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Environmental factors influencing lek site selection in the red bird of paradise (*Paradisaea rubra*) in Raja Ampat, Southwest Papua, Indonesia

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Abstract. *Budhiana R, Hamidi A, Hernowo JB, Setiawan Y. 2025. Environmental factors influencing lek site selection in the red bird of paradise (*Paradisaea rubra*) in Raja Ampat, Southwest Papua, Indonesia. Biodiversitas 26: 5277-5286.* Understanding the ecological determinants of lek site selection is crucial for the conservation of lek-breeding species, such as the red bird-of-paradise (*Paradisaea rubra*), which is endemic to Waigeo and Batanta Islands in Raja Ampat, Indonesia. This study aimed to identify the primary habitat characteristics that influence lek-site preferences in *P. rubra* by employing a spatially explicit, multivariate methodology. Ten environmental variables (tree diameter, tree height, lek height, lek diameter, lek angle, lek length, altitude, slope, temperature, and humidity) were documented across known lek sites, and Principal Component Analysis (PCA) was employed to address collinearity and capture ecological gradients. A multiple linear regression model was then applied to the principal components to assess their association with lek suitability (Y). Three principal components were extracted: PC_1 (topographic openness), PC_2 (microclimate), and PC_3 (vertical structure). Regression results identified PC_1 as the strongest predictor of lek suitability (B: -2.629, p: 0.002). PC_1 represents a topographic canopy gradient, with higher values indicating denser canopy and steeper terrain at higher elevations. The negative regression coefficient, therefore, indicates that males preferentially select leks in structurally open habitats with gentler slopes, reduced canopy density, and moderate elevations. PC_2 and PC_3 had positive but non-significant effects ($p>0.1$), though both suggest that lek preference may also be influenced by microclimate comfort and vertical signal projection. Lek site selection in *P. rubra* is strongly influenced by structural and spatial habitat features, especially canopy openness and elevation. The findings emphasize that lek selection in *P. rubra* is shaped by the interplay of topography, microclimate, and vertical structure. Conservation strategies should prioritize protecting ridge top forest zones and limiting forest infill from secondary growth or plantation encroachment, which may disrupt lek functionality and reduce reproductive opportunities in this iconic species.

Keywords: Conservation, ecology, habitat, Raja Ampat, red bird of paradise

INTRODUCTION

Paradisaea rubra, commonly known as the red bird-of-paradise, is an iconic endemic species of the family Paradisaeidae restricted to Waigeo and Batanta Islands in the Raja Ampat Archipelago, Indonesia (Birdlife International 2022). Celebrated for its elaborate plumage and courtship displays, *P. rubra* is legally protected under Indonesian law (Indonesian Ministry of Environment and Forestry 2018) and listed as Near Threatened (NT) on the IUCN Red List, primarily because of habitat degradation and illegal wildlife trade (Indonesian Ministry of Environment and Forestry 2018; Birdlife International 2022). As a polygynous species, males engage in conspicuous sexual displays in designated arenas called leks, which serve as central locations for female mate choice (Frith 1976; Beehler 1983b).

Lekking-based mating systems have been widely studied in avian taxa and are known to be shaped by intricate interactions between social behavior, environmental cues, and sexual selection mechanisms (Bradbury et al. 1986; Alatalo et al. 1988). Females often exhibit strong preferences for particular display sites or lek characteristics, including visibility, structural complexity, and spatial distribution of males, which influence both the intensity of sexual selection and the spatial organization of leks (Lank and Smith 1992; Alonso et al. 2012). Studies in lekking species such as white-throated manakin (*Corapipo gutturalis*) and ruffs (*Philomachus pugnax*) have demonstrated that lek site selection is not only influenced by male clustering or female movement patterns, but also by fine-scale ecological features such as microtopography, light exposure, and vegetation openness (Lank and Smith 1992; Westcott 1994; Endler and Thery 1996). Other species case like in male green peafowl (*Pavo muticus*) prefer and occupy open, undisturbed sites that maximize visual and acoustic signal transmission during lek displays (Hernowo 2017). In other Paradisaeidae species such as lesser bird of paradise (*Paradisaea minor*), males consistently select branches that receive optimal morning sunlight, maximizing plumage contrast and improving signal transmission during courtship displays (Beehler and Foster 1988).

In lek ecology, males benefit from selecting lek sites that enhance their conspicuousness while balancing predation risks and environmental constraints (Gibson et al. 1991; Wiley 2013). Previous studies have shown that environmental features such as slope, canopy height, habitat openness, and spatial proximity to female activity centers significantly shape lek attractiveness and influence male reproductive success (Gibson et al. 1991; Westcott 1994; Endler and Thery 1996; Alonso et al. 2012). Furthermore, the apparent paradox of lek evolution, why females continue to prefer certain males despite strong directional selection, has been addressed through hypotheses such as indirect genetic benefits, particularly the "sexy son" model, which suggests that females may gain fitness advantages by producing attractive male offspring (Kirkpatrick and Ryan 1991).

Research on *P. rubra* has primarily focused on ethological descriptions, while the role of habitat structure and landscape scale in shaping behavioral preferences such as lek selection and display behavior remains underexplored. There is a notable absence of integrative studies that combine behavioral ecology, remote sensing, and conservation planning. Given the rapid pace of land-use change in Raja Ampat, including potential threats from infrastructure and extractive development, the lack of data on lek habitat specificity represents a critical gap in conservation research.

