Research in Ecology

https://journals.bilpubgroup.com/index.php/re

ARTICLE

Foraging Dynamics, Dietary Preferences, and Niche Specialization of Two Bulbul Species in Sri Lanka's Dry Zone

Hiruni Kumarasinghe **,** ***Sriyani Wickramasinghe*** *

Department of Biological Science, Faculty of Applied Science, Rajarata University of Sri Lanka, Mihintale 50300, Sri Lanka

ABSTRACT

Two widespread bird species in Sri Lanka's dry zone, *Pycnonotus cafer* (Red-vented Bulbul, RVBB) and *Pycnonotus luteolus* (White-browed Bulbul, WBBB), were studied to understand their foraging dynamics and ecology. The research was conducted from October 2022 to February 2023 in Mihintale Sanctuary (80.30′11.24″ E, 8.21′04.63″ N) and the Faculty of Applied Sciences, Rajarata University of Sri Lanka (80.502206″ E, 8.353090″ N). Data were obtained through focal sampling, opportunistic observations, and mist netting. Both species predominantly foraged on twigs, using gleaning as the dominant food-handling technique. RVBB foraged mostly at the canopy level, while WBBB foraged primarily at the sub-canopy level. Fruits constituted the major food type for both species. RVBB and WBBB utilized 10 and 7 plant species, respectively, with *Grewia helicterifolia* being the primary foraging plant. Minimal foraging was observed on *Croton* sp. (RVBB) and *Hugonia mistax* (WBBB). The correlation between nutritional components and the consumption of both species revealed a preference for foods with lower protein, higher fat, and ash content. There was no linear correlation between gape width and fruit size ($r = -0.21$, $P = 0.69$) for both species. The standardized dietary niche breadth indicated both species are specialists, with a high pairwise dietary niche overlap (0.9854). These findings highlight the niche-specific foraging adaptations of RVBB and WBBB within Mihintale, emphasizing their distinct strategies in utilizing plant species, fruit sizes, and foraging heights. Understanding such ecological dynamics is essential for habitat conservation efforts and ensuring the availability of key foraging resources for these species in the dry zone.

*CORRESPONDING AUTHOR:

Sriyani Wickramasinghe, Department of Biological Science, Faculty of Applied Sciences, Rajarata University of Sri Lanka, Mihintale 50300, Sri Lanka; Email: sriwick@as.rjt.ac.lk

ARTICLE INFO

Received: 27 January 2025 | Revised: 3 March 2025 | Accepted: 4 March 2025 | Published Online: 19 March 2025

DOI: https://doi.org/10.30564/re.v7i1.8567

CITATION

Kumarasinghe, H., Wickramasinghe, S., 2025. Foraging Dynamics, Dietary Preferences, and Niche Specialization of Two Bulbul Species in Sri Lanka's Dry Zone. Research in Ecology. 7(1): 62–81. DOI: https://doi.org/10.30564/re.v7i1.8567

Keywords: Pycnonotus Cafer; Pycnonotus Luteolus; Foraging Behaviour; Food Preferences; Niche Breadth

1. Introduction

Sri Lanka has the highest biodiversity per unit area of land among South Asian countries [1]. Recently, it has been acknowledged as a home to significant bird species [2]. Sri Lanka is a bird diversity hotspot, with 244 breeding species, 87 vagrant species, and 179 species that purely migrate there. Among the other resident species, 34 and 68 subspecies are currently recognized as endemic to Sri Lanka [3].

Dry mixed evergreen forests dominate more than 70% of Sri Lanka's dense forest area, yet they remain understudied, despite their ecological significance. These forests support a wide array of species and exhibit complex ecological interactions that contribute to their resilience and functionality [4]. Plants within these ecosystems rely heavily on seed dispersers to maintain population dynamics and community structure. The presence of diverse dispersal agents, particularly frugivorous vertebrates, highlights the importance of fruit production and associated nutritional traits that have evolved to attract a broad spectrum of dispersal agents [5, 6]. In tropical forests, seed dispersal is primarily facilitated by birds, mammals, and other vertebrates [7]. Birds are among the most effective seed dispersers due to their diversity, abundance, and ability to consume and excrete or regurgitate seeds without damaging them [8, 9]. Several factors influence avian fruit preferences, including species morphology, dietary specialization, behavioral patterns, and the availability of alternative food sources. Concurrently, plants exhibit a range of traits—such as fruiting phenology, taste, color, and spatial distribution—that can influence avian selectivity [10].

Fruit colors function as prominent long-distance signals, advertising the availability of fruit crops and significantly influencing avian preferences for specific colors [7]. However, factors beyond external coloration, such as the chemical composition and nutritional properties of fruits, also play a critical role in determining their suitability and appeal to birds [11]. Birds use a combination of sensory cues, including taste and smell, to evaluate fruit edibility and nutritional quality. The presence of certain chemical compounds, such as sugars, acids, and secondary metabolites, can indicate ripeness and nutritional value. For a fruit to be considered edible, it must meet the nutritional demands of its consumers. Additionally, some birds have evolved to prefer specific fruit types based on their own dietary needs, ensuring they select fruits that provide the necessary energy, vitamins, and minerals [12].

Moreover, the dietary requirements of birds and other vertebrates are influenced by various life cycle stages. Seasonal shifts in nutritional needs drive these animals to diversify their diet by consuming fruits with varying chemical compositions to meet specific demands [13]. For instance, species like bulbuls and thrushes tend to consume protein-rich fruits during the breeding season to support egg production and chick development, as observed in hornbill species in Central Africa, which prioritize calcium- and protein-rich diets during early breeding stages [14]. The seasonal gradient in plant-bird evolutionary adjustments has been concurrently brought about by seasonally changing demands of dispersers and the differential coevolutionary potentials open to the plant-bird system through changing spatiotemporal asymmetry in relationships between vegetation and avifauna [13]. Birds that are seasonally specialized on particular resources are the most flexible in switching to alternative fruit sources across seasons [15]. The seasonal shifts in fruit selection not only reflect birds' physiological needs but also play a crucial role in shaping interspecific interactions. As multiple species may rely on similar fruiting plants, competition arises, influencing dietary strategies and niche partitioning. Birds that can adapt their foraging behavior or exploit alternative fruit resources may gain a competitive advantage, reducing direct resource overlap with other species [16, 17].

Therefore, birds are widely recognized as a key group for investigating competition and niche partitioning, providing critical insights into species coexistence. Analyzing their dietary niches helps identify the factors that enable coexistence among species. Ecological niche segregation reduces competition among species with similar ecological demands and is essential for the coexistence of phylogenetically related species [18]. Species do not exist in isolation, as interactions with others are fundamental to ecological communities. The concept of differential niche selection suggests that closely related species can coexist by minimizing competition for shared resources[19]. Both individual and species-level interactions shape resource allocation. According to Svardson[20] and Root[21] the balance between interspecific and intraspecific competition plays a pivotal role in avian niche partitioning. Interspecific competition promotes specialization, whereas intraspecific competition often drives generalization, influencing resource use and coexistence dynamics.

Foraging behavior encompasses food-searching techniques, foraging locations, dietary choices, and food-handling methods. Food-handling techniques, in particular, are essential for understanding the cost-benefit dynamics of various food types, exploring adaptive morphology, and examining plant-frugivore interactions[22]. Birds are not rigidly specialized in their diets; seasonal and locational variations often influence their dietary preferences. Additionally, long-term changes in diet may correlate with shifts in status or distribution[23]. Consequently, studying the foraging behavior of bird species is crucial for their conservation.

Bulbuls (Aves: Pycnonotidae) belong to the Order Passeriformes, which contains over half of all extant bird species and represents one of the most diverse groups of terrestrial vertebrates[24]. Sri Lanka hosts six bulbul species: Black-capped Bulbul *(Rubigula melanicterus)*, Red-vented Bulbul *(Pycnonotus cafer)*, Yellow-eared Bulbul *(Pycnonotus penicillatus)*, White-browed Bulbul *(Pycnonotus luteolus)*, Yellow-browed Bulbul *(Iole indica)*, and Square-tailed Bulbul *(Hypsipetes ganeesa humii)*. Among these, the Yellow-eared Bulbul and Black-capped Bulbul are endemic to Sri Lanka[25]. The Yellow-eared Bulbul inhabits the wet zone highlands, while the Black-capped Bulbul is frequently observed in wet lowland forests, nearby gardens, and the dry zone forests of the North-central Province[25]. The Red-vented Bulbul, highly adaptable, thrives in gardens across urban areas and all climatic zones of Sri Lanka. The White-browed Bulbul is primarily associated with dry lowlands but can be found ascending to mid-hills. In contrast, the Yellow-browed Bulbul is more prevalent in wet zone forests extending into mid-hills. The Square-tailed Bulbul predominantly inhabits the wet zone and hill forests[26]. While the Red-vented Bulbul and White-browed Bulbul are more widespread in the dry zone, the Black-capped Bulbul is rarely seen in this region. The Red-vented Bulbul *(Pycnonotus cafer)* typically measures approximately 20 cm in length. It is characterized by a black head with a tufted crest, brown upperparts adorned with white scaly fringes, a white rump and tail tip, and a brown breast with pale margins that transition into a striking scarlet vent and under tail coverts[25]. The White-browed Bulbul *(Pycnonotus luteolus)*, also about 20 cm in length, is easily identifiable by its prominent white eyebrow, a feature unique among local bulbuls. It possesses a brown crown, olive-green upperparts, brown wings, and a brown tail. Its underparts are off-white, with a brownish tinge on the breast that fades into yellow at the vent and under tail coverts[25].

