A STUDY OF TEMPORAL NICHE SEPARATION OF FOUR PHEASANTS IN THE SUBTROPICAL REGION OF CHINA: AFFECTED BY SEASON, ALTITUDE AND TEMPERATURE

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Abstract. To explore the temporal niche separation of four pheasants (*Syrmaticus ellioti*, *Arborophila gingica*, *Bambusicola thoracicus*, *Pucrasia macrolopha*). The kernel density estimation and randomization test were employed to analyze the daily activity rhythms patterns. The results showed that (1) the overlap coefficients of activity rhythms between different pheasant species were generally high. Pairwise comparisons revealed significant temporal niche differentiation only between *Pucrasia macrolopha* and *Syrmaticus ellioti*, and between *Pucrasia macroloph* and *Bambusicola thoracica*. (2) Seasonal analysis indicated that temporal niche differentiation among species was not significant in spring. Significant differentiation occurred between *Pucrasia macrolopha* and *Syrmaticus ellioti*, and between *Pucrasia macrolopha* and *Bambusicola thoracica* in both summer and winter. In autumn, significant temporal niche differentiation was found only between *Pucrasia macrolopha* and *Bambusicola thoracica*. (3) Temporal niche differentiation among pheasant species became increasingly pronounced with rising altitudinal gradient. (4) Compared to temperatures below 10°C, the number of significant temporal niche instances of differentiation among pheasant species increased at temperatures above 10°C. In summary, compared to seasonal and altitude changes, temperature changes had a greater impact on the activity rhythms of four pheasants. These findings demonstrated that divergent activity patterns across environmental gradients facilitated pheasant coexistence.
Keywords: *infrared-triggered camera, activity rhythm, sympatric species, animal conservation, Interspecific competition*

Introduction

Sympatric species with similar ecological niches often confront competitive pressures. For such species to coexist, one or more must undergo niche differentiation in aspects such as time, space, or diet (Hardin, 1960; Dinna, 1991; Pastore et al., 2021). Temporal differentiation is driven by two key factors. Firstly, periodic changes in abiotic factors (such as light, temperature) provide the fundamental rhythmic framework. Lehmann et al. (2012) found that temperature affects the circadian rhythm and activity duration of *Parus major*. Secondly, biological factors (such as behavioral interactions of coexisting species) further regulate the allocation of temporal resources (Pianka, 1981). Daily activity rhythms and their seasonal dynamics are core metrics

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for quantifying the temporal niche (Schoener, 1974). These rhythms, recorded by changes in animal activity intensity across diel (day-night) and seasonal scales, reveal adaptive strategies for partitioning time resources (Kronfeld-Schor and Dayan, 2003; Rowcliffe et al., 2014). Key evidence showed that the photoperiod (seasonal fluctuations in day length and sunrise/sunset times) directly drove phase adjustments in the timing of activity peaks (Seri et al., 2018; Amichai and Kronfeld-Schor, 2019). This manifests as activity peaks advancing or delaying in response to changing daylight. For example, nocturnal animals start activity earlier in winter than in summer, while diurnal species significantly extend their active period during the breeding season. Hou et al. (2022) studied *Tragopan caboti*, *Bambusicola thoracica*, *Lophura nycthemera*, *Arborophila gingica*, and *Pucrasia macrolopha* in the Xianxia Ridge area of Zhejiang. They found that, to some extent, shifts in the temporal niche likely help reduce interspecific competition among these sympatric pheasants, while differences in the altitudinal distribution of each species' activity areas further facilitate their coexistence. Xu et al. (2024) studied the *Arborophila rufipectus* populations in the Laojunshan national nature reserve and the Ma'anshan nature reserve in Sichuan province. They found that, overall, there was no significant difference in activity patterns between the Laojunshan and Ma'anshan populations. However, differences in active time periods and activity peaks were observed between the two populations.

China harbors rich pheasant species diversity, harboring numerous endemic, rare, and endangered species (Cao, 2021; Zheng et al., 1985). They serve as crucial ecological indicators for assessing forest ecosystem health. Furthermore, as typical ground-dwelling birds, their relatively large size and limited mobility make them well-suited for field monitoring using infrared camera traps (Linnebjerg et al., 2013; Xie et al., 2022). For instance, Xin et al. (2021) studied the winter foraging time allocation and differentiation between *Syrmaticus humiae* and *Lophura nycthemera*. Their results revealed differentiation in peak foraging times between males and females of different pheasant species. During the harsh winter conditions characterized by cold temperatures and food scarcity, this differentiation in foraging temporal niches helps mitigate competition and benefits population survival. Tang et al. (2024) analyzed *Lophura nycthemera* population data obtained via infrared camera traps. Their research found a high degree of overlap in the timing of activity selection within the *Lophura nycthemera* population. Activity time overlap was high during the warm season and moderate during the cold season. Li et al. (2025) compared the daily activity rhythms of *Lophura nycthemera* and *Chrysolophus pictus*. They discovered a high activity overlap coefficient and no significant difference in activity rhythms between the two species. This suggests that interspecific competition exists, but temporal niche differentiation has not occurred. Studies on the seasonal differences in daily activity rhythms among various pheasant species indicated a tendency for temporal avoidance between species, with distinct coexistence patterns across different seasons (Xie et al., 2022).