This study addresses two main research gaps: (i) the limited understanding of environmental factors influencing lek site selection in *P. rubra*; (ii) the scarcity of integrative approaches that connect spatial modelling, lek ecology, and community-based conservation. The objective of this study is to examine ecological determinants of lek-site occurrence. Ten habitat variables representing structural, topographic, and microclimatic conditions were documented. Principal Component Analysis (PCA) was applied to address collinearity among variables. By investigating the habitat correlates of lek preference in this species, we aimed to provide a scientific foundation for habitat-based management strategies tailored to the ecological requirements of *P. rubra* within a dynamic socioecological landscape.

MATERIALS AND METHODS

Study area

The study area is in Warkesi and Sarpokren Villages on Waigeo Island and Wailebet Village on Batanta Island (see Figure 1), Raja Ampat Islands, Southwest Papua Province, Indonesia. Waigeo and Batanta islands extend geographically from 0°45' to 2°15'S and from 129°15' to 132°00'E. This study was conducted from November to December 2023, with an average precipitation range of 231.3-186.3 mm/month. The temperature ranged from 26°C to 31°C, and the percentage of sunshine ranged from 55.4%-66.5%.

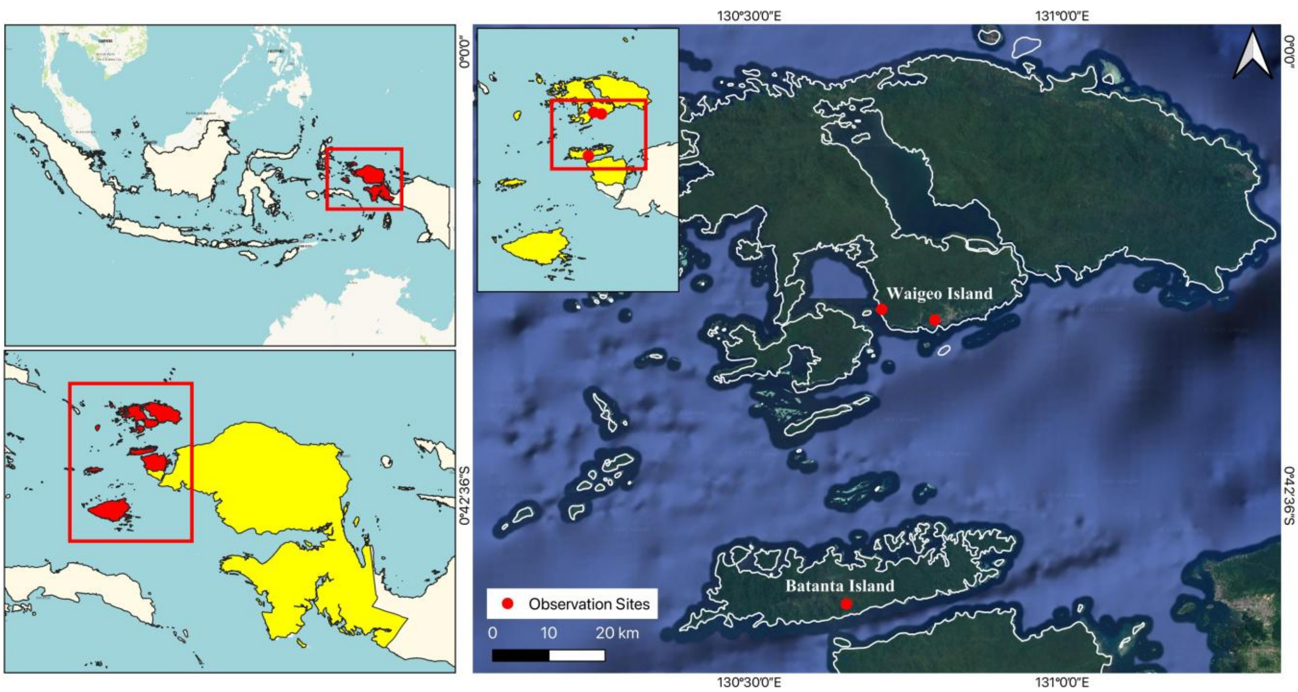

Figure 1. The map presents the topographic variation across the study area, covering Waigeo and Batanta Islands in Raja Ampat, Southwest Papua, Indonesia

Elevation in Raja Ampat are generally modest, with the highest peak on Batanta Island about 1,200 m asl, whereas most other islands do not exceed 1,000 m asl (King 2017). The region comprises small islands, with elevation changes occurring almost directly adjacent to the sea, resulting in a pseudo-mountain effect (Wibisono and Rinawati 2016). This phenomenon contributes to the classification of the lower montane forest type, based on the characteristics of its constituent vegetation (Webb 2005; Widyatmoko 2013). Waigeo Island is the largest island in Raja Ampat District, with land cover dominated by forests classified by function and legal designation. The forest area on Waigeo Island consists of a nature reserve (CA), conversion production forest (HPK), protected forest (HL), and other use areas (APL) (BPS Raja Ampat 2023). Most of Waigeo Island's land is primary forest, covering 263,929 ha (80%), with a small portion of secondary forest covering 33,094 ha (9%). In Batanta, 90% of the island is an undisturbed forest due to its topographical characteristics. Batanta Island is a protected forest based on its ecological characteristics. In Warkesi and Saporkren, *P. rubra* has become the main attraction for birdwatching. Shack shelters made of plastic tarps or palm leaves in Warkesi and Saporkren are used as observation stations to get the observer as close as possible to the lek tree without disturbing the *P. rubra* activities (Figures 2.A and 2.B). In contrast to the previous site, we identified the lek tree in Wailebet at the boundary between agricultural fields and forest, within a dryland farming area managed by local communities (Figure 2.C).

