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Research Article

Temporal Foraging and Ranging Patterns Suggested the Niche Partitioning of Two Sympatric Herbivores, *Axis axis* and *Bubalus bubalis*, in the Nijhum Dweep National Park of Bangladesh

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For proper conservation measures and to elucidate coexistence mechanism of sympatric herbivore, we assessed the temporal foraging and ranging patterns of the *Axis axis* (spotted deer) and feral and/or semi domesticated *Bubalus bubalis* (buffalos) in the Nijhum Dweep National Park (NDNP) of Bangladesh. We have collected the data by day long scan sampling method for 12 months. We found that spotted deer and buffalos, respectively, spent 50.34% and 36.41% of their total day time in foraging. To avoid clash with the larger sized buffalos in the grazing ground, the spotted deer choose a slightly different time for grazing. At least three foraging peaks were found for spotted deer, whereas, buffalos showed two foraging peaks in a day. More importantly, spotted deer relied more on browsing for their food collection although they are natural gazer, whereas, buffalos relied more on their natural grazing habit for food collection. Spotted deer spent most of their time inside the forest and forest edges, whereas, buffalos mostly spent their time in the open grazing grounds. The range of total distance moved (TDM) per day for spotted deer and buffalos was 1.56 to 2.67 km and 1.02 to 3.30 km, respectively. The total area ranged (TAR) per day were 0.23 km^2 to 0.8 km^2 for spotted deer and 0.03 km^2 to 0.35 km^2 for buffalos. Although, these two parameters varied seasonally for both species, only in case of TAR of spotted deer the variation was statistically significant ($P < 0.05$). We conclude that because of the presence of a larger sympatric herbivore, the spotted deer did some alterations in their temporal foraging and ranging pattern (TFRP) to survive in the small island which has very limited resources for their existence and survival.

1. Introduction

Since its introduction in the late 1980s, the spotted deer *Axis axis* (Erxleben, 1777) population in the Nijhum Dweep Island of Bangladesh, which is later officially declared as the Nijhum Dweep National Park (NDNP) in 2001 as per International Union for Conservation of Nature (IUCN) protected area category II [1]. The number of the species has increased rapidly in the absence of any natural predators to encounter a population burst in the late 1990s [2]. Feeroz and Uddin [3] reported the estimated number of spotted deer to be 10,000 and 14,000, respectively, for 2001 and 2006 census in the island. Thereafter, the population size has been gradually decreasing in the island, which estimated about 2000 or less spotted deer in the island [3]. One of the reasons for this decline may be due to the increasing human population. The consequence of human activities resulted in habitat fragmentation and subsequence destruction, and also other anthropogenic disturbances. It is now almost universally accepted that habitat loss and over exploitation are putting many of the world's mammal species at

risk of extinction [4]. Hunting, habitat degradation, and invasive species are some of the main leading factors which are responsible for the poor status of many mammal species [4].

Local people in the NDNP nurture a lot of buffalos *Bubalus bubalis* (Linnaeus, 1758) in a semidomesticated manner, which means all buffalos have an owner but always remain in the forest under the supervision of cowboys, and some of these sometimes become feral in the forest. Since both spotted deer and buffalos are herbivores having a more or less similar food preference [5], they compete for forage resources. The high diet similarity between the sympatric species indicates competitive interaction at high density and with limited food resources [5]. Although smaller in size, the spotted deer still remain and coexist with the buffalos in the island. However, sympatric species differ in their feeding styles [6] due to differences in morphological [7] and physiological [8] characteristics among them. Hence, the spotted deer might have done some modification in their activity patterns to cope with the competitors.

Information on the temporal activity and ranging patterns of animals is crucial for the implementation of suitable conservation measures, as it reflects the responses of subject animal to anthropogenic disturbance [9]. Moreover, the coexistence of animals ecologically rely on the temporal activity pattern information [10]. Among the closely related sympatric species, the temporal activity patterns are critically important to understand their coexistence mechanism in relation to interspecific competition and/or niche separation [11]. Home range extents of an animal depend largely on resource requirements [12]. Animals not only need sufficient space to procure food and other resources, but also have to stay away from predators [13] and other larger competitors. The present study is aimed to perform the comparative analysis of foraging activity (FA) and ranging patterns (RP) of spotted deer and buffalos in the NDNP of Bangladesh. The objective of this study was to understand how the two sympatric species of herbivore, having very close and/or similar feeding habits, partition their ecological niche to coexist in a small island with limited resources.

2. Materials and Methods

2.1. Study Area. The Nijhum Dweep National Park (NDNP) comprises of a cluster of several small islands, located about 31 km southwest of Hatiya Upazila under Noakhali District, Bangladesh. The geographical extent of the NDNP is in between latitude 22°01′25″ to 22°06′11″N and longitude 90°56′44″ to 91°06′07″E. The NDNP is located at the confluence of the Meghna River mouth on the Bay of Bengal (Figure 1).

The main island is about 10 km long in north-south and 8 km wide in east-west directions [3]. The NDNP is separated from the main land Hatiya by Mokteria channel and bounded by the Meghna River in the eastern part, Mokteria channel in the northern part, the Shahabaj River in the eastern part, and the Bay of Bengal in the southern part. There are three major types of land use available in the NDNP, such as, forested area, grazing land, and human habitation.