The study focused on the RVBB and the WBBB due to their widespread distribution and ecological significance in Sri Lanka. These species are key frugivores, playing a crucial role in seed dispersal and influencing plant regeneration. Their ability to thrive in diverse habitats, including urban areas, makes them ideal for studying avian adaptation to environmental changes. Additionally, examining their fruit selection behavior helps assess potential competition with endemic species and the impact of anthropogenic changes on avian frugivory. While endemic birds are valuable for conservation, these non-endemic bulbuls provide insights into broader ecological interactions within Sri Lanka's ecosystems[27, 28].

Limited research has been conducted on the RVBB and WBBB in Sri Lanka, particularly in the dry zone. While some studies have examined the Yellow-eared Bulbul in the wet zone, such as the research on its foraging behavior and parental care in the montane cloud forests of Horton Plains National Park[29, 30], these findings do not extend to the RVBB and WBBB or the dry zone. Additionally, studies focusing on the vocalizations of RVBBs[28] primarily address urban development impacts rather than foraging behavior or ecological interactions. Furthermore, no research has specifically investigated the foraging ecology of the WBBB in Sri Lanka, highlighting a critical knowledge gap that this study aims to address by exploring the status, distribution, and ecological roles of these species in the dry zone.

So, this research aims to explore diverse foraging strategies and the ecological contributions of these bulbuls. It hypothesizes that the RVBB and WBBB occupy distinct ecological niches that facilitate coexistence through resource partitioning and habitat differentiation. By filling critical gaps in our understanding of these species, this study seeks to contribute valuable insights into their conservation and ecological significance.

2. Methodology

2.1. Study Area

The research was carried out within the Mihintale Sanctuary, located at approximately 8°21′04.63″ N and 80°30′11.24″ E, as well as on the grounds of the Faculty of Applied Sciences at the Rajarata University of Sri Lanka, located at approximately 80.502206″ E and 8.353090″ N. Both sites are situated in the Anuradhapura District in Sri Lanka's North Central Province.

The Mihintale Sanctuary (**Figure 1**) predominantly comprises dry mixed evergreen forest types, along with scrublands, water-edge habitats, highly degraded tertiary forests, and vegetation associated with archaeological sites. This sanctuary hosts a rich biodiversity, including several endemic floral and faunal species [31]. Volk, and Vidanage [32] reported that these woodlands harbor approximately 40 tree species.

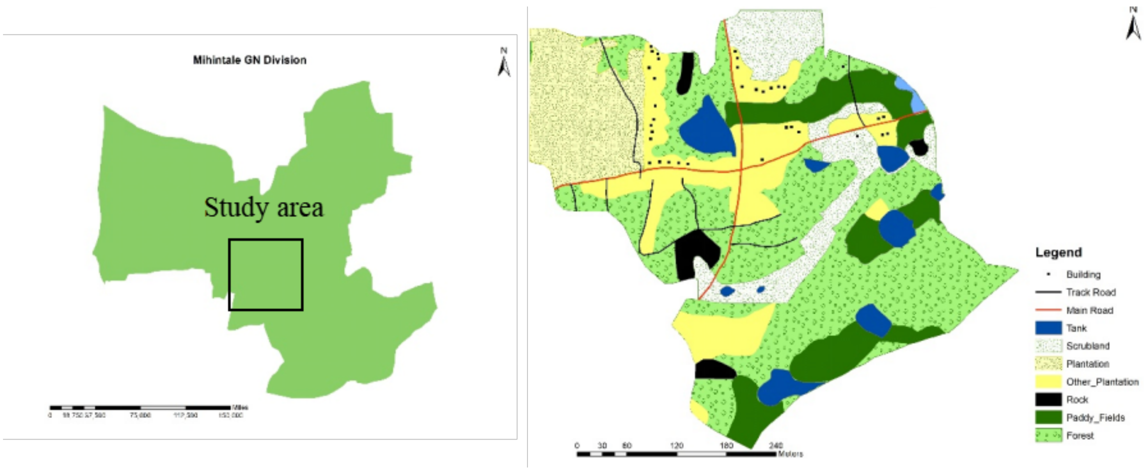


Figure 1. Map of Study Area 1 (Mihintale Sanctuary).

Located approximately 1.5 km from the sanctuary, the Faculty of Applied Sciences (**Figure 2**) at Rajarata University of Sri Lanka features a landscape that includes wooded areas, gardens with diverse plantings, and urbanized spaces, forming a mosaic of habitats. These environments support diverse wildlife, such as birds, insects, and small mammals, offering valuable opportunities for ecological research. However, the level of disturbance within the faculty premises is significantly higher compared to the relatively undisturbed Mihintale Sanctuary.

Figure 2. Map of study area 2 (Faculty of Applied Sciences, RUSL).

The study sites were selected to examine bird behavior in both urban, human-disturbed environments, and forested environments, allowing for a comparative analysis of their behavioral adaptations. This approach provides a broader understanding of how RVBB and WBBB respond to varying levels of human activity, offering insights into their behavioral flexibility and ecological adaptations across different habitats.

2.2. Population Data

The population count for both bulbul species was conducted daily from October 10, 2022, to January 3, 2023. Observations were made at 12 locations within the Mihintale Sanctuary and 3 locations on the Faculty of Applied Sciences premises. The counts were performed manually using Pentax 8 × 40 binoculars. The point count method was employed to collect abundance data, with observers stationed at predefined points. During fixed time intervals, all sightings of the two bulbul species were recorded, allowing for an estimation of their relative abundance across the study sites.

2.3. Behavioral Data Collection

The focal sampling method [33] was used to observe individual bird behaviors. A preliminary survey was conducted in both urbanized and forested areas to identify locations where birds were frequently sighted. Observations were carried out daily from 0700 h to 1800 h, excluding rainy days, using Pentax 8 × 40 binoculars to minimize disturbance to the birds during feeding activities. The duration and type of each observed activity were recorded. Microhabitat details for foraging attempts were also documented, including height above ground (measured with a clinometer), substrate type, and food-handling techniques. Field tools such as a stopwatch, digital camera, notebook, and relevant field guides, e.g., Ashton plant guide [10] and Harrison bird guide [25] were utilized.

- General activities during the day: scanning, flying, feeding, preening, and resting.
- Foraging height: ground (0 m), shrubs (0–4 m), subcanopy (4.1–8 m), canopy (8.1–12 m), and top canopy (>12 m).
- Foraging substrates: trunk or main branches, twigs (small branches), foliage (leaves, including leaf blades and petioles), and flowers.
- Food handling techniques: gleaning, reaching, hanging, pecking, and sally.

In the urbanized setting, foraging height was determined by categorizing observed feeding locations into predefined height classes using a clinometer. Since the urban landscape lacked a continuous canopy, birds were often observed foraging in alternative vertical structures such as shrubs, small trees, artificial perches (e.g., building edges, fences, utility wires), and garden vegetation. The same height classification system used for forested areas was applied, ensuring comparability.

The study was conducted over the entire day, divided into five time intervals. Food types were classified into fruits, flowers, insects, and worms.

2.4. Fruit Morphological Characters

The characteristics of fruits consumed by bulbuls over time were identified using focal observations and measured into the groups of characteristic parameters shown below. Fruits were collected from frequently cited locations of bulbuls. Mature fruits were collected from the lower branches of trees where both species consumed. Parameters included:

- The color of the fruit - the color of the outer court of the fruit was recorded, e.g., red, yellow, black, and green.
- Seed number - the seed number per fruit was counted and measured.
- Life form of the plant (structural and functional characteristics of the plant) - e.g., tree, shrub, climber
- Physical characters - e.g., weight of fruit, diameter of fruit.

2.5. Nutrient Analysis of Frequently Consumed Fruits

This study analyzed the nutrient content of fruits frequently consumed by the two bulbul species, examining components such as protein, lipids, fat, ash, moisture, and carbohydrates [34]. The nutrient analysis followed the standard methods established by the Association of Official Analytical Chemists (AOAC) [35] to ensure the accuracy and reliability of the results.

2.5.1. Determination of Moisture Content

The moisture content of the fruit samples was determined using the oven-drying method. Empty dishes and lids were thoroughly washed and dried in an oven at 105 °C for 3 hours before being transferred to a desiccator to cool. The weight of the empty dish and lid was recorded. Approximately 3.0 g of each sample was weighed into the dish, spread uniformly, and dried in the oven at 105 °C for 3 hours. After drying, the dishes were transferred to a desiccator to cool before being reweighed [35, 36].

2.5.2. Determination of Protein Content

The protein content was analyzed using the Kjeldahl method. Approximately 1.0 g of each sample was weighed into a digestion flask, followed by the addition of 5 g Kjeldahl catalyst (a mixture of 9 parts potassium sulfate and 1 part copper sulfate) and 200 ml concentrated sulfuric acid (H_2SO_4). A blank sample containing the reagents without the sample was also prepared. The flask was gently heated until frothing ceased and then boiled until the solution cleared. The mixture was cooled, and 60 ml of distilled water was cautiously added. The flask was connected to a condenser, with the tip immersed in 0.2 N HCl containing 5–7 drops of a mixed indicator (methyl red and bromocresol green). Ammonia was distilled and absorbed into the acid. The excess acid was titrated with 0.2 N NaOH solution [35, 37].

