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RESEARCH ARTICLE

Fruiting Tree Used by Greater Bird-of-Paradise (*Paradisaea apoda*) in Logging Concession in South Papua

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ABSTRACT

The greater bird-of-paradise (*Paradisaea apoda*), known as an endemic bird of the Papuan region, plays a vital role in seed dispersal. While habitat conversion threatens populations, empirical data on foraging ecology within managed landscapes remain scarce. This study evaluated the structural characteristics and dietary preferences of fruiting trees utilized by *Paradisaea apoda*. Fieldwork was conducted in the PT Inocin Abadi concession, South Papua, for 75 days from July to September 2023 and September 2024. Feeding trees were confirmed at nine observation points based on direct observation, relatively extended periods with fruit-handling movements, and evidence of fallen fruits. Vegetation structural attributes were quantified across 18 sampling sites using squared line transects. Species dominance was evaluated using the Importance Value Index (IVI). Of the five tree species recorded, six were identified as food sources, with direct consumption observed for *Myristica inspida* and *Oncosperma tigillarium*. The consumed fruit dimensions ranged from 5.97 to 40.07 mm in length and 6.19 to 25.40 mm in diameter. The IVI analysis revealed no single species dominance, reflecting an even co-dominant structural profile within the concession area. Two food plants (*Calophyllum soulattri* and *Myrstica fatua*) overlap with commercial timber species. To maintain habitat suitability, concession areas must enforce non-harvesting policies within river buffer zones and integrate food plants into retention-tree guidelines and enrichment planting programs.

Introduction

The greater bird-of-paradise (*Paradisaea apoda*) has long been recognized globally for its stunning plumage and complex behavioral ecology. This endemic species of Papua Island (Indonesia and Papua New Guinea) has a limited distribution from the southern part of Papua to the Aru Islands [1] and inhabits lowland tropical forests [2]. Similar to other frugivorous birds, the greater bird-of-paradise feeds primarily on fruits and plays an important ecological role as a seed disperser in tropical forest ecosystems [3,4]. Despite their crucial role in the ecosystem, information regarding their diet composition remains limited. This species is legally protected under Indonesian law through the Ministry of Environment and Forestry Regulation No. P.106 of 2018 concerning the Protected Species of Plants and Animal, and is currently listed in the CITES Appendix II. However, the population of the greater bird-of-paradise is declining. Hunting for trade, traditional usage by indigenous communities, and land-use change are serious threats to this species [5,6]. The lack of ecological and behavioral data in scientific publications exacerbates this vulnerability. One ecological aspect that remains poorly understood is feeding ecology, which includes diet composition, foraging behavior, food

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availability, and feeding habitat. Food is a fundamental requirement for all living organisms, and its availability may influence reproductive capabilities and the timing of breeding [7] and interspecies interactions [8]. It is important to identify the fruits consumed by the greater bird-of-paradise.

Several previous studies have identified fruiting tree families, such as Meliaceae (*Chisocheton lasiocarpus* and *Dysoxylum pettigrewwianum*), Moraceae (*Ficus obliqua*), Myristicaceae (*Myristica* sp.), and Podocarpaceae (*Podocarpus nereifolius),* as vital food sources for Paradisaeidae [9,10]. Typically, frugivorous birds select these plants based on fruit traits that match their bill morphology and metabolic demands, such as lipids and carbohydrates [3]. However, information on the greater bird-of-paradise remains limited. Raggiana bird-of-paradise (*Paradisaea raggiana*)*,* a closely related species is more commonly referenced in comparison studies [11]. Recent studies focusing on *Paradisaea apoda* offer only generalised descriptions of its broad feeding habitats, without describing the specific attributes of tree it visits [12–14]. Consequently, a gap persists in our understanding of the diet and foraging ecology of *Paradisaea apoda*, particularly within disturbed or managed landscapes [9,12–15].

Lekking behavior (part of the greater bird-of-paradise) was confirmed to occur within the concession area of PT Inocin Abadi, near human settlement and logging activities [16]. This record highlights the ecological importance of the area in supporting greater bird-of-paradise populations. Simultaneously, it raises challenges for sustainable forest management that also considers the ecological needs of endemic species, such as the greater bird-of-paradise. In addition to lekking areas, the greater bird-of-paradise also requires sufficient food sources [17]. In the context of a concession area, food availability is particularly crucial, as tree species harvested for timber may also serve as fruiting trees for the greater bird-of-paradise. This study aimed to evaluate the fruiting tree species utilized by *Paradisaea apoda* within a logging concession area by identifying food plant species, quantifying their general structural attributes, and assessing their spatial distribution patterns. We hypothesized that *Paradisaea apoda* does not depend on a single fruiting tree species for its diet but rather utilizes available fruit resources based on their abundance within the managed forest landscape. The findings are also expected to provide a basis for designing forest management policies that consider the ecological needs of the greater bird-of-paradise while maintaining the sustainable use of timber sources.

Materials and Methods

Study Area

This study was conducted within the timber concession area of PT Inocin Abadi, South Papua Province, Indonesia, from July to September 2023 and September 2024. The observation period was selected to coincide with the breeding season of the greater bird-of-paradise. This breeding season normally occurs from early July to late September [16]. Observations were carried out over 75 days, totalling approximately 600 h of field monitoring (ranging from 6 to 9 h per day, depending on weather conditions and site location). Fieldwork was performed by two personnel: one primary observer and one employee from PT Inocin Abadi, who served as a local guide and assisted with vegetation data measurement.

The total concession area of PT Inocin Abadi encompasses 99,665 ha (Figure 1). However, less than half of this area (approximately 40,000 ha) was logistically accessible during the study period. This limitation was primarily due to the absence of logging roads in undisturbed areas where logging activities had not yet commenced, compounded by restricted access to several post-harvest areas where former tracks had become inaccessible. To establish sampling within the accessible area, the study area was divided into 500 × 500 m grid cells to facilitate boundary delineation, generating 4,119 grid cells. Rather than utilizing the entire grid, sampling plots were selectively narrowed based on historical report data and preliminary studies. Initially, 20 encounter points from 2022 PT Inocin Abadi report and 12 observation points from preliminary study (5–20 July 2023) were identified. Through curation process based, 9 observation sites were established across 9 distinct grid cells.