In terms of the diet of animals, the habitat selection behavior of animals indicated their feeding preferences, which also affected their survival and reproduction (Lack, 1993). For example, *Syrmaticus ellioti* primarily fed on the nuts from fagaceae plants, seeds of herbaceous plants, berries, and grains during autumn. In winter, its diet included *Ophiopogon japonicus*, *Aster ageratoides*, *Carex tristachya*, *Gymnocladus chinensis*, *Albizia kalkora*, and *Boehmeria siamensis* (Shi and Zheng, 1997).

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Arborophila gingica mainly fed on the fruits and seeds of plants, such as acorns and berries. It also ate insects and other small invertebrates. During the autumn and winter seasons, wild plant seeds and fruits (such as *Castanopsis hystrix*, *Toxicodendron sylvestre*, *Lindera strychnifolia*) (Zhao, 2001). *Bambusicola thoracica* was a typical omnivorous bird, mainly feeding on plant shoots, grass seeds, termites, and worms (Yao et al., 2008). *Pucrasia macrolopha* primarily fed on the flat seeds, *Carex*, *Elaeagnus pungens*, *lmus parvifolia*, fern, *Quercus aliena*, and *Indocalamus tessellatus*, fruits of plants in the Rosaceae family (Wang and Hu, 1983). When there were significant differences in the overlap coefficient of activity rhythms between species, it indicated that this factor was the primary cause of intense interspecies competition. To gain more living space, species used temporal partitioning of their activities to reduce niche overlap and lower interspecies competition (Liu et al., 2017). It was also the result of the species adapting their activity rhythms to the environment.

Overall, previous research on temporal niche separation among pheasants was relatively limited (Wang et al., 2020), especially concerning niche differentiation along altitudinal and temperature gradients. There was a notable gap in understanding the mechanisms of sympatric species coexistence within communities based on wildlife activity rhythms (Bu et al., 2016). Here we presented the study on the temporal niche separation of four pheasants using infrared-triggered camera data. The objectives of this study were to 1) measure whether there are significant differences in the co-occurrence patterns between pheasant species; 2) explore whether its activity patterns show significant differences with respect to variations in season, altitude and optimal temperature.

Materials and methods

Study location

This research was conducted in the Longyou County region (28°44'-29°17'N, 119°02'-119°20'E), Zhejiang province, China. The study area encompasses a total area of 145.8 km². The elevation range of the study area is from 33 to 1442 m. The Longyou County region has a subtropical monsoon climate with distinct wet and dry seasons (Zeng et al., 2019). The average annual temperature is 17.3°C, with annual precipitation of 1602.6 mm. The wet season typically lasts from April to September, with the highest rainfall occurring from June to August, when over 60% of annual precipitation falls. The dry season spans from October to March, characterized by lower rainfall, cooler temperatures, and reduced humidity, especially from December to February of the following year.

Data collection and collation

This study was conducted from January 2021 to December 2024 in Longyou County, Zhejiang Province. The distribution map of 203 infrared-triggered camera sites and the surrounding habitats were drawn using ArcMap 10.8 (*Fig. 1*). The data download is sourced from the National platform for Common GeoSpatial Information Service (https://www.tianditu.gov.cn/). Four pheasant species were captured by 123 of the 203 camera points. (*Syrmaticus ellioti*, *Arborophila gingica*, *Bambusicola thoracica*, and *Pucrasia macrolopha*) (*Fig. 2*). We used an infrared-triggered camera H805 that used sensing technology to detect the temperature of animals, thereby automatically

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capturing high-definition images and videos. The manufacturer is Hong'e Electronics Technology Co., Ltd., located in Kunshan, Jiangsu Province, China. Camera trap deployment and parameter settings strictly followed standardized protocols (Zhang et al., 2024). Seasons were defined as: Spring (March-May), Summer (June-August), Autumn (September-November), and Winter (December-February of the following year) (Lu et al., 2007). Based the distinct distribution of main vegetation types across different altitudes from lower to higher altitudes, we found mixed Moso bamboo (*Phyllostachys edulis*) and *Cunninghamia lanceolata* forest, followed by mixed *Cunninghamia lanceolata* and broadleaf forest, and finally, mixed broadleaf and shrub dominated by *Rhododendron simsii* and *Hydrangea paniculata*. The optimal altitudinal gradients were divided into three levels: 0-500 m, 500-1000 m, and 1000-1500 m. The optimal temperature gradients were divided into three levels: <10°C, 10-20°C, and >20°C. We collected infrared-triggered camera data every six months. An independent photographic event was defined as consecutive images of the same species captured at a single camera station within 30-min interval, counted as one independent record (O'Brien et al., 2003). Species identification was based on a field guide to the birds of China (John and Karen, 2000).

