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Cover: Leaves and fruits of *Terminalia arjuna* in water colour artwork on cold pressed water colour paper by Bhama Sridharan.

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ARTICLE

Spatial, temporal and trophic resource partitioning among the four egret species (Aves: Pelecaniformes: Ardeidae) in a tropical wetland ecosystem, India

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Abstract: The diversity of micro-habitats in tropical wetlands allows the coexistence of several species. These sympatric species interact with each other, either directly or indirectly, to optimally use the available resources. They achieve this through niche separation or minimal overlap to avoid competition. India's wetland ecosystems are home to various sympatric species, such as the Great Egret *Ardea alba* (GE), Median Egret *Ardea intermedia* (IE), Little Egret *Egretta garzetta* (LE) and Cattle Egret *Bubulcus ibis* (CE). These egret species are closely related, and as a result, have similar niche requirements, which could lead to high intra-specific competition. However, there have been few studies on how these species utilize resources. This study aims to understand the possible mechanisms that enable the coexistence of these species in a tropical wetland. We have examined habitat characteristics, feeding behaviour, timings of seasonal and daily activities, and spacing patterns to evaluate possible models of species coexistence. We discovered that these four sympatric egret species have differences in microhabitat selection, activity patterns, both daily and seasonally, and feeding preferences. The study further indicates that there is a relationship between the niche dimensions, but it is only partially dependent on each other.

Keywords: Co-existence of sympatric species, competition, interspecific interaction, niche separation.

ان آبی علاقوں میں جو کرہ ارض کی استوائی زمین پر پائے جاتے ہیں، باریک فرق والی رہائش گاہوں کا تنوع متعدد انواع کے بقائے باہمی کی اجازت دیتا ہے۔ یہ انواع ایک دوسرے سے دیرینہ تعلق رکھتے ہیں اور دستیاب وسائل کو بہترین طریقے سے استعمال کرنے کے لیے براہ راست یا بالواسطہ طور پر ایک دوسرے کے ساتھ تعامل کرتے ہیں۔ مقابلہ سے بچنے کے لیے وہ طاق علیحدگی یا کم سے کم مخل کے ذریعے اپناتے ہیں۔ ہندوستان کے دَل دَل، جھیل اور تالاب کے ماحولیاتی نظام مختلف ایسی انواع کی پناہ ہیں، جیسے یہ چار بگلے جن کے نام ہیں عظیم بگلا یا آرڈیا البا (GE)، درمیانہ بگلا یا آرڈیا انٹرمیڈیا (IE)، چھوٹا بگلا یا ایگریٹا گارزیٹا (LE)اور مویشی بگلا یا بوبلکس ابیبس (CE)۔ ان چاروں بگلوں کی نسلوں کا آپس میں گہرا تعلق ہے، اور اس کے نتیجے میں، اسی طرح کے مخصوص تقاضے ہیں، جو اعلیٰ درجہ کے بین انواع مقابلہ کا باعث بن سکتے ہیں۔ تاہم، اس مقالہ میں کچھ مطالعات ہوئے ہیں جو ان نسلوں کے وسائل کے استعمال کے اسلوب پر روشنی ڈالتے ہیں۔ اس مطالعے کا مقصد ان ممکنہ اقدام کو سمجھنا ہے جو آبی زمین میں ان انواع کے بقائے باہمی کے لیے قدرت میں رایج ہیں۔ اس نظام کا جائزہ لینے کے لیے رہائش کی خصوصیات، خوراک کی روش، موسمی اور روزمرہ کی سرگرمیوں کے اوقات، اور وقفہ کاری کے نمونوں کا مطالعہ کیا گیا ہے۔ ہم نے دریافت کیا کہ ان چار دیرینہ بگلوں میں باریک سطح پر رہائش کا انتخاب،روزانہ اور موسمی طور پر سرگرمی کے رموز، اور اکل و شرب کی ترجیحات میں باریک فرق ہے۔ مطالعہ مزید اشارہ کرتا ہے کہ طاق طول و عرض کے درمیان تعلق ہے، لیکن یہ صرف جزوی طور پر ایک دوسرے پر منحصر ہے۔

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Author contributions: FA conceived the study, collected data as a part of her PhD programme. FA and MSK analyzed data and wrote the manuscript.

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INTRODUCTION

Tropical wetland ecosystems are important habitats for migratory birds and also support the avian diversity of native species (Junk 2006). The great diversity of micro-habitats allows the coexistence of the species in the wetland (Junk 2006). The species' coexistence is generally perceived as a consequence of the interspecific interactions among the sympatric species (Siepielski 2021). The sympatric species may or may not have direct interaction but the chances of interspecific interactions in terms of competition for resource utilization (in spatial, temporal and trophic dimensions) increase in the case of closely related species (Ye et al. 2021). The Lotka-Volterra approach suggested that the stable coexistence of competitive species is only possible when intraspecific competition is stronger than interspecific competition (MacArthur 1967; Gavina et al. 2018). Further, the behaviour of the species such as pattern of habitat use, daily activity, foraging and interspecific behaviours also govern the social spacing and tolerance, to allow biologically similar sympatric species to coexist (Perri & Randall 1999; Oviedo et al. 2018).

Great Egret *Ardea alba* (GE), Median Egret *Ardea intermedia* (IE), Little Egret *Egretta garzetta* (LE), and Cattle Egret *Bubulcus ibis* (CE) are ubiquitous in the wetland ecosystems across India. As generalist top predators, the egrets exert a top-down influence on the structure of lower trophic levels, altering the abundance and distribution of multiple prey species and, in turn, the effects of their prey on other species (Huang et al. 2015). Studies focusing on their habitat and behaviour ecology are critical in understanding their ecological requirements and their role as top predators in sustaining the richness of life in wetland ecosystems (Jennings 2017).

Despite the separate studies on feeding ecology, habitat selection and seasonal or daily behaviour of the species, a comprehensive understanding of niche partitioning that integrates the temporal, spatial and trophic dimensions of sympatric egret species is still lacking (Ye et al. 2021). Hence, the possible mechanism permitting the coexistence of GE, ME, LE, and CE in a tropical wetland has been studied.

Habitat characteristics, feeding behaviour, timings of seasonal and daily activities and spacing patterns have been examined to evaluate possible models of species coexistence. The research has been carried out to understand the partitioning of niche dimensions based on niche theory and inter-specific effects as the primary mechanism to structure the communities (Hairston et al. 1960; Schoener 1982; Kelt et al. 1985; Bardsley & Beebee 1998; Beckerman 2000). It appears that the four sympatric egret species in the study area are using the resources available to them in the tropical wetland habitat. However, due to variations in their microhabitat selection, daily and seasonal activity patterns, and feeding preferences, it is hypothesized that there exists some form of niche separation over the spatial, temporal and trophic scales amongst them.

