Effect of species richness and composition on foraging niches in mixed-species bird flocks

A Thesis in partial fulfillment of the requirements for the

BS-MS Dual Degree Programme

By

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May 2020

Submitted to Department of Biology

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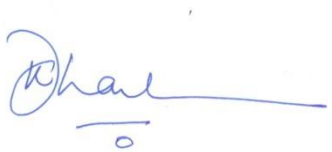
Certificate

This is to certify that this dissertation entitled “Effect of species richness and composition on foraging niches in mixed-species bird flocks” towards the partial fulfillment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents study/work carried out by Zakhiya PC at Indian Institute of Science, Bangalore under the supervision of Dr. Kartik Shanker, Associate Professor, Centre for Ecological Sciences, Indian Institute of Science, Bangalore during the academic year 2019-2020.



Dr. Kartik Shanker

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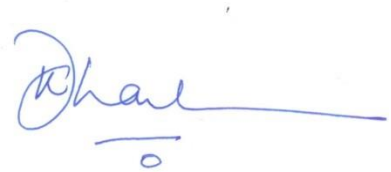
Declaration

I hereby declare that the matter embodied in the report entitled “Effect of species richness and composition on foraging niches in mixed-species bird flocks” are the results of the work carried out by me at the Centre for Ecological Sciences, Indian Institute of Science, Bangalore under the supervision of Dr. Kartik Shanker and the same has not been submitted elsewhere for any other degree.



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ABSTRACT

Facilitative relationships and non-trophic interactions are important contributors to determining the ecological niche of an organism. One such non-trophic interaction occurs in mixed-species bird flocks (flocks, hereafter). Flocks are examples where a niche of an individual bird is potentially modified by the presence of other species while foraging. The niche of an organism has been defined as ‘a multi-dimensional hyper volume’ of many variables. This aspect of the ecology of mixed-species flocks – namely their niches– remains under-studied. I studied mixed-species bird flocks in the semi-evergreen forests of Anshi National Park in the Western Ghats of India to understand the effect of richness and composition of the flock on the foraging niches of individual participants. I sampled a total of 113 flocks during the months January 2020 - March 2020. I used foraging height and behavior as representatives of the foraging niche which are the most relevant in the flock context. Foraging height ranges were correlated with species richness whereas average flocking heights were not. The results suggest that two of the nuclear gregarious species – which are key to flock formation and maintenance - are likely to determine the height of flock. Further, these gregarious species may influence the height of two other important sallying species that often follow the flock nucleus. Overall, this study contributes to the understanding of the foraging niche modifications that act on an individual level while influencing interactions at the group level in flocks.

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ACKNOWLEDGEMENTS

This thesis wouldn't have been possible without the many people who have supported me taught me and loved me through this year and before. I would like to especially thank the following people in this context.

Kartik has given me an opportunity, the resources and guidance at a point in life where I didn't expect or think I deserved any. I cannot thank you enough for your encouraging presence. You have taught me a lot of new things but more importantly things I was starting to forget. I won't be exaggerating if I say this was my rehab year.

Priti has been my drongo, (trying to (indirectly) advise me :P) I am happy I met you. You have patiently walked with me one of the most turbulent and important periods in my life. You have made me feel comfortable and in control, which were very crucial this year. Also thank you for not losing your calm with me prolonged tomorrows.

Sutirth has been an anchor and a point of self belief and confidence for me through IISER. I am happy that we are professionally related now. Thank you for understanding, accepting, mentoring and supporting me on the roads I choose at every turn. I hope I make you proud someday.

In Dinkar mama, Harshita, Pushpa did, Dadi and Nithu mama I found a family and home. Through the uncertain times in the field they have sensitively reassured and supported me.

Pandurang mama came with me for most of my forest walks so willingly with an attitude of a grandfather who wants his grandchild's work to not face any problems. I am eternally grateful that he is one year away from retiring. He made tiring terrains warm.

R.G. Naik for being considerate in arranging for field assistance every day, and his family for being a pleasant neighbor.

Prasad for spreading cheerfulness and energy and enthusiasm about my work.

Sada mama and Suresh for amazing me with their dutifulness and humbleness.

Hugo and Varsha for being my lab buddies and lifting my spirit to go one more step every time I felt I can't do more.

Gokul, Mihir and Amir for keeping IISER in CES. Princia, Deepa, Anne, Bharath, Bharti, Varun, Gowri, Priyanka, for the life in the lab.

Mahua aunty and Aurnab uncle for being my go to chill people in Bangalore. Soudamini aunty for constantly checking on me, George (mess) uncle and cycle uncle for their help and warmth. Chotu for his thoughtful services and Brahmalingeshwara for their breakfast.

Harsha, Vaishnavi, Rithwik, Akhil, Feroz, Vishnu, Faz, Shreya, Das, Sreelakshmi, Gayathri, Shefali, and Kiran for being family in Bangalore.

Vyshnav, Hrishidev, Mukul, Naveen, Charvee, Anwesha, Nithin, Bagi, Sidharthettan, Prashanthettan, Sidharth, Malavika, Santhosh for listening to me and believing in me.

Varun, Adwaith, Omkar, Unmesh, Lagachu, Ashrith, Kaustubh, Shilpi, Prasham Siri, Rohith, Shyam, Ananth, Yogesh, Vyshnavettan, Jyothish, Sohan, Kush, Nibras, Mohid, Sidharth, Sachin, Sourabh, Sandeep, Sandeep, Vikram and the entire IISER community for making me feel loved.

Akhi, Ranju, Vimi, Dee, Ammu, Mani, Megha, Anjitha, Swathi, Hari, Vaishakh, Vishnu, Jithin, Bharath, Prachan, Rohith, Nivedya, Ashwathi, Sneha and many more of my school friends for keeping me motivated and reassuring I can do what I want to. Also for always being a call away.

My family and neighbourhood, for tolerating me.

INTRODUCTION

'Why do all these penguins and flamingos stay so close to each other? Don't they have enough homes?' My three year old sister asked me when I was going through a children's book by the Discovery channel.

As for a child, a pink sea of flamingos, a V-shaped formation of birds in the sky or a massive dynamic herd of wildebeest migrating long distances are intriguing to many biologists. Studies across and within species suggest that food and predators influence group sizes in social animals (Krebs & Davis, 1987). Grouping provides anti predatory benefits through dilution effect and increased vigilance and may also increase the time that individuals can spend foraging (Krebs & Davis, 1987). On the other hand, there are costs of group living including increased competition and conspicuousness to predators (Krebs & Davis, 1987).

Groups can have individuals from a single species (flamingoes, sardines, penguins) or from multiple species (wildebeest and zebras). Groups in which more than one species participate are called multi-species or mixed-species groups. Individuals belonging to different species often associate with each other to form groups while foraging within bird communities (Sridhar et al., 2009). Such associations are observed in tropical and temperate bird communities, and are known as mixed-species bird flocks. Various studies have demonstrated that birds participate in mixed-species foraging flocks for two main reasons – 1. Increased foraging efficiency, and 2. Protection from predators (Morse, 1972; Sridhar et al., 2009).

Many of the benefits that species in multi-species groups derive from larger group sizes are similar to those from single species groups (Goodale et al 2020). According to the many-eyes effect (Pulliam 1973), as the number of individuals increases, the vigilance of the entire group goes up, while according to the dilution effect (Foster & Treherne 1981) and the confusion effect (Neill & Cullen 1974), the chance of an individual being singled out and attacked by a predator decreases. This means that individuals can spend more time in activities other than vigilance in a larger group. Given the heterospecific nature of mixed-species bird flocks, there are added complexities of

niche and behavioral differences amongst the flocking individuals as opposed to conspecific groups. These differences between participants within mixed-species bird flocks could contribute to significant changes in their selection pressures due to the proximity of other species. But the selection would work at an individual level and hence modify individual behaviors of the participants in such heterospecific groups (Farine & Montiglio, 2015). The costs and benefits that each species derive from participating in flocks are likely to be very different. Studies have shown that tropical flocks occur around the year and have a large number of participating species (Sridhar & Sankar, 2008; Develey & Peres, 2014; Munn & Terborgh, 1979; Powell, 1989; Terborgh, 1990; Thiollay, 1998). Thus, mixed-species flocks are an important part of the bird community.

In the forests of Western Ghats, birds belonging to the families Phylloscopidae, Sylviidae, Trogonidae, Pyconotidae, Tephrodornithidae, Muscicapidae, Campephagidae, Sittidae, Dicruridae, Zosteropidae, Pellorneidae, Timaliidae, Picidae, Sturnidae are known to participate in mixed-species flocks (Sridhar & Shanker, 2013). Of these, birds of the family Timaliidae, Phylloscopidae and Dicruridae commonly lead flocks, or attract flock participants (Sridhar & Shanker, 2013). Some species in these regions are known to be obligate flock participants (Sridhar & Shanker, 2013). While some species that participate in flocks are endemic to the Western Ghats of India, some winter migratory birds to the Western Ghats are also known to participate in these flocks.

Some of the species that participate in mixed-species flocks are known to provide benefits as well as pose costs to the co-participants. Sallying species like the greater racket-tailed drongo (*Dicrurus paradiseus*) aggressively mob and chase predators and are also known to be vigilant alarm callers (Ali and Ripley 1987; Nijman 2004). But they are also known to be kleptoparasites in flocks (Flower, 2010; King & Rappole, 2001; Satischandra, Kudavidanage, Kotagama, & Goodale, 2007; Sridhar & Shanker, 2014; Styring & Ickes, 2001). Therefore, their presence in a flock can have multiple effects on the flock depending on the richness, composition or size of the flock. This in turn can have diverse effects on their behavior and niche. This can for example be by preventing addition of a particular species, accelerating the increase in flock size, increase in

speed or enabling species to forage in a larger area. Some species are known to be flock leaders while others are followers (Moynihan, 1962), and some are known to be occasional participants. Different species take part in the flocks for varying reasons and have their own costs and benefits (Goodale & Kotagama, 2005b; Sridhar & Shanker, 2013).