These nine observation sites were used for monitoring the foraging behavior of the greater bird-of-paradise and were subsequently designated as vegetation sampling plots to characterize the foraging habitat. Vegetation sampling was expanded to one to three adjacent grid cells around these nine primary grid cells based on the visible movement of the greater bird-of-paradise and terrain feasibility. Although this sample size was relatively small and unevenly distributed relative to the entire study area, further expansion was strictly constrained by the inaccessible and limited logistics available in the remote terrain. Consequently, research efforts have focused on these accessible grid cells.

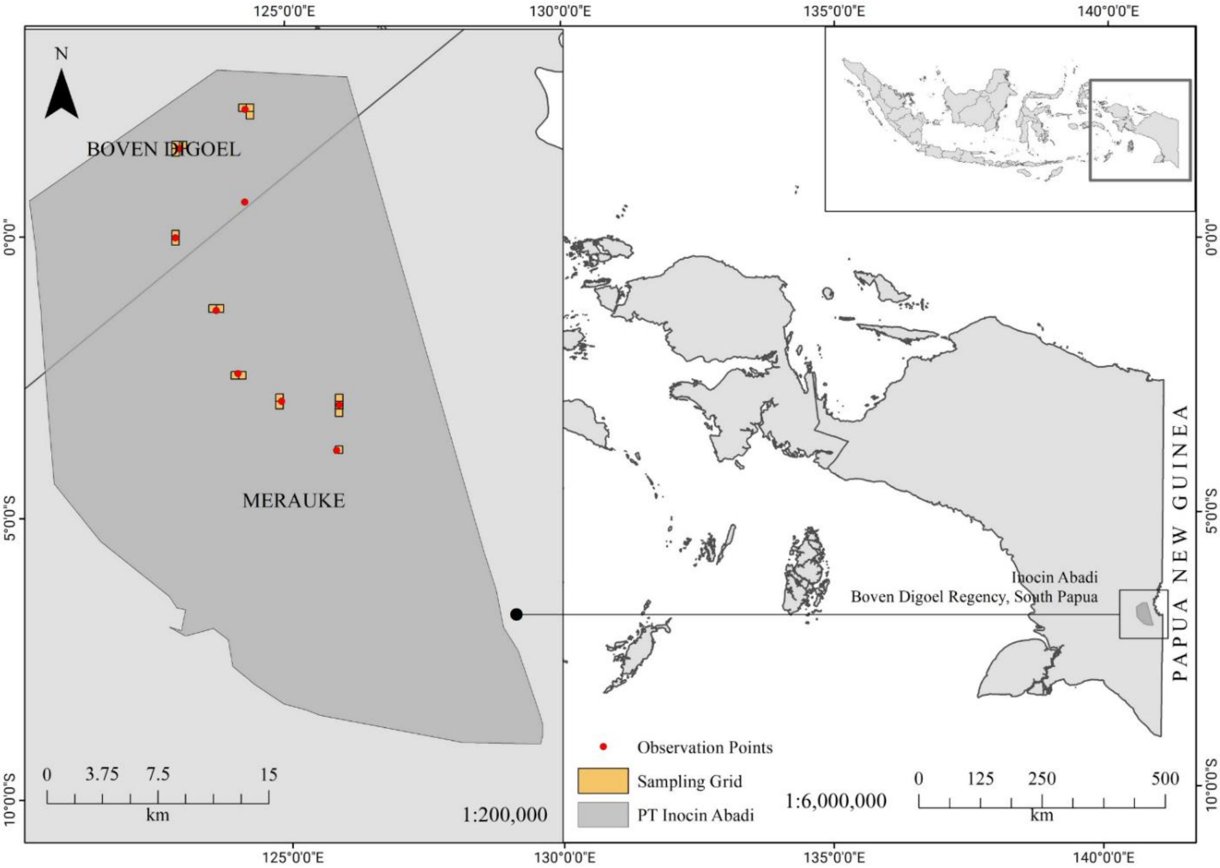

Figure 1. Map of the study area located within the timber concession of PT Inocin Abadi. A total of 9 observation points and 18 sampling grids are distributed based on ecological conditions, greater bird-of-paradise encounter intensity, and site accessibility.

Data Collection

A literature review and informal discussions with local communities were conducted to gather information on the feeding ecology, preferred foraging habitats, and fruiting tree species of the greater bird-of-paradise. These sources provided an initial understanding of where the foraging habitat and activities of the greater bird-of-paradise are most likely to occur. During the preliminary study in the first two weeks, individuals were located using a combination of habitat features, such as creeks, rivers, and swamp patches, at nine observation points. This information was then used to guide subsequent field observations and sampling efforts.

Tree species with fruits considered potential food sources were identified based on direct observations of feeding, bird activities on fruiting trees, fruit characteristics, and information from local communities. The greater bird-of-paradise is often difficult to observe while foraging in fruiting trees because of the dense surrounding canopy. Therefore, a tree species was categorized as a feeding tree when a bird spent more than 2 min within the canopy while exhibiting fruit-handling movements (i.e., maneuvering toward fruit patches, head movement toward fruits, or movement between branches), accompanied by evidence of fruit consumption (e.g., fallen or partially eaten fruits beneath the tree). Trees on which individuals were only perched without visible feeding cues were excluded.

Each observation did not occur on the same tree. The foraging behavior of the greater bird-of-paradise was immediately recorded upon an individual's arrival at a feeding tree and ended when the bird flew away or was no longer visible for observation. Individuals were rarely observed for extended periods. This brief duration of behavior minimized the likelihood of recording the same individual within a short period. This ensures sampling independence. Additionally, the total number of fruits consumed during each foraging behavior was quantified.