MATERIALS AND METHODS

Study Area

Sheikha lake is situated in the Gangetic Plains (Rodgers & Panwar 1988) between 78.204°–78.234° N & 27.870°–27.839° E at about 17 km from Aligarh district (Uttar Pradesh, India) and it is a perennial lake spread over 2.50 km^2 (Image 1). The region experiences extreme temperature conditions with a maximum of 47°C during summers and 0°C during winters. Average annual rainfall ranges from 650–750 mm. The lake is home to a large number of waterfowl both migratory and resident. The site has also been designated as IBA (Important Bird Area) as it provides a good habitat for the birds (Islam & Rahmani 2004).

The Upper Ganga Canal (UGC) divides the area into two blocks i.e. 'A' and 'B'. The main lake is in Block A on the western side of the canal. Block B becomes patchy in the dry season and segregates into several small pools. The permanent waterbody and seasonal expansion of the water lodging in surrounding areas, diverse weather conditions, shelter belt trees and agriculture field around the lake and the canal going through the wetland favour a broad spectrum of living conditions for diverse life forms. The major tree species on the periphery of the lake are *Terminalia arjuna, Syzygium cumini*, *Acacia leucocephala, Acacia nilotica, Holoptelia integrifolia, Ficus religiosa, Dalbergia sissoo, Azadirachta indica* and *Prosopis juliflora* (Saxena 1999). These trees provide good roosting and heronry sites for the egrets.

The lake is surrounded by agricultural fields and livestock grazing is also common in the area. A small amount of fishing, fuel wood, fodder extraction and utilization of the Block B pools for the cultivation of water chestnut *Trapa bispinosa* by the local communities, are a few minor anthropogenic disturbances in the area.

Methods

Data Collection

The study was conducted between August 2000

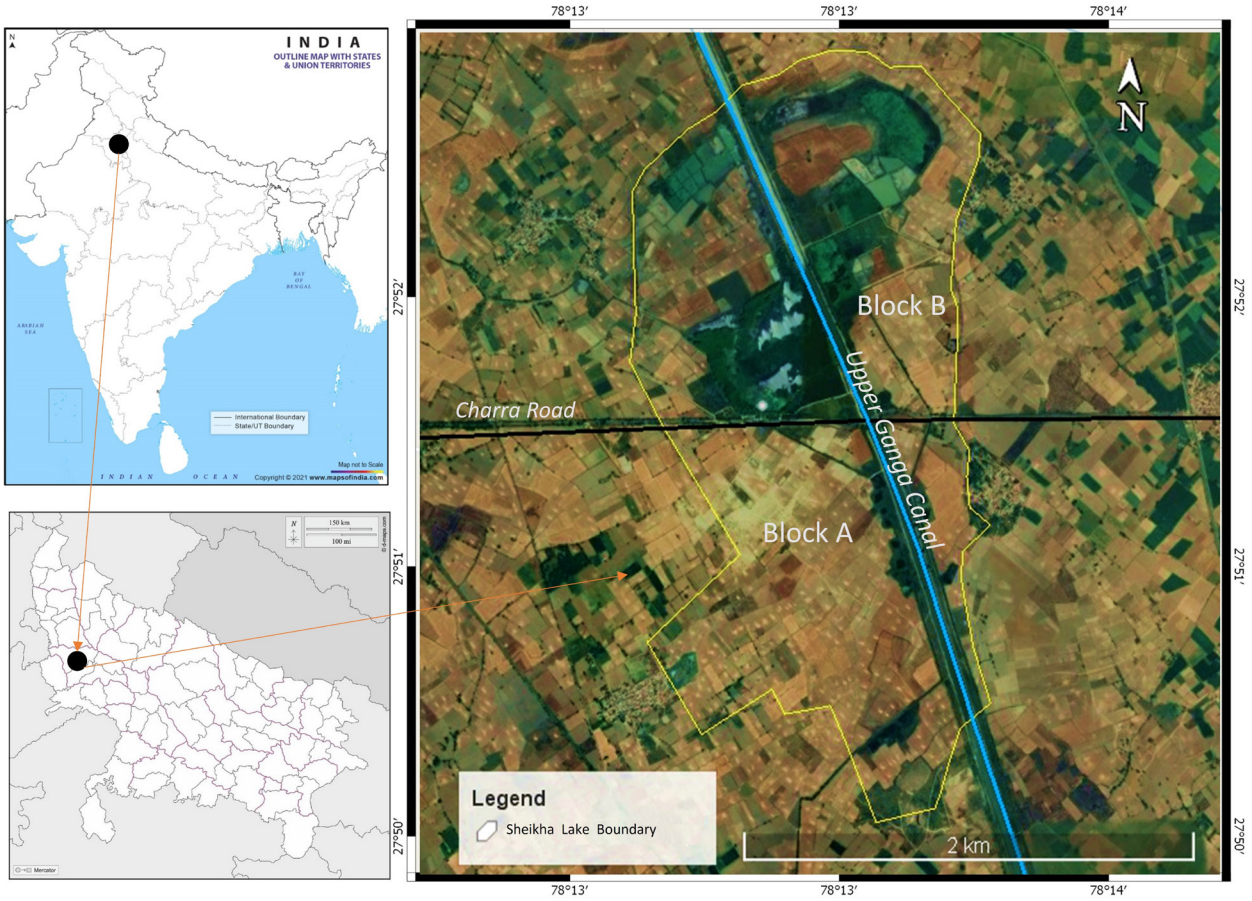

Image 1. Location map of Sheikha Lake, a tropical perennial wetland in Gangetic Plains.

and March 2004 in Sheikha Lake (Image 1). Field data collection was conducted three days a week in all study years, which amounts to 140 to 160 days. Therefore, in each season namely spring, summer, monsoon and winter, 45 to 50 days were spent in the field studying the egrets. Observation shifts of four hours each for focal animal sampling in the morning, noon and afternoon were done once a week in all seasons.

To cover all possible habitat types used by the egrets, the trails were identified and monitored on a bi-weekly basis. Seasonal data on the population, spatial distribution, activity budgeting and feeding preferences of the four sympatric species of egrets were collected through repeated sampling during the study period. Data on foraging and feeding was recorded during the observations of the egrets. Ocular estimation for prey type identification was done during the feeding attempt, and prey size was estimated using the bill length method following Bayer (1985). Established bill lengths were taken from Grimmett et al. (1998).

Spatial dimension of niche

The population of egrets were estimated using the point count method on the selected trails on a seasonal basis. Each count took place three days a week in all study years. The birds flying overhead were not recorded as per the standard point count method (Bibby et al. 1992). The seven micro-habitats were identified as open water, paddy field, grassland, lake shore, reed bed, canal bank, and ploughed field. The habitat characteristics, disturbance factors, and distance from the closest human habitation were also recorded.