Two-species flocks are the simplest unit of the mixed-flock system and have been studied in the past few years (Sridhar & Shanker, 2014). In such two-species flocks, at least one species directly benefits from the other and the costs and benefits are easy to observe and measure, but as the flock size and richness increases, there are several direct and indirect benefits that are difficult to observe and quantify. One such benefit could be the expansion of foraging niche. 'Niche' is considered as organism's place in the ecosystem, with respect to its relationship to resources, predators and habitat (Pocheville, 2015). This is determined by biotic as well as abiotic factors and the relationship the organism has with these.

The foraging niche of birds may have several elements. Foraging heights are an overarching representation of spatial niches as they will include the strata of the canopy or the substrates that are accessible. Foraging behaviours point to what kind of prey/substrate is being accessed. Foraging behavior can determine the perceived risks by individual birds since a bird's foraging behaviour can make it more or less vulnerable and vigilant for predators.

Hence, understanding changes in foraging height, foraging behavior and movement activity as the composition, richness and size of the flock varies can help us understand effect of flock participants on each others' niches. Farine & Milburn (2013) suggest that species might have to adjust their "preferred" niche to maintain the benefits that they derive from these flocks. This leads to the question of the effect of composition and richness on foraging heights. Flocks have been suggested as examples where in species can expand their foraging niches and forage at a different height which they may not explore alone or in conspecific groups (Chen, 2011; Harrison & Whitehouse, 2011).

Birds often experience different foraging rates and use different substrates when foraging alone (or in conspecific pairs or groups) as opposed to foraging in heterospecific flocks (Hino, 1998). Such increased rates could be due to decreased vigilance time, from following species that flush out prey or from being able to forage in risky areas. Species in mixed-flocks in Madagascar were seen to use similar locations when feeding in mixed flocks (Hino, 1998). Some other species were also seen to use diverse foraging substrates when in heterospecific groups (Hino, 1998). Buskirk (1976) also suggests that opportunities for imitative foraging might be a considerable factor for the participation of subordinate individuals in flocks.

Depending on the foraging habit of different species, the opportunities that a flock creates might be different. As flocks grow, they tend to open up more niche spaces. This can result in the flock being more diverse in species and enabling existing participants to exhibit diversity in behaviour. These positive interactions expand habitat use and the realized niches of sympatric species (Letten et al., 2018). Hence, mixed-species bird flocks could be examples of “niche construction” (Harrison & Whitehouse, 2011).

The niches of individual species in flocks may be affected by the behaviour of the nuclear species in the flock that are regular participants in flocks, known to be flock leaders and responsible for flock cohesion and maintenance. Nuclear species are also known to be gregarious in nature (Moynihan, 1962; Sridhar, Jordán, & Shanker, 2013). Associations with nuclear species are known to create foraging opportunities for birds in areas where the nuclear species forage (Chen, 2011).They consistently perform certain functions like alarm calling (enabling eavesdropping) (Goodale & Kotagama, 2005) or flushing insects (causing beater effect) (Hino, 1998; Munn & Terborgh, 1979; Powell, 1989). By taking up these roles they modify their own niche and the niche of other participating species.

Different species experience benefits depending on whether the nuclear species occupy a strata that is higher/lower in the canopy and showed different departure rates based on how the foraging of the nuclear species shifted in the canopy structure (Chen, 2011). Follower species would have to decrease foraging rates when foraging alone so as to

be vigilant, or adopt a different foraging strategy to find food which might not be efficient. Hence, the foraging heights and behaviors of non-gregarious flock followers like the greater racket tailed drongo in the presence of different gregarious species is of interest.

Eguchi et al.(1993) suggested that overlapping foraging height with other species might help flock participants of the same guild enhance their efficiency at finding food. This can possibly be through local enhancement (Krebs et al. 1972; Krebs 1973; Croxall 1976; Greenberg, 2000) or social learning regarding food type, food location or a new foraging technique (Avery, 1994; Hino, 1998; Palameta & Lefebvre, 1985; Rubenstein, Barnett, Ridgely, & Klopfer, 1977). A better coordination of activity while flocking is regarded as another benefit of niche overlap between flock members (Eguchi et al., 1993).

Flocking with similar/ dissimilar species and flock richness might determine how species change their niche. Flocking with heterospecific partners that are similar in their foraging niche might not allow for significant additional foraging opportunities. However, in flocks with dissimilar participants in terms of foraging niche, individuals might be able to exploit new niches. A dissimilar co-participant in this situation might also provide additional complementary vigilance benefits. Large groups tend to have greater anti-predation benefits along with more dissimilar partners. Species with different foraging habits (search, attack and in between movements) would perceive different threats and “risky” behaviors might be different for each of these species (Suhonen, 1993)

Two functionally important guilds of birds have been identified as key to mixed species flocks–intraspecifically gregarious species and sallying species (Sridhar & Shanker, 2014)**.** While the former are typically seen in groups of 2 or more individuals, the sallying species are known to forage alone or in pairs (Sridhar et al., 2013)**.** I aimed to examine foraging niche shifts in these two guilds.

The goal of this study is largely to understand the effect of flock parameters on the individual niches of participating species. The study was carried out with the following objectives:

1. To study overall variation in flock height with flock richness and composition
2. To understand the effect of flock richness on foraging heights of select intraspecifically gregarious species and sallying species.
3. To study the effect of composition (i.e. presence of functionally important species) on foraging heights of select species.

I find that flock foraging height ranges were correlated with flock species richness as well as gregarious species richness whereas average flocking heights were not. The results suggest that two of the nuclear gregarious species – which are key to flock formation and maintenance – are likely to determine the average height of the flock but not the flock ranges. At the same time, a difference was observed in the average heights of all three gregarious species. This might mean that the flock range increases with increasing species richness owing to accumulation of gregarious species and their followers that differ in terms of their average foraging heights/ foraging strata. The two sallyers studied show increase in their height ranges with increasing richness unlike the three gregarious species. Dark fronted babblers were unlike the other two gregarious species; their average height was very different from the flock average and its foraging height range reduced with increasing richness. This can either be a property of this individual species or understory birds in general.

METHODOLOGY

Study Area

The study was conducted at the Anshi National Park in the Kali Tiger Reserve in the state of Karnataka, Western Ghats, India. The habitat in Anshi is semi-evergreen and moist deciduous. Our study was done in the Anshi Range within the National Park. This was a suitable study site also because of the background work that has already been carried out in this region by researchers (Bangal, 2020; Sridhar, 2013). We thus carried out our field sampling in this area.

Flock data

A mixed-species flock was defined as a group of two or more species within 10 m of each other that are moving together. An individual bird was noted to be part of a flock if it was within 10 m of at least one other heterospecific individual. The chain rule (Whitehead 2008) was used in determining the flock members, i.e. 2 individuals that are not within 10 m of each other can be considered to be a part of the same flock if they both are within 10 m of a third individual. Benefits of flocking are not limited to this 10 m but the 10m cutoff is commonly used for flocks in forest habitats mainly due to poor visibility (e.g.Hutto,1994; Sridhar & Shanker, 2013).

Aggregations of birds at static resources such as fruiting trees were excluded since clumped resources such as fruits are an external stimulus. Mixed-species flocks, on the other hand are moving associations between species independent of distribution of foraging resources.

Sampling was conducted from January–March 2020; this period coincides with the non-breeding season of most evergreen forest bird species, when flocking activity is highest (Sridhar & Shanker, 2013). Six trails were walked between 08:00 hours and 18:00 hours to search for mixed-species bird flocks. No two trails were walked twice the same day or at the same time on two consecutive days to minimize the chances of pseudo replication. All observations were recorded using the Version 1.2.1_f4f7a0c_181101 recorder of an OPPO A3S mobile phone. Once a flock was encountered it was

observed for a minimum of 5 minutes to make sure the association is not a chance occurrence of species.

Flock composition and behavioral observations

A continuous record of flock composition based on the species seen and heard was maintained. The total number of species in the flock and the number of individuals of each species was noted. When there was difficulty in recording the exact number of individuals, each species was assigned to a group size class. Every time a species was visually detected, the height at which it is foraging was noted and the individuals within a 5 m radius of the focal bird were recorded as its local neighborhood. Focal animal sampling was carried out to record the foraging behaviour of the bird in the local social context within the flock (Altmann, 1974). Since we could not predict for how long we would be able to record from a focal bird at the start, recording was done at every available opportunity. Very short records (<5s) were removed from the data. Focal sampling was carried out without any upper or lower duration limits. The start and stop time of each focal observation was noted. It was often difficult to distinguish between individuals of the same species within a flock. So, to avoid pseudo-replication, the rates of foraging maneuvers used from focal data from all the individuals of the same species in a particular flock were averaged. The feeding technique / foraging maneuver of the bird every time it made a foraging attempt during the focal were noted. Foraging maneuvers are identified and classified as – gleaning, reaching, hanging, pecking, sallying, sally-strike, searching and probing (Remsen and Robinson 1990). The movement behaviour was recorded every time the bird moved and was not foraging. All the substrates that an individual bird used during a focal sampling were also recorded.

Characterizing foraging maneuver

Birds can be classified into foraging guilds on the basis of their foraging habits. Remsen & Robinson, 1990 have proposed a classification for foraging maneuvers. The species in the study area broadly fell into the following categories. Assignment of birds to any category was decided based on their most common foraging maneuvers. The birds in each category may also use other techniques for foraging.

Sallyers: These are the vigilant species. Sallyers in mixed-species flocks are known to associate with very specific species that provide benefits from flushing insects. Some sallyers also associate with species from which they can potentially steal.

Gleaners: Leaf gleaners feed by picking insects off leaves and hence are constantly moving and searching through the canopy for food. Although this seems like an intense foraging strategy, it also is a very active foraging habit and depending on whether the species is an understory or canopy forager, it means different things for each of these species. If the species typically (when on its own) forages in the understory, being with a flock would help it explore the canopy resources and on the other hand if the gleaner is a canopy forager, it could explore the understory resources when with heterospecific partners.