2.5.3. Determination of Ash Content

The ash content was determined by incinerating the samples in a muffle furnace. Crucibles and lids were heated at 550 °C overnight to remove impurities, cooled in a desiccator for 30 minutes, and weighed. Approximately 5.0 g of each sample was placed into the crucible, which was heated over a low Bunsen flame until the fumes ceased. The crucibles were then placed in the furnace at 550 °C overnight. After ashing, the crucibles were cooled in a desiccator and reweighed [35, 36].

2.5.4. Determination of Crude Fat Content

The crude fat content was analyzed using the Soxhlet extraction method. Extraction bottles and lids were dried in an oven at 105 °C overnight to stabilize their weight. Approximately 3.0 g of each sample was wrapped in filter paper, placed in an extraction thimble, and transferred to the Soxhlet apparatus. The extraction bottle was filled with 250 ml of petroleum ether and connected to the apparatus. The extraction was carried out at a rate of 150 drops per minute for 14 hours. After extraction, the solvent was evaporated using a vacuum condenser, and the extraction bottles were dried at 80–90 °C until the solvent was completely removed. The bottles were cooled in a desiccator and reweighed [35, 37].

2.5.5. Determination of Carbohydrate Content

Carbohydrate content was calculated by difference, using the proximate analysis values for moisture, protein, ash, and fat. The formula used is as follows:

$$\begin{aligned}\text{Total Carbohydrates (\%)} &= 100 - (\text{Moisture (\%)} \\ &+ \text{Protein (\%)} + \text{Ash (\%)} + \text{Fat (\%)}\end{aligned} \tag{1}$$

This calculation provides the total carbohydrate content, encompassing both soluble carbohydrates (e.g., sugars and starches) and insoluble carbohydrates (e.g., dietary fiber). It assumes that the sample's composition is limited to moisture, protein, ash, fat, and carbohydrates, with negligible contributions from other components [35].

2.6. Niche Overlapping

The study investigated niche overlap between RVBB and WBBB using mist netting and morphological measurements. Mist netting was conducted over five days at four sites within the Mihintale Sanctuary and three sites on the Faculty of Applied Sciences premises, utilizing 12-meter nets with a 20 mm mesh size (**Figure 3**). This research was conducted under the authority of wildlife permit number WL/3/2/16/22. Captured birds were tagged and marked with colored rings for identification, and morphological data, including body weight and beak dimensions (length and width), were recorded for niche breadth analysis.

2.7. Correlation between Morphometric Measurements and Fruit Size

The gape width and head-to-beak length of both species were calculated. The size of each fruit consumed by both bulbul species was also recorded.

Figure 3. Mist netting and bird ringing.

2.8. Data Analysis

The study employed Levins' niche breadth estimation[38] and the Simplified Morisita index[39–41] for calculating dietary niche overlap.

That was,

$$\widehat{B} = \frac{1}{\Sigma Pj^2} \quad (2)$$

Where,

$\widehat{B}$ = Levins' measure of niche breadth

P_j^2 Fraction of items in the diet that are of food category *j*

The range of B is from 1 to *n*, where *n* is the total number of resource states

$$\widehat{B}A = \frac{\widehat{B} - 1}{n - 1} \quad (3)$$

Where,

$\widehat{B}$- Levins' measure of niche breadth

$\widehat{B}A$- Levins' standardized niche breadth

n = Number of possible resource states

$$C_H = \frac{2\sum_i^n P_{ij}P_{ik}}{\sum_i^n P_{ij}^2 P_{ik}^2} \quad (4)$$

Where,

C_H - Simplified Morisita index of niche overlap between species *j* and species *k*

Pij - Proportion resource *i* is of the total resources used by species *j*

Pik - Proportion resource *i* is of the total resources used by species *k*

n - Total number of resource states (I = 1, 2, 3 . . . n)

Data analysis was conducted using Microsoft Excel™ for data storage and visualization, while statistical analyses were performed with R 4.2.2. The Shapiro-Wilk normality test was employed to assess the normal distribution of the data. Chi-square tests were employed to assess relationships between time intervals and bird food preferences, and a two-sample t-test was used to compare population differences between the RVBB and WBBB across different locations. Pearson correlation tests examined the relationship between gape width and average fruit size, while cluster analysis was used to identify patterns in foraging height across habitats. Spearman's correlation test was used as a non-parametric analysis.

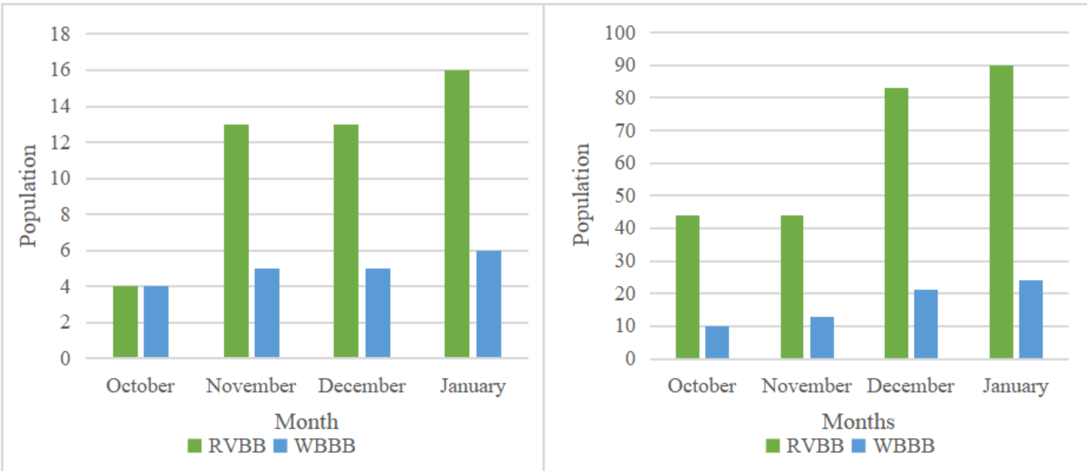
3. Results

3.1. Abundance of Bulbul Species

The observed abundance of bulbul species varied between the two study locations. In the Mihintale Sanctuary, 95 individuals of RVBBs and 29 individuals of WBBBs were recorded within their foraging areas. In contrast, the faculty premises recorded 16 RVBBs and 6 WBBBs. The results indicate a higher abundance of both bulbul species in the Mihintale Sanctuary compared to the faculty premises (**Figure 4**).

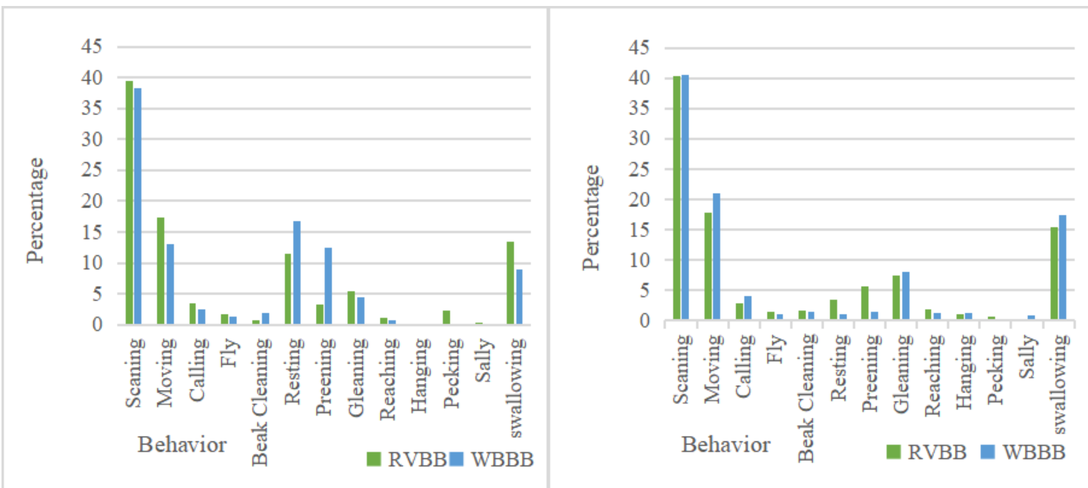
3.2. Foraging Behavior

The categories of foraging behavior were determined based on established methodologies from previous avian foraging studies such as Remsen and Robinson[42]. The focal bird's behavior was categorized into preening, beak cleaning, flying, scanning, calling, and foraging. RVBB and WBBB allocated similar amounts of time to foraging activities across the two study sites. However, behavioral differences were noted in other activities. Within the sanctuary, RVBB exhibited higher resting and preening frequencies than WBBB. Conversely, at the faculty premises, WBBB demonstrated higher levels of resting and preening than RVBB (**Figure 5**).



(**a**) (**b**)

Figure 4. Monthly bulbul abundance within the study area: (**a**) FAS RUSL, and (**b**) Mihintale Sanctuary.