2.2. Methods of Data Collection

2.2.1. Activity Pattern. The comparative activity patterns of spotted deer (*Axis axis*) and feral buffalos (*Bubalus bubalis*) were studied during March 2018 to February 2019 in the NDNP of Bangladesh. The scan sampling technique [14] was used to record the activity budget, foraging behaviour, and habitat use of the two species. Although many deer species are crepuscular in nature [15, 16], spotted deer are inclined to be diurnal [17, 18] and buffalos are completely diurnal animal, hence the data collection was carried out during the day.

Before starting the data collection, one herd of spotted deer was selected which forage mostly on the remote side of the island where least anthropogenic activities were evident. After that, the herd was habituated to continuous presence of the observer(s) in the vicinity wearing local dress as they appeared to recognise external clothing and persons. A scan interval of 2 minutes was chosen. The field observations were carried out with naked eyes and with the aid of one pair of binoculars (10×4 binoculars (Model: Zen-Ray 2015 ZRS HD (Summit) 8×42) depending upon the prevailing field conditions, from a distance of 100 to 150 m, so the focal herd did not get disturbed. The behavioural states were as follows: *Moving* (when an animal is in motion in the form of walking or running without doing any other activities); *Resting* (when an animal take rest either standing or laying without ruminating); *Ruminating* (when an animal ruminate either standing or laying); *Foraging* (when an animal move either for grazing or browsing); *Social Behaviour* (it included fighting and sniffing for spotted deer, and fighting, sniffing, and bathing for buffalos); *Alarm* (when an animal give alarm to its herd members. Here, standing alert and call alert for spotted deer, and standing alert alone for buffalos.

The sampling was carried out once in a month for each species continuously from dawn (06.00 h) to dusk (18.00 h). Five individuals from each herd of the two species were selected each time—of different age and sex—for recording different activities. As in every two minutes a single activity record was taken, so for five individuals, 150 activities were recorded in every hour, and in this way a total of 1,800 activities were recorded, in 12 hours (06.00 h to 18.00 h), in a single day of the representative month for each of the two species.

Data recordings were started from March 2018 as this month represents the first month of summer in Bangladesh. In the present study, three broad seasons were considered—summer (March to June), monsoon (July to October), and winter (November to February). The focal spotted deer and buffalo herds were followed on foot from dawn to dusk in the field and recorded their activities. The samples for each activity were averaged on a daily basis and their standard deviations were calculated. The detailed activities were merged into broader activities for monthly, seasonal, and yearly analysis. For analysis of data, IBM SPSS statistics 20 programme was used.

2.2.2. Ranging Pattern. Two parameters were considered for the analysis of ranging pattern of the two species, viz., total distance moved (TDM) per day and total area ranged (TAR) per day. For determining these parameters for both the