Sally-gleaners: The sally-gleaning foragers often perch for some time and make flights to pick insects off leaves once they have been spotted. It might sometimes require them to hover around leaves for a successful feeding opportunity. Such hovering flights might make them more vulnerable to predators. Depending on the social context and foraging partners that are present in the flock, birds in this feeding guild might vary their foraging rates. They might be more risk taking (reflected in increased foraging attempts) in larger groups or with more vigilant partners.

Searchers: The searching foraging habit is perhaps the most intense, high effort, which needs looking through different substrates and surfaces through the canopy and understory and leaving little room for vigilance during feeding. Such behaviours make these species vulnerable to predation. For understory “search” foragers and associating with different flock partners might allow them to expand their foraging range through the vertical stratification in the canopy.

Bark probers: Bark probing species, move up and down along tree trunks searching for insects and spend a lot of time digging/probing tree trunks for insects. Foraging on trunks, surrounded by dense understory would be a safe strategy when foraging in a solitary context. Being in a flock would allow them to forage in slightly more open spaces and higher up in the canopy that would otherwise seem risky in terms of predation threat.

Ground foragers: Ground foragers strictly stick to the understory in the canopy stratification when in conspecific groups or when foraging solitarily. However, when accompanied by more vigilant social partners, they could potentially move higher up in the canopy to explore other substrates that are resource rich but inaccessible when foraging on the ground or lower in the canopy.

Table 1: Characterizing foraging maneuver:

S.No.	Terminology	Definitions
1	Sally	To take off from a perch in a fluid motion without flapping wings towards the prey. The bird land on a perch (same or new) with or without flapping wings after a successful or unsuccessful attempt.
2	Sally hover	Involves an initial sallying followed by a hovering (constant moving of wings so as to remain in a same location in the air, e.g. hummingbird) near the substrate followed by a flight or perch.
3	Sally stall	Involves a sallying motion followed by a brief (shorter than hover, less aggressive and limited wing motion) pause at the substrate.

4	Peck	Forcing the bill at the surface and retreat back the neck to remove parts of the substrate (e.g. hen).
5	Reach	Stretching out body parts, especially neck or legs towards a definite target to procure prey from a constant position.
6	Probe	Reaching into crevices or variations along the substrate surface in search of prey. Can involve brief reaching, but differentiated from reaching due to an absence of a definite target.
7	Hammer	Series of pecks without pause (e.g. Woodpecker).
8	Flake	To brush aside loose surfaces like outer surfaces of bark, dead leaves in the foliage or leaf litter using leaves or beak to reveal underlying prey.
9	Glean/perch glean	Picking food items from a nearby substrate, no extension of legs or neck. This is usually preceded and followed by fast, rapid hoping walking or flying.
10	Hang	Reaching with the legs held onto a halt in a head down fashion.

Substrates

The foraging substrate used by the bird during a focal was recorded. The substrates identified in the study area are – ground, trunk, branch, twig, stem (vines and creepers), leaves, flowers, fruits, air, moss on the branches, dead leaves/leaf clusters on trees. These were broadly classified as in the table for the purposes of this study.

Table 2: Classification of substrates

S.No.	Classification	Constituents
1.	Branches	Trunk, branch, bark, twig, stem and moss over the tree.
2.	Leaves	Green and dead leaves on the tree, flowers and fruits
3.	Ground	Fallen leaves, branches twigs etc. on the ground, grass, mud and debris

Foraging Height

A range finder (Olympus) was initially used to adjust the observer's estimation of heights. The height observations were then estimated by visual approximation. In addition to noting the height at which the individuals were seen foraging, the canopy height in the area was also noted. This was used to then classify the height of foraging into different strata of the canopy (as opposed to what is available). This was also used to infer the total height range and strata of the entire flock.

ANALYSIS

I examined variation in foraging height means and ranges with respect to flock species richness (index of size) and flock species composition. First, I examined the effect of species richness on foraging heights and ranges. Here, I explored the effect of species richness on the average height and range of the entire flock. I then examined the effect of species richness on individual focal species including orange minivets, western crowned warbler, dark fronted babbler, ashy drongo and greater racket tailed drongo.

I also compared the foraging heights of different species with each other as well as with average flock foraging heights.

Secondly, I examined the effect of species composition on foraging heights and ranges. I followed Sridhar & Shanker's (2014) classification of the participant bird species of the study area into gregarious (*g),* sallyers (*s)* and non gregarious, non sallyers (*n*). This classification was used in the analysis involving species composition. I focus on three gregarious species (*g*) and two sallyer species (*s*) amongst the participants for further individual species based analysis. These two groups were identified as the functionally important nuclear species in flocks (Goodale & Kotagama, 2005; Sridhar et al., 2009; Srinivasan U, Raza RH, 2010) in the first analysis. I examined the effect of composition on both overall flock foraging heights as well as of individual species.

I carried out the analysis with both normalized and observed heights. Normalized heights were calculated by dividing the observed height with total canopy height to obtain the relative positioning of the birds in the strata. Since the results were similar, absolute heights have been used for representing most of the results.

I used Microsoft Office Excel 2007 and Graph Pad Prism 8.4.1 (676) to tabulate, analyze and plot the graphs. I carried out correlations and other analyses in R (R Core Team, 2018). I used Spearman’s rank correlations to test the relationship between richness and foraging heights (averages and ranges). Mann Whitney U-test was used to compare individual and flock heights (average and range) and Kruskal Wallis non-parametric tests to compare the flock heights and sallying species heights at different flock compositions.

RESULTS

I. DESCRIPTIVE

A total of 43 species (species codes are provided in Appendix, Table 3) were observed in 113 flocks during the study period from January– March 2020. The average flock richness and abundance were 4.9 and 13.7 respectively. Five species flocks were the most common followed by three and four-species flocks (Fig.2). Most flocks had either less than 7 individuals or between 12-17 individuals. Among the very large flocks which were observed, up to 20-25 individuals were seen. Flocks of approximately 50 individuals were also observed on rare occasions. The species richness and flock size had a positive relationship (Fig.1; Spearman's rho = 0.75, $p<0.05$).

Of the 43 species, 7 were intraspecifically gregarious and 5 were solitary sallyers. As observed by Sridhar et al. (2013), western crowned warbler (wclw), orange minivets (scmin), yellow browed bulbul (ybb), brown cheeked fulvetta (quak) and greater racket tailed drongo (grtd) were common participants in flocks (Fig. 3, Fig.4, Fig. 5). Apart from these ashy drongo was also found frequently in flocks (Fig.3, Fig. 5).

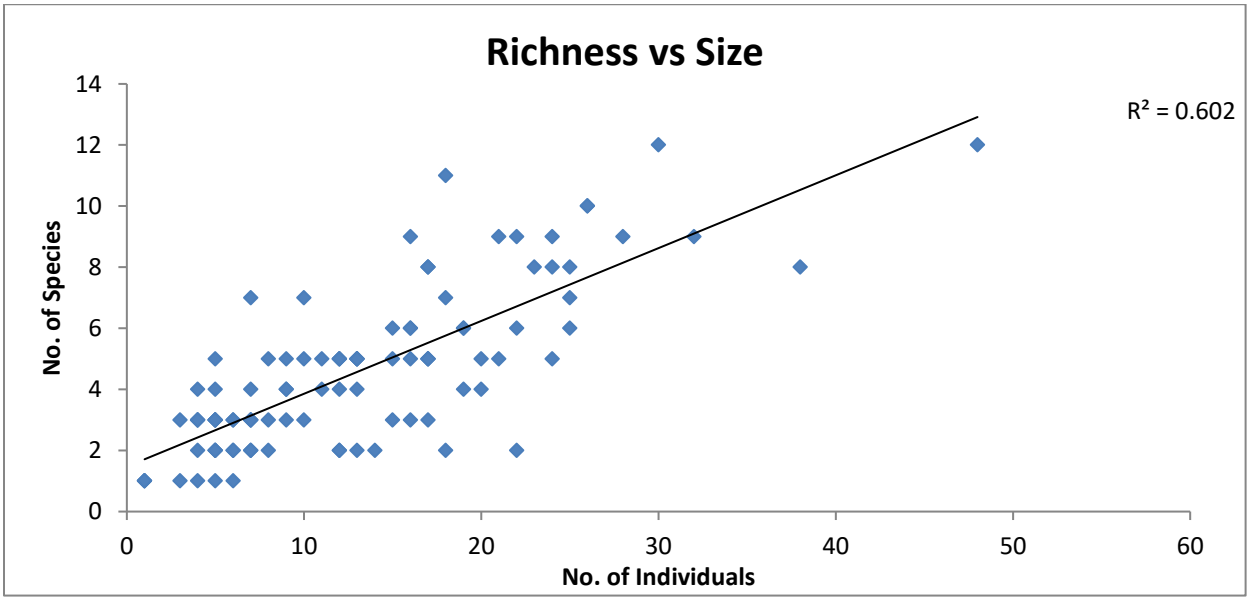


Figure 1 Relationship between flock richness and flock size.

