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Avian Behavior, Ecology, and Evolution

The Amur Paradise Flycatcher (*Terpsiphone incei*) with distinct male dichromatism: implications for nest-site selection and nesting success

El Monarca del Paraíso Chino (*Terpsiphone incei*) con un distintivo dicromatismo en machos: implicancias para la selección del sitio de nidificación y el éxito de la nidificación

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ABSTRACT. Nest-site selection plays a crucial role in reproductive success and survival of birds, particularly for territorial birds. Therefore, it is important to understand how birds identify and select their nesting sites. The Amur Paradise Flycatcher (*Terpsiphone incei*) is a medium-sized species of the Monarchidae family with dichromatism in males. To investigate the differences in nest-site utilization strategies between different male morphs and identify the nest-site variables that influence the nest success of the species, we conducted a study on nest-site selection and nest success during the breeding seasons of 2020 to 2022 in Yangxian County, Shaanxi Province, China. During our study, we recorded a total of 98 nests and found that the Amur Paradise Flycatcher preferred nesting in forests with lower illumination, specifically on cedrela trees, and exclusively near residential areas. Interestingly, we did not find any significant difference both in nest-site selection and nesting success between the two male morphs. The overall nesting success was 51.06% (n = 94), with nest predation being the primary cause of nest failure. Our principal component analysis identified several significant factors affecting nest-site selection, including nest tree factors (14.168%), interference factors (13.145%), nest concealment factors (10.87%), terrain factors (10.262%), altitude factors (10.046%), and stability factors (8.438%). Furthermore, the results of binary logistic regression analysis indicated that successful breeding nests were located closer to the forest edge, had a sunnier aspect, and a smaller slope compared to failed nests. Similarly, the multiple linear regression analysis showed that slope, aspect, and nest tree species had significant effects on breeding success. Our findings suggest that the Amur Paradise Flycatcher seeks a balance between nest concealment and a view of the surroundings. The lack of a significant difference in reproductive outcomes between the two male morphs could potentially be attributed to the greater experience of white morph individuals, which may help mitigate the higher risk with their more attractive plumage for predators. Understanding the factors affecting nest-site selection and nest success is crucial for conservation efforts aimed at protecting this fascinating species and ensuring its long-term survival.

RESUMEN. La selección del sitio de nidificación cumple un rol crucial en el éxito reproductivo y la supervivencia de las aves, particularmente para las aves territoriales. Entonces, es importante entender cómo las aves identifican y seleccionan sus sitios de nidificación. El Monarca del Paraíso Chino (*Terpsiphone incei*) es una especie de tamaño mediano de la familia Monarchidae con dicromatismo en machos. Para investigar las diferencias en las estrategias de uso de los sitios de nidificación entre diferentes morfotipos de machos e identificar las variables del sitio de nidificación que influencian el éxito de la nidificación, realizamos un estudio sobre selección del sitio de nidificación y éxito de la nidificación durante las temporadas reproductivas de 2020 a 2022 en el Condado de Yangxian, Provincia de Shaanxi, China. Durante nuestro estudio, encontramos un total de 98 nidos y descubrimos que el Monarca del Paraíso Chino prefirió nidificar en bosques con menor iluminación, específicamente en árboles de caoba china, y exclusivamente cerca de áreas residenciales. Sorprendentemente, no encontramos ninguna diferencia significativa en la selección del sitio de nidificación y el éxito de la nidificación entre los dos morfotipos de machos. El éxito de nidificación general fue 51,06% (n = 94), siendo la depredación de nidos la causa principal de falla de la nidificación. Nuestro análisis de componentes principales identificó varios factores significativos que afectaron la selección del sitio de nidificación, incluyendo factores del árbol del nido (14,168%), factores de interferencia (13,145%), factores de ocultamiento del nido (10,87%), factores del terreno (10.262%), factores de altitud (10,046%) y factores de estabilidad (8,438%). Además, los resultados del análisis de regresión logística binaria indicaron que los nidos exitosos estaban ubicados más cerca del borde del bosque, tenían mayor exposición al sol y estaban sobre pendientes más pequeñas comparados con los nidos fallidos. De manera similar, el análisis de regresión lineal múltiple mostró que la pendiente, exposición y especie de árbol del nido tuvieron efectos significativos en el éxito reproductivo. Nuestros resultados sugieren que el Monarca del Paraíso Chino busca un equilibrio entre el ocultamiento del nido y la visibilidad de los alrededores. La ausencia de una diferencia significativa en el éxito reproductivo entre los dos morfotipos de machos podría atribuirse potencialmente a la mayor experiencia de los individuos del morfotipo blanco, lo cual podría ayudarles a mitigar el mayor riesgo con su plumaje más atractivo para los depredadores. Comprender los factores que afectan la selección del sitio de nidificación y el éxito de nidificación es fundamental para los esfuerzos de conservación que se focalizan en proteger a esta fascinante especie y asegurar su supervivencia a largo plazo.