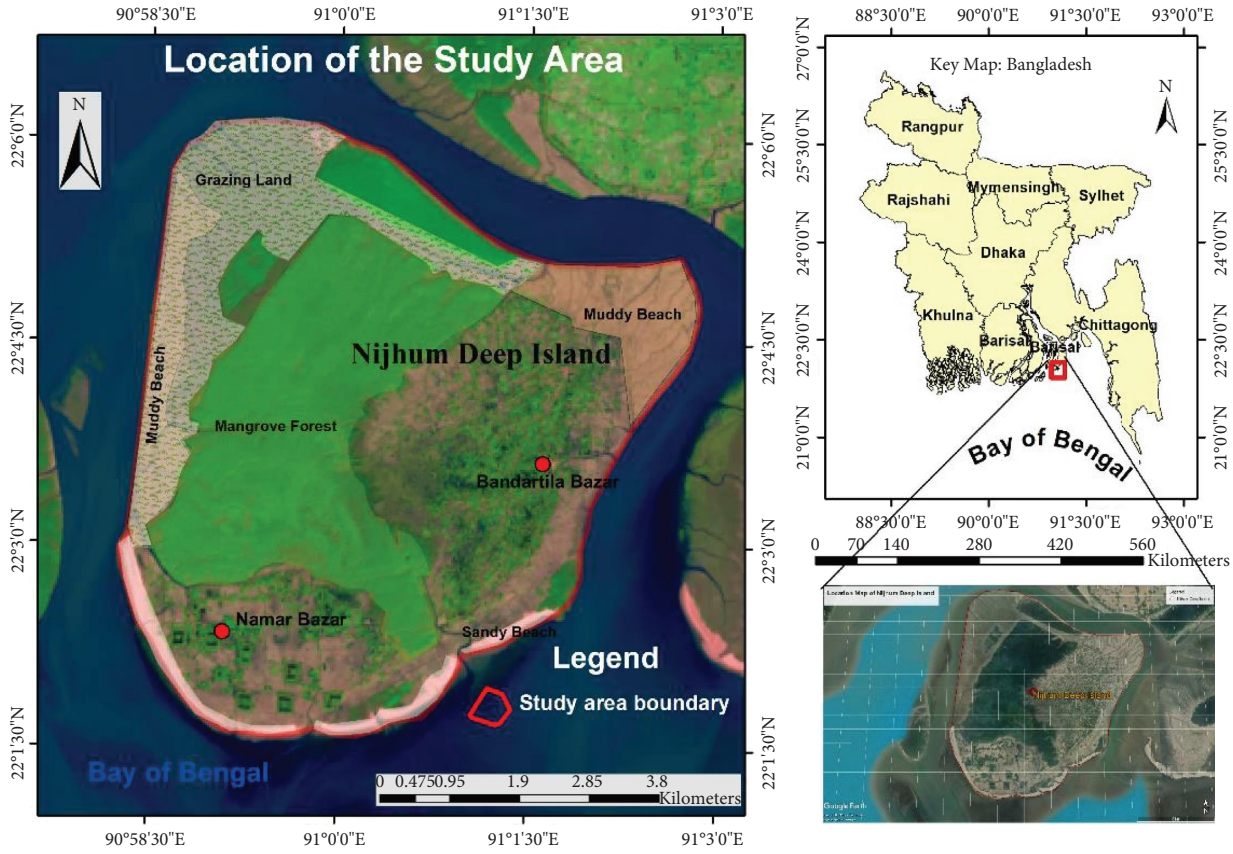

Figure 1: Location of the study area: the inset right bottom image indicate Google Earth Pro satellite image shows the study location overview and in the left, zooming view of Landsat 9 satellite image (acquisition date: 02 Dec 2022; band combination used in background image as R:G:B = 7, 5, 4) and red points represent important locations of the NDNP of Bangladesh.

species, 7 to 9 GPS (using a hand held GPS, model: GARMIN GPSmap 60 CSx) readings were taken, which represented the major activities (waking, resting, grazing and browsing, and bathing in case of buffalos) performed in the whole day (06.00 h to 18.00 h). By connecting the GPS points in ArcGIS 10.8 programme, the TDM for each species in each month was calculated. For determination of TAR, a polygon was constructed by connecting the GPS points in the same software and resulting areas of the polygon was considered as the ranging area of the respective species in the respective months. The seasonal data of both species have been presented in real earth image of "Google Earth," and also the TAR of both species were overlaid on seasonal basis (summer, monsoon, and winter) in the same image to compare the ranging areas and activity partitioning.

3. Results

3.1. Comparative Activity Budget of Spotted Deer and Buffalos. During the study periods, both the species were found to spent more time, 50.34% and 36.41%, respectively, for spotted deer (*Axis axis*) and buffalos (*Bubalus bubalis*) for foraging than those of the other activities (Table 1). Within the foraging activity, spotted deer relied more on browsing activity (32.91%), whereas buffalos relied more on grazing (28.19%) (Table 1).

3.2. Temporal Variations in Foraging. According to GPS tract records, both species overlapped with each other frequently during foraging, other than this activity they remained separated; that is why, day long comparison of foraging of both species was made.

In all seasons, spotted deer started their foraging long before dawn (06.00 h) and continued up to 10.30 h (Figures 2–4). Mostly before and after sunrise they respectively grazed and browsed. From 11.00 h to 14.00 h, they did not forage at all, rather they rested at that time; after 14.00 h, they again started foraging and became more and more active towards the dusk (18.00 h) and to continue it after sunset (Figures 2–4). On the other hand, buffalos started the day with resting in all seasons; they did not start foraging as late as 07.00 h—seasonally this time varied—became fully active in foraging at about 08.00 h (Figures 2–4). Their foraging was predominated by grazing, especially in the morning, but some browsing activity was also noticed before noon. From 13.00 h to 15.00 h, they stopped foraging and went for resting/ruminating (overall resting) (Figures 2–4). After 15.00 h, they again started foraging and continued up to 17.00 h, after that they reduced foraging and started returning to the resting place (Figures 2–4).

Spotted deer showed three foraging peaks, whereas buffalos showed two in all seasons (Figures 2–4). The first

Table 1: Proportion of time (%) spent in different activities by spotted deer and buffalos at the NDNP of Bangladesh in 2018–2019 (from Hossain 2020).

Activities		% of time spent in different activities			
		Spotted deer		Buffalo	
Moving	Walking	17.37	17.1	14.53	14.51
	Running		0.27		0.02
Resting	Standing	13.9	9.39	22.49	16.06
	Laying		4.51		6.43
Ruminating	Standing	14.09	0.99	12.92	6.02
	Laying		13.1		6.9
Foraging	Grazing	50.34	17.43	36.41	28.19
	Browsing		32.91		8.22
Social behaviour	Bathing	1.61	0.68	9.94	8.56
	Fighting		0.93		0.3
	Smelling		2.56		1.08
Alarm	Standing alert	2.72	0.16	3.7	3.7

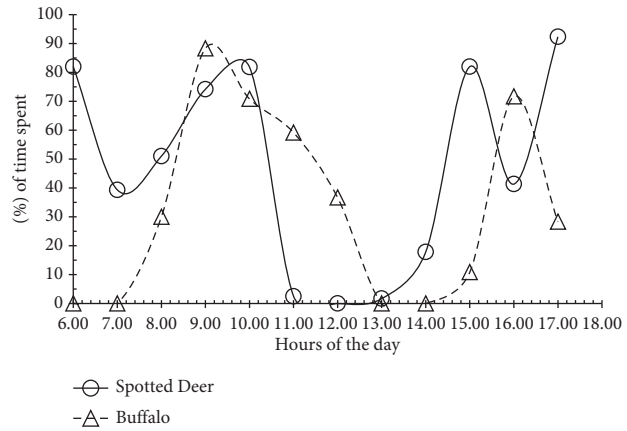

Figure 2: Temporal foraging patterns of spotted deer and buffalos in summer-2018.