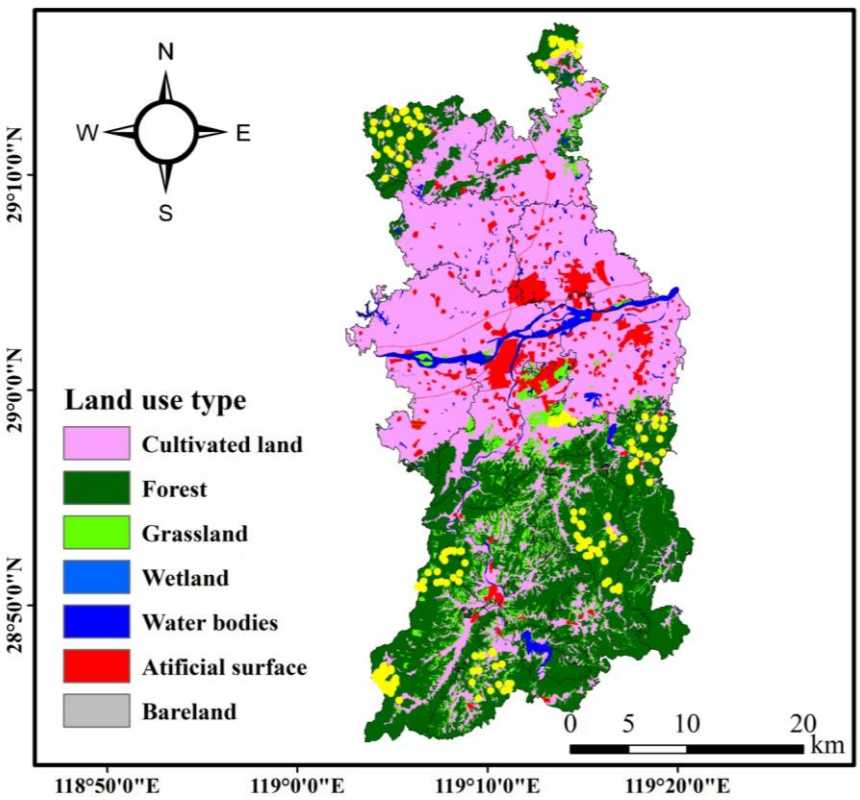

Figure 1. *Map of 203 infrared-triggered camera sites and surrounding habitats of four pheasant yellow circles: infrared-triggered camera sites*

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Figure 2. *Habitat sites of four pheasant in the subtropical region. (A) Syrmaticus ellioti, (B) Arborophila gingica, (C) Bambusicola thoracica, (D) Pucrasia macrolopha*

Statistical analysis

Daily activity rhythm analysis was performed in the version R4.4.0 (R Core Team, 2021). The overlap coefficient (Δ), representing the proportion of overlap between two daily activity rhythm curves, was calculated using the overlapEst function in the overlap package. Δ ranges from 0 (complete separation) to 1 (complete overlap) (Meredith et al., 2024). Statistical randomization tests (using the compareCkern function in the activity package) were conducted to determine whether the observed values corresponding to two activity rhythm curves originated from the same probability distribution. The test was performed with 1000 iterations (Chen et al., 2019a).

Results

Daily activity rhythm analysis of the four pheasant species

During the four-year infrared-triggered camera monitoring period, a total of 123 cameras captured 1693 independent records of the four pheasant species (*Syrmaticus ellioti*, n = 168; *Arborophila gingica*, n = 118); *Bambusicola thoracica*, n = 916; *Pucrasia macrolopha*, n = 491). The annual daily activity rhythm curves demonstrate that all four species are typically diurnal, exhibiting bimodal activity patterns with peak activity occurring around 06:00 (dawn) and 18:00 (dusk) (*Fig. 3*). Overlap analysis revealed significant variation in temporal niche partitioning: The highest activity

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rhythm overlap coefficient (Δ) occurred between *Syrmaticus ellioti* and *Bambusicola thoracica* (Δ = 0.9273). The lowest overlap coefficient was observed between *Bambusicola thoracica* and *Pucrasia macrolopha* (Δ = 0.8176), indicating that there is a difference in the temporal niche between different pheasant species. The overlap coefficient of daily activity rhythms of *Pucrasia macrolopha*, *Syrmaticus ellioti* and *Arborophila gingica* was extremely significant ($p < 0.01$), indicating that the *Pucrasia macrolopha* had a significant differention of temporal ecological niches from *Syrmaticus ellioti* and *Arborophila gingica*, respectively. No significant temporal niche differentiation was detected among the remaining species pairs.