Key Words: *Amur Paradise Flycatcher; dichromatism; nest-site selection; nest success*

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INTRODUCTION

The process of habitat selection is crucial for birds because it directly impacts their survival, fitness, and population dynamics (Jourdan et al. 2021). Nest-site selection, in particular, plays a vital role in determining the reproductive success and survival of territorial birds (Jones 2001, Mikula et al. 2014, Holopainen et al. 2015, Jourdan et al. 2021). Favorable nesting sites provide optimal microclimatic conditions for offspring development, which influences the physiological adaptations, survival rates, and growth of birds. However, numerous factors, such as intra- and interspecific competition, predation, parasitism, vegetation structure, and anthropogenic activities, can influence nest habitat selection (Amat and Masero 2004, Davis 2005, Hanane 2015, Pestana et al. 2020, Rebollo et al. 2020). Extreme natural events like flooding, droughts, fires, windstorms, and heavy rains also impact patterns of nest-site selection, which further affects breeding success and population dynamics (Hanane 2015). Therefore, understanding the features birds select for when choosing nesting sites can provide valuable insights into the behavioral and ecological mechanisms underlying nest-site selection. It can also offer guidance on the appropriate scale for implementing conservation planning for breeding birds of concern or those occupying endangered habitats (Zhu et al. 2012, Zhang et al. 2017, Rebollo et al. 2020). Numerous studies have been conducted to investigate the characteristics of nest sites and the selection process of different bird species because these features often play a determining role in bird breeding success (Jiao et al. 2014, Jiang et al. 2017, Zhang et al. 2017, Han et al. 2019, Loucif et al. 2021).

For decades, the Amur Paradise Flycatcher (*Terpsiphone incei*), a species of Monarchinae in the Passeriformes, has attracted the attention of ornithologists due to its elaborate plumage and interesting breeding behavior (Mizuta and Yamagishi 1998, Ngoenjun and Sitasuwan 2010, Janra et al. 2019, Hou et al. 2020). Male birds of this species exhibit two distinct color morphs: rufous and white. They possess eye-catching broad blue eye rings and prominently elongated central pairs of tail feathers. Conversely, female birds have a single morph, characterized by a dull rufous-brown coloration. They have gray eye rings and shorter tails compared to males. Breeding pairs of the species are monogamous, with both males and females actively participating in nesting, hatching, brooding, and feeding of the young (Ngoenjun and Sitasuwan 2009). Although there has been considerable research on the reproductive biology of the species (Mizuta and Yamagishi 1998, Ma et al. 2005, Ngoenjun and Sitasuwan 2009, Das and Adhikari 2019, Xi et al. 2020), there is relatively little knowledge on its nest-site selection, especially on nest-site variables and their effects on nest survival for the species and even for congeneric species. For example, Currie et al. (2003) conducted a comprehensive study in the inner Islands of Seychelles to assess the significance of native broadleaved woodland and wetland areas for the Seychelles Black Paradise Flycatcher (*T. corvine*). The investigation involved quantifying habitat use, territory composition, the impact of water on invertebrate abundance, as well as foraging and breeding success. Habitat differences in food abundance may have caused within-population variation in the timing of breeding in the Madagascar Paradise Flycatcher (*T. mutata*; Mizuta 2006). The nest sites of the Black Paradise Flycatcher (*T. atrocaudata*) tended to be located near roads or paths and near streams or wetlands (Suzuki et al. 2010).

It is worth noting that male dichromatism is observed in several species within the *Terpsiphone* genus. However, the mechanisms and evolutionary significance of these traits are still subject to debate. One perspective suggests that the variation in male plumage is partially attributed to age, with rufous males representing young adults and white males representing fully mature individuals. This pattern has been observed in species such as the Asian Paradise Flycatcher (*T. paradisi*; Mizuta and Yamagishi 1998) and the Madagascar Paradise Flycatcher (Mizuta 2002). On the other hand, the male paradise flycatchers seem to follow two alternative developmental pathways that lead to the exclusive acquisition of either white or rufous adult plumage (Mulder et al. 2002). This suggests that the rufous morph does not simply serve as a precursor to white plumage but represents a stable terminal type. Furthermore, it has been suggested white males have advantages in attracting mates and possessing more survival experience compared to rufous males (Mizuta and Yamagishi 1998, Mizuta 2000). The exact significance of this variation remains unclear, but an important question arises regarding whether the morphological differences between males are associated with behavioral differences and ultimately represent alternative mating strategies (Mulder et al. 2002).

In this study, we conducted an intensive investigation into the nest-site selection and nesting success of the Amur Paradise Flycatcher, with a particular focus on the differences between the two adult male plumage morphs. Our objectives were threefold: (1) to provide a descriptive analysis of the nest and nest-site microhabitats; (2) to evaluate the differences in nest-site use strategies between different morphs of adult males; and (3) to identify the nest-site variables that have an impact on the nesting success of the species.

METHODS

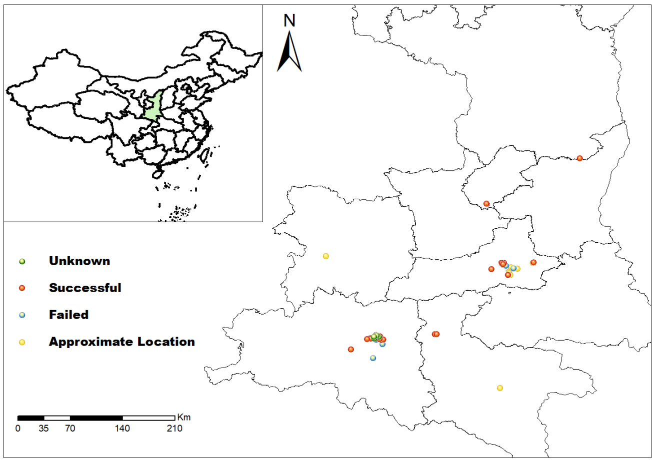
Study area

Our study was carried out in Shaanxi Province, China, which included Huanglong County situated in the south of the Loess Plateau in the north, Zhenping County in the Daba Mountain region in the south, Qianyang County in Baoji City in the west, and Hancheng County in Weinan City in the east (31°53′3″ N–35°48′54″ N, 107°8′19″ E–110°28′56″ E; Fig.1). The study area, characterized by distinct landforms and complex types, is divided into different geographical units (Nie 1981, Wang 1990, Zhang et al. 2021). The various landforms and climate types provide abundant material and energy conditions for vegetation and animals. The Amur Paradise Flycatcher is widely distributed in all geographical units south of the Loess Plateau of Shaanxi Province, with a particularly high abundance in Changan district and Lantian County of Xi’an City and, in Yangxian County of Hanzhong City (Fig. 1).