Data collection

The study applied purposive sampling to select lek trees recognized by local people as used by *P. rubra*, with each tree observed at three locations. Non-lek tree information was obtained through circular plot sampling (radius 12.56 m), with each lek tree serving as the center point of the plot. Specifically, in Warkesi and Saporkren, both lek trees are situated on the top of the hill and lead to the valley. We directly observed the *P. rubra* during active time (06.00-08.00 AM and 16.00-18.00 PM) for seven consecutive days on each location. The daily activity patterns of *P. rubra* were recorded using focal animal sampling with continuous recording throughout the observation period. All visible behaviors were categorized into standardized ethogram units (e.g., feeding, perching, vocalizing, displaying). Perching is one of *P. rubra* daily activity recorded, is categorization of some activity consist of sheltering (covering), probing, and vocalizing. Habitat related variables were obtained by measuring vegetation attributes and environmental characteristics directly associated with lek-site locations, such as tree species, diameter, tree height, lek height, lek diameter, lek angle direction, and lek length. We measured tree diameter and height using a metering band and laser rangefinder. Environmental variables such as elevation, slope, canopy cover, temperature, and humidity were recorded based on their hypothesized role in influencing lek functionality, particularly visibility, signal transmission, and microclimate regulation. These were measured using a clinometer, thermometer, compass, and GPS. Tree species were identified using local guide input and verified using botanical determinant keys; canopy architecture was assessed to evaluate crown openness and branching structure, which define spatial suitability for courtship displays.

Data analysis

The canopy in the forest is restricted to interior birds as a vegetation element associated with the diversity and availability of ecological niches, such as hiding, nesting, and lekking (Beehler and Mack 1999; Stein et al. 2014). Canopy cover quantification is an approach used to analyze biomass production and vegetation characteristics. We measured canopy cover using the Gap Light Analysis Mobile App (GLAMA) application. The GLAMA is a mobile application designed to analyze light gaps by estimating canopy cover using hemispherical photographs (Tichý 2014). GLAMA was used to describe the lek area from a canopy cover perspective using a smartphone. We used Huawei P30 Pro smartphones that are ideal for calculating the Canopy Cover index because of their powerful camera and processing capabilities (Tichý 2016). We also attached an external wide-angle or fisheye lens to the smartphone's built-in magnet to enhance its picture capabilities.

Figure 2. The observation stations differ in Raja Ampat, Indonesia: Warkesi (A), Saporkren (B) of Waigeo Island are used for birdwatching activity, while the station in Wailebet of Batanta Island (C) is in the farmland

We selected ten environmental variables based on their ecological relevance to lekking behavior, supported by previous studies (Beehler 1987; Alonso et al. 2012). We collected 234 data points across 10 environmental variables, including tree diameter, tree height, lek height, lek diameter, lek angle, lek length, altitude, slope, temperature, and humidity. Before analysis, we standardized each variable using z-scores and retained only those with standardized values ≥0.5 for the initial model (Tabachnick and Fidell 2018). All data were then analyzed using PCA to identify key habitat variables influencing lek site selection by *P. rubra*. We assessed sampling adequacy using the Kaiser-Meyer-Olkin (KMO) test and the anti-image correlation matrix. Two variables, lek height (LH; MSA: 0.478) and lek length (LL; MSA: 0.491), fell below the accepted MSA threshold of 0.5 and were excluded from subsequent analysis (Cahyana et al. 2015; Brillianti 2018). We validated the suitability of the refined dataset (8 variables) for PCA using a KMO value above 0.5 and a significant Bartlett's test ($p<0.001$).

Principal components were extracted from the correlation matrix using eigenvalue decomposition. We retained components with eigenvalues greater than one and confirmed the final selection through scree plot inspection (Ledesma et al. 2015). We interpreted the results based on the rotated component matrix, considering factor loadings ≥0.5 as substantively significant (Larasati and Suminto 2024). PCA allowed the identification of dominant ecological gradients associated with lek site characteristics. PCA reduced variable complexity while preserving essential information, enabling us to interpret habitat preferences more clearly (Vaughan and Ormerod 2005; Janekovi and Novak 2012). We used ANOVA to evaluate the regression model from PCA components and confirmed residual normality to validate linear analysis assumptions (Almais et al. 2023).

RESULTS AND DISCUSSION

Ethology description

Observations indicate that *P. rubra* initiates and concludes its daily activities with vocalization starting from 06.00 to 18.00. The daily behavioral patterns of *P. rubra* can be categorized into eight recurring activities: perching, vocalizing, displaying, feeding, stripping bark, shedding leaves, probing, and mating. Vocalizing, probing, and feeding activities were observed while perching during daylight hours. During the observation period, *P. rubra* appeared to utilize the canopy as a form of cover whenever larger birds or birds of prey approached. Conversely, stripping bark and shedding leaves occur after display or mating activities. A detailed ethological description of *P. rubra* is provided in the accompanying Table 1.