Temporal dimension of niche

Focal animal observations on activity budgets of egrets in non-roosting hours during the off-breeding seasons of the year were taken (Altman 1973). Seven major types of activities such as Preening (PR), Siesta (seizure of all activities during the daytime) (ST), Resting (intermittent rests during foraging) (RS), Foraging (FR), Chasing (CH), Display (DS) and Miscellaneous (The short duration activities such as defecating, scratching the body with feet, tilting the neck and fluttering their

wings) (MS) were recorded.

Observations were made in three shifts of four hours a day. The morning shift ranged between 0600 h and 1000 h, the noon shift from 1000 h to 1400 h and the evening shift from 1400 h to 1800 h (Lehner 1979; Yahya 1980; Maheswaran 1998). All observations of activity patterns were recorded at the lake rather than the nest or roosting sites.

Trophic dimension of niche

The foraging behaviour of the egrets was identified as walking slowly, standing, foot stirring, chasing prey, probing & pecking, walking quickly, hopping, and gleaning following Hancock & Kushlan (1984). These occurrences and time allocation for these behaviours were recorded during the species-wise focal animal sampling of general activity budgeting. Following Recher & Recher (1969), Seigfried (1971), Krebs (1974), Willard (1977), Kushlan (1978), Caldwell (1979), Quinney & Smith (1980), Hom (1983), Mock et al. (1987) and Forbes (1989), the prey type and its size was also recorded during the sampling. Each species was given equal observation time in a particular shift to avoid bias. The total observation time devoted to all species was 1622 hours in the entire study period.

Data Analysis

Spatial dimension of niche

The relative abundance of each of the four species of egrets in different habitats was compared using the Student's t-test (independent sample). Chi-square contingency analysis was performed to test the significance of associations between a species of egret and the micro-habitat type and different habitat parameters (Seigel 1956; Fowler & Cohen 1986) using SPSS ver. 7.3 (Norusis 1994). The niche relationships were analysed using the programme NICHE (Krebs 1989). Estimation of the micro-habitat niche breadth for all four species was performed by using the Shannon-Weiner Measure (Colwell & Fuentes 1975; Krebs 1989).

Temporal dimension of niche

The difference in the time allocation for different activities by the sympatric egret species was assessed using the One-way ANOVA with Post hoc Tukey Test following Fowler & Cohen (1986). The seasonal and diurnal variations in the activity patterns of each sympatric egret species were also analysed using One-way ANOVA with Post hoc Tukey Test, in SPSS ver. 7.3 (Norusis 1994).

Trophic dimension of niche

A comparison was made of the frequency with which each species used a foraging behaviour, food item and prey size with χ^2 for 'k' independent samples. Chi-square contingency analysis was performed to test the significance of associations between a species and a behaviour, prey item and prey size following Seigel (1956) and Fowler & Cohen (1986).

Food item and prey size in the categories of food and foraging behaviour in the categories of behaviour were considered as one resource type each and resource matrices for all species were structured following Pianka (1986). Levins' (1968) diversity index was used to estimate the extent of behaviour and resource use.

RESULTS

Spatial dimension of niche

The relative abundance measure indicated the population of the CE was highest (265.6 ± 54.5) followed by ME (114.6 ± 20.9), GE (12.6 ± 6.7) and LE (4.51 ± 3.5). Chi-square contingency analysis of the frequency with which each species used the micro-habitat types revealed that significant associations exist between the species and the micro-habitat types (Table 1). The CE used a variety of habitat types both aquatic and terrestrial and dry grassland amongst terrestrial habitat types while amongst the aquatic types, it preferred reed beds with low height vegetation growth and irrigated paddy fields (χ^2 = 213.6, P <0.05, df = 288). The LE mostly remained in open sheets of water within the lake and at the shore

Table 1. The percentage utilization of nine microhabitats by the four sympatric species of egrets and their micro-habitat niche breadth.

		*Proportion of individuals (Relative abundance)			
	Habitat Type	CE	LE	ME	GE
1	Marsh	6	14	9	10
2	Ploughed field	27	4	8	0
3	Pool	0	6	0	23
4	Open water	0	31	11	42
5	Paddy field	7	13	12	7
6	Dry grassland	34	7	12	0
7	Lakeshore	0	22	8	18
8	Reed bed	21	0	36	0
9	Canal bank	5	3	4	0
Shannon-Weiner's niche breadth index H'		**325.05**	**301.96**	**313.29**	**305.48**

Table 2. Habitat niche overlap (Morisita's measure of niche overlap) amongst the four sympatric species of egrets.

Species pairs	C (Morisita's measure of niche overlap)							
	Overall Habitat niche overlap	Aquatic habitat			Terrestrial habitat			
		Water depth	Water stretches	Vegetation cover	Tree height	Canopy cover	Ground cover	Distance from lake
CE-LE	0.030	0.108	0.170	0.000	0.214	0.422	0.240	0.085
CE-ME	0.016	0.675	0.682	0.000	0.237	0.464	0.425	0.115
CE-GE	0.011	0.054	0.076	0.000	0.319	0.568	0.384	0.100
ME-LE	0.062	0.411	0.129	0.235	0.280	0.411	0.506	0.794
ME-GE	0.024	0.260	0.057	0.212	0.422	0.556	0.634	0.864
LE-GE	0.045	0.274	0.028	0.979	0.363	0.492	0.957	0.948

(χ^2 = 232.7, P <0.05, df = 288). Amongst its less preferred ventures into the terrestrial area, it remained in short grasslands. The ME, however, (χ^2 = 256.8, P <0.05, df = 288) showed a high preference for reed beds (χ^2 =139.1, P <0.05, df = 288) and made equal use of paddy fields, lake shore and marshes. The GE (χ^2 = 297.3, P <0.05, df = 288) seemed to be specializing in open water feeding making use of the clear sheet of water within the lake and other pools.

The utilization pattern of resources within these micro-habitat types by the sympatric species of egrets was also found to be different (Table 2). The CE preferred to remain in shallow reaches (χ^2 = 234.2, P <0.05, df = 288) when feeding in water and treaded over vegetation, while the LE (χ^2 = 477.8, P <0.05, df = 288) and the ME (χ^2 = 285.4, P<0.05, df = 288) mostly stayed in water up to 30 cm deep. Owing to its longer legs, the GE (χ^2 = 274.3, P<0.05, df = 288) was the only species of the four, that ventured up to 70 cm.