A circular plot of 0.1 ha (radius 17.8 m) [18] was established around each fruiting tree that was confirmed to be consumed by the greater bird-of-paradise. Plots were created to describe the foraging habitat conditions surrounding each fruiting tree. The plot size was justified as the greater bird-of-paradise often leaves the area where foraging occurred when it has finished obtaining fruits in that area. A single representative individual was selected based on observations of the foraging behavior of the greater bird-of-paradise recorded on a particular tree. A circular plot was not established for *Oncosperma tigillarium* because it occurs widely across various habitat conditions and can be found easily across the study area. Only morphological information was recorded for each species. Squared-line transects were also established within the 18 grid cells to determine the frequency, density, and dominance of tree species within the foraging habitat of the greater bird-of-paradise. Within each grid cell, five plots were created along a 100 m transect line (Figure 2). Each transect comprised 10 × 10 m subplots for poles and 20 × 20 m subplots for trees.

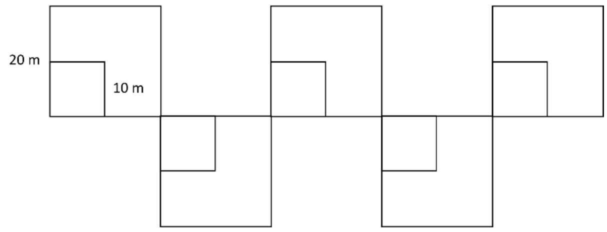

Figure 2. Schematic layout of the squared-line transects used for vegetation sampling. Nested 10 × 10 m subplots were designated for recording pole-phase individuals, while the 20 × 20 m subplots were used for tree-phase vegetation. Within each plot, the recorded data included diameter at breast height (DBH, cm), total height (m), clear bole height (m), and crown width (m). These variables were selected to represent the structural attributes of the foraging habitat. The distance and azimuth of each neighboring tree relative to the focal feeding tree were also recorded for the circular plot. All measurements were taken to the nearest centimeter (for DBH) and meter (height and tree width-related) due to equipment and visibility limitations.

Fruit dimensions (diameter, length, and mass of fresh fruit) were measured using available samples. Most fruiting trees did not produce fruits during the observation period, resulting in an uneven number of samples for each species. Sample fruits were obtained from fallen fruits or freshly picked from the tree if available. In the case of fallen fruits, fruits must be ensured from the same tree by observing and comparing the fallen fruits with fruits that are still on the tree. Fruit shapes were also classified based on the categories of fruit consumed by the raggiana bird-of-paradise *Paradisaea raggiana* [15].

The fruiting season of each tree species consumed by the greater bird-of-paradise was determined through field observations and data provided by PT Inocin Abadi. Field observations focused on identifying the presence of fruits or flowers on trees whose fruits were known to be consumed by the species. Additional data from PT Inocin Abadi were obtained from the nursery unit, which manages tree seedlings for future production forest plantation. These data were then combined to provide an overall overview of the fruiting phenology of greater bird-of-paradise food trees.

Data Analysis

The vegetation structure of the greater bird-of-paradise foraging habitat and the area surrounding each feeding tree was analyzed to describe the vertical and horizontal conditions of the habitat. The structural characteristics were illustrated using a diagram to visualize the spatial arrangement and canopy layering. The spatial distribution pattern of each feeding tree species was analyzed using the Morisita Index (I_d) (Equation 1). To standardize the indices across species with different sample sizes, the Standardized Morisita Index was used (I_p) (Equation 2). Standardized Morisita Index values of I_d greater than 1 indicate a clumped distribution, values equal to 1 indicate random distribution, and value less than 1 indicate a uniform distribution. The I_p values ranged from –1 to +1, where values close to +1 indicate a highly clumped distribution, values near 0 indicate a random distribution, and values close to –1 indicate a uniform distribution. Species with a low number of individuals were not included in the analysis to avoid misinterpretation. Feeding trees and other tree species recorded within the sample plot were analyzed using the Importance Value Index (IVI, Equation 3). This index was used to assess the dominance of tree species in the foraging habitat of the greater bird-of-paradise. Data processing and tabulation were performed using Microsoft Excel, utilizing pivot tables to facilitate efficient data filtering and synthesis.

$$I_d = n\frac{(\sum Xi^2 - \sum Xi)}{(\sum Xi)^2 - \sum Xi} \quad (1)$$

$$I_p = \begin{cases} \frac{0.5(I_d-1)}{n-1} + 0.5, \; if \; I_d \geq 1 \\ 0.5 - \frac{0.5(I_d-1)}{n-1}, \; if \; I_d < 1 \end{cases} \quad (2)$$

$$IVI = RF + RD + RDo \quad (3)$$

where I_d: Morisita Index, I_p: Standardizes Morisita Index, n: number of observation plots, $\sum X_i$: number of individuals each species on every observation plot, IVI: Important Value Index, RF: Relative Frequency, RD: Relative Density, RDo: Relative Dominance.

Results and Discussion

Results

Six plant species were identified as food sources for the greater bird-of-paradise (Table 1), with only two species, *Myristica inspida* and *Oncosperma tigillarium*, being directly observed to be consumed. When ripe, *Myristica inspida* fruits naturally split open along the midline, revealing the enclosed seed in an orange-to-red aril. The greater bird-of-paradise was observed consuming the aril, swallowing the seed along with it, and regurgitating the seed later. In contrast, *Oncosperma tigillarium* fruit is from a palm tree species (Arecaceae family). Many frugivorous birds, alongside the greater bird-of-paradise, also consume this fruit (e.g., variable pitohui (*Pitohui urophygialis*), red-cheeked parrot (*Geoffroyus geofroyi*), fruit-doves (*Ptilinopus* sp.), and king bird-of-paradise (*Cicinnurus regius*)).

Table 1. List of tree species utilized by the greater bird-of-paradise as food sources. Data were compiled from direct observations, secondary literature, and local ecological knowledge.