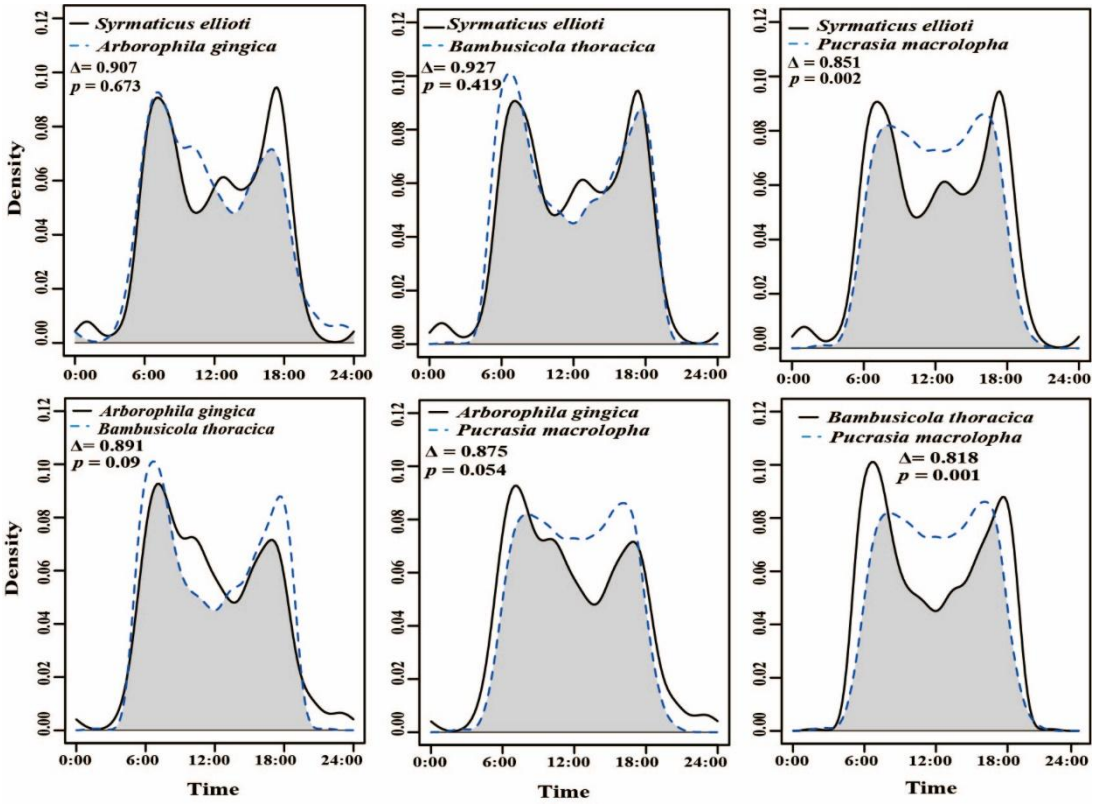

Figure 3. *Pairwise comparative analysis of daily activity rhythm curves among the four pheasants*

Seasonal variation in daily activity rhythms of four pheasant

Analysis across the four seasons revealed distinct *activity* patterns in species detection. *Syrmaticus ellioti* and *Pucrasia macrolopha* yielded the highest number of independent records in autumn. *Arborophila gingica* yielded the highest number in spring. *Bambusicola thoracica* yielded the highest number in summer. This indicates seasonal differences in relative abundance or detectability among the pheasant species (*Table A1*). Analysis of daily activity rhythm overlap across seasons revealed concrete differention of temporal ecological niches (*Fig. 4*). In the spring, no significant differences in pairwise activity rhythm overlap coefficients (Δ) were detected among any species pairs, indicating high temporal niche similarity and minimal differentiation during this spring. In the summer, the significant differentiation (Δ = 0.8079, $p < 0.05$) occurred between *Syrmaticus ellioti* and *Bambusicola thoracica*, indicating pronounced niche

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differentiation. Highly significant differentiation occurred between the *Pucrasia macrolopha* and *Arborophila gingica* ($\Delta = 0.6895$, $p < 0.01$) and between the *Pucrasia macrolopha* and *Bambusicola thoracica* ($\Delta = 0.7662$, $p < 0.01$), indicating pronounced niche differentiation for the *Pucrasia macrolopha* relative to these species. In the autumn, significant differentiation ($\Delta = 0.8504$, $p < 0.05$) occurred between the *Pucrasia macrolopha* and *Bambusicola thoracica*, indicating pronounced niche differentiation. In the winter, significant differentiation occurred between the *Pucrasia macrolopha* and *Arborophila gingica* ($\Delta = 0.608$, $p < 0.05$) and between the *Pucrasia macrolopha* and *Bambusicola thoracica* ($\Delta = 0.794$, $p < 0.05$), indicating pronounced niche differentiation for the *Pucrasia macrolopha* relative to these species. In summary, niche differentiation for the *Pucrasia macrolopha* relative to the other pheasant species was particularly pronounced during the summer, autumn, and winter seasons. Except for the species pairs showing significant differentiation (count = 6) under specific seasonal mentioned above, niche differentiation among the remaining species pairs was not significant.