Nest monitoring and nest-site characteristics

The Amur Paradise Flycatcher is a migratory species in Shaanxi Province (Zheng 2011), typically arriving in early May and departing in mid-August, resulting in a residence period of

Fig. 1. The study area and distribution regions of the Amur Paradise Flycatcher (*Terpsiphone incei*) in Shaanxi Province. The upper left portion of the figure shows the location of Shaanxi Province in China. The legend provides information about the fate of nests, with "Unknown" "Successful," and "Failed" representing different outcomes. "Approximate Location" denotes the location where the nest was observed.



approximately three months. For the sake of convenience, we will refer to breeding pairs consisting of rufous males and females as "rufous morph," while breeding pairs of white males and females will be referred to as "white morph." Nest-site surveys were conducted during three breeding seasons (from May to July in 2020, 2021, and 2022). To identify potential habitats and search routes, we relied on the experience of local birdwatching enthusiasts who had observed the species, based on the preliminary features of nest sites recorded on the China Bird Report website. Playback calls of the Amur Paradise Flycatcher were used to elicit reactions and responses from the birds, allowing for reliable surveys in large areas (Braun 2005, Jiao et al. 2014). Nest locations and actual birds were identified based on the repeat and loud call or incubation at the nests, and a GPS device was used for georeferencing. Once located, nests were visited every two days to examine nest contents and determine their fates. To minimize human disturbance, measurements of nest dimensions and characteristics were performed only after the chicks had fledged.

During the breeding season, we collected various measurements and data related to the nests and their surroundings. The nest itself was measured for its inside diameter (NID), outside diameter (NOD), height (NH), and depth (ND) using a Vernier caliper and straightedge. The ground diameter (GD) around the base of the tree trunk, the breast diameter (BD) of the nest tree trunk measured 1.3 m from the ground, and the average perimeter of stems supporting the nest (AP) were measured using a tape measure. The tree height (TH), nest-site height (NSH), distance to the nearest road (DR), distance to the forest edge (DF), distance to perennial water sources (DW), and distance to the nearest settlement (DS) were measured using an infrared rangefinder, and GPS measurements were collected when distances were too far to measure in the field.

Canopy density (CD) was calculated as the percentage of sky area blocked by plants within 1 m² directly above the nest. For the convenience of calculation, different nest tree species (NTS) are replaced with different serial numbers, such as 1- holly (*Ilex chinensis*) and 2- paper mulberry (*Broussonetia papyrifera*), whether the nest was located on the main or a lateral branch (using 1 to represent the main branch and 2 to represent a lateral branch, ML), and the number of nest-supporting branches (NSB) were recorded.

We also recorded the longitude, latitude, altitude, slope, and aspect of the nest sites. According to the direction of sunlight at the location of the nest and the orientation of the hillside, the aspect was divided into four grades of 0 (flat slope, slope < 5°), 1 (sunny slope), 2 (shade slope), and 3 (half-sunny and half-shady slope). Furthermore, we graded the visibility of nests (VN) based on the ease with which observers could identify local nests at a distance of three meters, using a scale of 1 (easy detection), 2 (medium case), and 3 (difficult detection).

In our previous observations, we have noticed a tendency among Amur Paradise Flycatchers to choose nest sites in darker forests. Building upon this observation, our study incorporated the nest-site illumination, as reported by some scholars (Podkowa and Surmacki 2017). We measured the illumination upon the nest twice and averaged the results. To ensure consistency, measurements were taken under constant weather conditions between 10:00 AM and 04:00 PM because changes in the sun's position could affect the brightness level inside the nest. To further account for this issue, we measured the illumination immediately outside the forest and calculated the relative illumination (in-nest illumination/out-of-forest illumination, RI, %) to represent the relative light intensity at the nest site. We used an ST-9813 lux meter with an accuracy of 0.1 lux to take all measurements of illumination.

Data analysis

To test for normality, we used the Kolmogorov-Smirnov *Z*-test for all variables. For normally distributed variables, we used an independent-samples *t*-test to test for differences in nest-site variables between different male morphs. For non-normally distributed variables, we used the Mann-Whitney *U* test to test for differences, and variables with significant differences ($P < 0.05$) were retained. We used Spearman's correlation coefficient for ranked data. For paired variables with strong correlations ($|rs| \geq 0.8$), we removed those with less ecological significance. Principal component analysis (PCA) was then performed on the remaining selected variables to identify which factors were most important in nest-site selection. Principal components with eigenvalues greater than or equal to 1 were selected.