Species name	Family	Notes	Source information
Calophyllum soulattri	Calophyllaceae	Tall-emergent trees with a narrow canopy, not a commercial timber species for veneer production but harvested for making bridges and other construction due to its strong wood.	Local information (fruit characteristics), secondary data [14]
Ficus obliqua	Moraceae	Strangler, the host tree was already dead when found, leaving a space in the middle, has a wide canopy, not a commercial timber species, often used by several bird species as food.	This study, secondary data [9]
Myristica fatua	Myristicaceae	Located at the edge of a small creek, many husks were found under the trees without any seed in them, tall trees, harvested as commercial timber.	This study
Myristica inspida	Myristicaceae	Mostly having small diameters of less than 20 cm and not qualified as harvested commercial timber species, they have a clumped fruit type.	This study
Oncosperma tigillarium	Arecaceae	A palm species with seasonally heavy fruit, easily found in many places, in some areas could reach above canopy of stratum B*.	This study
Syzygium sp.	Myrtaceae	Located in a dry swamp forest, tall but located at B stratum (non-emergent), the species name was still unidentified, not qualified as a commercial timber species harvested due to its hardness.	This study

*Main canopy, non-emergent.

Fruits from the other four food tree species were not directly observed to be consumed because of visibility limitations, as greater bird-of-paradise foraging activities mainly occur in dense crown areas. Otherwise, observations using binoculars showed individuals of the greater bird-of-paradise actively moving from one branch to another and moving towards the fruit patch. This behavior occurred over a relatively long period (> 2 min), and fruits that fell during the activities showed foraging behavior. This behavior was observed at least three times for each food tree species (except *Calophyllum soulattri*), suggesting that greater bird-of-paradise also utilized fruits from these tree species. Local information also provided additional information for interpretation. Nevertheless, further confirmation is required to verify the direct consumption of these four species.

Food tree species visited by the greater bird-of-paradise and their surrounding areas shared similar structural characteristics (Table 2, Figure 3. Vertically, most fruiting trees were categorized as canopy strata B and C (lower canopy) with an average height of 22.8 m. The only exception was *Calophyllum soulattri*, an emergent species (stratum A) that reached heights of over 40 m. The feeding activities of the greater bird-of-paradise were more frequently encountered around seasonal streams or small rivers (4 out of 5 encounters; 80%). The *Myristica fatua* sample tree (Figure 3-C), where the greater bird-of-paradise was observed foraging, was located right on the edge of a seasonal stream. Additionally, the area surrounding the sample tree also contained canopy gaps, resulting in a lack of dense tree canopy in the entire area.

Table 2. The characteristics of each representative food tree species were obtained from the circular plot. Numbers were taken to the nearest centimeter and meter.

	Calophyllum soulattri	*Ficus obliqua*	*Myristica fatua*	*Myristica inspida*	*Oncosperma tigillarium*	*Syzygium sp.*
Diameter (cm)	30	75	24	21	19	37
Height (m)	40	25	19	13	15	17
Clear-bole height (m)	20	18	9	8	14	10
Crown width (m)	5	13	5	4	4	9
Surrounding crown density*	Mid	High	Mid	Mid	Low	High
Stratum**	A	B	B	C	C	B

*High: 0–30% sunlight penetration to forest floor; Mid: 30–60 %; Low: 60–100%.
**A: emergent; B: main canopy; C: lower canopy; D: seedlings and shrubs; E: ground cover.

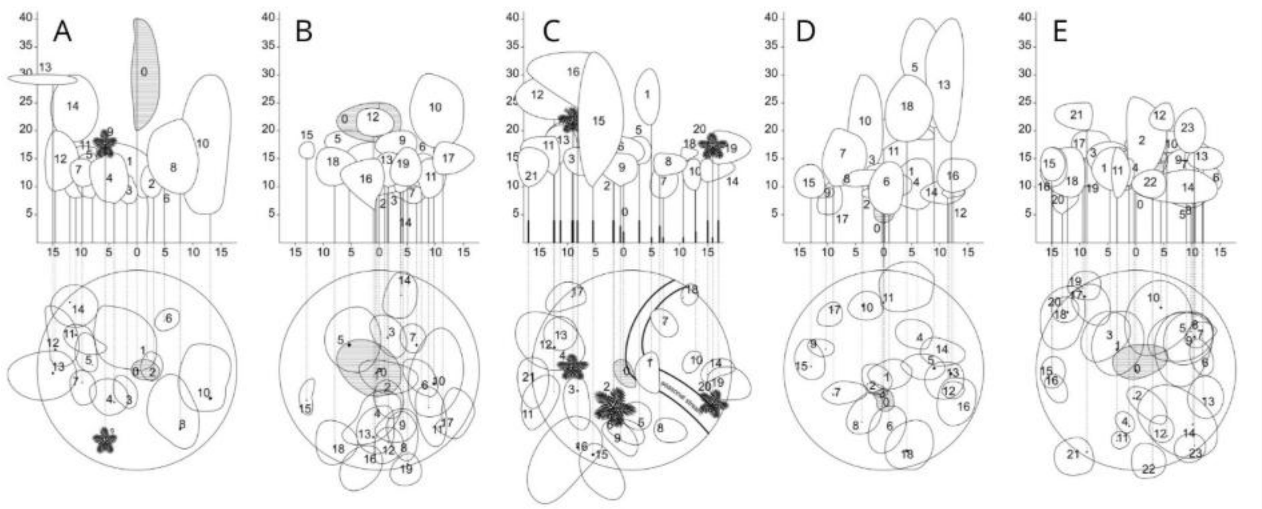

Figure 3. Veritcal and horizontal habitat structural diagrams centered on sample feeding trees (marked as number 0 with a darker shade) and their surroundings utilized by greater bird-of-paradise. Circular plots represent focal feeding tree species: (A) *Calophyllum soulattri*, (B) *Ficus obliqua*, (C) *Myristica fatua*, (D) *Myristica inspida,* and (E) *Syzygium* sp., complemented by a star-shaped diagram illustrating *Oncosperma tigillarium* stand.