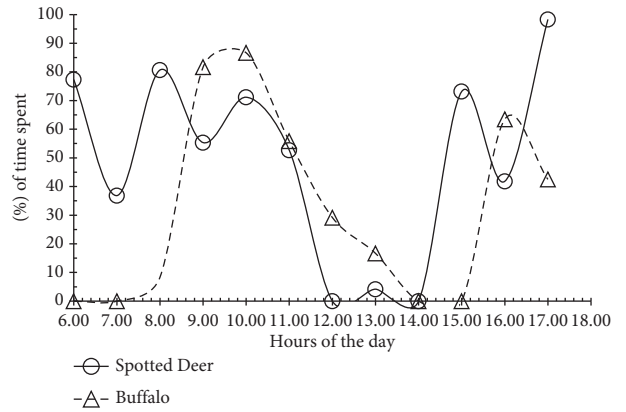

Figure 3: Temporal foraging patterns of spotted deer and buffalos in monsoon-2018.

and last peaks of spotted deer were diffused as they started foraging before sunrise and in the evening they continued foraging even after dusk.

During winter, the peak of spotted deer foraging was found to be sharper than that of the other two seasons (Figure 4), whereas in case of buffalos, foraging peak of winter was found to be broader than that of the other two seasons (Figure 4). The percentage of time spent in foraging was also more in winter than that of the other two seasons for both spotted deer and buffalos.

During summer, spotted deer and buffalos overlapped in foraging between 08.30 h and 10.00 h (i.e., before noon) and 15.30 h and 16.30 h (i.e., late afternoon) (Figure 2). Overlapping of resting in summer was not that evident as spotted deer started resting at 11.00 h and stopped at 13.00 h, whereas buffalos started resting at 13.00 h and ended at 14.00 h (Figure 2).

During monsoon, spotted deer and buffalos overlapped in foraging between 08.30 and 11.00 h and 15.30 h and 16.30 h (Figure 3). Overlapping of resting in monsoon was not that evident as spotted deer started resting at 12.00 h and finished at 14.00 h, whereas buffalos started resting at 14.00 h and finished at 15.00 h (Figure 3).

During winter, spotted deer and buffalos overlapped in foraging much less times—10.00 h in the morning and 15.30 h to 16.00 h in the late afternoon (Figure 4). Overlapping of resting in winter was not that evident as spotted deer started resting at 12.00 h and stopped at 14.00 h, whereas buffalo started resting at 14.00 h and ended at 14.30 h (Figure 4).

3.3. Ranging Pattern. TDM ranges were (1.56–2.67) km and (1.02–3.30) km for spotted deer and buffalos, respectively (Table 2). The yearly average TDM of spotted deer and buffalos were found to be 2.13 ± 0.33 km and 1.92 ± 0.61 km, respectively (Table 2), although they did not differ significantly ($t = 1.049$, $df = 22, P = 0.306$). Among different seasons, the highest average TDM was recorded in monsoon (2.34 ± 0.26 km) and the lowest was recorded in summer (1.94 ± 0.29 km) for spotted deer, whereas the highest average TDM was recorded in summer (2.15 ± 0.99 km) and the lowest was recorded in monsoon and winter (1.80 ± 0.46 and 1.80 ± 0.28 km) for buffalos (Table 2). TDM values of both species (spotted deer ($F = 1.775$; $df = 2, 9$; $P = 0.224$) and buffalo ($F = 0.388$; $df = 2, 9$; $P = 0.689$)) did not differ significantly among the seasons.

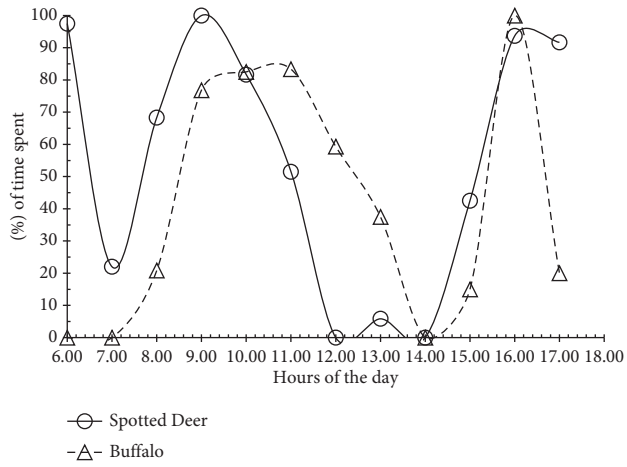

Figure 4: Temporal foraging patterns of spotted deer and buffalos in winter-2018-19.