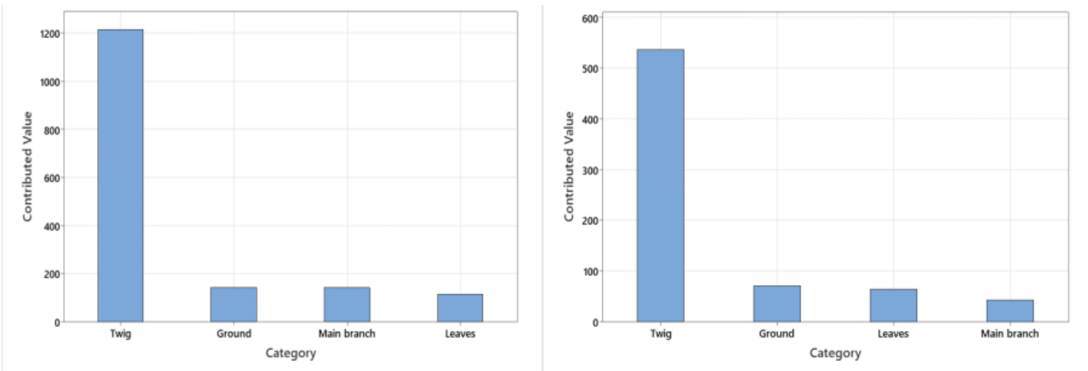


(**a**) (**b**)

Figure 5. The percentage of total observation time spent on foraging activities for common RVBB and WBBB in the (**a**) Mihintale Sanctuary, and (**b**) Faculty of Applied Sciences.

Within the Mihintale Sanctuary, scanning constituted the majority of observed behaviors for both RVBB and WBBB, with more time dedicated to scanning than foraging or other activities. Both species exhibited similar proportions of time spent scanning and engaging in other behaviors. The presence of conspecifics reduced scanning behavior while increasing foraging activity. Observations revealed that both species were more frequently seen alone than with conspecifics and significantly less often with heterospecifics. Foraging was most active during the middle of the day (1000 h–1600 h), contrary to the typical foraging pattern of many passerines, which peaks in the early morning and late evening. WBBB displayed notably higher foraging activity between 1400 h and 1600 h within the sanctuary. However, no significant behavioral differences were observed between the two species at the faculty premises. Both species utilized various substrate types, spending minimal time on bare ground and favoring tree branches. Additionally, both RVBB and

WBBB preferred slightly elevated substrates in both locations. Both RVBB and WBBB exhibited a strong preference for twigs as their primary foraging substrate. Among other substrates, RVBB showed the least preference for leaves, whereas WBBB demonstrated the least preference for the main branches. A chi-squared test confirmed a statistically significant difference in substrate preferences between the two species ($p < 0.05$) (**Figure 6**).



(**a**) (**b**)

Figure 6. Substrate types preferred by (**a**) RVBB and (**b**) WBBB.

The categories of food handling techniques such as gleaning, pecking, sallying, reaching, and hanging were determined based on established methodologies from previous avian foraging studies to provide a standardized framework for observing avian foraging strategies. The term "gleaning" refers to the act of gathering food from a surrounding substrate, such as the ground, that may be reached without fully extending the legs or neck. Reaching involves fully stretching the legs or the neck upward, outward, or downward. Hanging means suspending the body below the feet using the legs and toes to access food that could not be obtained from any other sitting posture. Pecking was the process of pressing the bill against the substrate to scrape off some of its surfaces. Sallying involved taking off from a perch to attack some food[42, 43]. Gleaning emerged as the predominant food-handling technique employed by both RVBB and WBBB. This was followed by reaching and hanging behaviors, with occasional instances of pecking and sallying observed during the study (**Table 1**).

Table 1. Food handling techniques of RVBB and WBBB.

Behavior	Number of Observations	%	Number of Observations	%
	RVBB		WBBB	
Gleaning	761	70.00	324	73.63
Reaching	164	15.08	53	12.04
Hanging	71	6.53	30	6.81
Pecking	69	6.34	9	2.04
Sallying	22	2.02	24	5.45

The majority of RVBBs foraged in the canopy position (8.1–12 m) (70.8%), while the ground level (0 m) (2.8%) was the least utilized. In contrast, most WBBBs foraged in the subcanopy (4.1–8 m) (75.9%), with the canopy position (8.1–12 m) being the least preferred (9.1%) across both study sites (**Figure 7**). The RVBB and WBBB demonstrated distinct foraging heights during feeding, with partial overlaps but no complete overlap in their foraging ranges. WBBB foraging heights deviated from those of RVBBs. Additionally, a significant association was observed between time intervals and food preferences ($p < 0.05$), with both species foraging more frequently in the morning compared to the late afternoon.

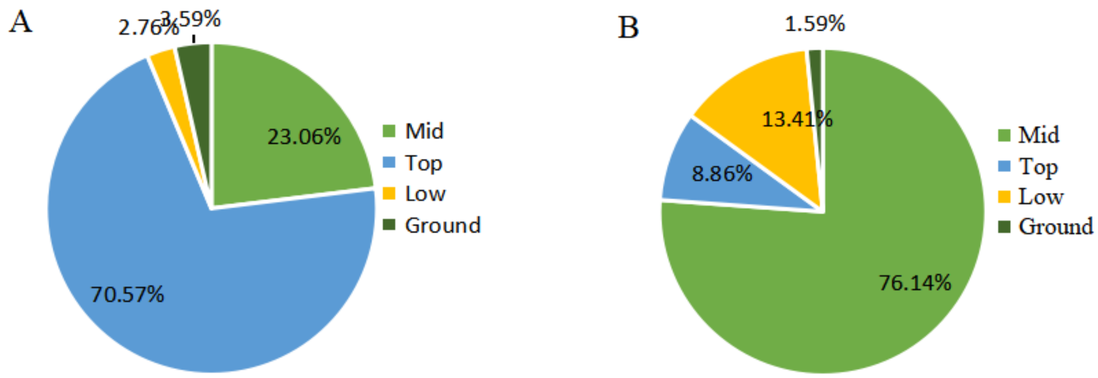


Figure 7. Percentages of vertical foraging positions in the foraging tree of (**A**) RVBB and (**B**) WBBB at both study sites.

3.3. Food Preferences of Bulbul Species

The diet composition of both bulbul species was categorized by the types of food items consumed. It was categorized into Fruit, Insect, Flowers and Worms. Both species exhibited a strong preference for fruits over other food types. A chi-squared test revealed a significant difference in food type preferences between the two species ($p < 0.05$). Though both species are considered frugivores, a certain portion of insects was included in their diet (**Figure 8**).

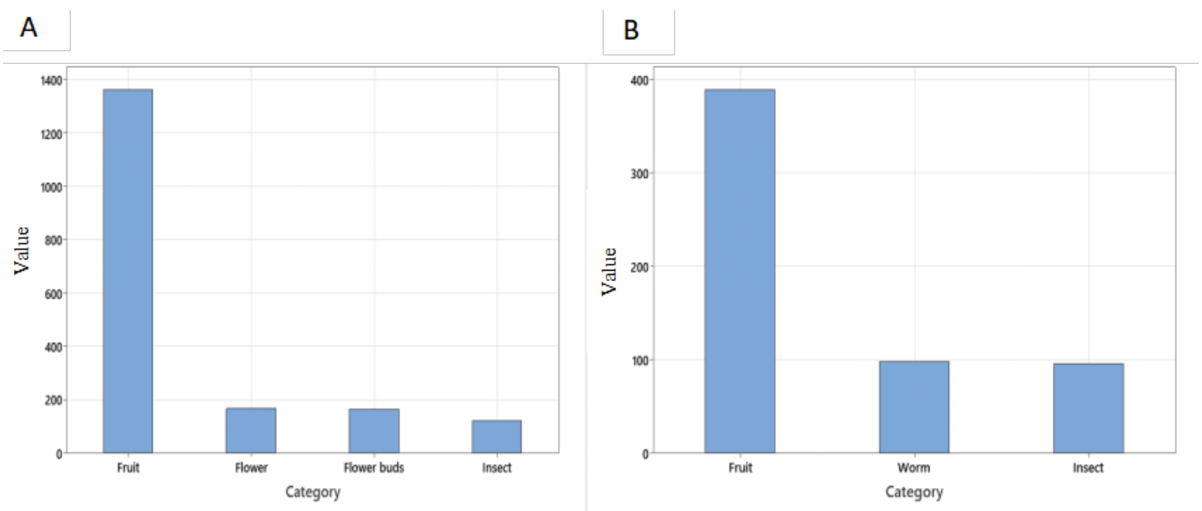


Figure 8. Food types preferred by (**A**) RVBB and (**B**) WBBB.

RVBB utilized ten species of plants for foraging. *Grewia helicterifolia* was the major foraging plant of RVBB. Minimum foraging observations were recorded on Croton sp. They frequently utilized *Tarenna asiatica, Flueggea leucopyrus,* and *Lantana camara*. Trees such as *Vitex pinnata* and *Benkara malabarica* are occasionally preferred (**Table 2**). WBBB utilized seven species of plants for foraging. *Grewia helicterifolia* was the major foraging plant of WBBB. Minimum foraging observations were recorded on *Hugonia mistax.* They frequently utilized *Hamelia patens, Benkara malabarica,* and *Tarenna asiatica*. Trees such as *Vitex pinnata* and *Lantana camara* are occasionally preferred (**Table 3**) (**Figure 9**).

Table 2. Description of foraging plant species of RVBB.

Plant Species	Family	Frequency %
Grewia helicterifolia	Malvaceae	49.85
Tarenna asiatica	Rubiaceae	13.88
Flueggea leucopyrus	Phyllanthaceae	13.03
Lantana camara	Verbenaceae	4.72
Vitex pinnata	Lamiaceae	4.43
Carmona retusa	Boraginaceae	3.87
Ficus microcarpa	Moraceae	3.30
Benkara malabarica	Rubiaceae	1.22
Hamelia patens	Rubiaceae	0.94
Azadirachta indica	Meliaceae	0.37
Croton sp	Euphorbiaceae	0.37

Table 3. Description of foraging plant species of WBBB.