The aquatic vegetation cover was also differentially used by the four species for foraging. The CE (χ^2 = 184.5, P <0.05, df = 288) and the ME (χ^2 = 109.6, P <0.05, df = 288) fed in highly vegetated areas, whereas the LE (χ^2 =119.2, P <0.05, df = 288) and the GE (χ^2 = 122.4, P <0.05, df = 288) fed in scantily vegetated areas. Out of the several categories of available water stretch in the wetland, there was a differential association of the four species with various categories. The CE (χ^2 = 248.6, P <0.05, df= 288) frequented the wetland with less than 50% open water while the LE (χ^2 = 194.7, P <0.05, df = 288) preferred the wetland with only 25% open water. The ME (χ^2 = 233.1, P <0.05, df = 288) frequented the lake when open water was up to 75% and the GE (χ^2 = 242.9, P <0.05, df = 288) fed in the lake when the open water was more than 50% and even while the lake was overflowing due to heavy rains.

The CE (χ^2 = 274.3, P <0.05, df = 288) frequented ground vegetation cover only where it was more than 30%, whereas the LE (χ^2 = 146.2, P <0.05, df = 288) frequented areas with less than 30% ground vegetation. The ME did not exhibit a significant association with the ground cover but the GE (χ^2 = 203.5, P <0.05, df = 288) showed a significant preference for ground vegetation cover of up to 60%. Significant associations were also found between the species and their distance to the lake. While the CE (χ^2 = 266.4, P <0.05, df = 288) was mostly found feeding away from the lake. The LE (χ^2 =313.5, P <0.05, df = 288) maintained strict proximity to the lake area. The ME (χ^2 = 186.7, P <0.05, df = 288) did venture away from the lake but remained within a distance of one kilometre. The GE (χ^2 = 302.8, P <0.05, df = 288) was found to feed only in the close vicinity of the lake and its adjoining pools and never beyond one kilometre distance.

Analysis of the niche breadth (Table 1) shows that the CE and the ME use a wide spectrum of habitat types hence they have a larger niche breadth. While the GE has a lesser diversity of habitat types used and a smaller niche breadth followed by the LE.

The degree of habitat niche overlap between the four sympatric species of egrets (Table 2) indicates that the maximum overlap exists between the LE and the GE. The CE has very little overlap with any of the species for all habitat parameters, in fact, no overlap exists between the CE and the other three species in the case of vegetation cover. The ME shows moderate habitat overlap with LE and GE. However, niche overlap inference cannot be made with regard to tree height and canopy cover, because the Chi-square contingency analysis used to derive Morisita's Index of niche overlap revealed that there was no significant correlation between the species and these habitat parameters.

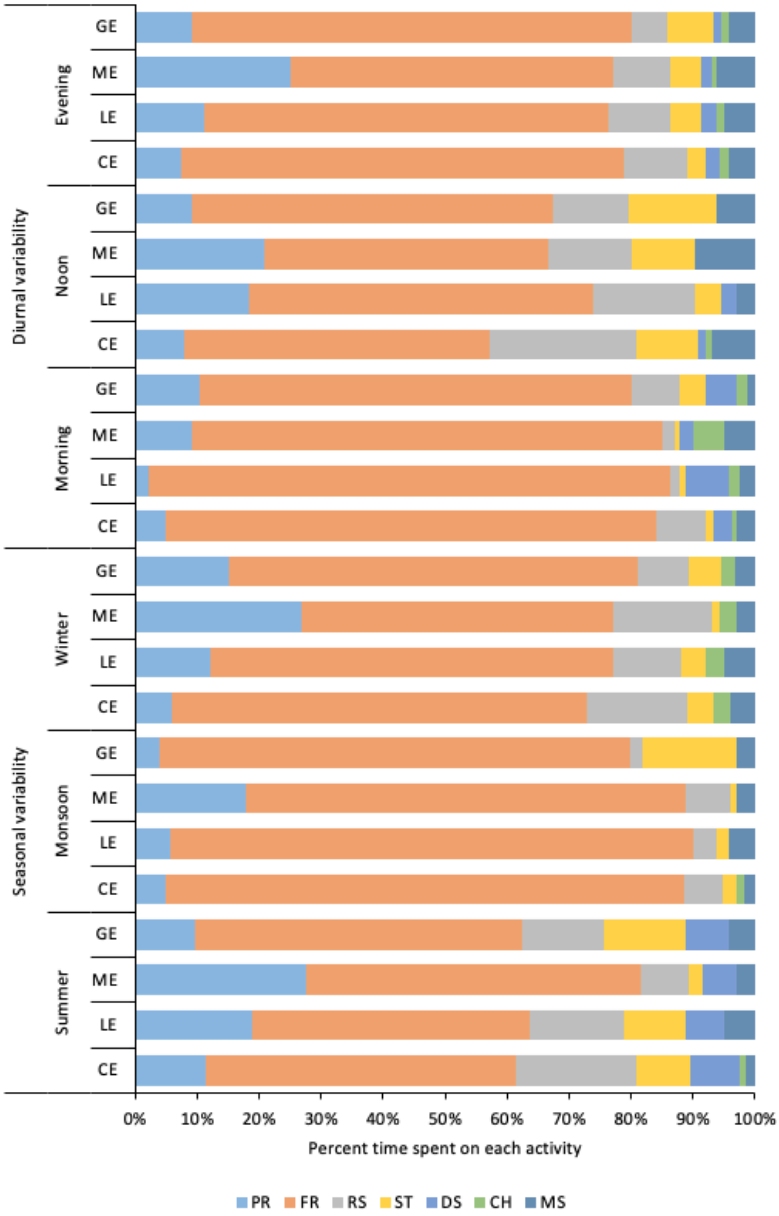

Figure 1. Seasonal and diurnal variability in the activity patterns among the egret species.

Temporal dimension of niche

All species of egrets were found to be variably utilizing the diurnal period throughout different seasons (Figure 1). In general, a significantly high proportion of their time was spent on foraging activity followed by preening and resting (Figure 1). Since the display behaviour was only recorded during the summers, therefore, its seasonal comparison was not possible.

The post hoc analysis of diurnal activity pattern suggested that preening time differs between all species except between LE and GE. Only CE & ME and LE & ME differ in foraging activity. Resting time differs between CE-ME, CE-LE and CE-GE while siesta and time devoted to miscellaneous activities differ amongst all species. Differences were also found between the display and chasing activity of CE-LE, LE-ME and ME-GE (Figure 2).