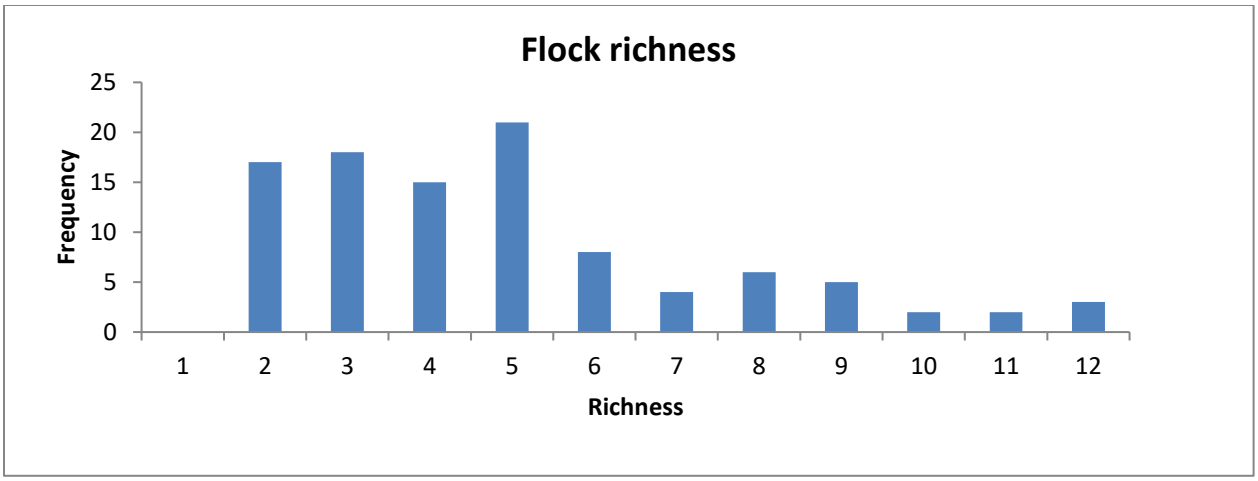
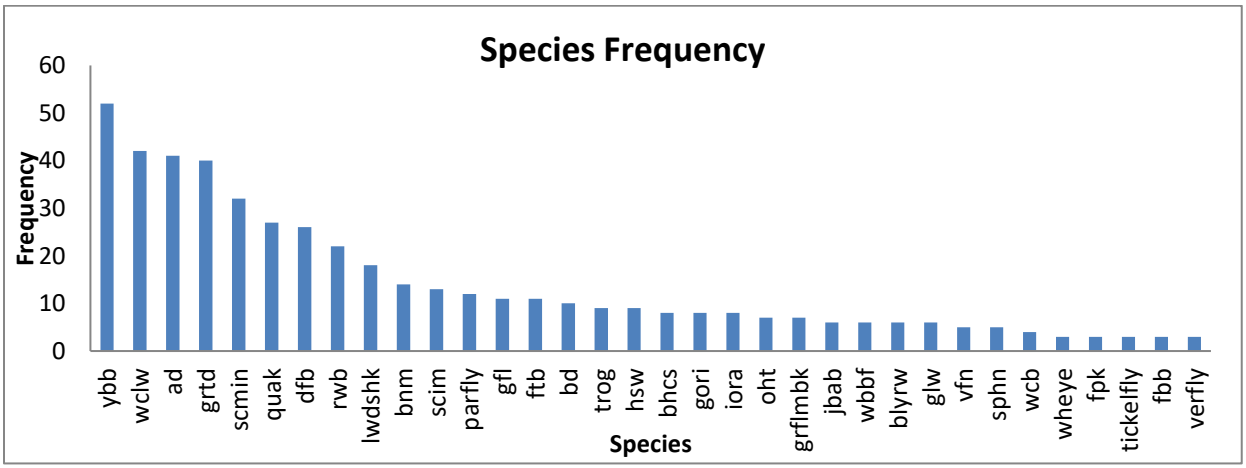
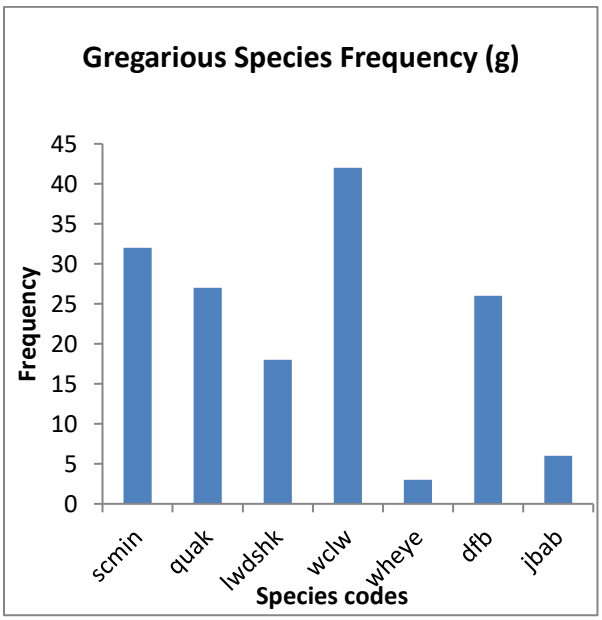


Figure 2 Frequency plot for flock richness.





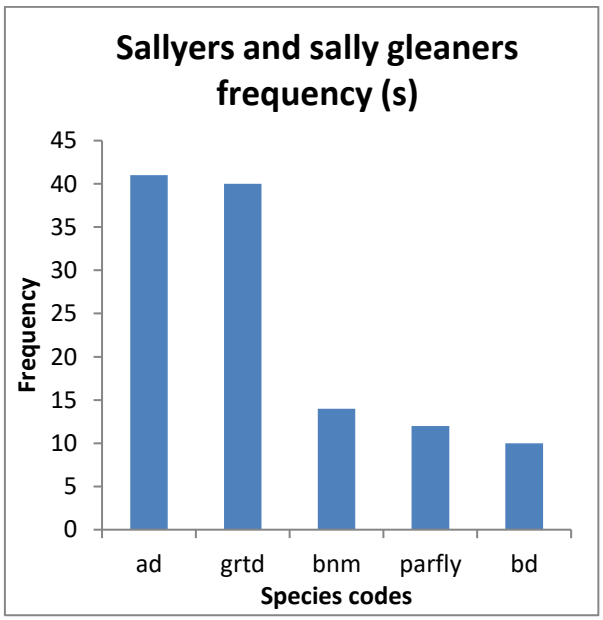


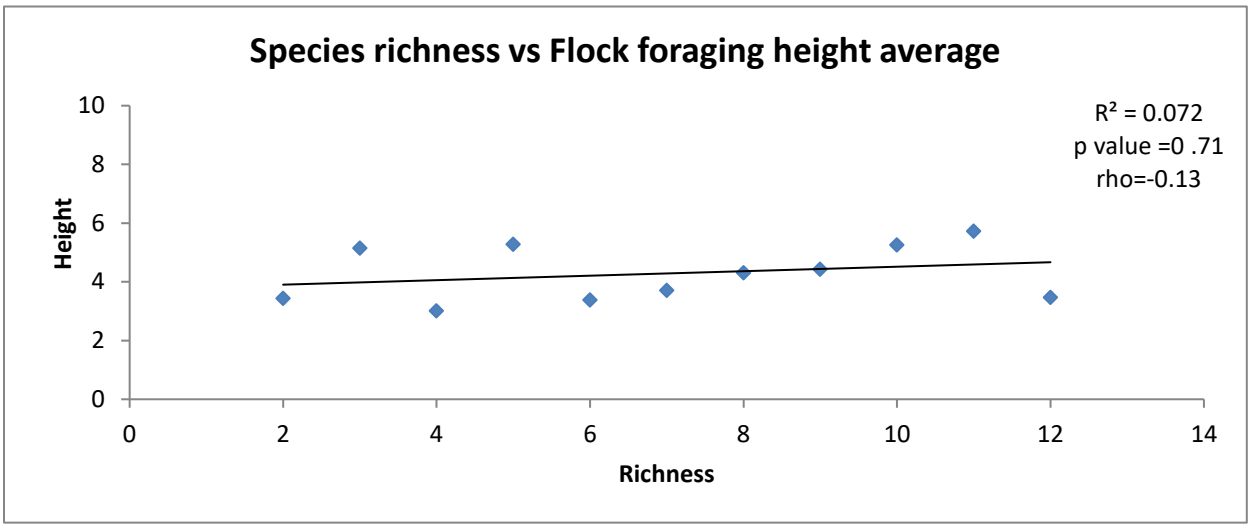
Figure 3, 4 & 5 Frequency Plots (Species, gregarious species and sallyers).

II.FORAGING HEIGHT

A. Richness (predictor)

1) Flock foraging height and Species richness

Average flock heights did not vary with species richness (Fig 6: Spearman's rho= -0.12, p = 0 .7). However, the height range of flocks increased with increasing species richness (Fig 7: Spearman's rho = 0.69, p = 0.01).



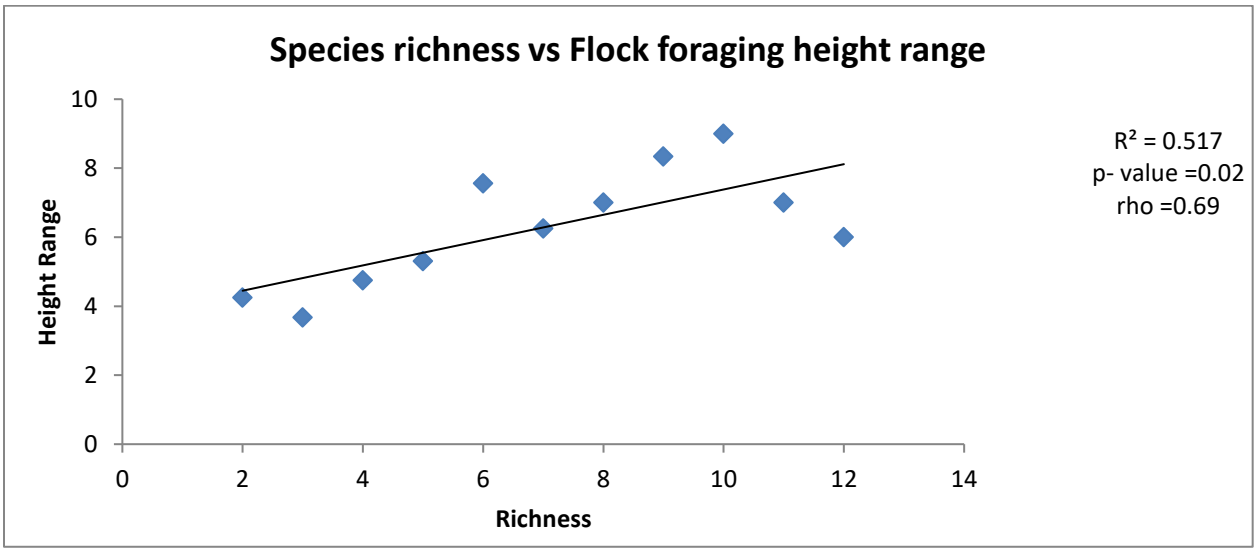


Figure 6 & 7 Relationship of flock height averages and ranges with species richness of flocks.