Plant Species	Family	Frequency %
Grewia helicterifolia	Malvaceae	48.96
Hamelia patens	Rubiaceae	18.93
Benkara malabarica	Rubiaceae	13.39
Tarenna asiatica	Rubiaceae	8.31
Lantana camara	Verbenaceae	5.54
Vitex pinnata	Lamiaceae	3.69
Hugonia mistax	Linaceae	0.92

Figure 9. Some of the dominant fruits during the study period: (**A**) *Grewia helicterifolia*, (**B**) *Benkara malabarica*, (**C**) *Tarenna asiatica*, and (**D**) *Lantana camara*.

Also, bulbul species change their diet periodically. RVBB mainly consumed *Grewia helicterifolia* in all three months. In November they also preferred *Flueggea leucopyrus* as the second most consumed fruit. In December they preferred *Carmona retusa* as the second most favourable fruit (**Figure 10**). WBBB also mainly consumed *Grewia helicterifolia* in all three months. In November and December, they preferred *Hamelia patens* as the second most favorable fruit (**Figure 11**).

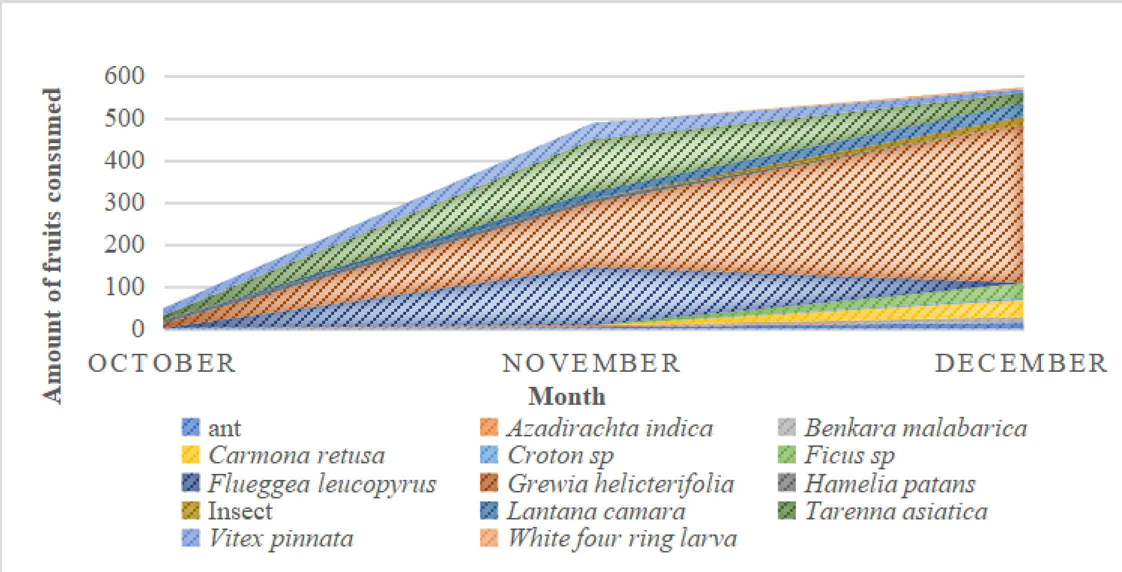


Figure 10. Monthly fruit selection of RVBB in both study sites.

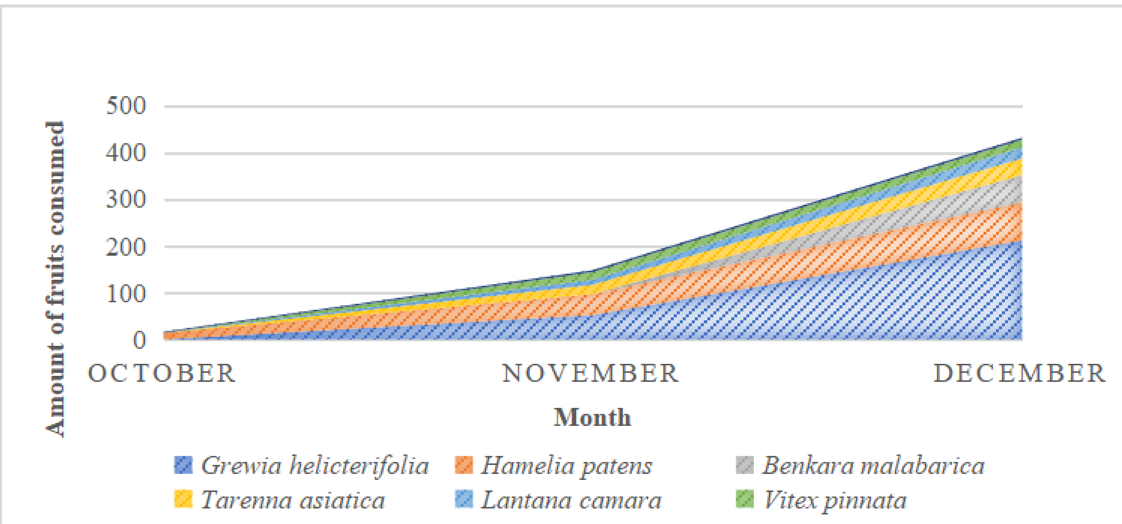


Figure 11. Monthly fruit selection of WBBB in both study sites

3.4. Fruit Morphological Characters

Morphological characteristics of the fruits chosen by RVBB and WBBB are crucial for understanding their foraging behavior and dietary preferences (**Table 4**).

3.5. Nutrient Analysis of Common Fruit Items

The nutrient analysis revealed significant variation in the composition of fruits consumed by Red-vented Bulbuls (RVBBs) and White-browed Bulbuls (WBBBs) (**Table 5**).

Table 4. Morphological characters of fruits selected by both bulbul species.

Plant Species	Color	Seed Number	Life Form of Plant	The Mean Weight of Fruit (g) (±0.001)	Mean Diameter of Fruit (cm) (±0.005)
Grewia helicterifolia	Green	1	Tree	0.115	0.55
Tarenna asiatica	Green	2	Tree	0.193	0.65
Flueggea leucopyrus	White	1	Shrub	0.071	0.45
Lantana camara	Black	1	Shrub	0.078	0.53
Vitex pinnata	Purple	1	Tree	0.252	0.72
Carmona retusa	Orange	1	Shrub	0.13	0.68
Benkara malabarica	Yellow	4	Tree	0.554	0.94
Hamelia patens	Red	1	Shrub	0.179	0.58
Hugonia mistax	Orange	5	Shrub	0.288	0.74

Table 5. Nutrient composition of fruits consumed by RVBBs and WBBBs.

Fruit Species	Protein (%)	Moisture (%)	Ash (%)	Fat (%)	Carbohydrates (%)
Tarenna asiatica	0.08	53.13	5.74	1.02	40.03
Vitex pinnata	4.50	60.43	0.13	0.89	34.04
Flueggea leucopyrus	5.34	74.43	0.97	3.55	15.71
Grewia helicterifolia	0.03	68.97	1.95	2.15	26.89
Lantana camara	4.12	80.46	1.13	1.78	12.51
Benkara malabarica	0.10	58.82	1.68	0.60	38.84
Hamelia patens	3.44	87.40	0.49	0.96	7.71

The Shapiro-Wilk normality test was employed to assess the distribution of the data. Since the data were not normally distributed, a non-parametric test, Spearman's correlation test was used to analyze the relationship between nutrient content and the consumption patterns of these bulbul species. RVBBs showed a strong positive correlation with fat content (r = 0.7143) and a moderate positive correlation with ash content (r = 0.5429). In contrast, protein content exhibited a moderate negative correlation (r = −0.4857), while moisture and carbohydrates displayed very weak correlations (r = 0.0857 and –0.0857, respectively). For WBBBs, a very strong negative correlation was observed with protein content (r = −0.9429) and a strong positive correlation with ash content (r = 0.7714). Moisture (r = −0.3714) and fat (r = −0.2571) showed weak negative correlations, whereas carbohydrates had a weak positive correlation (r = 0.3714).

These results indicate that RVBBs preferred fruits with higher fat content, whereas WBBBs favored fruits with higher ash content. Both species avoided fruits with elevated protein levels, reflecting dietary selectivity. Carbohydrate and moisture contents appeared to have minimal influence on their consumption preferences, underscoring the importance of fat and ash as key nutritional factors in their food preferences.

3.6. Niche Breadth and Niche Overlap

To find the patterns of resource use of both bulbul species, dietary niche breadth was used. The mean standardized dietary niche breadth value for both bulbul species was 0.0334. RVBB has the highest niche breadth (0.0484), while WBBB has the lowest niche breadth (0.01855). Niche breadth values of both species indicate that they are specialists in both locations (**Table 6**).

Both species required almost the same environmental conditions and the same resources. So, dietary niche overlap value was used to check whether both species partition resources in the environment. The pairwise dietary niche overlap value between RVBB and WBBB is 0.9854. This shows that dietary niches between both species strongly overlap.

Table 6. Dietary niche breadth - Levin's niche breadth (B) and Levin's standardized niche breadth (B_A).

Species	B	B_A
Red-vented bulbul	1.145245	0.048415
White-browed bulbul	1.037102	0.018551

3.7. Correlation between Morphometric Measurements and Fruit Size

Gape size plays a crucial role in birds' reproductive and feeding behaviours, as it directly influences their ability to capture and consume prey or forage for food [44]. To examine the relationship between gape size and fruit size, a Pearson's correlation test was conducted. The results indicated no significant linear correlation between gape width and average fruit size ($r = -0.21$, $p = 0.6922$). Additionally, no linear correlation was found between the ratio of gape width to head-to-beak length and fruit size for both species ($r = 0.35$, $p = 0.4972$). These findings suggest that gape size may not directly influence the selection of fruit size in the two bulbul species.