Lek tree profile

Waigeo and Batanta Islands are situated within a chain of small islands in the Bird's Head Peninsula (Vogelkop) region of Western Papua (Fenner 2018). No areas in Raja Ampat District exceed 1200 meters above sea level, with Batanta Island containing the highest elevation (Kartikasari et al. 2012). Birds-of-paradise typically inhabit humid tropical rainforests across lowland and montane regions (Switzer 2008). In this study, we observed lek trees in hilly lowland forests with varied topographic features (Mambrisaw et al. 2006). We identified the canopy architecture of these lek trees based on distinct structural forms, including Roux, Rauh, and Leeuwenberg models (Hallé et al. 1978; Vivin et al. 2022). In Warkesi and Saporkren, lek trees occurred on elevated slopes at 310 and 228 meters above sea level, respectively, while in Wailebet, they were located on relatively flat terrain. The species of lek trees identified in Warkesi, Saporkren, and Wailebet included *Gyrinops* sp., *Callophylum inophylum*, and *Ficus lawesii*. The fig species is one of the common trees used by the birds of paradise for their daily activity (Raunsay 2020).

The observations showed that the lek trees in Warkesi and Saporkren share common characteristics, notably their positions at the edge of hills overlooking valleys where the terrain becomes flatter. The lek tree heights in Warkesi and Saporkren are 32 m and 16 m, respectively. The Wailebet lek tree stands out as the tallest, reaching a height of 40 m, whereas the other two lek trees exhibit an average height comparable to the surrounding vegetation. The lek tree in Wailebet is close to community plantations. The lek branches' size and length are approximately 2.7-7 cm and 60-180 cm. Figure 3 illustrates the spatial position and structural context of the lek trees.

The environmental variables affecting lek behavior are architecture, elevation, and slope. Elevation and slope are important in the sexual selection process. The climate on both islands is likely to have a daily temperature of 26°C and moisture between 80% and 90% (Table 2).

Table 1. Ethogram of daily behaviors of the red bird of paradise (*Paradisaea rubra*)

Activity	Description
Perching	Birds sit on tree branches, remaining still, often as a basis for other activities
Vocalizing	distinctive sounds at a fast tempo with short (call) and long (song-like call) durations, as well as sounds like clicking their beaks (bill-clicked call) while perched
Display	Series of distinctive movements made by males to attract females
Feeding	Eating fruit while perching
Stripping bark	Peeling the bark with its beak
Shedding leaves	Pulling leaves on the branch used as lek until they detach and fall off
Probing	Cleaning feathers and ornamental plumage with the beak while perching
Mating	Copulation between the male and female, which occurs briefly in the lek arena

An interesting aspect of the lek trees is the angle at which the branch stems are inclined (Table 3). In Warkesi and Saporkren, male red birds of paradise selected lekking perches with steep branch angles, often approaching 90°. In contrast, within Wailebet, the inclination angle of branches in the lekking areas varied between 30° and 60°. Observation in Wailebet indicate that, red birds of paradise select smaller twigs and generally prefer branches with lower inclination angles compared to Warkesi and Saporkren. Males perform on vertical or nearly vertical perches and prefer bare branches in open area (Frith 1976). The Lek space illustration is shown in Figure 5.

Figure 4 illustrates the lek site's position, characterized by a relatively open canopy and sparse leaves. According to the GLAMA results, the canopy cover index in Warkesi is the lowest at 38.93% and the densest is the lek tree in Wailebet at 69.19%. In Warkesi and Saporkren, males of *P. rubra* tend to select lek trees with relatively narrow crowns, likely due to spatial constraints, in contrast to the broader-crowned trees observed in Wailebet. Although Wailebet recorded the highest canopy cover value, this measurement did not exclusively represent the lek tree canopy. Instead, it likely reflected overlapping crowns of underlying vegetation that were inadvertently included during data collection.

This research revealed that arboreal structures that serve as lek sites are instrumental in meeting diverse habitat necessities for the species in question. These trees serve as essential sites for courtship displays and offer vital resources such as nourishment and protective cover from potential threats. Specifically, the species *P. rubra* exhibited notable courtship behaviors, critical for mating rituals. Additionally, these trees provided feeding opportunities, allowing *P. rubra* to access food sources necessary for their survival. Furthermore, they offered a refuge from larger avian predators, including raptors, thereby enhancing the overall safety and well-being of the species within these habitats. This multifaceted support highlights the importance of preserving such trees to maintain ecological balance and support biodiversity. We documented various behaviors of *P. rubra* on lek trees, as illustrated in Figure 5.

Principal Component Analysis (PCA) result

The communal value was >0.5 for each variable, which showed the relationship between particular variables and the factors formed (Cahyana et al. 2015). The smaller the communality's value, the weaker the relationship between the variable and the presence of the red paradise. The total value of the Measure Sampling Adequacy (MSA) for all variables is 0.629, indicating that all variables can continue for further analysis (Table 4).