To compare the nest success of different morphs, we used the χ^2 goodness-of-fit test. A nest was considered successful if at least one nestling fledged. To determine the most important nest-site characteristics affecting the nesting success or failure, we used binary logistic regression. Breeding success was calculated based on clutch size and the number of fledging birds. To explore which factors influence the reproductive success of the species, we used multiple linear regression analysis for all successful nests. All the nest site data from the rufous and white male morphs were used in the study of the above mode and all statistical analyses were performed using SPSS 26.0 software for Windows (IBM Inc., USA). Results were presented as mean ± SE, and all significance values were based on two-tailed tests with a significance of 0.05. We used Graph Pad Prism 9.0 software to create all relevant graphs, and Adobe Photoshop CS6 was used for image processing.

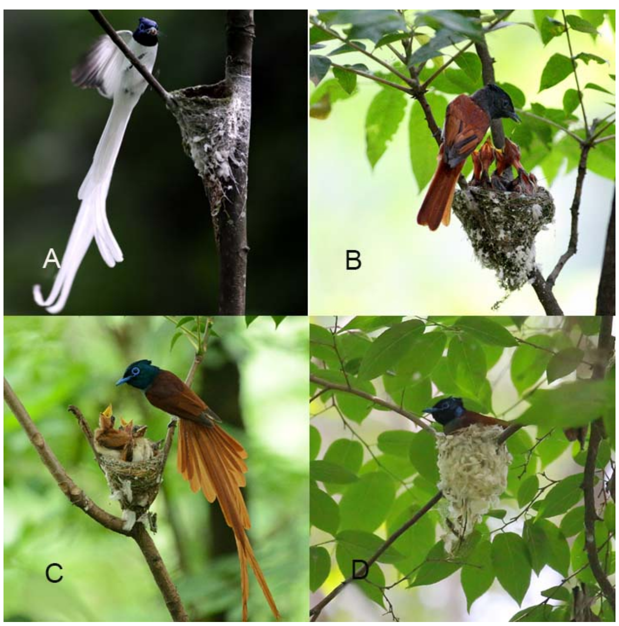
RESULTS

Nest parameters

The nest structure of the Amur Paradise Flycatcher was very delicate, usually supported by two or three branches. The inner wall was composed of fine grass roots, leaves, stems, brown fibers, and other materials, while the outer wall was often woven with moss, cobwebs, feathers, fluffy catkins from blooming willows and poplars, and other materials. The birds used abundant cobwebs to secure the loose nest walls and hold the nest tightly to the branches (Fig. 2A). The Amur Paradise Flycatcher preferred to use locally sourced materials for nest building. Palm trees (*Trachycarpus fortunei*) were the most commonly used nesting material, and the brown fiber and silk from these trees were permeable, ensuring that the nest would not store water, which could affect normal reproduction. Additionally, the materials appeared to have helped camouflage the nest (Fig. 2). Moss, feathers, and a few plant catkins were more frequently used in the outer wall of nests (Fig. 2A, B, C), while very few nests were exclusively made of poplar catkins (Fig. 2D).

The nests of the Amur Paradise Flycatcher were open, deep, cup-shaped, and cone-like in appearance. The average height, depth, outer diameter, and inter diameter of the nests are shown in Table 1, respectively. The average height of nest sites above the ground was 5.14 ± 0.35 m (n = 98; Table 2). We found significant differences in nest height between different color morphs (Mann-Whitney U test, Z = 2.101, P = 0.032).

Fig. 2. Different types of nests of the Amur Paradise Flycatcher (*Terpsiphone incei*). (A) a white male weaving its nest with cobwebs; (B) (C) the outer wall of a nest mainly made of moss, feathers, and plant catkins; (D) the outer wall of a nest exclusively made of poplar catkins.



Nest-site selection

Nest tree species

A total of 98 nest trees were recorded, comprising 24 species (Fig. 3). The most frequently used tree species was cedrela (*Toona sinensis*; n = 32), followed by poplar (*Populus* × *canadensis*; n = 20), paper mulberry (n = 12), holly (n = 5), and others. Cedrela was the most common nest tree species, accounting for 32.65% of all nests, followed by poplar at 20.41%, and paper mulberry at 12.24%. Among the 24 species, 21 were used by individuals of the rufous morph, and the most commonly used trees were cedrela and poplar. For individuals of the white morph, nine tree species were used, with cedrela being the most commonly used (Fig. 3).

Table 1. Nest parameters of different color morphs of the Amur Paradise Flycatcher (*Terpsiphone incei*).

Variables†	Combined (n = 17)	Rufous (n = 13)	White (n = 4)	z value	Sig.
ND/mm	39.19 ± 1.39	39.75 ± 1.50	37.38 ± 3.59	-0.570	0.624
NH/mm	87.82 ± 3.62	83.09 ± 3.00	103.20 ± 8.73	2.101	0.032*
NOD/mm	78.79 ± 1.71	79.23 ± 2.11	77.36 ± 2.78	-0.284	0.785
NID/mm	58.62 ± 1.33	59.07 ± 1.67	57.17 ± 1.81	-0.681	0.549

†ND = nest depth, NH = nest height, NOD = the nest outside, and NID = the nest inside diameter.
*P < 0.05; **P < 0.01.

Table 2. Comparison of nest-site variables between the different color morphs of the Amur Paradise Flycatcher (*Terpsiphone incei*). Note: NTS = nest tree species, TH = tree height, BD = breast diameter, GD = ground diameter, NSH = nest-site height, CD = canopy density, ML = nest on the main or lateral branch, NSB = the number of supporting branches, AP = the average perimeter of supporting branches, VN = visibility of nests, DR = distance to the nearest road, DF = distance to the forest edge, DW = distance to the nearest water source, DS = distance to the nearest settlement.