The range of the total area ranged was 0.23 km^2 to 0.8 km^2 for spotted deer and 0.03 km^2 to 0.35 km^2 for buffalos (Table 2). The yearly average TAR of spotted deer and buffalos was 0.48 ± 0.19 km^2 and 0.17 ± 0.11 km^2, respectively (Table 2). However, they differed significantly ($t = 4.829$, $df = 22$, $P = 000$). Like TDM, the highest TAR of spotted deer was also recorded in monsoon (0.61 ± 0.17 km^2), whereas the lowest was recorded in summer (0.29 ± 0.09 km^2) (Table 2). On the other hand, the highest TAR of buffalo was recorded in summer (0.22 ± 0.16 km^2), whereas the lowest was recorded in monsoon (0.14 ± 0.10 km^2) (Table 2). TAR values of spotted deer differed significantly ($F = 5.740$; $df = 2, 9$; $P = 0.025 < 0.05$) among seasons, whereas that of buffalos it did not vary significantly ($F = 0.576$; $df = 2, 9$; $P = 0.082 > 0.05$).

3.4. Habitat Preference for Different Activities by Spotted Deer and Buffalos. The GPS data of ranging pattern revealed that spotted deer grazed mostly in the early morning and late evening in the grass land of the forest edges and small grassy patches within the forest; whereas buffalos grazed mostly in the open grassland in the late morning and during evening (Figures 5–10). The foraging pattern of the spotted deer was dominated by browsing within the forest, whereas in case of buffalos that was dominated by grazing in the open grassland (Figures 5–10). The resting pattern of both species also showed dissimilarities, such as the spotted deer rested entirely within the forest, whereas buffalos rested in the open field or at the edge of the forest (Figures 5–10). When the seasonal TAR of both species overlaid on each other, it revealed that both species share some common areas but there were differences in time of the activity within the shared areas during all seasons (Figures 5–10). The TAR of both of the species moved from north to south with the advent of monsoon, whereas again they shifted from south to north during winter and summer (Figures 6, 8, and 10).

4. Discussion

In the present study, the foraging behaviour accounted for 50.34% and 36.41%, respectively, for *Axis axis* (spotted deer) and *Bubalus bubalis* (buffalo) in the Nijhum Dweep National Park (NDNP) (Table 1). Foraging included both grazing and browsing. However, grazing included all feeding on grass and other low height vegetation, whereas browsing included feeding on leaves, soft shoots, or fruits/pods of high-growing, generally woody plants [19]. Relatively high amount of time spent in foraging by both species indicated that there is shortage of food or competition for food for both species in the island. Dave [5] also found that spotted deer and buffalos spent more than 30% time in foraging in the Gir National Park, which has similar results of this study. According to previous theoretical [20, 21] and empirical [22] studies, greater time spent in foraging always indicated poor habitat resources, especially food resource. The present study indicated poor food resources for both the sympatric species, especially very poor food resources for spotted deer. Although spotted deer is smaller in body size than that of the buffalos, it had to forage more to fill up its relatively smaller stomach further indicated very poor food resources available for spotted deer in this national park.

Table 2: Mean TDM (total distance moved per day) and TAR (total area ranged per day) with standard deviations of spotted deer and buffalos in the NDNP in 2018–19 (from Hossain 2020).

Seasons	Spotted deer		Buffalo	
	TDM (km)	TAR (km^2)	TDM (km)	TAR (km^2)
Summer	1.94 (±0.29)	0.29 (±0.09)	2.15 (±0.99)	0.22 (±0.16)
Monsoon	2.34 (±0.26)	0.61 (±0.17)	1.80 (±0.46)	0.14 (±0.10)
Winter	2.11 (±0.36)	0.55 (±0.15)	1.80 (±0.28)	0.16 (±0.05)
Year average	2.13 (±0.33)	0.48 (±0.19)	1.92 (±0.61)	0.17 (±0.11)
Range	1.56–2.67	0.23–0.84	1.02–3.30	0.03–3.35

Spotted deer grazed very limited amount of time than that of the buffalos (Table 1). Generally, spotted deer were found to be grazing in the forest edges and small grassy patches of the forest, whereas buffalos grazed mostly in the open field. This might be due to anthropogenic disturbances (agricultural works, sound of engine boats, and so on) that prohibited spotted deer to graze in the open field during the day; as earlier research [5] mentioned that spotted deer spent more time in grazing than browsing in the Gir National Park of India. On the other hand, spotted deer were found to be browsing high amount of time than that of the buffalos, as they were found preferring feeding on keora (*Sonneratia apetata*) leaves and fruits from the forest floor, which were easy options for them.

The foraging patterns of spotted deer and buffalos showed clear differences as the former showed three distinct peaks of foraging, whereas the later showed two (Figures 2–4). This result disagreed with the observations of Dave [5], who found two peaks for both spotted deer and buffalos in the Gir National Park of India. The second foraging peak of the spotted deer was formed during 08.00 h to 10.00 h, and it is exceptional for most of grazing ungulates might be formed due to walking of the species in search of available food in the forest as they could not avail the food from the grassland at that time because of anthropogenic