Table 2. Environmental variables measured at each lek tree site, including structural, topographic, and microclimatic parameters. These variables were used as input for subsequent multivariate analyses to identify habitat preferences of *Paradisaea rubra*

Environment variable	**Location**		
	Warkesi	**Saporkren**	**Wailebet**
Architecture type	Roux	Rauh	Leeuwenberg
Tree species	*Gyrinops* sp.	*Callophylum inophylum*	*Ficus lawesii*
Elevation (m asl)	310	228	63
Slope (%)	5	5	0
Temperature (°C)	26	26	26
Moisture (%)	90	90	80

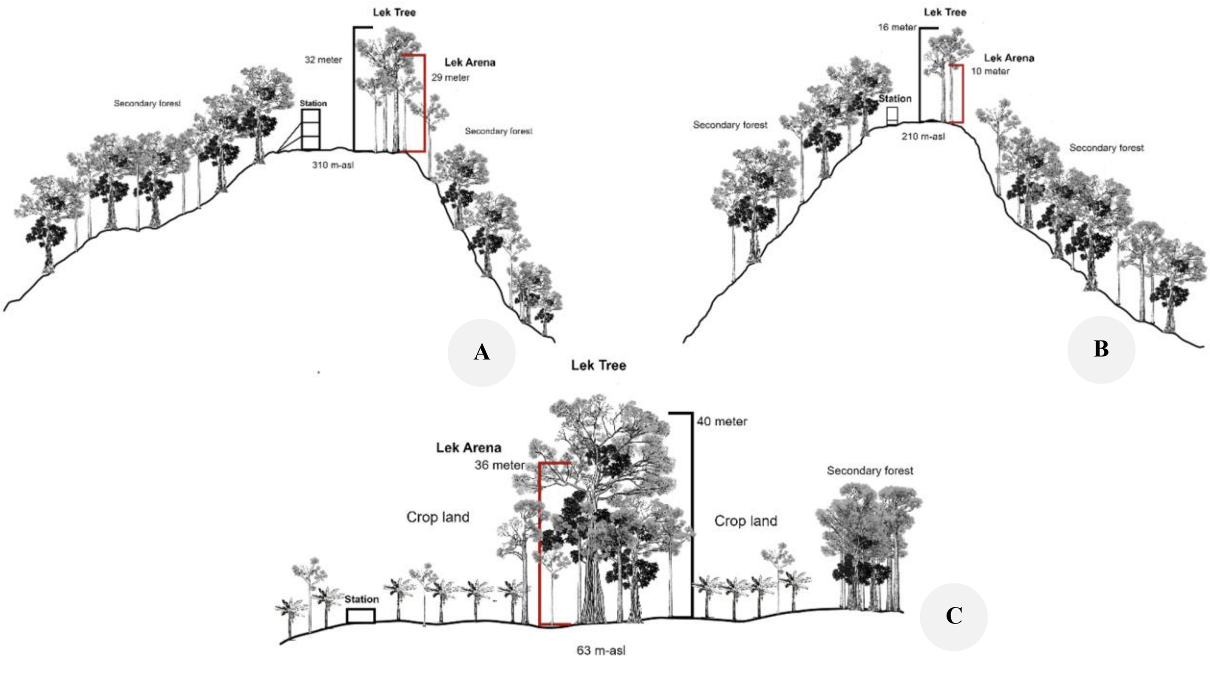

Figure 3. Lek tree used by red bird of paradise (*Paradisaea rubra*) position and situation comparation in Raja Ampat, Indonesia: A. Warkesi, B. Saporkren, C. Wailebet

PCA results showed the formation of three main components with eigenvalues greater than 1 (Hernowo 2017). The first component had an eigenvalue of 2.377, accounting for 29.714% of the total variance. The second component had an eigenvalue of 1.411, contributing 17.633% of the variance. The third component adds a further 13.450% with an eigenvalue of 1.076 (Table 5). Together, these three components accounted for 60.796% of the total variation in the data, which represents a reasonably strong explanatory value for socioecological studies (Hair et al. 2013), especially given the complexity and interdependence among variables.

The results of the varimax rotation on the component matrix produced three main components (PC_1, PC_2, and PC_3) that explained the structure and quality of environmental variables influencing the location of the red bird-of-paradise's lek (Table 6). Elevation (0.774), lek angle (0.754), and canopy cover (CCI: 0.667) primarily shaped the first component (PC_1), while humidity (0.766) and temperature (TMP: 0.718) formed the basis of the second component (PC_2). Tree height (0.732) and slope (0.54) characterized the third component (PC_3), while lek diameter showed a strong negative loading (-0.547) within this component. These three components reflect a complex environmental structure, where lek preference is determined not only by a single ecological dimension but also by a combination of strategic microhabitat position, microclimatic factors, and complementary structural qualities of tree space. These results reinforce the view that lek selection by the red bird-of-paradise is multidimensional.