2) Individual foraging heights

The foraging heights of orange minivets were marginally higher than western crowned warbler (KW chi squared= 21.465, p =0.07) and both these were significantly higher than dark fronted babblers (KW chi squared = 21.465, p<0.05). The foraging height ranges of all three species were not significantly different from each other (p>0.05 for all pair wise comparisons) (Fig 8 & 9).

The normalized foraging heights and height ranges of individual species were compared with the flock heights and flock height ranges respectively (Fig 10-19). In all species except dark fronted babblers (MW = 40, p = 0.055), the individual heights were similar to the flock heights (p>0.05 for all comparisons). The individual heights of dark fronted babblers were lower than the average flock heights. The individual height ranges of the 5 nuclear species namely orange minivets (MW =140.5, p <0.01), western crowned warblers (MW = 329.5, p<0.01), dark fronted babblers (MW = 139, p<0.001), greater racket tailed drongo (MW=1013, p< 0.0001), ashy drongo (MW =86, p< 0.0001), was much lower than the respective flock ranges.

Individual foraging height averages and ranges were plotted against species richness. There was no relationship between individual foraging height average and species richness for all 5 species including orange minivets (Spearman's rho = -0.25, p = 0.47), western crowned warblers (Spearman's rho = -0.43, p = 0.18), dark fronted babblers (Spearman's rho = -0.12, p = 0.72), greater racket tailed drongo (Spearman's rho = -0.15, p = 0.67) and ashy drongo (Spearman's rho = -0.31, p = 0.35) (Fig 20-24). Foraging height ranges (Fig 25-29) of two of the three gregarious species namely orange minivets (Spearman's rho =0.13 p =0.71), western crowned warblers (rho = -0.12, p = 0.72) did not show any trend with species richness whereas the understory gregarious bird species, dark fronted babblers showed a negative correlation with species richness (Spearman's rho = -0.65, p = 0.03). The height ranges of both the sallying species, greater racket tailed drongo (Spearman's rho = 0.50, p = 0.12) and ashy drongo (Spearman's rho = 0.28, p = 0.41) did not show a significant correlation with flock richness.

a) Comparing between foraging heights of gregarious species.

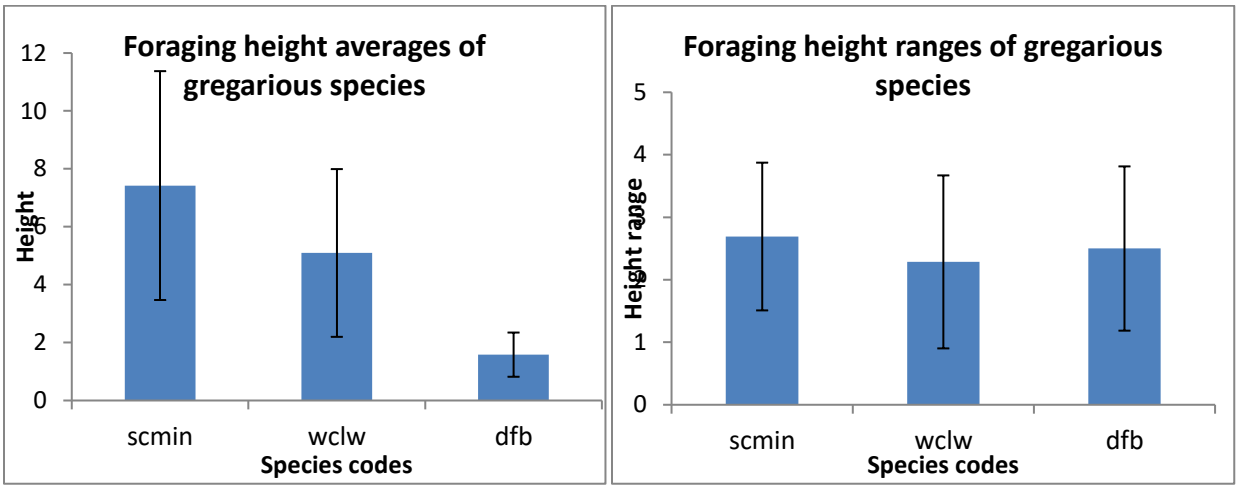


Figure 8 & 9 Foraging height averages and ranges of different gregarious species (Error bars represent Standard deviation).

b) Comparing individual foraging heights (average and range) with flock heights.

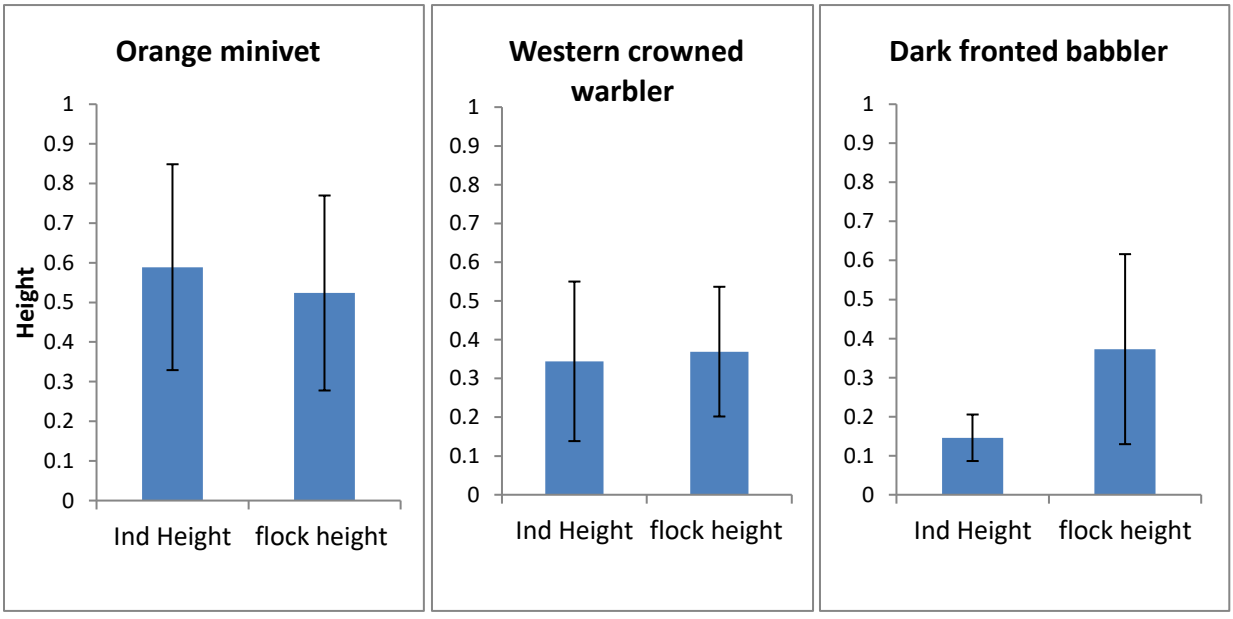


Figure 10, 11 & 12 Comparison of Individual height averages of gregarious species with respective flock heights (Error bars represent Standard deviation).

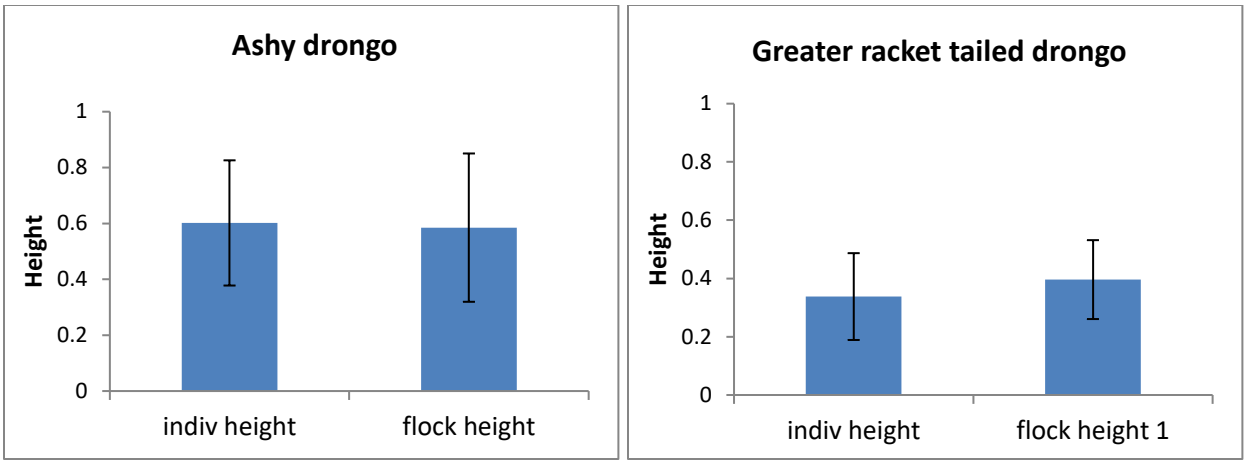


Figure 13 & 14 Comparison of height averages of sallyer species with respective flock heights (Error bars represent Standard deviation).