4. Discussion

The study of foraging habits is an essential aspect of bird species conservation, as it provides insights into their ecological roles and adaptive strategies. Foraging behaviour encompasses various elements, including searching techniques, foraging sites, dietary preferences, and food-handling methods. Understanding these behaviours is vital, as variations in food intake can offer valuable information about ecological niches, bill morphology, and energy dynamics [42]. Foraging strategies are often influenced by environmental conditions, species interactions, and food availability, shaping a bird's overall ecological niche [45, 46]. In this study, RVBB displayed a more tolerant and easily noticeable behaviour, making it easier to observe and document its foraging activities. In contrast, WBBB was more secretive and difficult to detect, making observation significantly more challenging. This difference in behaviour may be attributed to differences in predation risk perception or habitat use, as has been observed in other bird species [47].

This study revealed that RVBBs and WBBBs allocate their time equally between foraging, scanning, and other behaviours. This study revealed that both RVBB and WBBB were observed more frequently in solitary contexts than in the company of conspecifics, and significantly less often in association with heterospecifics. This solitary behaviour is consistent with findings from previous research, which indicate that many bird species exhibit social foraging patterns shaped by factors such as predation risk and food availability. Under certain conditions, these pressures can lead to increased solitary foraging as a strategy to optimize resource acquisition and minimize competition [48].

The distinct vertical positions and partitioning of foraging sites within the same habitat by the two species may reflect the influence of past competition on their current distribution. RVBBs predominantly foraged at the canopy level, while WBBBs were more frequently observed at the subcanopy level. These vertical stratifications in foraging height have been documented in multiple bird species, including bulbuls and tanagers, suggesting that niche differentiation reduces interspecific competition [49, 50]. Also, previous studies have shown that bird foraging height selection is significantly shaped by factors such as vegetation structure, plant species composition, food availability and distribution, and interspecific competition [42, 51]. This study identified four primary foraging substrates: twigs, leaves, flowers, and ground. Both RVBBs and WBBBs strongly preferred twigs as their main foraging substrate. These findings are consistent with previous research, which identified plants, particularly twigs, as the primary foraging substrate for forest-dwelling bird species [52, 53].

In this study, gleaning emerged as the primary food-handling technique for both RVBBs and WBBBs, followed by reaching and hanging behaviours. Previous research has highlighted that leaf morphology and arrangement such as the size, shape, petiole length, and position of leaves along branches play a crucial role in shaping the foraging behaviour of birds that capture prey from surrounding substrates [54]. Birds that forage on vegetation and the ground typically employ "gleaning" as their predominant foraging technique, as it is considered the most energy-efficient method [42]. The preference for gleaning may be explained by its low energy expenditure, making it the most cost-effective foraging strategy for many bird species [55]. For some bird species, specific morphological traits are closely associated with their ecological behaviours [53]. For example, studies on passerines have shown that species with shorter bills and compact body structures rely heavily on gleaning, whereas those with longer bills may employ probing or sallying techniques [56]. Also, species with long bills, such as the small Bee-eater, are better adapted to capturing fast-moving insects, while species with shorter bills, like the RVBB and WBBB, are predominantly gleaners [57]. Additionally, foraging behaviours are influenced by the abundance of food items available [58].

This study identified fourteen plant species consumed by RVBBs and eight species consumed by WBBBs, including some insect species. *Grewia helicterifolia* was the primary fruit foraged by both bulbul species and was the most common tree species in the Mihintale Sanctuary. *Hamelia patens*, another frequently consumed fruit, was the most common shrub on the faculty premises. Other notable species in their diet included *Tarenna asiatica*, *Vitex pinnata*, and *Benkara malabarica*. Additionally, *Flueggea leucopyrus* and *Carmona retusa* were consumed exclusively by RVBBs, while *Hugonia mistax* was only consumed by WBBBs. Overall, both bulbul species showed a preference for fruits over other food types such as flowers and insects, confirming their frugivorous diet [59]. This preference for fruits over other food sources is well-documented in many frugivorous birds, as fruit consumption plays a key role in energy acquisition and seed dispersal dynamics [60, 61]. The morphological characteristics of the fruits chosen by RVBB and WBBB are crucial for understanding their foraging behaviour and dietary preferences. Morphological traits, such as fruit size, shape, and colour, can influence a bird's ability to access and consume these resources [62]. For instance, larger fruits may be easier for birds with specific bill sizes to manipulate, while colour can impact fruit visibility and palatability [63, 64]. Fruit colour has been identified as a significant factor influencing avian dietary preferences, as it serves as an advertisement for ripe fruits, aiding in long-distance recognition [7]. The most common colours in mature fruits are red, black, and blue, with white, orange, and green appearing less frequently [10]. In this study, both bulbul species consumed fruits of all the aforementioned colours, except blue. However, no significant relationship was observed between fruit colour and diet selection for either bulbul species.

The study also found that both RVBBs and WBBBs adjusted their diet seasonally, with foraging activity and food intake increasing in December compared to the other two months. Seasonal changes in food intake have been linked to energy demands, reproductive cycles, and environmental conditions in many bird species [65]. Birds often increase food consumption during periods of higher metabolic demand, such as winter months or breeding seasons, to maintain body condition and survival [66]. This seasonal fluctuation in diet is consistent with findings from previous studies, such as Grouse [67], which suggested that seasonal variations in body weight, particularly in small birds, play a critical role in survival strategies. The increased food intake observed in December may reflect an adaptive strategy to store fat reserves, ensuring survival during periods of lower food availability or increased thermoregulatory demands [68].

This study underscores the critical influence of both the abundance and nutritional quality of fruits in shaping the foraging behaviour of fruit-eating birds. Foraging decisions in these birds are influenced by a complex set of factors, where the availability of food resources plays a dominant role in determining their foraging patterns [69, 70]. Both RVBBs and WBBBs displayed seasonal changes in their foraging activity, with higher food intake and foraging activity in December. This suggests that the birds' ability to adjust their foraging strategies based on seasonal availability is likely driven by the overall quantity of fruits available in the environment, reflecting the importance of food abundance in their foraging ecology [71, 72]. While the abundance of food resources appears to govern the general foraging strategies of these species, the nutritional content of fruits plays a crucial role in more specific, short-term decisions regarding fruit selection. This study supports this idea, as both bulbul species demonstrated a preference for fruits with higher fat and ash content, indicating that nutrient quality is a key factor influencing their foraging choices. Similar findings have been reported in previous studies, where nutrient content in fruits was found to affect feeding preferences in birds, with species selecting fruits that provide optimal nutritional rewards [73, 74]. In line with these observations, this study suggests that the interplay between the availability of food resources and the nutritional value of those resources influences the feeding habits of RVBBs and WBBBs. While the abundance of fruits is the primary driver of broad foraging strategies, the quality of fruits, especially in terms of fat and ash content, plays a significant role in the birds' specific fruit selection behaviours. This highlights the hierarchical nature of food selection in fruit-eating birds, where resource quantity dictates general foraging patterns and nutritional rewards shape more immediate dietary choices [70].

Understanding the dietary niche breadth of birds is essential for formulating effective conservation strategies. Species with a narrow dietary niche rely heavily on specific food resources, making them vulnerable to habitat alterations or resource depletion[75]. Conversely, species with a broad dietary niche can exploit a diverse array of food resources, allowing them to adapt to varying environmental conditions. In Central Europe, studies have shown that passerine birds with wider dietary niches tend to have larger distributional ranges and higher local abundances. This generalist feeding behaviour enables them to thrive in diverse habitats, suggesting that conservation strategies should aim to preserve a variety of food sources to support these species' ecological flexibility[75]. When a bird species relies heavily on a specific food source, conservation efforts should focus on safeguarding that resource or creating new habitats where it remains accessible[76]. In our study, both RVBB and WBBB exhibited characteristics of dietary specialists within the study sites. The pairwise dietary niche overlap values were close to 1, indicating a high degree of overlap in the food sources utilized by both species. This high degree of niche overlap suggests that these two species have similar dietary requirements, facilitating their coexistence without competitive exclusion[77]. Research on frugivorous bird communities in the tropical Andes supports this finding, showing that closely related species often exhibit substantial dietary niche overlap, which can promote species coexistence through shared resource use[78]. These findings highlight the importance of understanding niche overlap in the development of conservation measures, ensuring that both species can thrive in their shared habitats.

5. Conclusions

This study explored the foraging behaviour, dietary preferences, and ecological interactions of RVBB and WBBB, shedding light on their dietary niche overlap and foraging strategies. Both species exhibited high niche overlap, with a preference for fruits, particularly those rich in fat and ash. Seasonal fluctuations in foraging activity highlighted the influence of food availability on feeding behaviours. Despite their dietary similarities, the coexistence of both species within the same habitat indicates that niche partitioning allows for minimal competition. The findings emphasize the importance of considering both food quality and availability in conservation strategies for frugivorous birds, particularly in maintaining habitat diversity and resource accessibility. Long-term studies on the seasonal variations in dietary composition and their relationship with breeding success and survival rates would provide deeper insights into the ecological adaptability of these species.