Table 3. Structural and physical characteristics of lek trees observed across three locations in Raja Ampat, Indonesia (Warkesi, Saporkren, and Wailebet)

Physical measurement	Location		
	Warkesi	Saporkren	Wailebet
Diameter (cm)	48.3	49	120
Tree height (m)	32	16	40
Lek branch direction	North	Southeast	Northeast
Lek branch inclination (°)	60°-90°	45°-80°	30°-60°
Lek branch height (m)	29	10	36
Lek branch diameter (cm)	4.5-7	2.7-3.5	3-3.7
Lek branch length (cm)	110-180	70-100	60-90
Individual number of birds	10	12	21
Canopy cover index	38.93%	57.00%	69.19%

Table 4. KMO test result as initial process in PCA showed eligibility of the data for further analysis

	TH	ELE	SLP	TMP	MST	LD	CCI	LAG
MSA	0.558	0.653	0.76	0.694	0.652	0.769	0.759	0.596
KMT	0.617	0.719	0.611	0.550	0.596	0.542	0.530	0.697

Notes: TH: Tree Height, ELE: Elevation, SLP: Slope, TMP: Temperature, MST: Moisture, LD: Lek Diameter, CCI: Canopy Cover Index, LAG: Lek Angle, MSA: Measure Sampling Adequacy, KMT: Communality

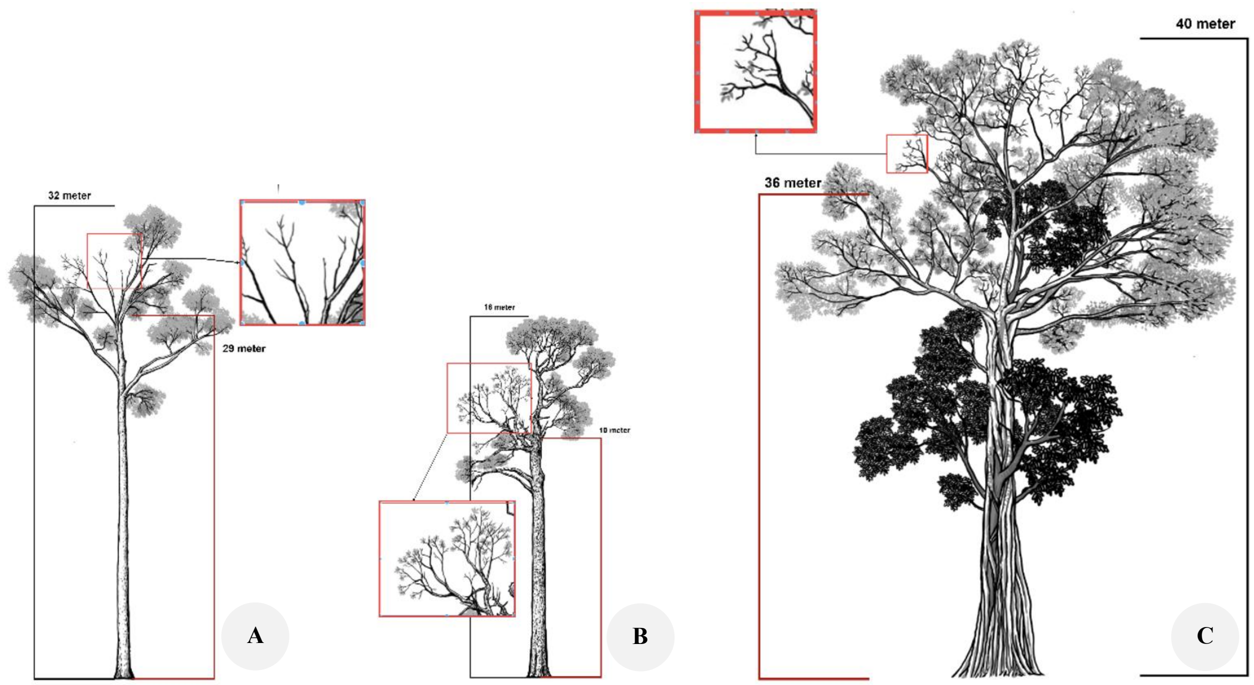

Figure 4. Comparison of lek height using the red bird of paradise (*Paradisaea rubra*) showed that it has less canopy cover or open spaces in Raja Ampat, Indonesia: A. Warkesi, B. Saporkren, C. Wailebet