Altitudinal variation in daily activity rhythms of four pheasants

Across altitudinal gradients (*Table A2*), *Arborophila gingica* had the lowest independent records (count = 7, < 500 m), while *Bambusicola thoracica* showed peak abundance (count = 599, > 1000 m). The number distribution of *Syrmaticus ellioti* tends to inhabit an area of 0-500 m. The number distribution of *Arborophila gingica* tended to live in 1000-1500 m, whereas both *Bambusicola thoracica* and *Pucrasia macrolopha* concentrated in 1000-1500 m ranges. Below 500 m, all pairwise overlap coefficients (Δ) indicated high temporal niche similarity with no significant differences. Within 500-1000 m, *Bambusicola thoracica* and *Pucrasia macrolopha* exhibited significant temporal niche differentiation ($p < 0.05$). Above 1000-1500 m, *Syrmaticus ellioti* showed significant differentiation from both *Arborophila gingica* and *Bambusicola thoracica*, and *Pucrasia macrolopha* similarly showed significant differentiation from *Arborophila gingica* and *Bambusicola thoracica*. The significant niche differentiation (count = 5) occurred only in these specified species pairs across altitudinal gradients (*Fig. 5*).

Temperature variation in daily activity rhythms of four pheasants

Across temperature gradients (*Table A3*), the number of independent records of *Syrmaticus ellioti* is the smallest in both lower temperature range (≤10°C; count = 33) and higher temperature range (≥20°C; count = 72). The highest distribution numbers of the *Arborophila gingica* and *Pucrasia macrolopha* concentrated in moderate temperatures, respectively (10-20°C; count = 54, count = 230). The *Bambusicola thoracica* tended to the habitant of optimal temperature gradient above 20°C (count = 443). Temporal niche differentiation exhibited thermal dependence (*Fig. 6*). Below 10°C, *Bambusicola thoracica* significantly diverged from *Arborophila gingica* and *Pucrasia macrolopha* ($p < 0.05$); within 10-20°C, *Bambusicola thoracica* differentiated significantly from all three congeners while *Pucrasia macrolopha* diverged from *Syrmaticus ellioti*; above 20°C, *Pucrasia macroloph* showed significant differentiation from *Syrmaticus ellioti*, *Arborophila gingica*, and *Bambusicola thoracica*, and *Arborophila gingica* diverged significantly from *Bambusicola thoracica*. The significant niche differentiation (count = 10) occurred exclusively in these species-temperature combinations, with non-significant differentiation in all other pairwise comparisons.

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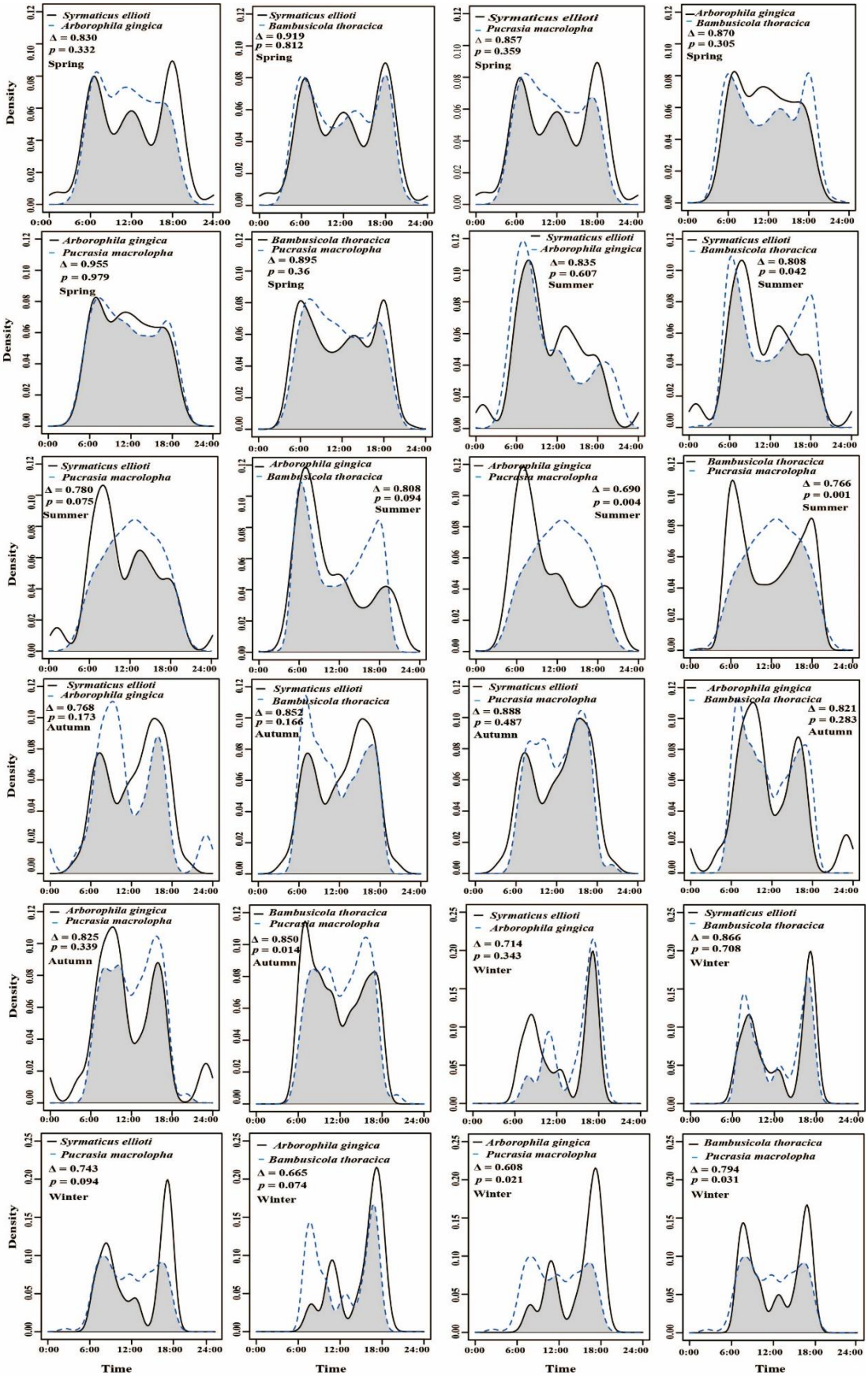