The Morisita Index indicated that most food tree species used by bird-of-paradise exhibited clumped distribution patterns, except for *Ficus obliqua* (Table 3). *Ficus obliqua* was excluded from the analysis to avoid unreliable spatial distribution interpretation, due to only two individuals found across all plots. *Myristica inspida* showed the highest density, with 50.0 trees/ha. In contrast, *Myristica fatua* had the lowest density at 11.9 trees/ha. The number of fruit samples obtained from each species varied owing to fruit availability. Some species were represented by only five samples. As a result, fruit size estimates for these species may not fully capture their variation. *Calophyllum soulattri* did not produce fruits during the observation period, whereas only a few fruits of *Myristica fatua* were collected. Most *Myristica fatua* fruits found on the ground were already split open and lacked seeds. Although the sample size is too small to provide a statistically reliable estimate for the entire species, these measurements are retained to offer an initial indication that *Myristica fatua* can exhibit a larger fruit dimension. The fruits of *Oncosperma tigillarium* were at heights that made direct collection impossible, and fallen bunches no longer contained fresh and intact fruits suitable for measurement.

Table 3. Spatial distribution of feeding tree species used by the greater bird-of-paradise. Spatial pattern is quantified using the Morisita Index (I_d) and the Standarized Morisita Index (I_p) where values of $I_p > 0.5$ indicate a clumped distribution pattern.

Tree species	Species density (tree/ha)	I_d	I_p	Distribution pattern
Calophyllum soulattri	18.0	9.33	0.745	Clumped
Ficus obliqua	0.5	0.00	n/a	-
Myristica fatua	11.9	5.48	0.632	Clumped
Myristica inspida	50.0	6.59	0.665	Clumped
Oncosperma tigillarium	15.2	7.33	0.686	Clumped
Syzygium sp.	14.7	7.96	0.696	Clumped

-: samples were too small for estimation.

The fruit consumed by the greater bird-of-paradise was small to medium in size (Table 4, Figure 4). Fruits under 10 mm in diameter were typically swallowed whole while the bird was perched on fruiting branches or clusters, as observed with *Oncosperma tigillarium* (Figure 5). Fruit color varies among fruiting tree species, including green, yellow, orange, red, brown, and black. Within the Myristicaceae family, species such as *Myristica inspida* and *Myrisitca fatua* produce brightly colored arils ranging from orange to red.

Table 4. Fruit dimensions (mean ± standard deviation) from each species fruit tree species within the study site. While the majority of species exhibit small to medium-sized fruit dimensions, sample sizes for *Calophyllum soulattri, Myristica fatua,* and *Oncosperma tigillarium* were limited or unavailable due to seasonal fruiting variation.

Tree species	n	Mean diameter (mm)	Mean length (mm)	Mean mass (gr)	Colour	Type
*Calophyllum soulattri**	n/a	n/a	n/a	n/a	n/a	n/a
Ficus obliqua	30	6.19 ± 0.55	5.98 ± 0.57	< 1.0	Orange to red	Fig
Myristica fatua	3	25.40 ± 1.28	40.07 ± 12.00	12.7 ± 4.2	Brown	Capsule
Myristica inspida	30	17.82 ± 4.93	18.88 ± 5.09	3.3 ± 0.8	Brown	Capsule
*Oncosperma tigillarium***	n/a	n/a	n/a	n/a	n/a	n/a
Syzygium sp.	15	22.48 ± 1.53	25.51 ± 1.77	8.3 ± 2.1	Greenish brown	Drupe

*Did not produce fruit during observation.
**Palm species.

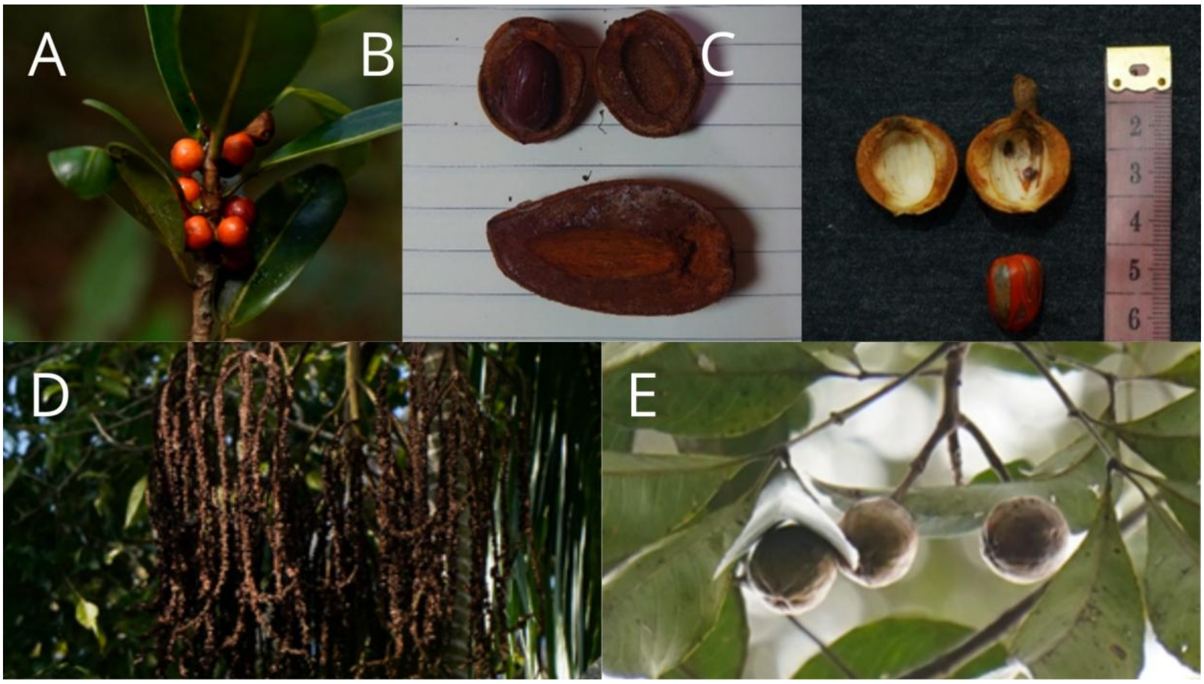

Figure 4. Fruit documentation from each species utilized by greater bird-of-paradise.Individual panels show ripe fruits of (A) *FIcus obliqua,* (B) *Myristica fatua*, (C) *Myristica* inspida, (D) *Oncosperma tigillarium*, and (E) Syzygium sp., highlighting distinct physical characteristics of the greater bird-of-paradise food sources.