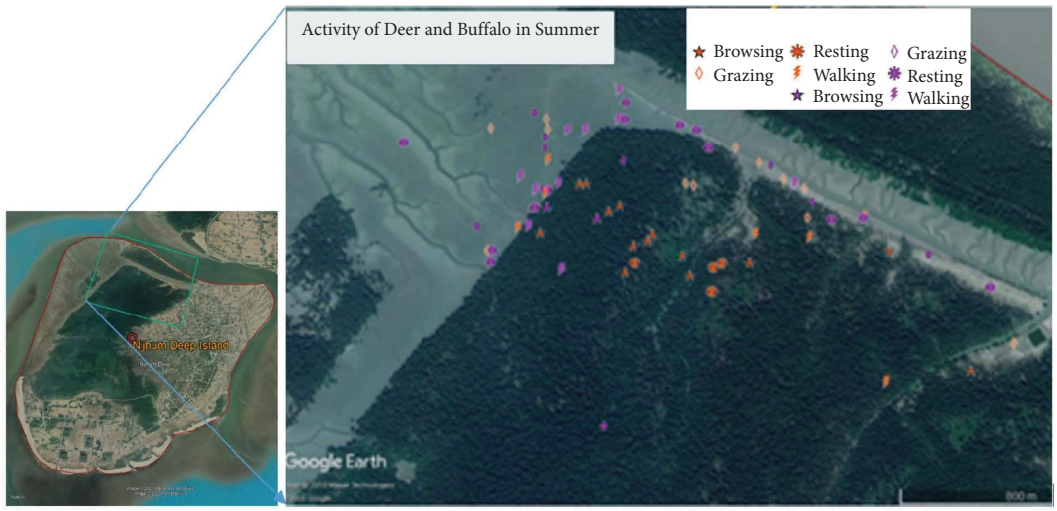

Figure 5: Ranging pattern of a single group of spotted deer (orange) and buffalo (pink) in the Nijhum Dweep National Park in summer-2018.

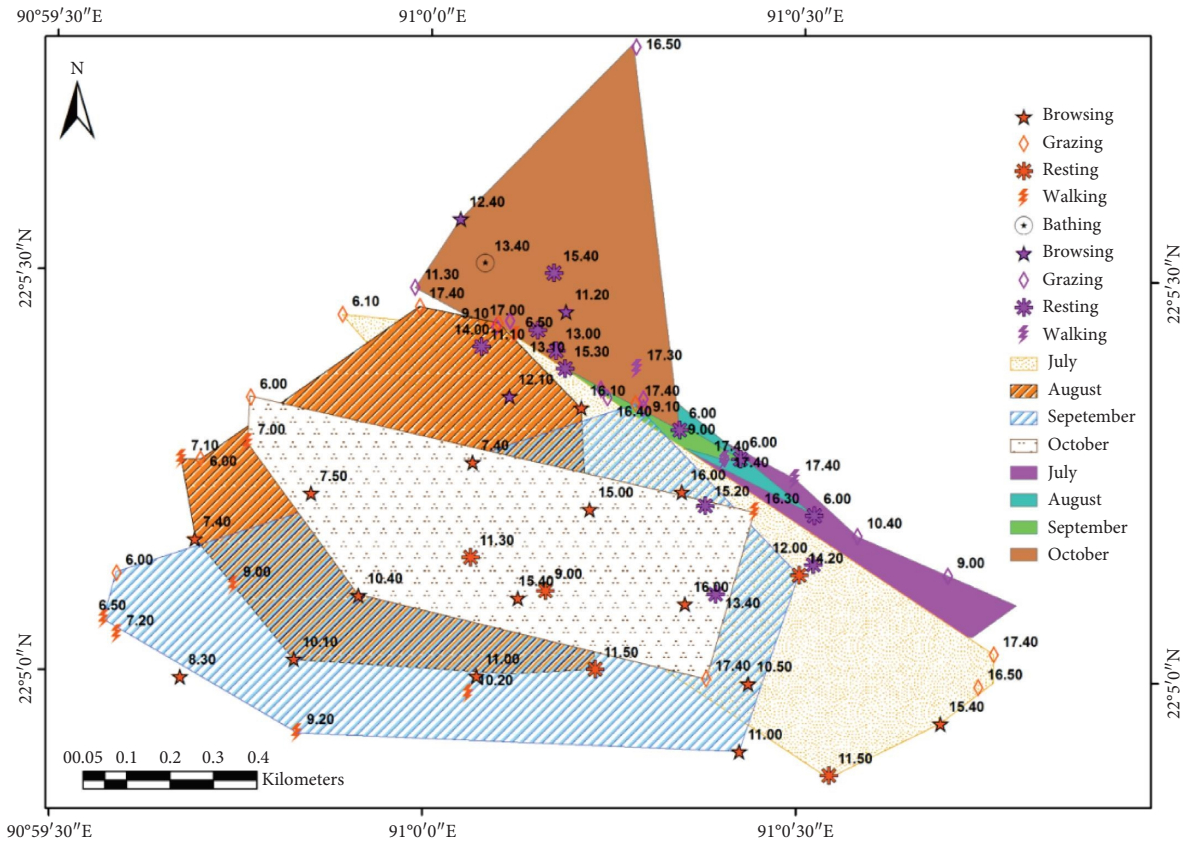

Figure 6: TAR (shaded spotted deer and solid buffalo) of a single group of spotted deer (orange) and buffalo (pink) in the Nijhum Dweep National Park in summer-2018.

activities and the presence of buffalos. Broad patterns of alternating foraging and resting for both species were little bit different.

Little difference in the seasonal patterns of foraging of individual species was also evident. Moreover, the morning and evening peaks of spotted deer were diffused and refers that the morning peak started much before the dawn and the evening peak ended after dusk (Figures 2–4). Distinct foraging peaks in the daily cycle were also found in most of the studies [23–26] with an intensive peak in the morning hours.