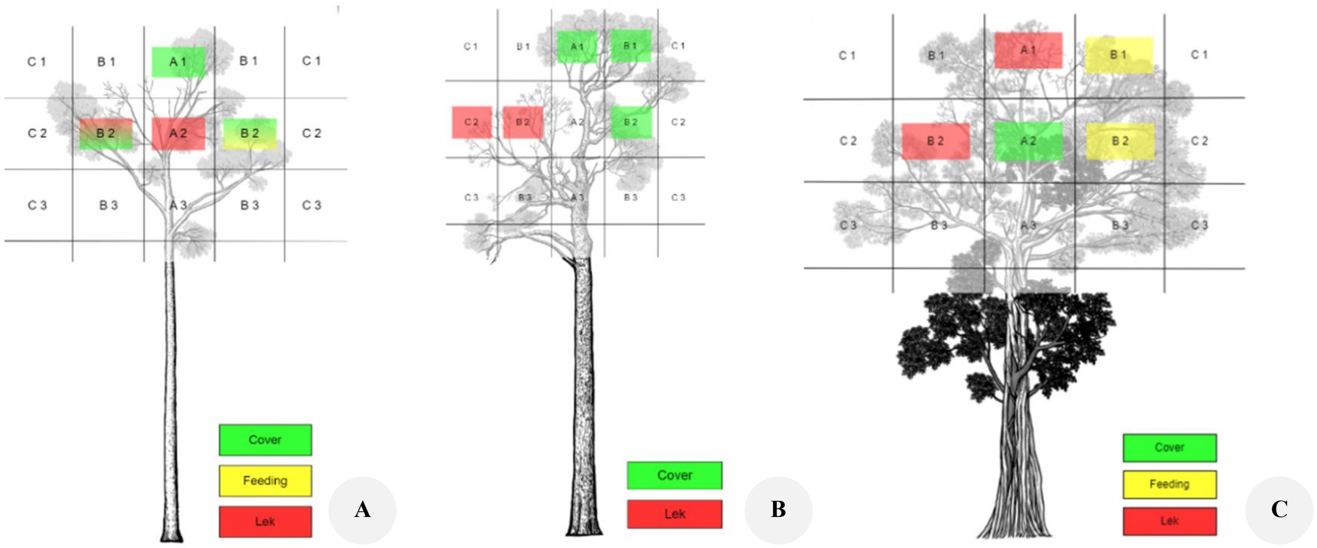

Figure 5. Canopy space using by the red bird of paradise (*Paradisaea rubra*) based on their activity in Raja Ampat, Indonesia: A. Waigeo, B. Saporkren, C. Wailebet showed a different characteristic

Table 5. Initial eigenvalues, percentage of variance, and cumulative variance explained by each principal component derived from PCA

Component	Initial eigen value		
	Total	% variance	% cumulative
1	2.377	29.714	29.714
2	1.411	17.633	47.347
3	1.076	13.450	60.796
4	0.775	9.687	70.484
5	0.745	9.309	79.792
6	0.678	8.479	88.272
7	0.571	7.140	95.411
8	0.367	4.589	100.000

Table 6. PCA results identified two principal components affecting lek preferences: PC, driven by canopy cover, elevation, and lek dimensions; PC, influenced by lek height and slope, reflecting key habitat features for *Paradisaea rubra*

New group	Composing variables	Rotated eigen value
PC_1	Elevation (ELV)	0.774
	Lek angle (LAG)	0.754
	Canopy cover (CCI)	0.667
PC_2	Moisture (MST)	0.766
	Temperature (TEMP)	0.718
PC_3	Tree high (TH)	0.732
	Lek diameter (LD)	-0.547
	Slope (SLP)	0.54

The ANOVA test shows that the regression model with three principal components explains a significant portion of the variation in lek site suitability ($F(3,30)$: 5.467, p: 0.004). The model explains 35.4% of the total variance (318.433 of 900.941), while 64.6% remains unexplained (582.508), likely due to additional ecological or behavioral factors not captured in this analysis. These results demonstrate that the principal components derived from PCA provide strong explanatory power for understanding the ecological gradients influencing lek site selection in *P. rubra*.

The results of the linear regression analysis showed that the value of the dependent variable Y could be partially explained by three principal components (PC_1, PC_2, and PC_3) obtained from the PCA extraction. The first component (PC_1) had a significant adverse effect on Y, with a coefficient of -2.629 and a significance value of p: 0.002 (Table 7). This indicates that an increase in the PC_1 score tends to significantly decrease Y. This interpretation is consistent with earlier findings regarding component loading. PC_1 captures lek site characteristics defined by increased canopy openness, higher elevation, and more robust structural features. This finding suggests that the environmental and spatial attributes associated with PC_1 create a setting that is not only visually expansive but also supports the development of more substantial and noticeable features within the landscape. Such characteristics are likely to influence lekking dynamics by shaping the spatial context in which mating and territorial behaviors occur, although direct behavioral measurements were not undertaken in this study. The second component (PC_2) and third component (PC_3) each showed a positive relationship with Y, with coefficients of 1.093 and 1.243, respectively. However, neither of these relationships was statistically significant (p: 0.165 and p: 0.116), indicating that microclimatic factors (PC_2) and vertical forest structure (PC_3) may play a secondary or context-dependent role compared to the more dominant topographical openness captured by PC_1. Further studies with larger sample sizes or finer spatial resolution may help clarify the extent of their influence.

Table 7. Regression coefficients of principal components affecting lek suitability in *Paradisaea rubra*. PC_1 had a significant negative influence (p: 0.002), while PC_2 and PC_3 showed non-significant positive effects

Component	**B**	**Std. error**	**Standardized β**	**t**	***p*-value**
(Constant)	8.176	0.756	-	10.820	0.000
PC_1 (Topographic openness)	-2.629	0.767	-0.503	-3.427	0.002
PC_2 (Microclimate)	1.093	0.767	0.209	1.424	0.165
PC_3 (Vertical structure)	1.243	0.767	0.238	1.620	0.116

Discussion

Ecological determinant of lek site

Our Principal Component Analysis (PCA) identified three main ecological dimensions influencing lek site selection in *P. rubra*: topographic openness, microclimatic conditions, and vertical structure. Male birds consistently preferred display trees at higher elevations, with semi-open canopies and steep vertical angles. These characteristics enhance visual exposure, acoustic projection, and spatial mobility, critical for successful courtship display. This pattern supports Frith's (1976) ethological observations, which noted that males favor vertical perches and often engage in active vegetation clearing to optimize signal transmission.