The post hoc analysis of significant seasonal variability in the activity pattern showed that during winters all species except LE-GE differ in the preening activity. The ME and CE, LE and GE differ in their foraging time. For the resting activity CE-LE, CE-GE and LE-ME differed significantly while for the rest of the activities in the time budget, only ME-GE showed a significant difference regarding the siesta activity (Figure 2). In

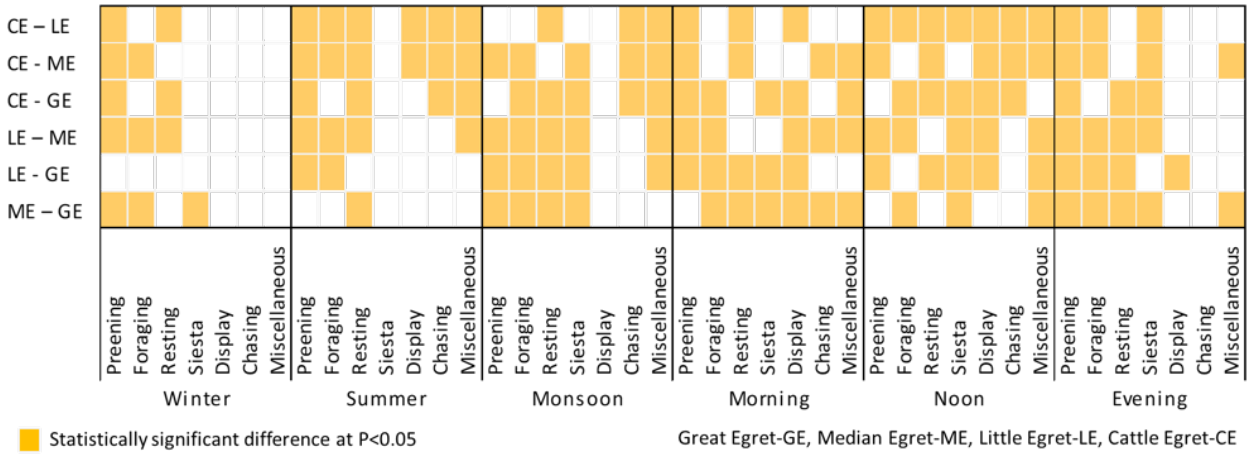

Figure 2. Significant differences in the seasonal and diurnal activity pattern between the sympatric species of egret.

the summer season, the preening activity pattern was different between all pairs of species except LE-GE. The time spent on foraging was also different between all pairs of species except CE-GE and ME-GE. Resting and miscellaneous activity patterns were different in all species pairs except LE-GE. The CE-LE, CE-ME and ME-GE differed significantly in their display behaviour whereas CE-ME, CE-LE and CE-GE adopted differential time budgets for chasing (Figure 2).

In monsoon, all pairs of species except the CE-LE and CE-GE were different in preening activity pattern. Time spent on foraging was significantly different between all pairs of species except CE-LE. In time allocation to the resting, siesta and miscellaneous types of activities, half of the pairs of species differed significantly (CE-GE, ME-LE and LE-GE) and the remaining half performed without any significant differences (CE-LE, CE-ME and ME-GE). The chasing time was found significantly different between the pair CE-LE, CE-ME and CE-GE (Figure 2).

Trophic dimension of niche

The Chi-square contingency analysis of the frequency suggested that associations between the species and the behaviour types are highly significant. CE used a variety of feeding behaviours such as walking slowly, standing and walking quickly most often (χ^2 =32.7, P <0.05, df = 21) and LE used walking quickly and foot stirring most often (χ^2 =33.4, P <0.05, df = 21). The behaviour of foot stirring was unique to the LE. The ME used walking slowly most often but gleaning, probing and pecking and standing were also used with an equal thrust (χ^2=37.9, P <0.05, df = 21). The GE almost specialized in using the walking slowly and standing behaviour (χ^2 =34.3, P <0.05, df = 21) with minuscule use of probing and pecking and chasing.

A total of 7,826 observations on the foraging behaviour of the different egret species were possible during the study period (Figure 3). The chi-square suggested a significant association between species and preferred prey items. CE preyed mostly upon terrestrial insects and small vertebrates such as amphibians, molluscs and crustaceans (χ^2 = 44.5, P <0.05, df = 30), the LE was most significantly associated with small fish but also include crustaceans, amphibians and aquatic insects (χ^2 =48.9, P <0.05, df = 30) in its diet, the ME most often fed upon small fish but larger fish and aquatic insects too formed a considerable portion of the diet (χ^2 = 46.2, P <0.05, df = 30), whereas the GE almost exclusively fed upon large sized (more than 8 cm) fish (χ^2 = 43.8, P <0.05, df = 30). The rest of the dietary items were also consumed by the GE but in smaller quantities (Figure 4).

A clear preference of prey size has been indicated by the egret species (Figure 5). CE subsisted on smaller prey of less than 6 cm (χ^2 =22.8, P <0.05, df = 12), prey eaten by LE ranged from 2 cm to 8 cm (χ^2 =27.1, P <0.05, df = 12); similarly, the ME too preyed upon intermediate size fish and crustaceans less than 8 cm in size (χ^2 =25.2, P <0.05, df = 12) but the GE maximized on fish larger than 8 cm (χ^2 =24.7, P <0.05, df = 12) (Figure 5). However, since they fed on small fish as well, some of their prey was less than 6 cm.

The measurement of niche breadth (Table 3) indicates that CE and ME use almost the same diversity of foraging behaviours and the LE and GE use a very small variety of behaviours – practically only walking quickly and foot stirring, and walking slowly and standing. The CE and LE showed equal diversity in the choice of food items and the ME and GE showed a lower diversity than the former two. Regarding prey size, the LE showed a very high diversity followed by the ME, and the GE and CE

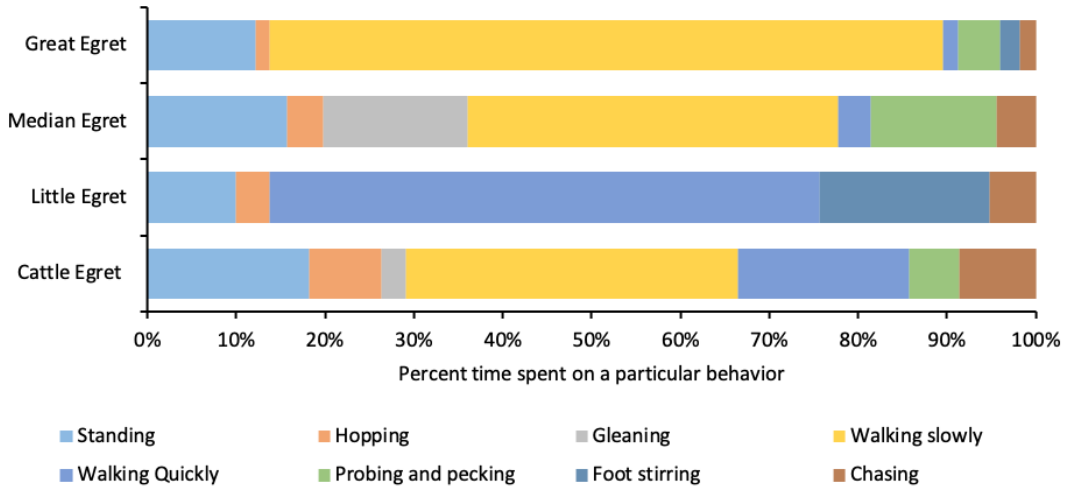

Figure 3. Time devoted to different foraging behaviours by four sympatric species of egrets.