Author Contributions

Methodology, S.W.; formal analysis, H.K.; investigation, H.K.; data curation, H.K.; writing—review and editing, H.K.; supervision, S.W.; project administration, S.W.; All authors have read and agreed to the published version of the manuscript.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Institutional Review Board Statement

This study followed ethical guidelines under wildlife permit number WL/3/2/16/22, following standard bird mist-netting and handling protocols approved by the Department of Wildlife Conservation, Sri Lanka.

Informed Consent Statement

Not applicable.

Data Availability Statement

The data supporting the findings of this study are available upon reasonable request from the corresponding author.

Acknowledgment

The authors extend their heartfelt gratitude to Dr. Asanga T. B. Wijethunga, Senior Lecturer in the Department of Biological Sciences, Faculty of Applied Sciences, Rajarata University of Sri Lanka, for his invaluable support in plant species identification and for providing valuable comments. Sincere thanks are also extended to the academic and non-academic staff members of the Zoology, Botany, and Chemistry laboratories at the Faculty of Applied Sciences, Rajarata University of Sri Lanka, for their assistance with laboratory work. Special appreciation is given to the Faculty of Agriculture, Rajarata University of Sri Lanka, for their support in analyzing the nutrient content of the samples.

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this article.

References

[1] Secretariat of the Convention on Biological Diversity, 2011. Convention on biological diversity. Available from: https://www.cbd.int/doc/legal/cbd-en.pdf (cited 30 January 2025).

[2] Rasmussen, P., Anderton, J., 2005. The birds of South Asia: The Ripley guide. Lynx Edicions. 1, 916–918.

[3] Biodiversity Secretariat, Ministry of Environment, 2021. The national red list conservation status of the birds of Sri Lanka-2021. Available from: www.env.gov.lk (cited 30 January 2025).

[4] Gunatilleke, N., Pethiyagoda, R., Gunatilleke, S., 2008. Biodiversity of Sri Lanka. Journal of the National Science Foundation of Sri Lanka. 36, 25–61. DOI: https://doi.org/10.4038/jnsfsr.v36i0.8047

[5] Corlett, R.T., 2017. Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: An update. Global Ecology and Conservation. 11, 1–22. DOI: https://doi.org/10.1016/j.gecco.2017.04.007

[6] Snow, D., 1971. The study of bird migration patterns. International Journal of Avian Science (IBIS). 113(1), 1–15. DOI: https://doi.org/10.1111/j.1474-919X.1971.tb05144.x

[7] Willson, M.F., Graff, D.A., Whelan, C.J., 1990. Color preferences of frugivorous birds in relation to the colors of fleshy fruits. The Condor. 92(3), 545–555.

[8] Fleming, T.H., John Kress, W., 2011. A brief history of fruits and frugivores. Acta Oecologica. 37(6), 521–530. DOI: https://doi.org/10.1016/j.actao.2011.01.016

[9] Traveset, A., Heleno, R., Nogales, M., 2014. The ecology of seed dispersal. CABI. Volume(issue number), 62–93. DOI: https://doi.org/10.1079/978117880641836.0062

[10] Thompson, J.N., Willson, M.F., 1979. Evolution of temperate fruit/bird interactions: Phenological strategies. Evolution. 33(3), 973–982.

[11] Ashton, M.S., 1997. A field guide to the common trees and shrubs of Sri Lanka. WHT Publication (Pvt.) Ltd. for the Wildlife Heritage Trust of Sri Lanka: Colombo, Sri Lanka. pp. 29–400.

[12] Nevo, O., Razafimandimby, D., Valenta, K., et al., 2019. Signal and reward in wild fleshy fruits: Does fruit scent predict nutrient content? Ecology and Evolution. 9(18), 10534–10543. DOI: https://doi.org/10.1002/ece3.5573

[13] Herrera, C.M., 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. Ecology. 63(3), 773–785.

[14] Lamperti, A.M., French, A.R., Dierenfeld, E.S., et al., 2014. Diet selection is related to breeding status in two frugivorous hornbill species of Central Africa. Journal of Tropical Ecology. 30(4), 273–290. DOI: https://doi.org/10.1017/S0266467414000236

[15] Bender, I.M.A., Kissling, W.D., Böhning-Gaese, K., et al., 2017. Functionally specialised birds respond flexibly to seasonal changes in fruit availability. Journal of Animal Ecology. 86(4), 800–811. DOI: https://doi.org/10.1111/1365-2656.12683

[16] Palacio, F.X., Siepielski, A.M., Lacoretz, M.V., et al., 2020. Selection on fruit traits is mediated by the interplay between frugivorous birds, fruit flies, parasitoid wasps and seed-dispersing ants. Journal of Evolutionary Biology. 33(7), 874–886. DOI: https://doi.org/10.1111/jeb.13656

[17] Naoe, S., Masaki, T., Sakai, S., 2018. Effects of temporal variation in community-level fruit abundance on seed dispersal by birds across woody species. American Journal of Botany. 105(11), 1792–1801. DOI: https://doi.org/10.1002/ajb2.1173

[18] Toyama, M., Kotaka, N., Koizumi Toyama, I.M., et al., 2015. Breeding timing and nest predation rate of sympatric scops owls with different dietary niche breadth. Canadian Journal of Zoology. 93(11), 1–30. DOI: https://doi.org/10.1139/cjz-2015-0060

[19] Rosenzweig, M.L., 1981. A theory of habitat selection. Ecology. 62(2), 327–335.

[20] Svardson, G., 1949. Competition and habitat selection in birds. OIKOS. 1(2), 157–174.

[21] Root, R.B., 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecological Monographs. 37(4), 317–350.

[22] Howe, F., Smallwood, J., 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics. 13, 201–228. DOI: https://doi.org/10.1146/annurev.es.13.110182.001221

[23] Gibb, J., Hartley, P.H.T., 1957. Bird foods and feeding-habits as subjects for amateur research. British Birds. 50, 278–291.

[24] Dekker, R.W.R.J., Dickinson, E.C., 2002. Systematic notes on Asian birds. 25. A preliminary review of the Pycnonotidae. National Museum of Natural History. Available from: https://www.aviansystematics.org/systematic-notes-on-asian-birds (cited 1 February 2025).

[25] Harrison, J., 2011. A Field Guide to the Birds of Sri Lanka, 2nd ed. Oxford University Press: Oxford, UK. pp. 18–144.

[26] Wijerathne, I., Wickramasinghe, S., 2018. Behavioral pattern of endemic Sri Lanka grey hornbill (Ocyceros gingalensis) within the breeding and nonbreeding seasons. International Journal of Biodiversity. 2018, 1–7.