The spotted deer found to be grazing less during the day than that of the buffalos, when the later occupied the grazing

Figure 7: Ranging pattern of a single group of spotted deer (orange) and buffalo (pink) in the Nijhum Dweep National Park in monsoon-2018.

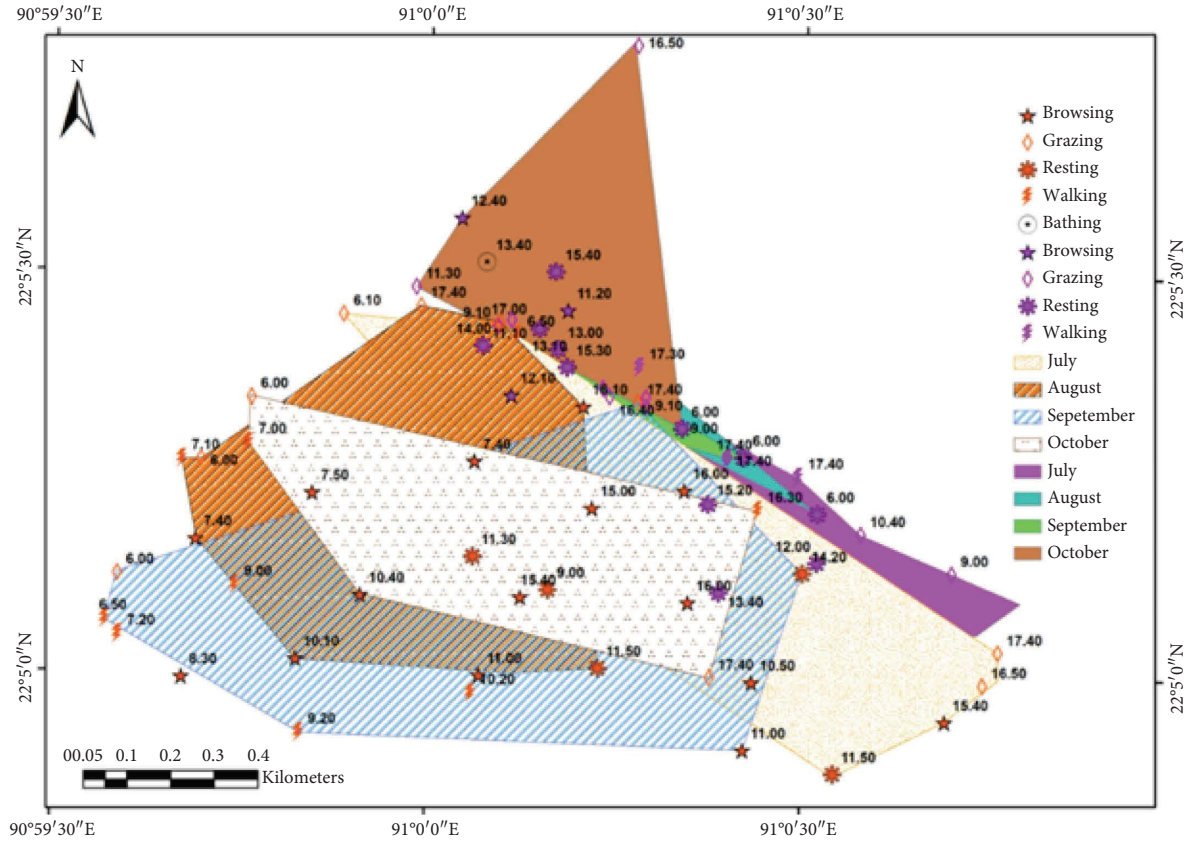

Figure 8: TAR (shaded spotted deer and solid buffalo) of a single group of spotted deer (orange) and buffalo (pink) in the Nijhum Dweep National Park in monsoon-2018.

land. Fisler [27] mentioned the influence of larger body size in determining the dominance among the species of the same trophic level. In this case, interspecific behavioural hierarchy of the two species probably determined the partitioning of the ecological niche [28], as spotted deer, although predominantly a grazer [5], had become a predominant day time browser in the NDNP. In areas where larger species of the same trophic levels got established, the larger one either monopolizes the resources directly from the smaller one or caused smaller species to shift niches [5]. The difference in the foraging patterns could also be attributed to the size, quality, and quantity of the food items; gut capacity and process; and digestion of the forage [29–31].

Both abiotic factors (such as slope and distance to water) and biotic factors (such as forage quality and quantity) might govern the foraging or ranging pattern of large herbivores

Figure 9: Ranging pattern of a single group of spotted deer (orange) and buffalo (pink) in the Nijhum Dweep National Park in Winter-2018.