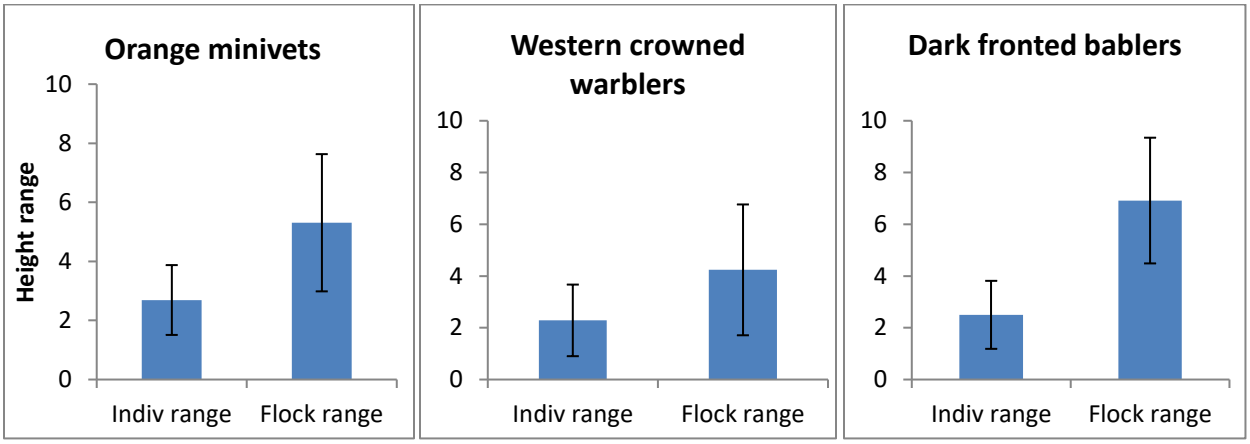


Figure 25, 16 & 17 Comparison of Individual height ranges of gregarious species with respective flock heights (Error bars represent Standard deviation).

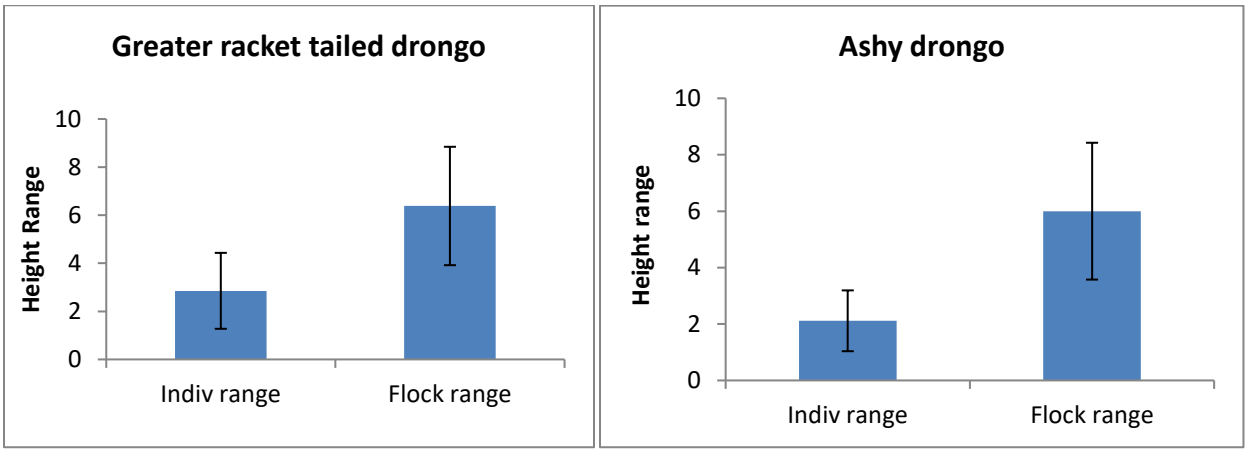


Figure 38 & 19 Comparison of Individual height ranges of sallyer species with respective flock heights (Error bars represent Standard deviation).

c) Individual foraging height (average and range) vs. Species richness.

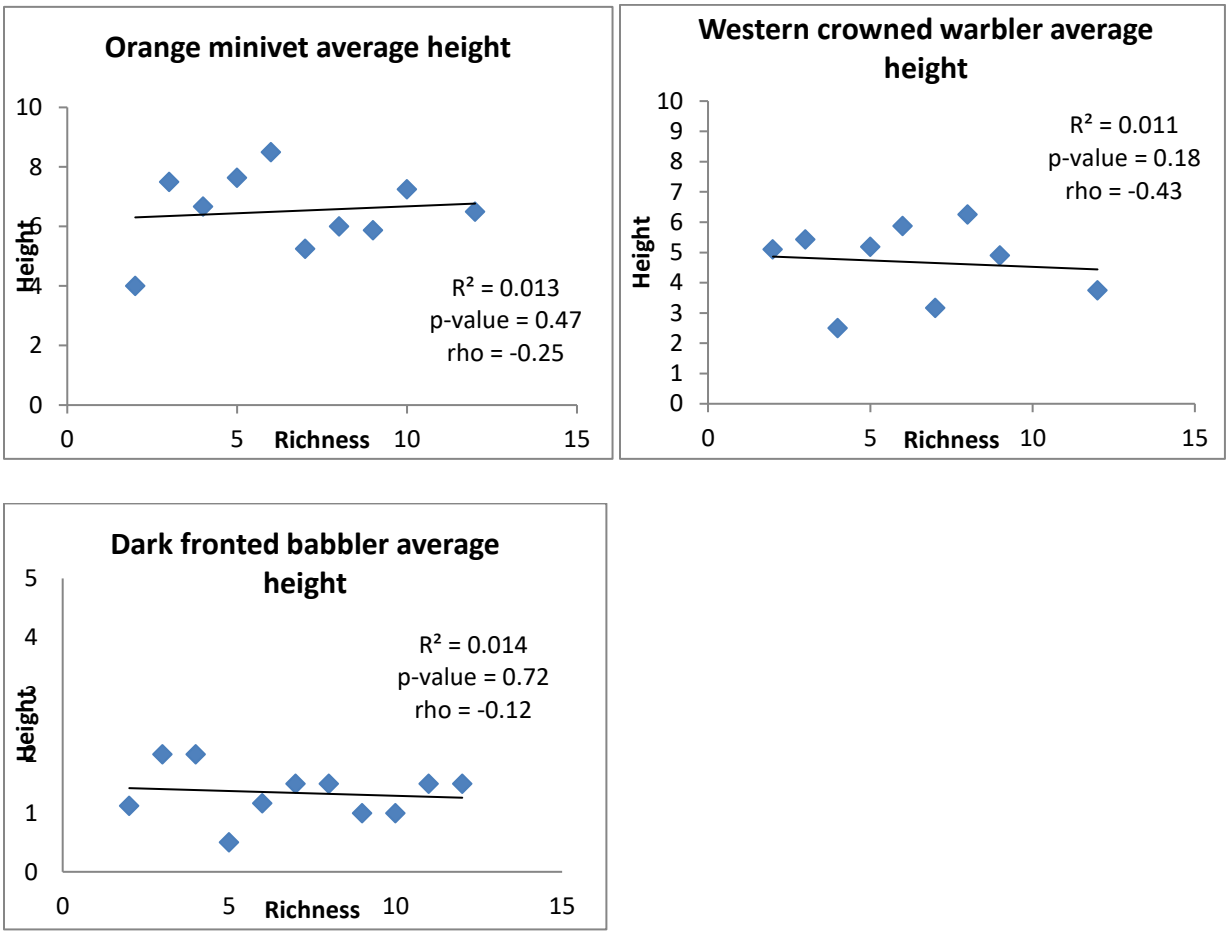


Figure 20, 21 & 22 Relationship between species richness and foraging height averages of gregarious species.

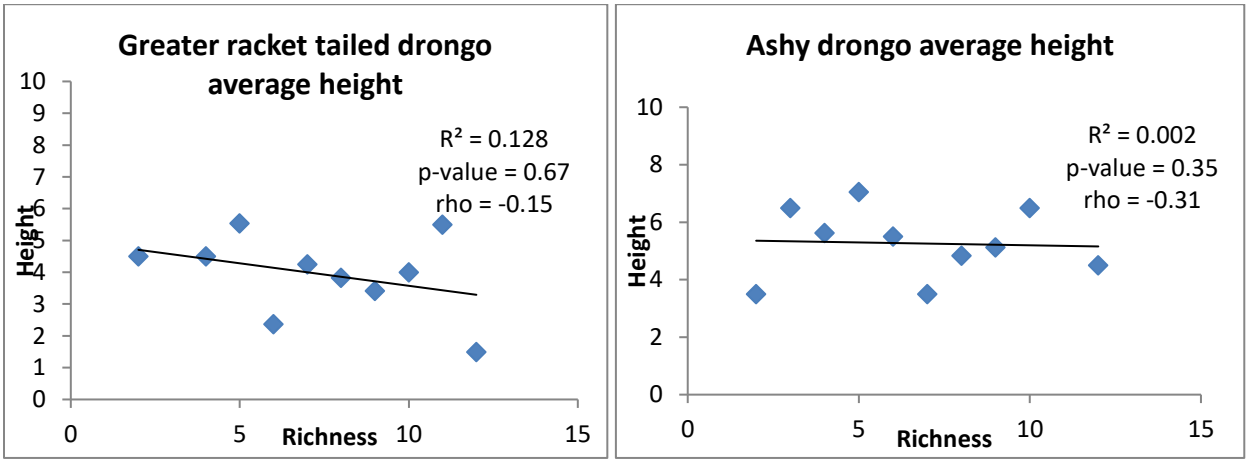
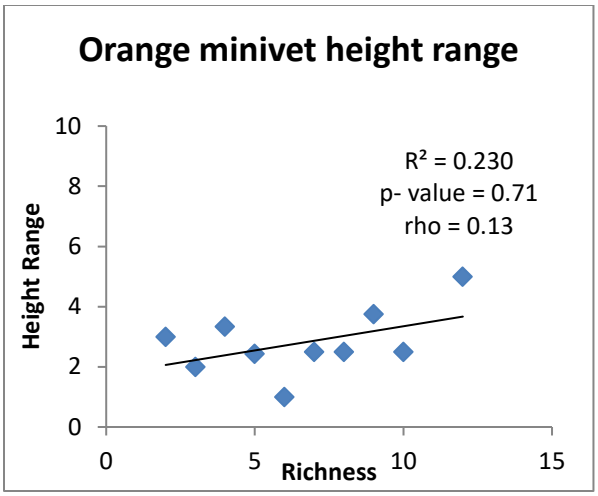
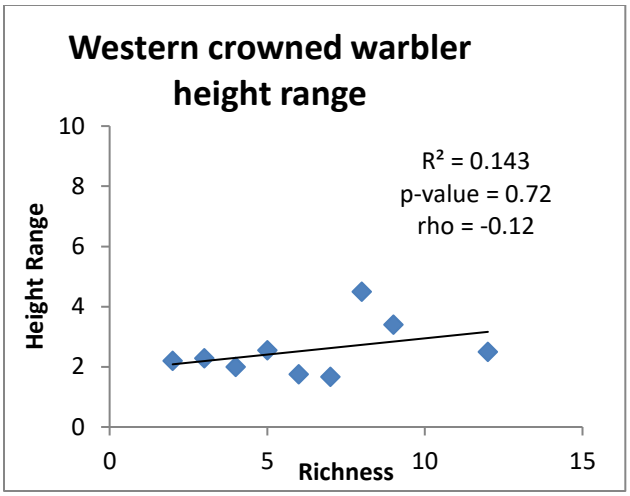


Figure 23& 24 Relationship between species richness and foraging height averages of sallying species.