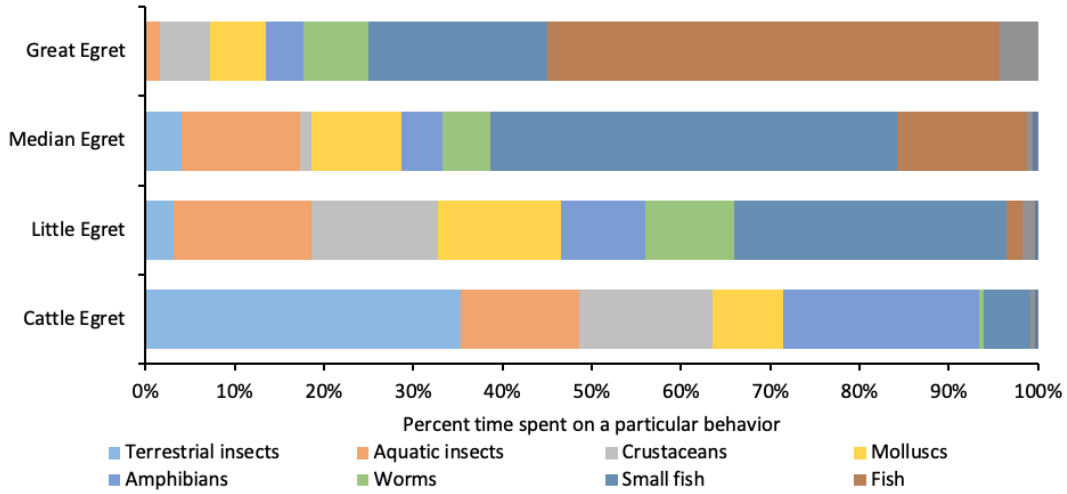

Figure 4. Food resource matrix for prey items of the four sympatric species of egrets.

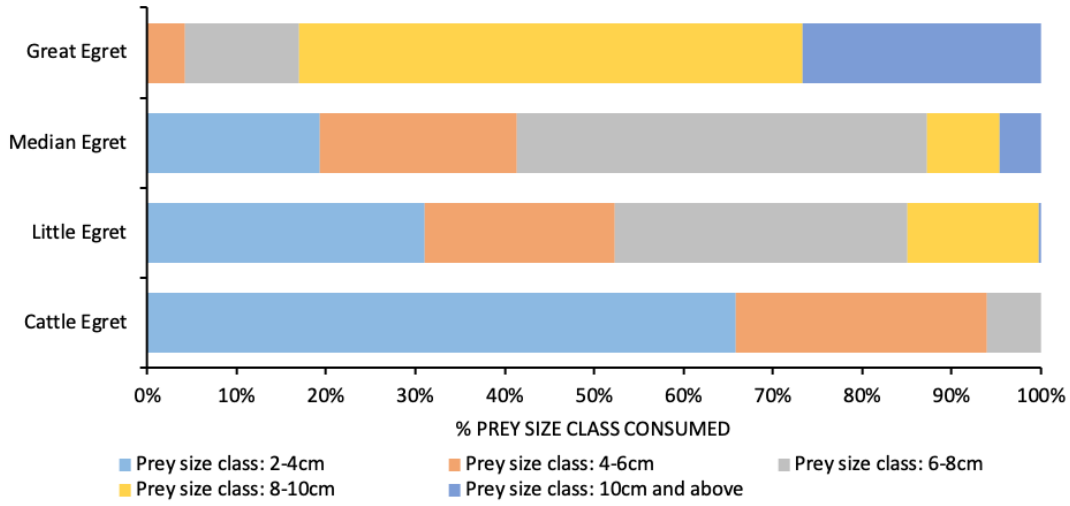

Figure 5. Food size matrix for prey size of the four sympatric species of egrets.

Table 3. Levin's measure of niche breadth (B) and Hulbert's standardized measure of niche (B_A) diversity of foraging behaviour and food resource of four sympatric species of egrets.

Species	Resource state					
	Foraging behaviour		Prey item		Prey size	
	(B)	(B_A)	(B)	(B_A)	(B)	(B_A)
CE	4.3835	.4834	4.8105	.3811	2.0022	.2506
LE	2.3195	.1885	4.3534	.3353	3.5845	.2461
ME	3.9776	.4254	3.8184	.4818	3.2688	.5672
GE	1.6683	.0955	3.1491	.2149	2.4621	.3655

exhibited a comparatively lower diversity.

Analysis of resource overlap amongst the four sympatric egrets (Table 4) reveals high overlap between CE and GE regarding behaviour, moderate overlap with prey type but very little overlap in prey size. GE and ME showed a high overlap in foraging behaviour and considerable overlap in prey size and prey type. ME and LE exhibited almost total overlap in prey type but little overlap in foraging behaviour. GE and LE coexist with very little overlap in foraging behaviour and considerable overlap in prey type and prey size. LE and CE have a high overlap in prey type and prey size and a moderate overlap in foraging behaviour. CE and ME have high degrees of overlap in all categories.

Table 4. Horn's resource overlap (R_0) between the sympatric species of egrets for foraging behaviour, prey type and prey size. The overall overlap between the species in resources dependent and resource independent conditions.

Species pairs	Resource state			Overall resource overlap (dependent conditions)	Overall resource overlap (independent conditions)
	Foraging behaviour	Prey type	Prey size	Product	Mean
CE- GE	.825	.492	.180	.073	.499
GE-ME	.841	.677	.549	.312	.689
ME-LE	.313	.935	.959	.280	.735
GE-LE	.269	.677	.549	.099	.498
LE-CE	.573	.807	.808	.373	.729
CE-ME	.895	.742	.720	.478	.785

DISCUSSION

The study demonstrated significant differences in habitat use, diurnal time utilization and feeding habits among the four species of egrets at Sheikha lake. Thus, they segregated in the use of the temporal, spatial and trophic niche dimensions, resulting in reduced interspecific competition.