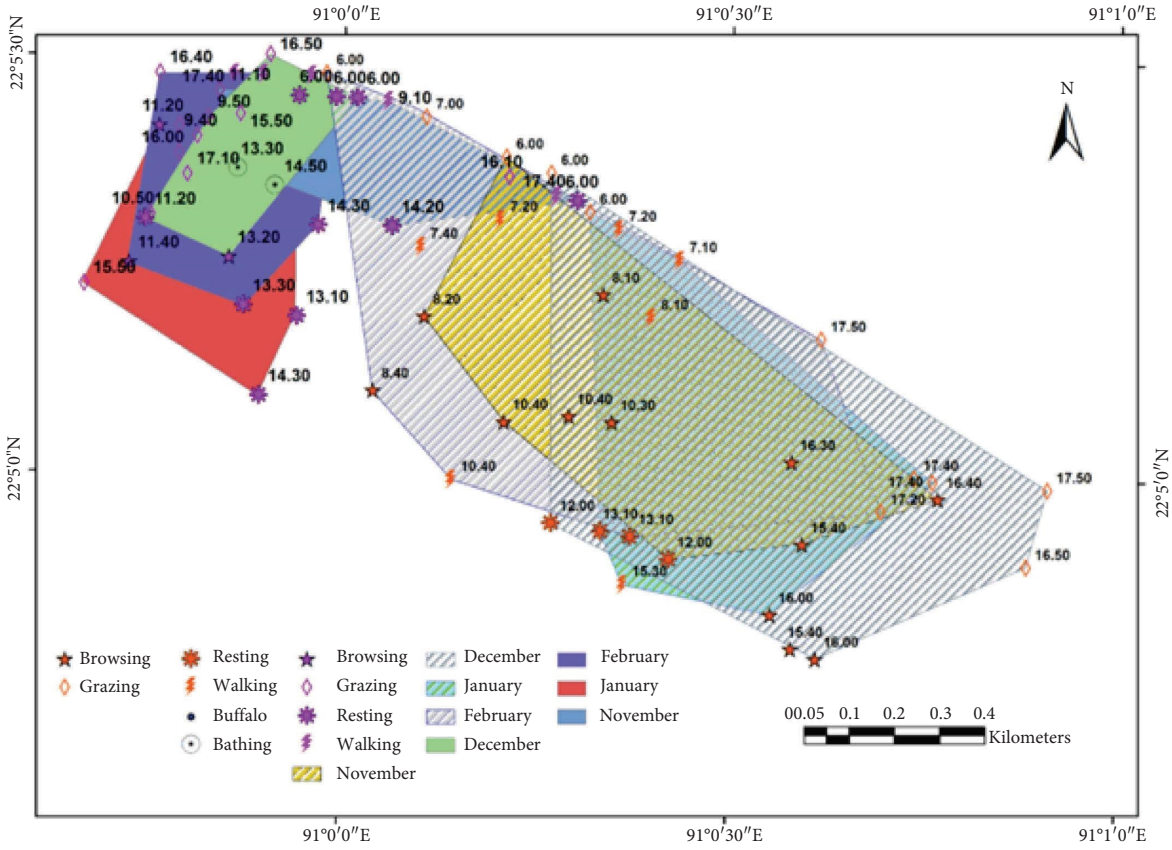

Figure 10: TAR (shaded spotted deer and solid buffalo) of a single group of spotted deer (orange) and buffalo (pink) in the Nijhum Dweep National Park in winter-2018.

[32]. In this study, the major abiotic factors that influenced the ranging pattern of both the species might be the tidal water and anthropogenic disturbances; major biotic factors might be forage quality and quantity, and the species themselves as resource competitors. The average TDM and TAR of spotted deer were higher than that of the buffalos, indicating that the resources available for spotted deer were limited in the island compared to the buffalos. Seasonally, spotted deer moved more during monsoon, whereas buffalos moved more in summer. Both spotted dear and livestock (cattle and buffalo) move more in summer than winter and monsoon in the Gir National Park, India. This is because during summer, increased walking appeared to be the expense of foraging time, although other activities did not

change much [5]. But in the NDNP, due to regular tidal periods, the grazing land never get completely dried; hence, no notable differences in grass availability were evident. On the other hand, during monsoon, the grazing and forest lands got submerged more intensely, so food became very limited for spotted deer as they could not tolerate high water levels, hence they moved towards the high dry land. In contrast, buffalos are more comfortable in the water by nature, so they do not face any problem in finding foods during monsoon, and as a result they moved less in this season; Moreover, their TAR is also found less during this period of the year. During summer period both TDM and TAR of buffalos were found to be more than that of the other two seasons. This might be due to searching of suitable bathing place, as during this period the island become very hot and dry, so the available water pools in the open grassland for bathing become limited.

The abovementioned findings supported the general concept of the negative relationship between the foraging area and resource availability for herbivores as mentioned by Cohen et al. [33, 34] in case of white-tailed deer and Dave [5] in case of spotted deer and buffalos. But seasonal data of TDM and TAR deferred with that of Dave [5], who found greater foraging area during summer for the spotted deer in the Gir National Park of India; this might be due to the difference of the geographical position of the two study areas. Animals ranging in an area with better food availability have a lower net displacement and decrease the chance of leaving the high resource density area, thereby increasing the utilization of resources [35–38].

As information on resource distribution is considered to be limited in animals [39], so a number of past studies used random movement strategy while foraging within the theory of optimal foraging [38, 40]. On the other hand, Bailey et al. [32] observed that prior information on the resource distribution increases their chances of encountering the target, hence form a definite shape of animal foraging path. In this study, the ranging pattern and foraging path of both the species indicate that they probably have a clear idea about the resource distribution of the island as they are more or less specific in terms of timing and use of resources.

5. Conclusion

An animal's foraging and ranging habits may help to solve the issue of adequate management and conservation measures, which are important considerations for park managers. This study can be utilized as a starting point, and long-term research may reveal more information about these two sympatric ungulates.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Acknowledgments

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