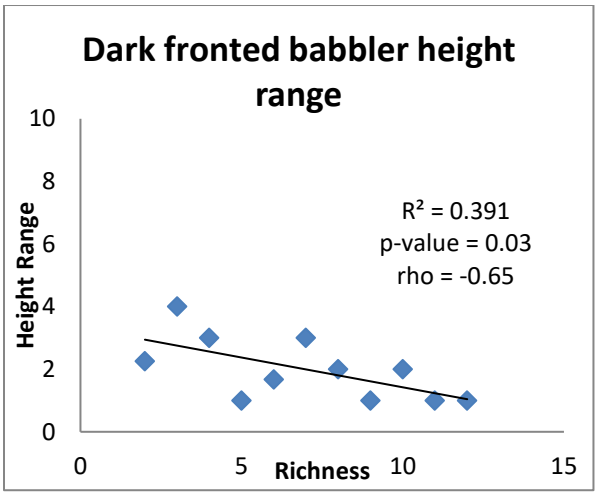
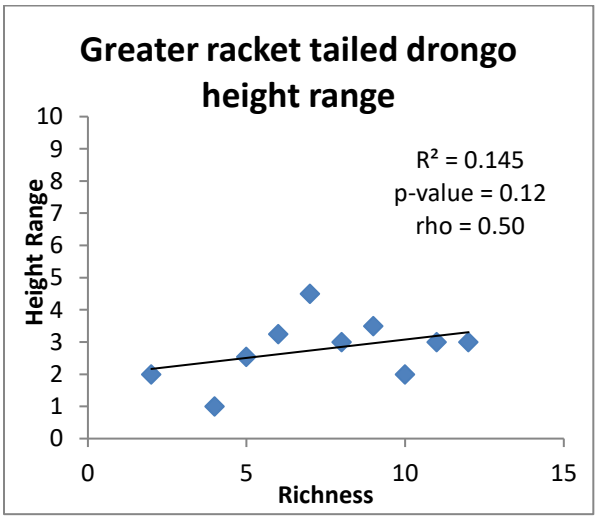


Figure 25, 26& 27 Relationship between species richness and foraging height ranges of gregarious species.



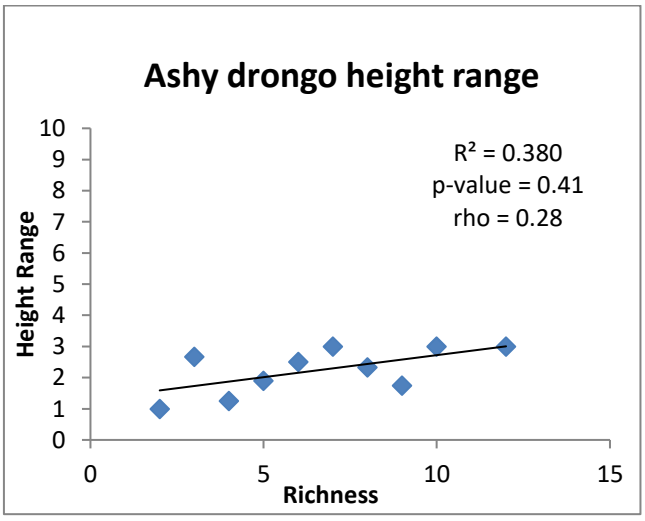


Figure 48& 29 Relationship between species richness and foraging height range of sallying species.

B. Composition (predictor)

Flock foraging height averages (Fig 30) did not show any pattern with different compositions (p>0.05 for all pair wise comparisons).The foraging height range (Fig 31) was higher when all three guilds (gregarious (*g),*sallyers (*s)* and non gregarious, non sallyers (*n*)) were present as opposed to when any of them was absent (p-values: *gsn-gn*=0.004, *gsn-gs*=0.0001, *gsn-sn*=0.14, *gs-gn*=0.98, *sn-gn*=0.82, *gs-sn*=0.70).

The number of gregarious species in the flocks observed varied from zero to four. The flock height averages (Fig 32) did not vary with increasing gregarious species richness (Spearman's rho = 0.1, p= 0.95). Flock foraging height ranges (Fig 33) also did not increases with an increasing number of gregarious species (Spearman's rho = 0.6, p= 0.35).

The foraging height averages and ranges of the two sallying species, greater racket tailed drongo and ashy drongo, in the presence of the three different gregarious species (scmin, wclw and dfb) were compared (Fig 34-37). The foraging heights of both greater racket tailed drongo and ashy drongo did not vary in the presence of different gregarious species (p>0.05).

1) Species composition vs Flock foraging heights

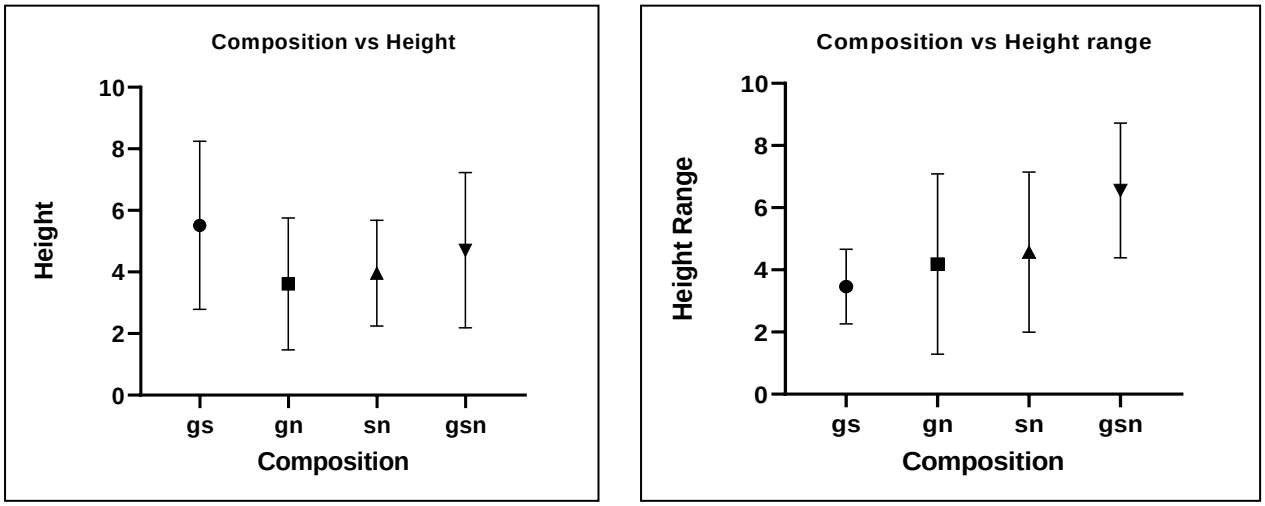
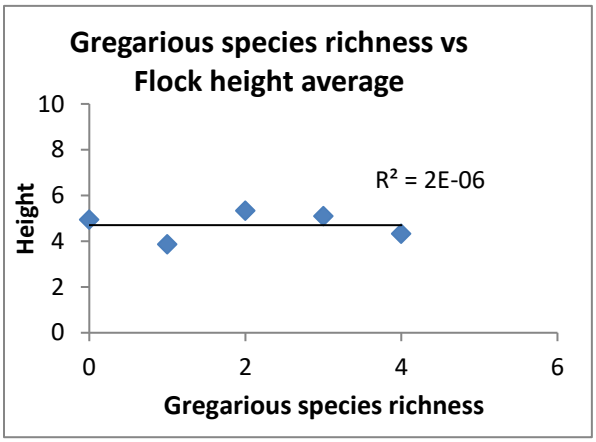


Figure 30&31 Flock foraging height averages and ranges at different flock compositions (Error bars represent Standard deviation).

2) Gregarious species richness vs. Flock foraging heights



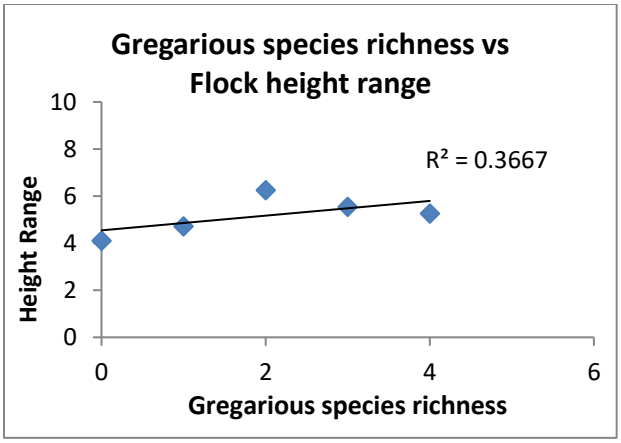
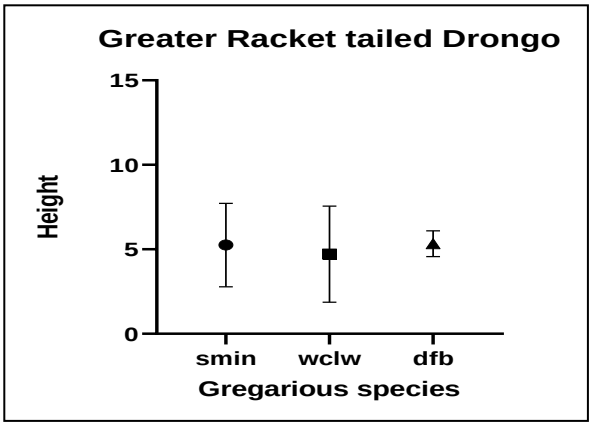


Figure 32 & 33 Foraging height averages and ranges of flocks with increasing number of gregarious species.

