, we only carried out the breeding monitoring of the red junglefowl for 2 years, which may be the reason that the breeding season in Hainan subspecies differs from other subspecies. There should be a long-term monitoring to the subspecies in the wild.

Studies have found that red junglefowl tend to choose areas with well-developed herbs and patches for nesting (Collias and Collias, 1967). However, some studies have suggested that deciduous trees and bamboo forests with scattered patches are the favorite nesting habitats of red junglefowls during the breeding season (Johnson, 1963). In this study, it was observed that female birds mostly nested on patrol roads or in open areas near the edge of forests with fewer deciduous leaves. This reflects the geographical differences in the selection of nesting sites among different subspecies. The edge effect hypothesis indicates that because the edge area of the habitat has more abundant vegetation resources and a more complex environment, the predation pressure is usually greater than that of the central area (Ewers and Didham, 2007). However, studies on the Reeves's pheasant (Syrmaticus reevesii) do not support this hypothesis, as this species tends to nest in marginal areas with more human interference (Luo et al., 2017). Our results are consistent with that study, as the female birds of the Hainan subspecies chose to nest on patrol roads or at the edge of the forest. It is possible that human activities in these areas are more frequent, and some predators are forced to enter the central area where there are fewer disturbances, thereby



FIGURE 12 Domestic chicken near the artificial nest.



FIGURE 13 Red junglefowl near the artificial nest.

reducing predation by natural enemies. Nest predation is the main factor in the failure of pheasant reproduction (Lu and Zheng, 2001; Sherry et al., 2015). In the predation events we observed, eggshells were either left in the nest or no trace of the predator was left after the eggs were preyed upon. Therefore, we speculated that rodents and reptiles may be the main nest predators. This is because rodents usually leave eggshells or debris behind after predation, and some reptiles leave no traces when preying on nests (Klug et al., 2010). In addition, in the study area, small carnivorous mammals, such as leopards, falcons, and raptors are the main natural enemies of the subspecies (Zheng et al., 1978; Evans



FIGURE 14 Hainan muntjac near the artificial nest.

et al., 1993), and snakes are also the main predators of red junglefowls (Anwar et al., 2016).

In our study, although artificial nests were set up in the same study area, their predation rate was lower than that of natural nests, and the types of predators were also different. This result is consistent with the results of a study of the reed parrotbill (*Paradoxornis heudei*) (Chen et al., 2020). This is different from the results of other studies. For example, snakes were found to be the main predators of natural nests, while mammals were found to be the main predators of artificial nests (Thompson and Burhans, 2003; Chen et al., 2020).

The use of infrared camera technology to monitor artificial nests is ideal for the determination of nest predator species (Anthony et al., 2006; Kross et al., 2013). In this study, the infrared cameras captured a number of wild animals, such as greater coucals, lesser coucals, and Hainan Eld's deers. Among them, the greater coucal was the main predator of the experimental eggs, and the feeding activity of Hainan Eld's deers caused female birds to abandon nests. Studies have shown that wild boars can change the terrain by overturn large areas of soil, thereby changing the vegetation structure and composition of their habitats (Singer et al., 1984; Lacki and Lancia, 1986), which is particularly harmful to ground-nesting birds (Barrios-Garcia and Ballari, 2012; Sanders et al., 2020). Therefore, the wild boar may be an opportunistic predator of nests.



A recent study has shown that gray squirrels (*Sciurus carolinensis*) are widely considered to be important predators of bird eggs and chicks (Broughton, 2020). We photographed red-bellied squirrels in the vicinity of artificial nests many times and speculate that the red-bellied squirrel is a potential nest predator. In addition, studies have found that bats are the main nest predators of tropical forest birds (Perrella et al., 2019). In our study, we did not find predation of eggs by bats. In follow-up work, we intend to carry out effective and continuous monitoring of breeding nests and clarify the antipredation strategies of red junglefowl.

In this study, the predation rates of artificial nests varied in Datian. The main reason is that the artificial nest experiments were done at the buffer zone in 2020, while at the core zone in 2021. The habitats in the two regions are significantly different, and so are the predation rates. The predation rate was 0% in Bangxi. There are two possible reasons. Firstly, our sample size is not large enough, secondly, there is a relative lack of potential predators for red junglefowl eggs. Although the survival rates of the artificial nests in the two study sites were higher than those of the natural nests. The possible reason is that the experiment was conducted in May 2020, while in March 2021, the birds had just started breeding, and most of them were in the hatching period in May. Most previous studies used the quadrat survey method (Johnson, 1963; Kalsi, 1992; Arshad and Zakaria, 2009; Yuan et al., 2009a,b) or radio tracking technology (Arshad and Zakaria, 2011) to investigate habitat selection and habitat utilization in red junglefowls. Satellite tracking technology is a tool to effectively track the small-scale movement of highly mobile and inaccessible species (Cagnacci et al., 2010; Coxen et al., 2017). The application of this technology to the study of ground-dwelling pheasants such as red junglefowl is very important for understanding how these birds use their habitat, the motivation for their movements, and the process of space utilization, to ultimately improve pheasant protection.

Conclusion

Red junglefowl are ground-nesting pheasants that are highly alert, which makes field research and tracking difficult (Arshad and Zakaria, 2011; Anwar et al., 2016). Human interference or direct observation of brooding parent birds may lead to abandonment of the nest and reproduction failure (Yuan, 2009). Therefore, there is limited information on the survival rate of red junglefowl nests. Protecting the habitat and reducing human disturbance will play a positive role in the growth of the red junglefowl population in our study areas. Datian and Bangxi are both protected areas with the main goal of protecting Hainan Eld's deer. Burning grassland vegetation, thinning, plowing, and manual removal of waste can alleviate the degradation of Hainan Eld's deer habitat quality (Fu et al., 2016, 2018). We suggest that the conservation area should take into account the impact on the reproduction of ground-dwelling pheasants when rebuilding or reconstructing the suitable habitat of Hainan Eld's deer. In addition, domestic chickens were photographed in the Bangxi Nature Reserve, indicating the possibility of hybridization between wild red junglefowl and domestic chickens. It is recommended that free-range domestic chickens be banned within protected areas to avoid the problem of genetic contamination of wild red junglefowls.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Ethics statement

Ethical review and approval was not required for the animal study because we have obtained the administrative licensing decision of Hainan Forestry Bureau on the study of Red Junglefowl [Hainan Forestry Bureau approval (2019) 083].

Author contributions

XR designed the study. XR, JL, BH, HW, GW, and TT carried out field experiments. XR and QL performed cartography and statistical analyses. XR wrote the draft manuscript. All authors contributed to the article and approved the submitted version.

Funding

This work was supported by the Joint Fund of the Natural Science Foundation of Hainan Province (no. 320RC506 to XR) and the National Natural Science Foundation of China (no. 31800320 to XR). XR was funded by the project supported by the Scientific Research start-up Fund of Hainan University [no. KYQD (ZR) 20057] and the Teaching Research of Hainan University (no. Hdsz20-9).

Acknowledgments

We are grateful to Datian and Bangxi Nature Reserves for their help and co-operation. We thank Biaoyi Tang for assistance with field work.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1127139/full#supplementary-material

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