Variables	Combined (n = 98)	Rufous (n = 68)	White (n = 30)	z value	Sig.
Altitude (m)	519.52 ± 9.76	524.96 ± 12.97	507.20 ± 12.34	0.000	1.000
Slope (°)	19.29 ± 2.24	18.07 ± 2.47	22.03 ± 4.75	0.004	1.000
Aspect	1.62 ± 0.11	1.56 ± 0.13	1.77 ± 0.20	0.888	0.638
NTS	6.10 ± 0.57	6.63 ± 0.72	4.90 ± 0.85	-1.183	0.620
TH (m)	9.04 ± 0.69	9.63 ± 0.86	7.72 ± 1.13	-0.979	0.620
BD (cm)	9.86 ± 1.01	10.59 ± 1.28	8.20 ± 1.57	-0.786	0.668
GD (cm)	13.19 ± 1.40	14.47 ± 1.81	10.31 ± 1.93	-1.021	0.620
NSH (m)	5.14 ± 0.35	5.44 ± 0.45	4.46 ± 0.55	-1.137	0.620
CD (%)	68.51 ± 1.53	68.74 ± 1.80	68.00 ± 2.96	-0.004	1.000
ML	1.48 ± 0.05	1.53 ± 0.06	1.37 ± 0.09	-1.479	0.620
NSB	2.19 ± 0.04	2.22 ± 0.05	2.13 ± 0.06	-1.002	0.620
AP (cm)	3.45 ± 0.14	3.39 ± 0.16	3.58 ± 0.26	0.698	0.687
VN	2.48 ± 0.06	2.50 ± 0.07	2.43 ± 0.12	-0.376	0.925
DR (m)	16.5 ± 2.21	18.46 ± 2.93	12.04 ± 2.71	-1.137	0.620
DF (m)	7.42 ± 0.99	7.89 ± 1.17	6.59 ± 1.94	-1.323	0.620
DW (m)	101.29 ± 15.26	77.36 ± 15.27	155.54 ± 34.29	1.716	0.620
DS (m)	72.20 ± 18.00	43.86 ± 8.18	136.44 ± 54.63	-0.089	1.000

(All P-values are corrected by Benjamini and Hochberg).

Fig. 3. Species and number of nest trees used by the Amur Paradise Flycatcher (*Terpsiphone incei*).

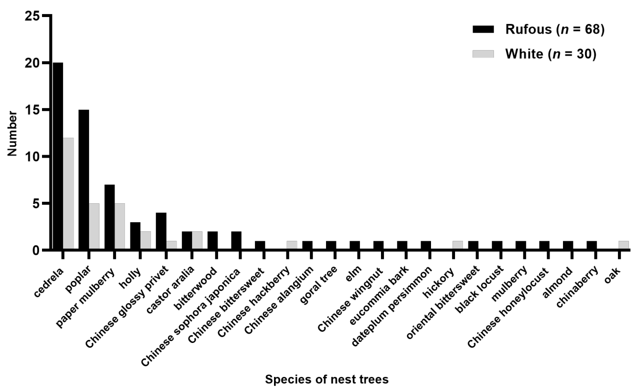
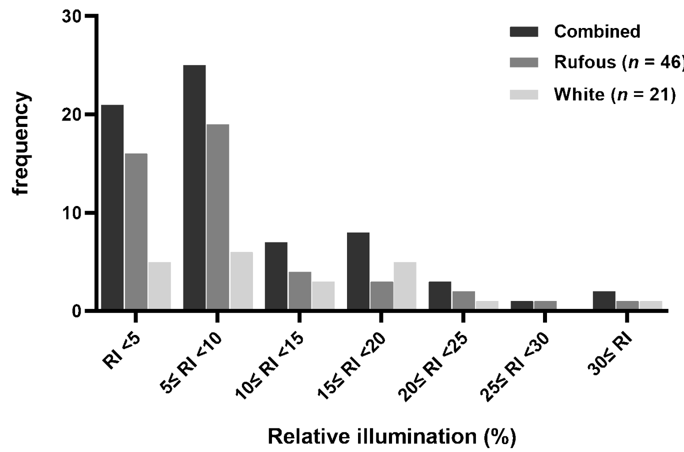


Fig. 4. Relative illumination of nest sites under the canopy in forests of the Amur Paradise Flycatcher (*Terpsiphone incei*).



Nest-site relative illumination

The Amur Paradise Flycatcher tends to select nest sites under forests with low light intensity. To investigate this, we measured the illumination of 67 nest sites in Yangxian County. The results (Fig. 4) showed that an RI of less than 10% accounted for approximately 68.66% of the values. The maximum RI was 35.81%, and nests with an RI greater than 25% failed to reproduce ($n = 3$). However, we found no significant difference in RI between the nests of different color morphs (Mann-Whitney *U* test, $z = 1.546$, $P = 0.122$). Similarly, there are no significant differences in RI between successful and failed nests (Mann-Whitney *U* test, $z = -1.169$, $P = 0.243$).

Nest-site characteristics of different morphs

Having identified the important variables of nest-site selection in the Amur Paradise Flycatcher, we compared the nest-site selection variables of 98 nests used. However, the results did not reveal any significant differences between the nest-site selection variables for the different color morphs (Table 2).