3) Foraging heights of sallying species in presence of different gregarious species.



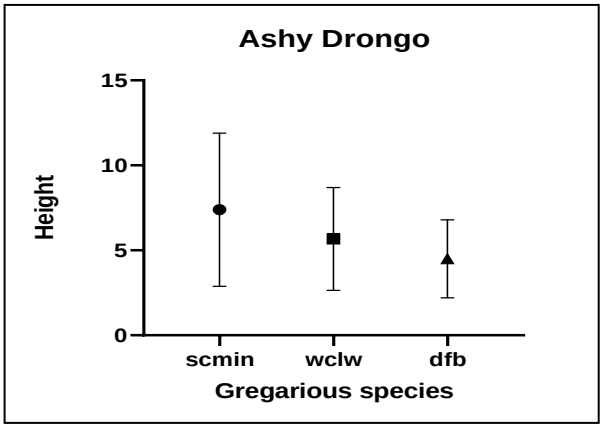
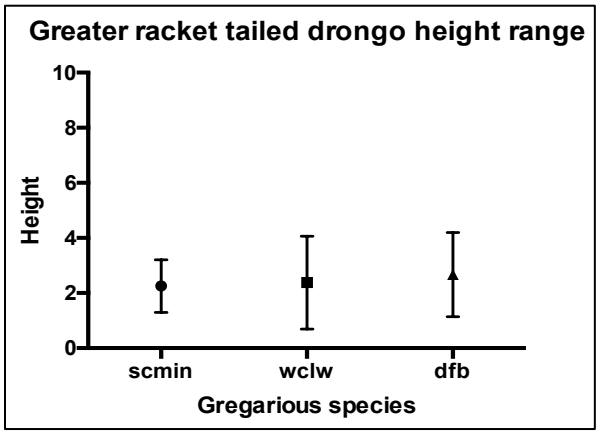


Figure 34 & 35Foraging height averages of Sallyers in the presence of gregarious species (Error bars represent Standard deviation).



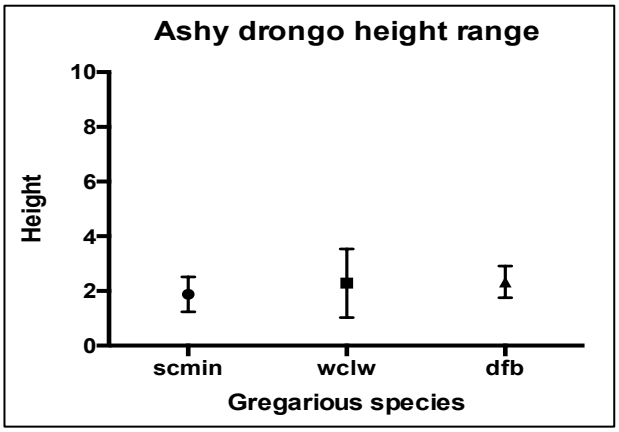


Figure 36 & 37 Foraging height ranges of Sallyers in the presence of gregarious species (Error bars represent Standard deviation).

DISCUSSION

This study aimed at understanding the consequence of flocking on the foraging niche of participating individuals. The foraging niche of an organism has multiple factors shaping it, which has been described as an ‘n- dimensional hyper volume’ (Hutchinson, 1958). In this study, we examined a parameter which represents one or more dimensions of the niche, namely foraging height, in terms of average height and range. I find that the two flock parameters - richness and composition – have an effect on foraging heights or ranges of the flock as a whole as well as of individual species.

Five out of the six species noted as important for mixed species flocks (Sridhar, Jordán, & Shanker, 2013) namely yellow browed bulbul, western crowned warblers, orange minivets, brown cheeked fulvetta and greater racket tailed drongo were the most common species in the mixed species flocks of Anshi during my study period. Additionally, ashy drongo and dark fronted babblers, species that were not in the top 6 common species in the past, were seen commonly in flocks. But such variations between years have been previously recorded (Sridhar et al., 2013, Hariharan, 2018). For further individual species based analysis, five of these species (western crowned warblers, orange minivets, greater racket tailed drongo, ashy drongo and dark fronted babblers) were considered. Of these, three were gregarious species and 2 were sallyer species according to the classification used in Sridhar & Shanker, 2014.

Foraging niche overlap between participating species can lead to facilitative interactions or cause competition (Chen, 2011). It is important to note here that we are only looking at a part of the niche. The overlap in this dimension can be compensated for by separation in other dimensions (Eguchi et al., 1993) i.e. though there is overlap in height, they might be separated along other axes (like their horizontal positioning or choice of substrate). In this study, the average foraging height of orange minivets and western crowned warblers were higher than dark fronted babblers. All their foraging height ranges are comparable.

The 5 nuclear species did not show a significant relationship in their foraging height averages or ranges with species richness. Similarly, the flock foraging height average also did not show any correlation with species richness, but the foraging height range occupied by the flocks increased with increasing species richness. This could be because dissimilarity between the members of the flocks increases with increasing species richness in terms of preferred foraging heights. As the number of species increases, there may be more nuclear species that occupy different strata hence averaging the flock height to similar values but increasing the range occupied. This could potentially lead to an increasing trend in flock foraging height ranges with increasing gregarious species richness.

The average foraging height of the nuclear species however does not show variation with species richness. Orange minivets, western crowned warblers and dark fronted babblers were the most frequent gregarious species. Orange minivets and dark fronted babblers are known to be canopy foragers and understory birds, respectively. Western crowned warblers are known to occupy a height range in mid-canopy strata (Bangal, 2020). Except for dark fronted babblers, the foraging height averages of four of the five species were found to be very close to the flock foraging height averages. Among intraspecifically gregarious species, the flock foraging height averages are not very different from individual foraging heights of orange minivets and western crowned warblers whereas flock height seems independent of dark fronted babblers foraging height. This could solely be a species-specific trend or a common property of understory birds. However, further comparative studies between understory gregarious birds in flocks will be necessary.

The comparison of the heights of the two most frequent sallying species– greater racket- tailed drongo and ashy drongo– in the presence of the three main nuclear species was carried out to see the effect of the latter on sallying species. Drongos are known for using flocking as a way to increase efficiency in foraging mainly through the beating effect (Morse 1977; Diamond 1981; Hino 1998). Satischandra et al. (2007) observed that the greater racket-tailed drongo (Satischandra et al., 2007) and the bronzed drongo (Chen, 2011) adjust their perching heights according to the foraging

heights of nuclear species. In this study, the greater racket- tailed drongo maintained similar average heights regardless of the presence of the three gregarious species whereas the ashy drongo showed some variation. This was not found to be significant but this could be because of low sample size and needs further observations.

This study contributes to the understanding of foraging niches in mixed species flocks. The results suggest that species richness and composition can affect individual niches, with some birds having more impact on niches of other participants than the others. This warrants further enquiry into how these affect flocking tendencies.

FUTURE WORK

This study is focused on the spatial niche overlap. As Buskirk et al (1972) and Munn & Terborgh (1979) suggests, behavioral compatibility and diet similarity are also significant determinants in flocking. I plan to carry out a similar analysis for foraging behavior data which were collected along with the foraging height during this study. I also plan to carry out additional analyses to study the effect of composition on individual niches.

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APPENDIX

Table 3: Species codes and guilds

The birds are classified into 3 guilds namely gregarious (g), sallyers and sally gleaners (s) and non gregarious non sallyers (n).

Species code	Common names	Guild
ad	Ashy Drongo	s
bd	Bronzed Drongo	s
bhcs	Black-headed Cuckoo-shrike	n
blyrw	Blyth's Reed-warbler	n
bnm	Black-naped Monarch	s
bwfs	Bar-winged Flycatcher-shrike	n
cmflmbk	Common Flameback	n
ctb	Malabar Barbet	n
ctstar	Chestnut-tailed Starling	g
dfb	Dark-fronted Babbler	g
fbb	Fairy blue bird	n
forwag	Forest Wagtail	n
ftb	Flame throated Bulbul	n
gfc	Golden-fronted Leafbird	n
glw	Greenish Warbler	n
gori	Indian golden Oriole	n
grflmbk	Greater Flameback	n
grtd	Greater Racket-tailed Drongo	s
hsw	Heart-spotted Woodpecker	n
iora	Common Iora	n
jbab	Jungle Babbler	g
jnmn	Hill Myna	n
lblw	Large-billed Leaf-warbler	n
lwdshk	Malabar Woodshrike	g
lynpe	Lesser Yellownape	n
oht	Orange-headed Thrush	n
parfly	Indian paradise Flycatcher	s
pic	Speckled Piculet	n
quak	Brown-cheeckedFulvetta	g
rwb	Red whiskered bulbul	n
scim	Scimitar Babbler	n
scmin	Orange Minivet	g
sphn	Little spider hunter	n

tickelfly	Tickell's Blue-flycatcher	n
trog	Malabar Trogon	n
verfly	Verditer Flycatcher	n
vfn	Velvet-fronted Nuthatch	n
wbbf	White-bellied Blue-flycatcher	n
wbt	White-bellied Treepie	n
wcb	White-cheecked Barbet	n
wclw	Western Crowned Warbler	g
wheye	Oriental White-eye	g
ybb	Yellow-browed Bulbul	n
bbfly	Brown-Breasted Flycatcher	n

Thank you.