Given the lack of interspecific territoriality and aggression, this suite of ardeid assemblage exhibits a pattern of spatial segregation that relies on slight differences in micro-habitat utilization with a varying overlap in various spatial niche dimensions (Table 1 & 2). A positive correlation has been found between Shannon-Weiner's niche breadth of the egret species and their local abundances (Table 1). CE and ME were using both the terrestrial as well as water-based micro-habitats hence their niche breadths are wider so do their population abundance. Whereas the GE and LE are more wetland-oriented species therefore narrower niche breadth and lower local abundance. These results are in line with the ecological phenomenon proposed by Hanski (1982) that the species occupying most sites (i.e., wider habitat-based niche) also have higher local abundances within those sites and vice versa.

The egret species were found to be variably utilizing the daytime throughout different seasons and shifts of the day (Figure 1). In general, a significantly high proportion of their time was spent on foraging activity followed by preening and resting (Figure 1). The results are the first example of diurnal temporal partitioning in the four major egret species of tropical wetlands. Such partitioning is likely to be driven by a combination of physiological and morphological constraints of each species and behavioural mechanisms, including a species' potential for behavioural plasticity (Lear et al. 2021). Due to varied body sizes there use to be a hierarchy in the Egret species in which the bigger body sizes have the advantage to get the most suitable place for hunting. Hence the egrets make opportunistic adjustments in their activity patterns in response to the sympatric species exploiting the same habitat. Perhaps to avoid interspecific conflict the egrets use temporal niche partitioning as a mechanism for co-existence in the overlapped portion of microhabitats (Ye et al. 2019), which could also maximize their fitness (Sanz-Aguilar et al. 2015).

The Egrets are visual predators that use the sit-and-wait technique (Kushlan & Hancock 2005). They are predominantly small fish and insect eaters. The dependency on the smaller prey is reasonable as they are usually r-selected species and suffice the energy requirements of the species (Britto & Bugoni 2015). Furthermore, during breeding, the egrets may select insects to deliver to chicks because they are unable to swallow large fish and other prey (Martinez-Vilalta &

Motis 1992). They are therefore called a biocontrol agent for insects, especially the CE as more than 60% of CE's diet comprise items less than size of 4cm (Seedikkoya et al. 2007). The size of consumed prey varies among the species and it is in accordance with their own body sizes, i.e., bigger egrets feed on big-size prey. 69.3% diet of CE (smallest of the studied egrets) comprised of prey size 2–4 cm. Similar to this, prey between the sizes of 2 and 8 cm made up 86.4% and 87.5% of the diets of LE and ME, respectively. Whereas the GE (largest of the studied egrets) fed on 83% of prey species that were between 8–10cm and above.

The study indicates that there is a relationship between the niche dimensions, but it is only partially dependent on each other. Little overlap existed in food selected by the four species but very different foraging behaviours are adopted. Considering the interplay of habitat selection and the feeding technique adopted, the nature of foraging niche differentiation is multi-faceted and may vary from region to region.

Our results are in agreement with the niche partition hypothesis, whereby morphologically, ecologically and closely related sympatric species segregate in at least one of the niche dimensions to allow coexistence (Ye et al. 2021).

REFERENCES

Altmann, J. (1973). Observational study of behaviour: Sampling methods. *Behaviour* 49(3–4): 227–267.

Bardsley, L. & T.J.C. Beebee (1998). Interspecific competition between *Bufo* larvae under conditions of community transition. *Ecology* 79(5): 1751–1759. https://doi.org/10.1890/0012-9658(1998)079[1751:ICBBLU]2.0.CO;2

Bayer, R.D. (1985). Bill length of herons and egrets as an estimator of prey size. *Colonial Waterbirds* 8(2): 104–109. https://doi.org/10.2307/1521059

Beckerman, A.P. (2000). Counterintuitive outcomes of inter-specific competition between two grasshopper species along the source gradient. *Ecology* 81(4): 948–957. https://doi.org/10.1890/0012-9658(2000)081[0948:COOICB]2.0.CO;2

Bibby, C., N.D. Burguess & D.A. Hill (1992). *Bird Census Techniques*. Academic Press, London, 257 pp.

Britto, V.O. & L. Bugoni (2015). The contrasting feeding ecology of great egrets and roseate spoonbills in limnetic and estuarine colonies. *Hydrobiologia* 744: 187–210. https://doi.org/10.1007/s10750-014-2076-1

Caldwell, G.S. (1979). Social dynamics of foraging herons and egrets in tropical mixed-species flocks. PhD Thesis, University of California, Berkley, 268 pp.

Colwell, R.K. & E.R. Fuentes (1975). Experimental studies of the niche. *Annual Review of Ecology, Evolution, and Systematics* 6: 281–310. https://doi.org/10.1146/annurev.es.06.110175.001433

Forbes, L.S. (1989). Coloniality in herons: Lack's Predation Hypothesis reconsidered. *Colonial Waterbirds* 12(1): 24–29. https://doi.org/10.2307/1521308

Fowler, J. & L. Cohen (1986). *Statistics for Ornithologists*. *BTO Guide No. 2*. British Trust for Ornithology, UK, 176 pp.

Gavina, M.K.A., T. Tahara, K. Tainaka, H. Ito, S. Morita, G. Ichinose, T. Okabe, T. Togashi, T. Nagatani & J. Yoshimura (2018). Multi-species coexistence in Lotka-Volterra competitive systems with crowding effects. *Scientific Reports* 8: 1198. https://doi.org/10.1038/s41598-017-19044-9

Grimmett, R., G. Inskipp & T. Inskipp (2016). *Birds of the Indian Subcontinent. 2nd Edition*. Oxford University Press & Christopher Helm, London, 528 pp.

Hairston, N.G., F.E. Smith & F.B. Slobodkin (1960). Community structure, population control, and competition. *American Naturalist* 94(879): 421–425.

Hancock, J. & J.A. Kushlan (1984). *The Herons Handbook.* Croom Helm, London and Sydney, 548 pp.

Hanski, I. (1982). Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38(2): 210–221. https://doi.org/10.2307/3544021

Hom, C.W. (1983). Foraging ecology of herons in a southern San Francisco Bay salt marsh. *Colonial Waterbirds* 6: 37–44. https://doi.org/10.2307/1520965

Huang, A.C., M. Essak & M.I. O'Connor (2015). Top-down control by Great Blue Herons *Ardea herodias* regulates seagrass-associated epifauna. *Oikos* 124(11): 1492–1501. https://doi.org/10.1111/oik.01988

Islam, M.Z. & A.R. Rahmani (2004). *Important Bird Areas in India: Priority Sites for Conservation. Indian Bird Conservation Network*, Bombay Natural History Society and BirdLife International (UK), xviii + 1133pp.

Jennings, S. (2017). Studying top predators to understand landscape habitat linkages. The Movement Ecology of Egrets. *The Ardeid* 1–3.