Principal component analysis of nest-site characteristics

Principal component analysis (PCA) was performed on the nest-site variables, which yielded six principal components explaining 66.928% of the total variation in the analyzed sample (Table 3). Principal component 1 (PC1) accounted for 14.168% of the total variance, with the strongest correlations observed for BD (0.898), NSH (0.899), and AP (0.582), all of which were positively correlated with nest-site selection. These three factors reflected the influence of nest trees on nest-site selection and were considered nest tree factors. Principal component 2 (PC2) accounted for an additional 13.145% of the total variance in the data. It had the highest correlation index of DR (0.767) and DF (0.771), indicating that these factors significantly influenced the nest-site selection of this species and were regarded as interference factors. Principal component 3 (PC3) accounted for 10.87% of the variance, with CD (0.697) and VN (0.884) selected as variables that represented the requirement of surrounding concealment and were thus considered concealment factors. Principal component 4 (PC4) accounted for 10.262% of the variance, with slope (0.763) and aspect (0.784) being the most dominant variables and these were regarded as terrain factors. Principal component 5 (PC5) accounted for 10.046% of the variance, with altitude (0.777) being the selected variable and it was treated as an altitude factor. Finally, PC6 accounted for 8.438% of the variance, with ML (0.804) and NSB (0.537) being mainly related to nest stability and thus considered as stability factors (Table 3 and Table 4).

Nest success

A total of 98 nests were discovered, and the outcomes of 94 of these nests were determined ($n = 30$ in 2020, $n = 33$ in 2021, and $n = 31$ in 2022). Of these nests, 48 (51%) were successful, while 46 (49%) failed. Nest success in 2020 was higher than that in 2021 and 2022. With the exception of the 2022 data, nest success for the white morph was lower than that for the rufous morph (Table 5), but there was no significant difference in nest success between the two morphs (χ^2 goodness-of-fit test, $\chi^2 = 0.341$, $P = 0.559$).

Table 3. Descriptions of nest-site characteristics for the Amur Paradise Flycatcher (*Terpsiphone incei*) with principal component analysis (PCA). Note: BD = breast diameter, NSH = nest-site height, AP = the average perimeter of supporting branches, DR = distance to the nearest road, DF = distance to the forest edge, CD = canopy density, VN = visibility of nests, ML = nest on the main or lateral branch, NSB = the number of supporting branches.

	Parameters	Eigenvalues	Nomination	Ratio of contribution	Accumulative ratio of contribution
PC1	BD (cm) NSH (m) AP (cm)	2.125	Nest tree factor	14.168	14.168
PC2	DR (m) DF (m)	1.972	Interference factor	13.145	27.313
PC3	CD VN	1.63	Nest concealment factor	10.87	38.183
PC4	Slope (°) Aspect	1.539	Terrain factor	10.262	48.444
PC5	Altitude (m)	1.507	Altitude factor	10.046	58.49
PC6	ML NSB	1.266	Stability factor	8.438	66.928

Table 4. The rotated loading matrix for the nest-site characteristics of the Amur Paradise Flycatcher (*Terpsiphone incei*). Note: NTS = nest tree species, BD = breast diameter, NSH = nest-site height, CD = canopy density, ML = nest on the main or lateral branch, NSB = the number of supporting branches, AP = the average perimeter of supporting branches, VN = visibility of nests, DW = distance to the nearest water source, DR = distance to the nearest road, DF = distance to the forest edge, DS = distance to the nearest settlement.

Nest-site variables	Components					
	1	2	3	4	5	6
Altitude (m)	-0.041	-0.084	0.027	-0.011	0.777	0.056
Slope (°)	-0.155	-0.175	-0.115	0.763	-0.106	0.134
Aspect	-0.03	-0.07	0.223	0.784	0.111	-0.274
NTS	-0.158	-0.077	-0.061	-0.002	0.701	-0.253
BD (cm)	0.898	0.067	-0.084	-0.054	-0.048	-0.037
NSH (m)	0.899	0.173	-0.03	-0.037	-0.047	0.027
CD (%)	-0.212	-0.271	0.697	0.069	-0.107	-0.141
ML	-0.152	-0.13	-0.055	-0.187	-0.09	0.804
NSB	0.092	0.315	0.185	0.335	-0.004	0.537
AP (cm)	0.582	-0.374	0.216	-0.116	-0.157	-0.153
VN	0.147	0.083	0.884	0.047	0.018	0.116
DW (m)	-0.1	-0.474	0.146	-0.288	-0.404	-0.157
DR (m)	-0.033	0.767	0.075	-0.184	-0.199	-0.146
DF (m)	0.11	0.771	-0.17	-0.169	-0.072	0.103
DS (m)	-0.011	0.382	-0.387	0.163	-0.362	-0.238

Table 5. Nest success of the Amur Paradise Flycatcher (*Terpsiphone incei*) from 2020 to 2022.

Year	Type	n	Successful	Failed	Nest success (%)
	All	30	19	11	63.33
2020	Rufous	20	14	6	70.00
	White	10	5	5	50.00
	All	33	12	21	36.36
2021	Rufous	21	8	13	38.10
	White	12	4	8	33.33
	All	31	17	14	54.84
2022	Rufous	23	12	11	52.17
	White	8	5	3	62.50
	All	94	48	46	51.06
2020-2022	Rufous	64	34	30	53.13
	White	30	14	16	46.67

The factors that affected nest success included nest predation (n = 12, 26.09%), human interference (n = 11, 23.91%), inclement weather (n = 3, 6.52%), and reproduction failure (n = 4, 8.70%). However, the reason for the lack of success in 34.78% of nests (n = 16) could not be determined.