Topographic openness (PC_1), which exhibited a significant negative relationship with lek suitability, captured this structural profile, comprising elevation, canopy cover, and branch inclination. Males appear to select trees that amplify their display effectiveness through enhanced visibility and sound propagation. Similar lek placement strategies have been documented in *Rupicola rupicola* and *C. gutturalis*, where birds utilize specific light environments to increase signal contrast (Kelley and Endler 2012), as well as in grouse species that prefer elevated, open terrains to maximize acoustic reach (Coates et al. 2014). In contrast, PC_2 (humidity and temperature) and PC_3 (tree height and slope) showed positive but statistically non-significant associations with lek suitability. These components may still influence lek behavior by providing thermally stable or acoustically favorable conditions, as observed in other lekking species such as manakins, where temperature affects display frequency and female attendance (McDonald 1989; Horng et al. 2009; Anderson et al. 2024). The vertical structure captured in PC_3 may also support refuge from predators or better acoustic dispersion, as seen in *Tetrao urogallus* (Horng et al. 2009).

Beyond the environmental features, lek architecture itself reflects ecological filtering. Display trees typically followed architectural models like Leeuwenberg or Roux, providing regular branching and structural support for movement. Males often selected lek trees that faced north or south, likely to improve plumage visibility by enhancing light contrast, particularly considering the importance of structural coloration in birds of paradise (Wilts et al. 2014). This suggests that males may strategically select display sites for structural advantage and to optimize their visual signaling under natural light. While male behavior dominates lek display, female strategy also plays a central role in shaping lek dynamics. In *P. rubra*, as in many lekking species, females actively assess multiple males across several sites before mating. This behavior exerts intense selection pressure on males to secure high-quality display platforms that offer optimal visibility, acoustic clarity, and safety (Ligon et al. 2018; Isvaran 2021). From the female's perspective, lek sites function as efficient environments for mate sampling. Structural traits, branch inclination, canopy openness, and elevation, directly affect the ability to evaluate male displays. Studies in manakins and ruffs show that lek structural configuration influences both female visitation and mate choice, thereby intensifying sexual selection (Endler and Thery 1996; Kelley and Endler 2012).

Importantly, female preferences are not random. Research shows consistency in mate selection based on display position, visual clarity, and male proximity within the lek (Beehler and Foster 1988; Westcott 1994). This reinforces habitat-based selection pressures, where specific trees or microhabitats are reused across breeding seasons. In this sense, lek sites act as ecological "hotspots", integrating spatial fidelity, sexual selection, and microhabitat suitability. Compared to other birds-of-paradise like *P. minor*, which lek communally within dense canopies, *P. rubra* displays a more solitary or semi-communal system on structurally prominent trees. This divergence supports the hotspot model of lek evolution, wherein environmental architecture, rather than male aggregation, determines lek location (Beehler 1983a; Bradbury et al. 1986). Similar patterns are found in *Pavo muticus*, which selects open, undisturbed ground for courtship to enhance display clarity and predator awareness (Hernowo 2017), and in manakins, which prefer forest gaps for optimal acoustic signaling (Brumm 2009; Austin et al. 2021).

Habitat openness, particularly canopy density, influences both visibility and sound propagation. In dense forests, males must increase call amplitude to overcome attenuation caused by leaf and branch scattering (Delgado and Penteriani 2007; Brumm 2009). This imposes energetic or social costs, rival aggression, that only high-quality males can bear (Brumm and Ritschard 2011; Zollinger et al. 2011; Clark and Areta 2023). Therefore, lek trees with semi-open canopies and elevated positions offer enhanced signal transmission and reduced signaling cost. Our findings suggest that lek site selection in *P. rubra* reflects behavioral plasticity in response to ecological constraints, rather than fixed preferences. Male birds dynamically adjust their site choices to enhance signal efficacy, while females reinforce these preferences through selective mate choice.

Integrating behavior and landscape in conservation planning

Given these ecological requirements, conservation of *P. rubra* must prioritize structurally complex forest habitats that include emergent trees with sufficient spacing, vertical structure, and north-south exposure. This study contributes to understanding habitat-specific reproductive behavior, with implications for conserving behaviorally critical microhabitats in the face of land-use change. Forest area authority should protect ridgelines and elevated terrain where leks are most likely to form. Additionally, ecotourism, although economically beneficial, must be carefully regulated near lek sites, as noise and visual disturbances could affect male display routines and female choice (Cita et al. 2019).

Effective conservation of *P. rubra* requires more than protecting forest cover alone. Our findings argue for integrating behavioral ecology into spatial planning frameworks, especially lek microhabitat requirements. Habitat degradation through agricultural expansion, infrastructure development, or unregulated tourism can disrupt lek formation and reduce reproductive success. Landscape-scale strategies should incorporate lek mapping, remote sensing data, and community stewardship to ensure lek stability over time. Encouragingly, many lek sites lie within customary forest territories, providing a strong foundation for community-based conservation. Understanding lek preferences in *P. rubra* reveals how fine-scale environmental features shape complex mating systems. This insight provides a theoretical contribution to sexual selection studies and a practical foundation for ensuring the long-term persistence of this flagship species in Raja Ampat.

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