DOI: https://doi.org/10.1155/2018/9509785
[27] Wijesundara, C.S., 2015. Significance of a forest fragment as a bird habitat and its importance in biodiversity conservation. Available from: https://www.researchgate.net/publication/311454285_Significance_of_a_Forest_Fragment_as_a_Bird_Habitat_and_its_Importance_in_Biodiversity_Conservation (cited 30 January 2025).
[28] Wickramarathna, S.M.A.S., Fernando, T.S.P., 2024. Effects of urban development on vocalizations and behaviour of Red-vented Bulbul (Pycnonotus cafer). Proceeding of the International Research Conference of the Open University of Sri Lanka (IRC-OUSL 2024); 7–8 November 2025; Nugegoda, Sri Lanka. pp. 300–308.
[29] Chandrasiri, P.H.S.P., Mahaulpotha, W.A.S., Lakmal, S.B.A.R., et al., 2018. Biodiversity and ecological health aspects of parental care approaches and nestling diet of Yellow-eared Bulbul (Pycnonotus penicillatus) in montane region of Sri Lanka. Available from: https://journals.sjp.ac.lk/index.php/fesympo/article/view/3665 (cited 2 February 2025).
[30] Chandrasiri, P.H.S.P., Mahaulpatha, W.A.D., 2017. Foraging behaviour of Sri Lanka Yellow-eared Bulbul (Pycnonotus penicillatus) in the montane cloud forests of Horton Plains National Park, Sri Lanka. International Journal of Science and Research (IJSR). 6(7), 695–699. DOI: https://doi.org/10.21275/art20175226
[31] Wimalasekara, C., Wickramasinghe, S., 2014. Species diversity and conservation of avifauna in three different habitat types within the Mihintale Sanctuary, Sri Lanka. Journal of Threatened Taxa. 6(5), 5718–5725. DOI: https://doi.org/10.11609/jott.o3119.5718-25
[32] Volk, R., 2012. Tropical Forest and Biodiversity Analysis, Sri Lanka. Report number: AID 383-0-11-00064, DOI: https://doi.org/10.13140/RG.2.2.27577.42084
[33] Altmann, J., 1974. Observational study of behavior: Sampling methods. Behaviour. 49, 227–265. DOI: https://doi.org/10.1163/156853974X00125
[34] Wijerathne, I., Panduwawala, P., Wickramasinghe, S., 2023. Food availability and food selectivity of Sri Lanka Grey Hornbill Ocyceros gingalensis Shaw, 1811 in Mihintale Sanctuary, Sri Lanka. Journal of Threatened Taxa. 15(1). DOI: https://doi.org/10.11609/jott.2023.15.1.22355-22558
[35] Latimer, G.W., 2019. Official Methods of Analysis of AOAC International, 21st ed. AOAC International: Gaithersburg, MD, USA. pp. 4–24. Available from: https://journals.sjp.ac.lk/index.php/fesympo/article/view/3665
[36] Nollet, L.M.L., 2004. Physical Characterization and Nutrient Analysis. In: Nollet, L.M.L. (ed.). Handbook of Food Analysis, 2nd ed. CRC Press: Boca Raton, FL, USA. pp. 60–80. DOI: https://doi.org/10.1201/9781482276459
[37] Breil, C., Abert Vian, M., Zemb, T., et al., 2017. "Bligh and Dyer" and Folch methods for solid–liquid–liquid extraction of lipids from microorganisms. Comprehension of solvatation mechanisms and towards substitution with alternative solvents. International Journal of Molecular Sciences. 18(4), 708. DOI: https://doi.org/10.3390/ijms18040708
[38] Levins, R., 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press: Princeton, NJ, USA. pp. 20–115.
[39] Horn, H.S., 1956. Measurement of "overlap". Comparative Ecological Studies. 100(914), 419–424. Available from: http://www.journals.uchicago.edu/t-and-c DOI: https://doi.org/10.1086/282436
[40] Krebs, C.J., 1999. Ecological Methodology, 2nd ed. Addison-Wesley Educational Publishers, Inc.: Upper Saddle River, NJ, USA. pp. 620–625.
[41] Vandercone, R., 2011. Dietary Shifts, Niche Relationships and Interspecific Competition Dietary Shifts, Niche Relationships and Interspecific Competition in Sympatric Grey Langur (Semnopithecus entellus) and Purple-in Sympatric Grey Langur (Semnopithecus entellus) and Purple-faced Langur (Trachypithecus vetulus) in Sri Lanka faced Langur (Trachypithecus vetulus) in Sri Lanka [Doctoral dissertation]. Washington University: Louis, MO, USA. Available from: https://openscholarship.wustl.edu/etd
[42] Remsen, J.V, Robinson, S.K., 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Studies in Avian Biology. 13, 144–160. Available from: https://www.researchgate.net/publication/281444922
[43] Houston, A.I., 1994. Avian daily foraging patterns: effects constraints and variability of digestive. Evolutionary Ecology. 8, 36–52.
[44] Wheelwright, N.T., Wheelwright, N.T., 1985. Fruit-size, gape width, and the diets of fruit-eating birds. Ecology. 66(3), 808–818.
[45] Barnea, A., Nottebohm, F., 1994. Seasonal recruitment of hippocampal neurons in adult free-ranging black-capped chickadees (learning/neurogenesis/neuronal replacement). Proceedings of the National Academy of Sciences of the United States of America (PNAS). 91, 11217-11221 DOI: https://doi.org/10.1073/pnas.91.23.11217
[46] Olivier, P.I., van Aarde, R.J., 2017. The response of bird feeding guilds to forest fragmentation reveals conservation strategies for a critically endangered African eco-region. Biotropica. 49(2), 268–278. DOI: https://doi.org/10.1111/btp.12402
[47] Lim, J.Y., Svenning, J.C., Göldel, B., et al., 2020. Frugivore-fruit size relationships between palms and mammals reveal past and future defaunation impacts. Nature Communications. 11(1), 4904. DOI: https://doi.org/10.1038/s41467-020-18530-5
[48] Gill, F.B., 1991. The social behavior of birds. American

Birds. 45(2), 218–223.
[49] Foster, M.S., 1990. Factors influencing bird foraging preferences among conspecific fruit trees. The Condor. 92(4), 844–854. DOI: https://doi.org/10.2307/1368720
[50] Carlo, T.A., Yang, S., 2011. Network models of frugivory and seed dispersal: Challenges and opportunities. Acta Oecologica. 37(6), 619–624. DOI: https://doi.org/10.1016/j.actao.2011.08.001
[51] Macarthur, R.H., 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology. 39(4), 599–619.
[52] Holmes, R.T., Recher, H.F., 1986. Determinants of guild structure in forest bird communities: An intercontinental determinants of guild structure in forest bird communities: An intercontinental comparison. The Condor. 88(4), 427–439.
[53] Gokula, V., Vijayan, L., 2000. Foraging pattern of birds during the breeding season in thorn forest of Mudumalai wildlife sanctuary, Tamil Nadu, Southern India. Tropical Ecology. 41(2), 195–208. Available from: https://www.researchgate.net/publication/252805623
[54] Holmes, R.T., Robinson, S.K., 1988. Spatial patterns, foraging tactics, and diets of ground-foraging birds in a northern hardwoods forest. Wilson Bulletin. 100(3), 377–394.
[55] Remsen, J.V, And, J.R., Krobinson, S., 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Studies in Avian Biology. (13), 144–160.
[56] Forstmeier, W., Keßler, A., 2001. Morphology and foraging behaviour of Siberian Phylloscopus warblers. Journal of Avian Biology. 32(2), 127–138.
[57] Asokan, S., Ali, A.M.S., 2010. Foraging behavior of selected insectivorous birds in Cauvery Delta region of Nagapattinam District, Tamil Nadu, India. Journal of Threatened Taxa. 2(2), 690–694. DOI: https://doi.org/10.11609/jott.o2201.690-4
[58] Poulin, B., Lefebvre, G., Mcneil, R., et al., 1994. Diets of land birds from northeastern Venezuela. The Condor. 96(2), 354–367.
[59] Ramaswami, G., Somnath, P., Quader, S., 2017. Plant-disperser mutualisms in a semi-arid habitat invaded by Lantana camara L. Plant Ecology. 218(8), 935–946. DOI: https://doi.org/10.1007/s11258-017-0741-y
[60] Jordano, P., 2014. Fruits and frugivory. Seeds: The Ecology of Regeneration in Plant Communities. CABI: Woking, UK. pp. 18–61. DOI: https://doi.org/10.1079/9781780641836.0018
[61] Karasov, W.H., del Rio, C.M., 2020. Physiological Ecology: How Animals Process Energy, Nutrients, and Toxins. Princeton University Press: Princeton, NJ, USA. pp.10-700
[62] Lord, J.M., 2004. Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. Austral Ecology. 29(4), 430–436.
[63] Moermond, T.C., 1990. Behavioral and theoretical considerations a functional approach to foraging: Morphology, behavior, and the capacity to exploit. Studies in Avian Biolog. 13, 427–430.
[64] Wheelwright, N.T., Wheelwright, N.T., 1985. Fruit-size, gape width, and the diets of fruit-eating birds. Ecology. 66(3), 808–818.
[65] Norberg, R.A., 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. Journal of Animal Ecology. 46(2), 511–529.
[66] Molokwu, M.N., Nilsson, J.Å., Olsson, O., 2011. Diet selection in birds: Trade-off between energetic content and digestibility of seeds. Behavioral Ecology. 22(3), 639–647. DOI: https://doi.org/10.1093/beheco/arr025
[67] Pendergast, B.A., Boag, D.A., 1973. Seasonal changes in the internal anatomy of spruce grouse in Alberta. The Auk. 90(2), 307–317. Available from: https://academic.oup.com/auk/article/90/2/307/5197724
[68] Desmond, M.J., Mendez-Gonzalez, C., Abbott, L.B., 2008. Winter diets and seed selection of granivorous birds in southwestern New Mexico. Studies of Avian Biology. 37, 101–112.
[69] Guitián, J., Munilla, I., 2008. Resource tracking by avian frugivores in mountain habitats of northern Spain. Oikos. 117(2), 265–272. DOI: https://doi.org/10.1111/j.2007.0030-1299.16316.x
[70] Blendinger, P.G., Giannini, N.P., Zampini, I.C., et al., 2015. Nutrients in fruits as determinants of resource tracking by birds. International Journal of Avian Science (IBIS). 157(3), 480–495.
[71] Herrera M., L.G., Hobson, K.A., Hernández C., P., et al., 2005. Quantifying differential responses to fruit abundance by two rainforest birds using long-term isotopic monitoring. The Auk. 122(3), 783–792. DOI: https://doi.org/10.1642/0004-8038(2005)122[0783:QDRTFA]2.0.CO;2
[72] Carnicer, J., Abrams, P.A., Jordano, P., 2008. Switching behavior, coexistence and diversification: Comparing empirical community-wide evidence with theoretical predictions. Ecology Letters. 11(8), 802–808. DOI: https://doi.org/10.1111/j.1461-0248.2008.01195.x
[73] Witmer, M.C., Van Soest, P.J., 1998. Contrasting digestive strategies of fruit-eating birds. Functional Ecology. 12(5), 728–741. DOI: https://doi.org/10.1046/j.1365-2435.1998.00242.x
[74] Bolser, J.A., Smith, A., Li, L., 2013. Dietary antioxidants attenuate the endocrine stress response during long-duration flight of a migratory bird. The Wilson Journal of Ornithology. 287(1929). DOI: http://dx.doi.org/10.1098/rspb.2020.0744
[75] Brändle, M., Prinzing, A., Brandl, R., 2002. Dietary niche breadth for Central European birds: Correlations with species-specific traits. Evolutionary Ecology Research. 4, 643–657.
[76] Contrasts, P., Brandl, R., Kristín, A., et al., 1994. Inter-

national association for ecology dietary niche breadth in a local community of passerine birds: An analysis using. Oecologia. 98(1), 109–116.

[77] Connell, J.H., Connell, J.H., 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos. 35(2), 131–138.

[78] Dehling, D.M., Riva, G.V.D., Hutchinson, M.C., et al., 2022. Niche packing and local coexistence in a megadiverse guild of frugivorous birds are mediated by fruit dependence and shifts in interaction frequencies. American Naturalist. 199(6), 855–868. DOI: https://doi.org/10.1086/718684