Influence of nest-site characteristics on nest survival

Nest-site factors affecting reproductive success or failure

According to the binary logistic regression model, slope, aspect, and the distance of nest to forest edge were the most important variables affecting nest-site selection of breeding successful or unsuccessful nests (Table 6). The Hosmer and Lemeshow test showed the model had a good fit to the data (χ^2 = 11.198, df = 8, P = 0.191). The percentage of correctly predicted classification for nest sites was 76.6% (with the best cut-off value being 0.5). Furthermore, the slope of the reproductively successful nests was significantly smaller than that of the failed nests (12.81 ± 2.55° vs 25.65 ± 3.61°, P = 0.043). The distance between the successful nest and the forest edge was also lower than that of the failed nest (6.08 ± 0.91 m vs 9.07 ± 1.87 m, P = 0.023). Finally, it was clear that the probability of reproductive success is higher on sunny slopes (1.38 ± 0.15 vs 1.91 ± 0.15, P = 0.036).

Table 6. The parameters in the binary logistic regression model of nest-site selection by the Amur Paradise Flycatcher (*Terpsiphone incei*). Note: DF = distance to the forest edge.

Variables	B	SE	Wald	df	Sig.	Exp (B)
Slope (°)	0.029	0.014	4.109	1	0.043	1.029
Aspect	0.691	0.329	4.414	1	0.036	1.996
DF (m)	0.134	0.059	5.14	1	0.023	1.144
Constant	1.257	3.213	0.153	1	0.696	3.515

Effects of nest-site characteristics on reproductive success

Multiple linear regression analysis was conducted on the characteristics of each nest site and reproductive success of 48 successful nests. It was found that the slope, aspect, and nest tree species reached a highly significant level (Table 7). Among these variables, slope and aspect showed significant levels, with slope being significantly negatively correlated with reproductive success. The nesting tree species also reached a highly significant level, indicating that the Amur Paradise Flycatcher is highly selective in choosing nesting tree species. The adjusted R^2 value in the study showed that the model has some explanatory power (R^2 (adj.) = 0.345, F_{47} = 2.628, P < 0.05).

DISCUSSION

Nest-site selection

Nest-site selection is a complex decision-making process for birds, including the Amur Paradise Flycatcher. Over time, this process has evolved under selection pressure, involving various factors of varying importance. The ultimate goal is to enhance reproductive success while minimizing risks, which requires a trade-off between visibility to detect potential threats and nest concealment. The result of PCA shows that several factors significantly influence the nest-site selection of the Amur Paradise Flycatcher. These include nest tree, interference, nest concealment, terrain, and nest stability factors. Among them, nest tree characteristics exert the greatest impact. It is evident this species prefers to nest at a specific height and on smaller branches, which can accommodate their tiny and delicate nests. Nesting on such branches allows them to raise their young and defend against predators effectively. They typically choose a slender twig that slants downward and has one or more little branches springing upward, providing suitable support for their open, cup-shaped nests (Moreau 1949). Interference factors and nest concealment are also critical in the nest-site selection process. Interference factors include variables such as the distance between the road and the forest edge, indicating the need for a visual field and the ability to adapt to human interference. The Paradise Flycatchers show a strong preference for building their nests on or close to the forest edge

Table 7. Effects of the nest-site parameters on reproductive success among successful nests of the Amur Paradise Flycatcher (*Terpsiphone incei*) based on multiple linear regression. Note: NTS = nest tree species, BD = breast diameter, NSH = nest-site height, CD = canopy density, ML = nest on the main or lateral branch, NSB = the number of supporting branches, AP = the average perimeter of supporting branches, VN = visibility of nests, DW = distance to the nearest water source, DR = distance to the nearest road, DF = distance to the forest edge, DS = distance to the nearest settlement.

Variables	B	SE	β	t value	Sig.
Altitude (m)	0	0	0.173	1.03	0.311
Slope (°)	-0.003	0.001	-0.331	-2.3	0.028*
Aspect	0.064	0.03	0.404	2.137	0.041*
NTS	-0.013	0.005	-0.477	-2.961	0.006**
BD (cm)	-0.001	0.003	-0.058	-0.282	0.780
NSH (m)	-0.006	0.01	-0.123	-0.596	0.555
CD (%)	0.003	0.002	0.265	1.348	0.187
ML	0.044	0.053	0.132	0.821	0.418
NSB	-0.068	0.056	-0.163	-1.205	0.237
AP (cm)	-0.02	0.021	-0.139	-0.962	0.343
VN	-0.008	0.046	-0.034	-0.182	0.857
DW (m)	0	0	0.109	0.728	0.472
DR (m)	0.002	0.001	0.241	1.582	0.124
DF (m)	-0.008	0.005	-0.301	-1.555	0.130
DS (m)	0	0	0.18	1.17 ns	0.251

0 indicates that < 0.001.
$*P < 0.05$; $**P < 0.01$.

and over water (Moreau 1949). Higher levels of concealment reduce the likelihood of nest detection by predators but also make it more challenging for parents to detect predators in advance and avoid them (Götmark et al. 1995). The Amur Paradise Flycatcher tends to select nest sites that offer a wide view while providing some degree of shelter, supporting the hypothesis of a trade-off between nest concealment and a view of the surroundings (Götmark et al. 1995). Terrain factors also play a role in nest-site selection. Our findings suggest that nests located on sunny slopes with smaller slopes, closer to the forest edge have a higher likelihood of successful reproduction. Such positioning strategy can expand the visual range of the Amur Paradise Flycatcher, enabling adults to effectively prepare for a swift escape when needed. Moreover, it allows the chicks to remain silent and delay any movements, promoting their safety and minimizing the risk of attracting predators. In addition, the species shows a preference for nesting in tree joints with two or three thin branches. The most common nest tree species observed were cedrela, accounting for 32.65% of all nests, followed by poplar at 20.41% and paper mulberry at 12.24%. Adequate shelter with low light conditions also helps protect them from exposure to elements. Our observations indicate that the species tends to nest in close proximity to their previous year's nesting site. These observations suggest a certain level of site fidelity and the importance of familiarity with the surroundings for successful nesting.