Figure 4. *Comparative analysis of activity rhythm curves across seasons of four pheasants*

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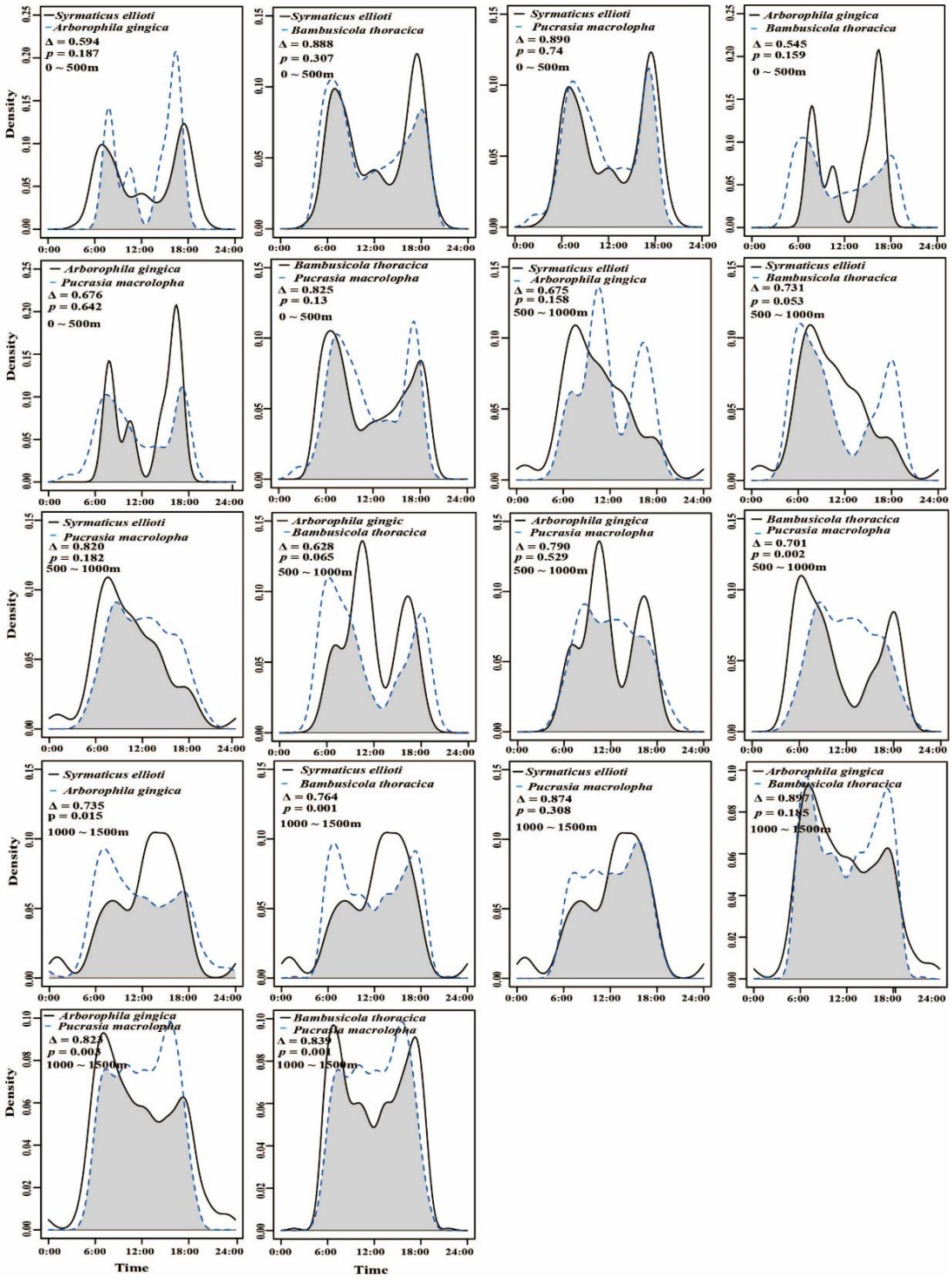

Figure 5. *Comparative analysis of activity rhythm curves across altitudinal gradients of four pheasants*

Discussion

Temporal niche differentiation in animals results from interspecific interactions and environmental adaptations (Sun, 2019). Our study reveals high annual activity rhythm overlap among the four pheasant species (*Syrmaticus ellioti*, *Arborophila gingica*,