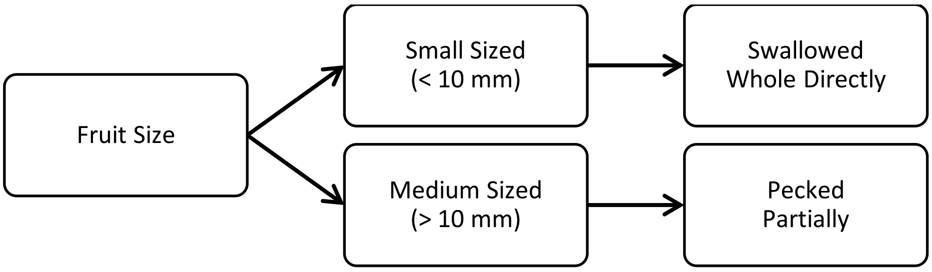

Figure 5. Conceptual figure of foraging behaviour of greater bird-of-paradise based on fruit size. Fruits with relatively small in size dimensions were swallowed directly, while the medium-sized-fruit were pecked partially.

Of the 45 tree species found (43 tree stage and 32 pole stage), *Myristica inspida,* which was identified as a food tree species consumed by the greater bird-of-paradise, had the highest IVI compared to other food trees, followed by *Calophyllum soulattri. Vatica rassak* was the most abundant species (313 individuals recorded) with highest IVI. However, the IVI of this species was only slightly higher than that of the other species, showing that no single species dominated the forest structure within the foraging habitat of the greater bird-of-paradise. When compared to the five species with the highest IVI, most of the fruiting trees utilized by the greater bird-of-paradise exhibited relatively low IVI (Table 5).

Table 5. Important Value Index (IVI) of tree and pole-stage vegetation recorded across the sampling grid, excluding *Oncosperma tigillarium.* Overal, *Vatica rassak* exhibited the highest IVI among all, whereas *Myristica inspida* recorded as the highest IVI among the fruiting tree used by the greater bird-of-paradise.

No	Tree species	Family	IVI (%)
Tree stage (total 43 species)			
1	*Vatica rassak*	Dipterocarpaceae	37.914
2	*Gironniera nervosa*	Cannabaceae	21.901
3	*Rhodamnia* sp.	Myrtaceae	19.709
4	*Gironniera* sp.	Cannabaceae	19.666
5	*Syzygium* sp.	Myrtaceae	19.300
6	*Syzygium* sp.	Myrtaceae	13.868
7	*Hopera iriana*	Dipterocarpaceae	12.258
8	*Myristica inspida**	Myristicaceae	11.455
9	*Calophyllum soulattri**	Calophyllaceae	10.425
10	*Hopea* sp.	Dipterocarpaceae	10.377
11	*Syzygium* sp.	Myrtaceae	10.306
12	*Gironniera* sp.	Cannabaceae	10.163
13	*Myristica fatua**	Myristicaceae	9.273
14	*Pometia pinnata*	Sapindaceae	8.659
15	*Syzygium* sp.*	Myrtaceae	7.863
16	*Aloxyllon brachicarpum*	Proteaceae	6.768
17	*Palaquium* sp.	Sapotaceae	6.376
18	*Eucalyptus* sp.	Myrtaceae	5.792
19	*Hopea papuana*	Dipterocarpaceae	5.244
20	*Calophyllum inophyllum*	Calophyllaceae	5.119
21	*Shorea similis*	Dipterocarpaceae	4.350
22	*Anisoptera* sp.	Dipterocarpaceae	4.175
23	*Dillenia* sp.	Dilleniaceae	4.132
24	*Campnosperma brevipetiolatum*	Anarcadiaceae	4.118
25	*Casuarina equisetifolia*	Casuarinaceae	4.058
26	*Litsea firma*	Lauraceae	3.823
27	*Nauclea orientalis*	Rubiacaeae	3.603
28	*Palaquium obtusifolium*	Sapotaceae	3.115
29	*Anisoptera costata*	Dipterocarpaceae	2.565
30	*Gironniera* sp.	Cannabaceae	2.193
31	*Gironniera* sp.	Cannabaceae	1.445
32	*Gnetum gnemon*	Gnetaceae	1.361
33	*Syzygium sp.*	Myrtaceae	1.228
34	*Ficus obliqua**	Moraceae	1.197
35	*Calophyllum* sp.	Calophyllaceae	1.006

No	Tree species	Family	IVI (%)
36	*Syzygium sp.*	Myrtaceae	0.971
37	*Acacia mangium*	Fabaceae	0.912
38	*Anisoptera* sp.	Dipterocarpaceae	0.721
39	*Cerbera floribunda*	Apocynaceae	0.590
40	*Podocarpus* sp.	Podocarpaceae	0.590
41	*Terminalia brassii*	Combertaceae	0.523
42	*Aquilaria* sp.	Thymelaeaceae	0.448
43	*Hopea* sp.	Dipterocarpaceae	0.439
Pole stage (total 30 species)			
1	*Myristica inspida**	Myrisiticaceae	26.896
2	*Gironniera* sp.	Cannabaceae	22.734
3	*Vatica rassak*	Dipterocarpaceae	20.237
4	*Gironniera nervosa*	Cannabaceae	19.424
5	*Syzygium* sp.	Myrtaceae	18.143
6	*Rhodamnia* sp.	Myrtaceae	16.926
7	*Hopea Iriana*	Dipterocarpaceae	16.536
8	*Gironniera* sp.	Cannabaceae	15.834
9	*Myristica* sp.	Myrtaceae	15.135
10	*Syzygium* sp.*	Myrtaceae	12.001
11	*Calophyllum soulattri**	Calophyllaceae	11.505
12	*Hopea* sp.	Dipterocarpaceae	10.713
13	*Syzygium* sp.	Myrtaceae	9.668
14	*Myritica fatua**	Myrisiticaceae	7.486
15	*Palaquium* sp.	Sapotaceae	7.425
16	*Eucalyptus* sp.	Myrtaceae	6.268
17	*Hopea similis*	Dipterocarpaceae	6.131
18	*Pometia pinnata*	Sapindaceae	5.906
19	*Calophyllum inophyllum*	Calophyllaceae	5.464
20	*Dillenia* sp.	Dilleniaceae	5.048
21	*Casuarina equisetifolia*	Casuarinaceae	4.604
22	*Calophyllum* sp.	Calophyllaceae	4.537
23	*Gironniera* sp.	Cannabaceae	4.537
24	*Hopea* sp.	Dipterocarpaceae	4.537
25	*Cerbera floribunda*	Apocynaceae	4.445
26	*Gironniera* sp.	Cannabaceae	4.183
27	*Campnosperma brevipetiolatum*	Anarcadiaceae	3.932
28	*Anisoptera costata*	Dipterocarpaceae	3.739
29	*Gnetum gnemon*	Gnetaceae	3.135
30	*Syzygium* sp.	Myrtaceae	2.871