It was observed that the Amur Paradise Flycatcher tends to build nests near human settlements. A majority of the nests (75 out of 98) were built less than 50 meters away from the nearest settlement, with some nests located as close as 0.4 meters. A few nests (n = 10) were situated between 50 and 100 meters away from the nearest settlement. The remaining nests were more than 100 meters away from the nearest settlement but were surrounded by vegetable or crop fields. This behavior suggests that although breeding near human settlements carries the risk of nest discovery and destruction, the threat from certain predators, including snakes, the Tiger Shrike (*Lanius tigrinus*), the Red-billed Blue Magpie (*Urocissa erythrorhyncha*), and other birds, may be greatly reduced (Ma et al. 2005). Additionally, it was also observed that the Amur Paradise Flycatcher exclusively selected nest sites in forests with lower light intensity, which spatially isolated them from predators such as the Red-billed Blue Magpie, known for nesting in higher positions (Yu et al. 2014). This observation leads to a speculation that the Amur Paradise Flycatcher's disproportionately large eyes and their potential adaptation for dark vision may be evolutionary responses to dark environments.

The dichromatism observed in male Amur Paradise Flycatchers, with white and rufous morphs, is believed to be influenced by genetics or age differences. However, the exact adaptive significance of this dichromatism remains unclear (Mulder et al. 2002, Mizuta 2003, 2006). In the present study, we found no significant difference in nest-site selection between males of different color morphs, except for nest height. Although there was no significant difference in nest success between the rufous morph (53.13%) and the white morph (46.67%), it is important to note that the smaller sample size of the white morph may have influenced these results. Previous studies suggested that the frequency of the white morph is only half or even 25% of that of the rufous morph (Ma et al. 2005), and our research supports this notion. Based on these findings, we hypothesize that the rufous morph may have an advantage in avoiding predators in dark environments, which could explain the adaptive significance of this color morph. However, further research is needed to fully understand the ecological and evolutionary implications of the plumage dichromatism in the Amur Paradise Flycatcher.

Nest success

Our study revealed a relatively low total nest success rate (36.36%) for the Amur Paradise Flycatcher in 2021. This finding aligns with previous studies reporting low nest success rates in other locations, such as Dongzhai, Henan (34.5%; Xi et al. 2020), and in the Madagascar Flycatcher (*Terpsiphone mutata*; 33.9%; Mizuta 2002, Xi et al. 2020). Nest predation and extreme natural events were identified as the main factors contributing to nest failures, similar to what we observed in the present study. Interestingly, we found that the Amur Paradise Flycatcher relies on other bird species like the Ashy Drongo (*Dicrurus leucophaeus*) and the Black-naped Oriole (*Oriolus chinensis*) to repel predators and protect their nests. This behavior highlights the importance of interspecies interactions in enhancing nest survival. Furthermore, human disturbance emerged as another important factor affecting nest success, leading to nest desertion. The species exhibited a tendency to increase nest height in response to frequent disturbances. During our field investigation, we encountered situations in which some farmers lacked awareness of environmental protection, resulting in the destruction of bird nests by cutting down young trees for personal use. In addition, human activities such as agriculture, construction, and other forms of development have extensively exploited bird habitats through land and water use (Hsu et al. 2019).

CONCLUSION

Our study provides insights into the nest site preferences of the Amur Paradise Flycatcher, indicating their tendency to select nest sites with a wide visual range, some degree of shelter, and lower illumination. The slope and aspect of the nest sites were found to be particularly influential in determining nesting success. Specifically, nests situated on sunny slopes with gentle inclines and closer proximity to the forest edge showed a higher likelihood of successful reproduction in our study. Furthermore, the observed differences in reproductive success between the two plumage morphs for males may indicate the evolutionary significance of predator avoidance. However, our study did not find significant differences in nest-site selection and nesting success between different adult male plumage morphs. Considering that all chicks exhibit rufous plumage and there is a transition from rufous to white plumage, it is plausible to speculate that white males may have greater age and survival experience, which could mitigate the potential risk associated with having more conspicuous white plumage, which may attract predators. To obtain a more comprehensive understanding of these findings, future studies should explore molecular aspects such as the evolution of dark vision and investigate reproductive behaviors such as hatching and brooding. These investigations could provide further insights into the evolutionary significance of the observed differences in reproductive outcomes between the two male plumage morphs of the Amur Paradise Flycatcher.

Author Contributions:

TP, SW, and X. Yu conceived and designed the study. TP, SW, FL, SD, NZ, and X. Yu conducted the field work. TP, SW, and NJ analyzed the data and drafted the manuscript, and X. Yu and X. Ye revised it. All authors read and approved the final manuscript.

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Data Availability:

The datasets used in the present study are available from the corresponding author on reasonable request.

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