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Bambusicola thoracica, *Pucrasia macrolopha*) (*Fig. 3*; $\Delta > 0.8$). All species exhibited diurnal bimodal activity patterns with peak activity at dawn and dusk, consistent with previous findings (Meng et al., 2022). Crucially, peak timing variations emerged: *Syrmaticus ellioti* and *Pucrasia macrolopha* showed significantly lower morning peaks than evening peaks, with pronounced differentiation between their activity rhythms. Conversely, *Arborophila gingica* and *Bambusicola thoracica* displayed higher morning activity intensity. Significant differentiation also existed between *Bambusicola thoracica* and *Pucrasia macrolopha*. These temporal divergences reflect niche partitioning strategies, likely representing adaptive responses among dietary-similar species to reduce competitive intensity among sympatric pheasants through temporal segregation (Cui et al., 2008).

Understanding temporal niche differentiation among sympatric species is crucial for elucidating coexistence mechanisms (Ridout and Linkie, 2009). Our study demonstrates seasonally-specific activity rhythms in four sympatric pheasant species within subtropical area (*Fig. 4*). The differentiation was minimal in spring but most pronounced in summer, followed by winter and autumn. *Bambusicola thoracica* and *Pucrasia macrolopha* exhibited significant activity rhythm differentiation across summer, autumn, and winter. This likely reflects limited food resources driving reproductive-phase adjustments during breeding seasons, birds optimize nutrient acquisition for reproduction and chick-rearing by temporally partitioning activity to avoid interspecific encounters (Yang et al., 1995), creating distinct non-breeding season patterns (Meng et al., 2022). Extreme temperatures further modulate behaviors that winter cold increases thermoregulatory energy expenditure (Yu et al., 2017), while excessive heat constrains survival activities (Farooq et al., 2010). Altitudinal analysis revealed key thresholds (*Fig. 5*): below 500 m, no significant pairwise differentiation occurred; within 500-1000 m, only *Bambusicola thoracica* and *Pucrasia macrolopha* showed significant divergence; above 1000 m, 60% of species pairs exhibited significant differentiation, potentially due to richer biodiversity and reduced anthropogenic disturbance in subtropical 1000-1500 m zones. These conditions provide expanded habitat and abundant resources, enabling reduced foraging time (Enoksson, 1990) and facilitating spatial-temporal niche segregation. Such rhythmic differentiation minimizes temporal conflicts and promotes stable coexistence among sympatric pheasants (Meng et al., 2022).

Temperature serves as a core environmental regulator of animal activity patterns, with species temporally adjusting behaviors to avoid extreme thermal stress (Zweifel-Schielly et al., 2009). Concurrently, weather conditions and their seasonal impacts on food resources further modulate activity rhythms (Bennie et al., 2014; Monterroso et al., 2020). Activity peaks typically align with optimal thermal gradients. In this study, *Syrmaticus ellioti* and *Bambusicola thoracica* peaked at >20°C, while *Arborophila gingica* and *Pucrasia macrolopha* optimized activity within 10-20°C. Among the four pheasant species, there are six pairwise combinations for comparing diel activity rhythms. Below 10°C, significant differentiation occurred only between *Bambusicola thoracica* and *Arborophila gingica,* as well as between *Bambusicola thoracica* and *Pucrasia macrolopha* (*Fig. 6*). Conversely, four pairwise combinations showed significant differentiation within both 10-20°C and >20°C gradients. This divergence among species sharing optimal temperatures likely reflects the limiting similarity hypothesis and competitive exclusion principle. The intensified competition for spatial and trophic resources within identical thermal regimes drives niche differentiation, enabling multi-species coexistence in shared habitats (Shine, 1989; Butler, 2007; Chen et al., 2019b). What is more, we found that temperature changes had the greatest

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significant impact on the activity rhythms of the four pheasants (count = 10), followed by seasonal changes (count = 6), and finally altitude changes (count = 5). Ultimately, wildlife activity rhythms represent energy-budget optimization strategies, with behavioral shifts constituting adaptive responses to spatiotemporal variations in ecological niches across seasonal, altitudinal, and temperature gradients.