*) food tree species.

PT Inocin Abadi operates a nursery unit that manages tree seedlings for replanting programs conducted after each harvesting cycle. The nursery unit records the phenology of harvested species, including *Calophyllum* sp. and *Myristica* sp., to obtain seedlings for replanting (Table 6). However, differences may occur between the phenological data observed in the field and those recorded by the nursery unit because the available data do not represent species-specific information. Instead, they represent all *Calophyllum* sp. from the Calophyllaceae family and all *Myristica* sp. from the Myristicaceae family throughout the concession area. This limitation suggests that phenological information from the nursery unit should be interpreted with caution, particularly when assessing fruit availability for the greater bird-of-paradise.

Table 6. Fruiting seasons of several food trees identified within the management area of PT Inocin Abadi, compiled from direct field observations and secondary company records. Due to limited phenological data, the fruiting periods are generally categorized at the genus level rather than detailed for each specific species.

Tree species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Calophyllum soulattri												
Myristica sp.												
Syzygium sp.												

Grey = seed or fruit, Black = seedlings. Not all tree species have their fruiting and flowering season record.

Few fruiting trees, particularly those whose fruits are consumed by the greater bird-of-paradise, were encountered during the study. Data on the fruiting and flowering phenology of plant species in the Trans Fly region (i.e., the lowland area stretching along the border between Indonesian Papua and Papua New Guinea) remain scarce, making it difficult to align field observations with existing theoretical frameworks.

Discussion

The only two fruit species confirmed to be consumed by the greater bird-of-paradise in this study were *Myristica inspida* and *Oncosperma tigillarium*. The four other tree species were not directly observed to be consumed by the greater bird-of-paradise. Some of these species have been reported in previous studies (Table 7), and all of the references mentioned nutmeg (*Myristica* sp.) as food sources for greater bird-of-paradise [9,12,13], although the reported species might vary among studies. In this study, the species confirmed to be consumed was *Myristica inspida*.

Table 7. Comparison of fruit tree species consumed by the greater bird-of-paradise compliled from four previous study. Across all four, almost all study mentions at least one species from the genera Ficus and Myristica as dietary sources for greater bird-of-paradise.

Tree species	Beehler and Dumbacher [9]	Sari [13]	Latupapua et al. [14]	Pramunandya [15]
Calophyllum soulattri				X
Chisocheton lasiocarpus	X			
Diospyros sp.		X		
Dysoxylum pettigrewianum	X			
Ficus benjamina		X		
Ficus drupacea		X		
Ficus nodosa		X		
Ficus obliqua	X			
Ficus sp.		X		X
Mangifera gedebe		X		
Myristica fragrans			X	
Myristica sp.	X		X	X
Podocarpus nereifolius	X			
Pometia pinnata				X
Rhodamnia sp.		X		
Syzygium sp.				X

Oncosperma tigillarium was considered as an opportunistic or fallback resource for the greater bird-of-paradise when preferred fruits, such as *Myristica inspida*, were seasonally unavailable. Vegetation sampling showed that while *Myristica insipida* exhibits high abundance, its fruiting phenology is highly seasonal, thereby creating temporal resource gaps. In contrast, *Oncosperma tigillarium* produces fruits almost continuously throughout the year and is widely distributed across the study site. Although there is no strong evidence regarding the nutritional traits of *Oncosperma tigillarium*, its temporal availability plays a vital role as a continuous food source for birds, including the greater bird of paradise. Energetically poor fruit are often preferred by frugivorous birds during periods of resource scarcity [19]. In the absence of *Myristica inspida,* this functional shift in ecological roles may indicate an adaptive response to temporal changes in food availability [17].

Calophyllum soulattri was reported to be the primary food source for the greater bird-of-paradise [14], supported by local community knowledge and fruit characteristics. During this study, *Calophyllum soulattri* did not produce fruits because its fruiting season occurs at a different time. The greater bird-of-paradise was not observed eating *Myristica fatua* directly, but bird movements between branches with some fallen fruits later showed potential foraging and feeding behavior. Several species of figs have also been recorded as food sources for *Paradisaea minor* and *Paradisaea raggiana* [9,17]. Moreover, figs are widely recognized as an important food source for a broad range of frugivorous birds in many habitats [20,21]. The greater bird-of-paradise spent approximately 3 min foraging on *Ficus obliqua* trees, and direct feeding behavior was not observed.

Although two individual trees of *Ficus obliqua* were found fruiting, their utilization was heavily dominated by fruit doves (Columbidae; *Ptilinopus* sp.), which were observed foraging in small to large groups. The greater bird-of-paradise tends to forage alone and avoid the presence of fruit-dove groups. Fruit doves also show different behaviors, often using the upper canopy of the tree [22], rather than the lower layer canopy, like the greater bird-of-paradise. Rather than risking interspecific conflict and predation by predators in the exposed upper canopy strata [23,24], the greater bird-of-paradise exhibited behavioral avoidance by restricting its activities to the lower canopy [19,24]. All food tree species showed a clumped distribution pattern, which was primarily influenced by geographical factors and further affected by climate, elevation, and slope gradient [25].