Junk, W.J., M. Brown, I.C. Campbell, M. Finlayson, B. Gopal, L. Ramberg & B.G. Warner (2006). The comparative biodiversity of seven globally important wetlands: a synthesis. *Aquatic Sciences* 68: 400–414. https://doi.org/10.1007/s00027-006-0856-z

Kelt, D.A., M.L. Taper, & P.M. Maserve (1995). Assessing the impact of competition on community assembly: a case study using small mammals. *Ecology* 76(4): 1283–1296. https://doi.org/10.2307/1940935

Krebs, C.J. (1989). *Ecological Methodology.* Harper & Row Publishers, New York, 654 pp.

Krebs, J.R. (1974). Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardeola herodias*). *Behaviour* 51: 99–134.

Kushlan, J.A. & J.A. Hancock (2005). *The Herons*. Oxford University Press, Oxford, xvii + 433 pp.

Kushlan, J.A. (1978). Feeding behaviour of North American herons. *Auk* 93(1): 86–74.

Lear, K.O., N.M. Whitney, J.J. Morris, & A.C. Gleiss (2021). Temporal niche partitioning as a novel mechanism promoting co-existence of sympatric predators in marine systems. *Proceedings of the Royal Society B* 288: 20210816. https://doi.org/10.1098/rspb.2021.0816

Lehner, P.N. (1979). *Handbook of Ethological Methods*. Garland SFPM Press, New York, 672 pp.

Levins, R. (1968). *Evolution in Changing Environments.* Princeton University Press, Princeton and New Jersey, 132 pp.

MacArthur, R. & R. Levins (1967). The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101(921): 377–385.

Maheswaran, G. (1998). Ecology and behaviour of Black-necked Stork *Ephippiorhynchus asiaticus* in Dudwa National Park, Uttar Pradesh, India. PhD Thesis, Centre of Wildlife and Ornithology, Aligarh Muslim University, Aligarh, India.

Martinez-Vilalta, A. & A. Motis (1992). Family Ardeidae (Herons), pp. 376–430. In: del-Hoyo, J., A. Elliott & J. Sargatal (eds.). *Handbook of the Birds of the World*. Lynx Edicions, Barcelona, 535 pp.

Mock, D.W., T.C. Lamey & B.J. Ploger (1987). Proximate and ultimate roles of food amount in regulating egret sibling aggression. *Ecology* 68(6): 1760–1772. https://doi.org/10.2307/1939867

Norusis, M.J. (1994). SPSS/PC + Statistic 7.3 for IBMPC/XT/AT and PS/2. SPSS International, Prentice Hall, Englewood Cliffs, N.J., USA.

Oviedo, L., M. Fernández, D. Herra-Miranda, J.D. Pacheco-Polanco, C.J. Hernández-Camacho & D. Aurioles-Gamboa (2018). Habitat partitioning mediates the coexistence of sympatric dolphins in a tropical fjord-like embayment. *Journal of Mammalogy* 99 (3): 554–564. https://doi.org/10.1093/jmammal/gyy021

Perri, L.M. & J.A. Randall (1999). Behavioural mechanisms of coexistence in sympatric species of desert rodents, *Dipodomys ordii* and *D. Merriami*. *Journal of Mammalogy* 80(4): 1297–1310. https://doi.org/10.2307/1383180

Pianka, E.R. (1986). *Ecology and Natural History of Desert Lizards.* Princeton University Press, Princeton, New Jersey, 222 pp.

Quinney, T.E. & P.C. Smith (1980). Comparative foraging behaviour and efficiency of adult and juvenile Great Blue Herons. *Canadian Journal of Zoology* 58(6): 1168–1173. https://doi.org/10.1139/z80-161

Recher, H.F. & J.A. Recher (1969). Comparative foraging efficiency of adult and immature Little Blue Herons (*Florida caerulea)*. *Animal Behaviour* 17(2): 320–322. https://doi.org/10.1016/0003-3472(69)90017-7

Rodgers, W.A. & H.S. Panwar (1988). Planning a wildlife protected area network in India. Vol. 2. Project FO: IND/82/003. FAO, Dehradun, India, 339pp.

Sanz-Aguilar, A., M. Carrete, P. Edelaar, J. Potti & J.L. Tella (2015). The empty temporal niche: breeding phenology differs between coexisting native and invasive birds. *Biological Invasions* 17(32): 3275–3288 . https://doi.org/10.1007/s10530-015-0952-x

Saxena, L. (1999). Description and classification of plant communities of Patna Bird Sanctuary and Sheikha Jheel. M.Sc. Dissertation, Department of Wildlife Sciences, Aligarh Muslim University, Aligarh, 56 pp.

Schoener, T.W. (1982). The controversy over inter-specific competition. *American Scientist* 70(6): 586–582.

Seedikkoya, K., P.A. Azeez & E.A.A. Shukkur (2007). Cattle egret as a biocontrol agent. *Zoos' Print* 22(10): 2864–2866.

Seigel S. (1956). *Nonparametric Statistics from the Behavioural Science.* McGraw Hill, New York 260 pp.

Seigfried, W.R. (1971). Feeding activity of the cattle egret. *Ardea* 59: 38 – 46.

Siepielski, A.M., W.A. Boys, J. Bried, M. Gómez-Llano, T. Lanzer & S.P. Tye (2021). Insect Species Coexistence and Conservation Amidst Global Change, pp. 370–377. In: DellaSala, D.A. & M.I. Goldstein (eds.). *Imperiled: The Encyclopedia of Conservation*. Elsevier, 2608 pp. https://doi.org/10.1016/B978-0-12-821139-7.00026-X

Willard, D.E. (1977). The feeding ecology and behaviour of five species of herons in southeastern New Jersey. *Condor* 79(4): 462–470. https://doi.org/10.2307/1367726

Yahya, H.S.A. (1980). A comparative study of the ecology and biology of Barbets *Megalaima* spp (*Capitonidae:Piciformes*) with special reference to *Megalaima viridis* (Boddaert) and *Megalaima rubricapilla malabarica* (Blyth) at the Periyar Tiger Reserve, Kerala. Ph.D. Thesis, University of Bombay, 210 pp.

Ye, P., C. Yang & W. Liang (2019). Nest site availability and niche differentiation between two cavity-nesting birds in time and space. *Evolutionary Ecology* 9(20): 11904–11910. https://doi.org/10.1002/ece3.5698

Ye, Y., C. Hu, Y. Jiang, G.W.H. Davison & C. Ding (2021). Three-dimensional niche partitioning between two colonially nesting ardeid species in central China. *Avian Research* 12: 33. https://doi.org/10.1186/s40657-021-00264-7

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