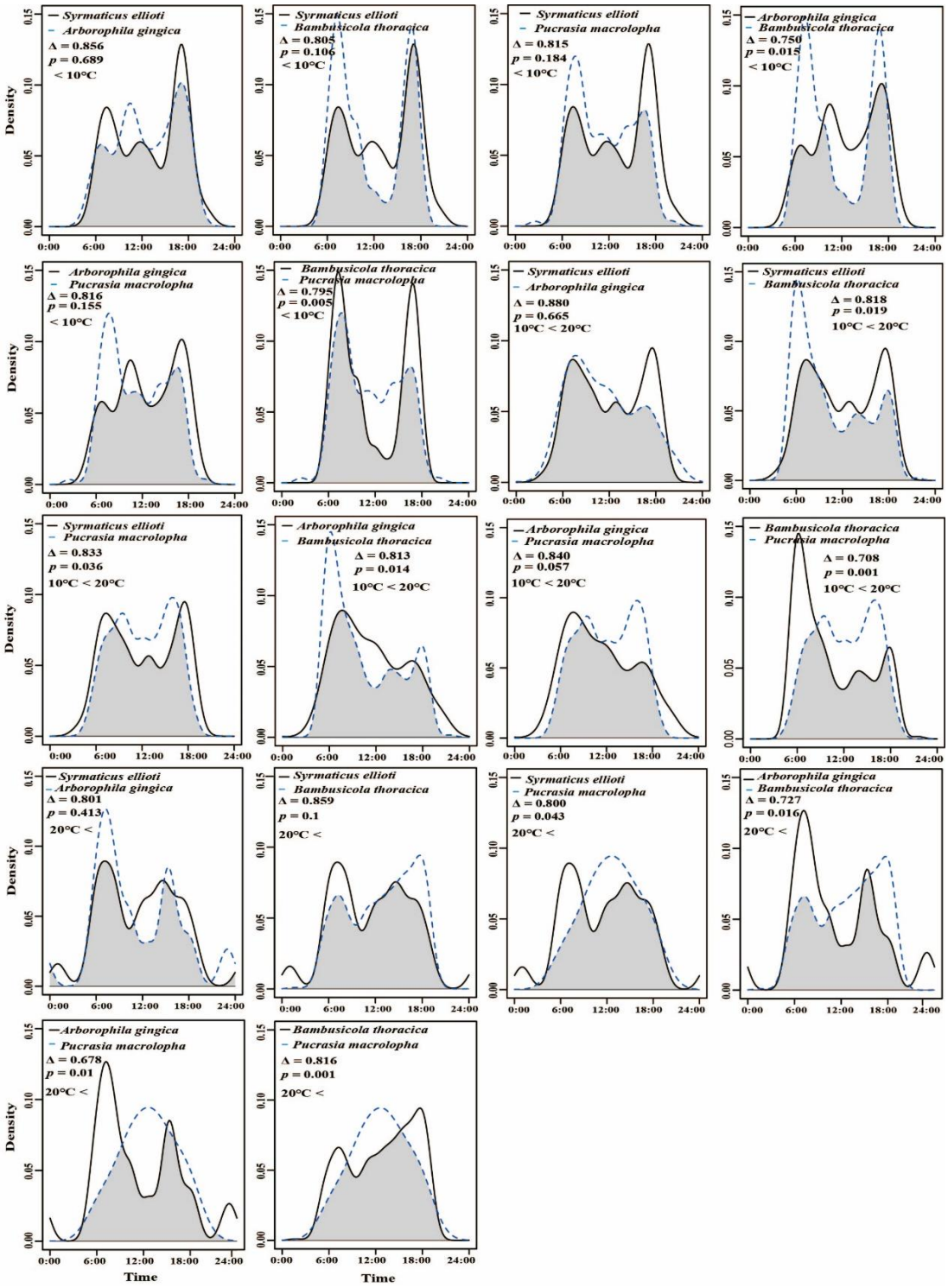

Figure 6. *Comparative analysis of activity rhythm curves across temperature gradients of four pheasants*

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Conclusion

In summary, the four pheasant species (*Syrmaticus ellioti*, *Arborophila gingica*, *Bambusicola thoracica*, *Pucrasia macrolopha*) in subtropical Longyou County, Zhejiang Province, exhibit substantial overlap in daily activity rhythms while demonstrating significant temporal niche differentiation. This pattern suggests sympatric pheasants mitigate interspecific competition through strategic temporal niche partitioning. Furthermore, species-specific adaptations across seasonal, altitudinal, and thermal gradients manifested through differential activity rhythm adjustments substantially enhance their coexistence potential. Compared to seasonal and altitude changes, temperature changes have a greater impact on the activity rhythms of the four pheasants. This study advances our understanding of how daily activity rhythms in subtropical pheasants respond to seasonal variations, altitudinal gradients, and shifting temperature regimes. It also provides novel perspectives for developing regional wildlife population management strategies.

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Conflict of interests. The authors declare no conflict of interests.

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APPENDIX

Table A1. *The number of valid photographs of four pheasants across different seasons*

Season	*Syrmaticus ellioti*	*Arborophila gingica*	*Bambusicola thoracica*	*Pucrasia macrolopha*
Spring	37	43	170	93
Summer	47	31	453	104
Autumn	56	31	207	178
Winter	28	13	86	116
Count	168	118	916	491

Table A2. *The number of valid photographic records of four pheasants across altitudinal gradient*

Altitude	*Syrmaticus ellioti*	*Arborophila gingica*	*Bambusicola thoracica*	*Pucrasia macrolopha*
0~500 m	93	7	270	51
500~1000 m	29	11	47	118
1000~1500 m	46	100	599	322

Table A3. *The number of valid photographic records of four pheasant species across temperature gradients*

Temperature	*Syrmaticus ellioti*	*Arborophila gingica*	*Bambusicola thoracica*	*Pucrasia macrolopha*
~10℃	33	34	143	151
10℃~20℃	63	54	330	230
20℃~	72	30	443	110

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