The mechanism of greater bird-of-paradise fruit consumption varied between the two confirmed resources. Greater bird-of-paradise utilize the fruit of *Myristica inspida* by swallowing the seeds whole and subsequently regurgitating them after digesting the aril. This can be achieved by the manageable size of the *Myritica inspida* seed. Fruit size and shape influence bird feeding preferences [26]. Frugivorous birds tend to select fruits that are easier to handle with their bills and can be swallowed efficiently, which is also correlated with their gape width [27]. Not many birds use nutmeg as their primary fruit source, while the greater bird-of-paradise, as a medium-sized frugivore, plays an important role in dispersing the seeds of *Myristica* sp. [28].

In contrast, due to the smaller size of *Oncosperma tigillarium* fruits, individuals were observed to consume up to 5–7 fruits per foraging activity recorded, with a duration of less than two minutes. During *Myristica inspida* scarcity, utilizing *Oncosperma tigillarium* could be an alternative strategy to obtain the required nutrition within a single foraging event. In addition, fruit color also influences bird preference; although not the sole determinant, red and purple hues are generally more attractive to frugivorous birds [29]. Although differences in mean fruit size are presented descriptively, these comparisons should be interpreted with caution due to the unbalanced sample.

Tree architecture could influence both visitation frequency and accessibility, as greater bird-of-paradise prefer trees with a circular branching pattern to move between branches while foraging [30]. Greater bird-of-paradise were most often observed perching near the main trunk, where the cover was denser and fruit was more concentrated, rather than in the upper part of the tree crown. In the case of *Oncosperma tigillarium*, birds were observed to prefer palm stands with heights ranging from 10 to 15 m, although this species can grow taller than 30 m, with trees surrounding the palm. This preference is an adaptive strategy to lower the effort for foraging and utilize cover from predation when food availability is low [31].

The vegetation analysis showed that *Vatica rassak* exhibited the highest IVI, although it was only slightly higher than that of the species below. As a member of Dipterocarpaceae family, *Vatica rassak* high relative density highlights its critical role in defining the canopy architecture and signifying a stable forest structure [32]. The high abundance and structural dominance of *Vatica rassak* closely linked to provide ideal microhabitat for the greater bird-of-paradise. The absence of dominant tree species within the foraging habitat of the greater bird-of-paradise is likely to be a defining characteristic of the tropical rainforest community [33]. This relatively even co-dominance exerted pressure on the greater bird-of-paradise to adapt to seasonal fruit availability, forcing individuals to utilize multiple fruiting tree species to fulfill their nutritional and energetic needs [2].

From a management perspective, this study shows that only two food-tree species of the greater bird-of-paradise were harvested in the PT Inocin Abadi concession area, namely *Calophyllum soulattri* and *Myristica fatua*. Although members of Myristicaceae are generally harvested for timber, *Myristica inspida* has a relatively small diameter that does not meet the qualification for commercial logging. This indicates that the availability of food trees for this species remains relatively secure in terms of the number of individual trees present. Continued monitoring is required to ensure that future logging activities do not reduce the abundance or distribution of fruiting tree species.

In practice, PT Inocin Abadi does not harvest timber within river buffer zones in accordance with existing regulations (Presidential Decree of the Republic Indonesia No. 32/1990 on the Management of Protected Areas). This measure is important for maintaining foraging habitat conditions, especially because greater bird-of-paradise are frequently observed feeding near watercourses. Habitat suitability can be further strengthened by designating conservation priority zones in areas known to have highly intensive greater bird-of-paradise activity (feeding habitat, lekking areas, and roosting areas), ensuring that vegetation within these zones remains protected. Additionally, enrichment planting of food trees and other potential fruit tree species by the PT Inocin Abadi nursery unit may help secure the long-term availability of foraging habitats, even within a production forest concession. Nevertheless, frugivorous birds, such as the greater bird-of-paradise, are more sensitive to habitat changes caused by logging activity [34]. Greater bird-of-paradise particularly rely on canopy conditions to forage effectively [35]. As the greater bird-of-paradise mostly forages in the lower canopy layer, it requires a structurally complex vegetation profile with non-food trees providing essential perches before accessing the fruits. Therefore, maintaining vegetation heterogeneity is crucial for supporting foraging behavior.

Conclusions

This study identified six tree species used as food sources by the greater bird-of-paradise within the logging concession area. Among these, *Myristica inspida* and *Oncosperma tigillarium* were confirmed through direct observation, whereas *Calophyllum soulattri, Ficus obliqua, Myristica fatua,* and *Syzygium* sp. were identified based on indirect evidence. These tree species generally exhibit a clumped spatial distribution and share prominent structural attributes, such as dense crowns and extensive branching. The foraging habitat of the greater bird-of-paradise is characterized by a relatively even co-dominance, which exerts greater bird-of-paradise to adapt to seasonal fruit availability by utilizing multiple fruiting species to fulfill their needs. Among the identified resources, *Calophyllum soulttri* and *Myristica fatua* are commercial timber species targeted for harvesting within the concession. Given the constraints of the current dataset, it is important to acknowledge that the available sample size remains limited, with the majority of records obtained primarily from indirect evidence. Given this constraint, preliminary management efforts by PT Inocin Abadi for greater bird-of-paradise conservation should focus on maintaining vegetation heterogeneity and securing habitat structures within river buffer zones where foraging encounters are concentrated. Continuous, long-term monitoring remains essential to validate these initial trends and ensure that future logging activities do not alter the spatial distribution of these essential fruiting resources.

Author Contributions

TANI: Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Writing – Original Draft; **YAM:** Conceptualization, Methodology, Supervision, Writing – Review & Editing; **AM:** Methodology, Supervision, Writing – Review & Editing; **RAP:** Investigation; and **VC**: Project Administration, Resources.

AI Writing Statement

During the preparation of this work, the authors used ChatGPT for grammar checking and translation. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Conflict of Interest

There are no conflicts to declare.

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