

Nest Space Partitioning among Colonial Nesting Waterbirds at Bhitarkanika Mangroves, India

G.V. Gopi and Bivash Pandav

Department of Endangered Species Management, Wildlife Institute of India,
Chandrabani, Dehradun-248001, India

Abstract: Bhitarkanika mangroves in Orissa harbours one of the largest mixed-species heronries in the country with more than 30,000 birds of 11 species breeding annually in a small mangrove patch of c.5 ha area between June and December. Patterns of spatial segregation was studied among nesting waterbirds as competition for space in waterbird colonies is known to be mitigated through habitat partitioning. Both vertical and horizontal associations among the nesting waterbirds in the heronry were studied. It was observed that Asian openbill (*Anastomus oscitans*), Large egret (*Ardea alba*), Intermediate egret (*Egretta intermedia*), Little cormorant (*Phalacrocorax niger*) and Little egret (*Egretta garzetta*) were associated more frequently than they would be expected at random. There was a significant avoidance trend between Grey (*Ardea cinerea*) and Purple (*Ardea purpurea*) herons and between Darter (*Anhinga melanogaster*) and Asian openbill. Interestingly, Black-headed ibis (*Threskiornis melanocephala*) was observed to nest away from most of the species within the heronry forming sub-colonies on its own. Results of the current analysis on vertical alignment of nests did not support the body mass-nest height hypothesis which postulated a direct positive correlation between body weight and nest height among colonial waterbirds. There was a significant radial zonation of species in the heronry with Asian openbill storks preferring the central portion of the heronry (KW $\chi^2=8.54$, $P<0.05$) whereas Darter and Grey heron nests were observed more towards the periphery of the heronry (KW $\chi^2=6.40$, $P<0.05$). On the other hand, nests of Little egret (KW $\chi^2=11.11$, $P<0.05$), Purple heron (KW $\chi^2=11.53$, $P<0.05$) and Night heron *Nycticorax nycticorax* (KW $\chi^2=10.61$, $P<0.05$) were found to have clumped distribution being restricted to select blocks of the heronry. The study supported the hypothesis that edge nests suffer higher level of predation and demonstrates that the highest level of predation occurs in the periphery and central nests have higher reproductive success than the peripheral nests.

Key words: Nest space partitioning • Colonial waterbirds • Vertical stratification • Heronry • Bhitarkanika mangroves

INTRODUCTION

Differential resource selection is one of the principal factors, which permit species coexistence [1, 2]. In studies of niche partitioning, nest site location has received much less attention than food or habitat, perhaps because suitable nest sites are presumed to be readily available for most species. However, when a species has specific nesting requirements, suitable nesting locations may be difficult to obtain [3, 4]. This may bring about the overlap of nest sites and consequently, predation costs for breeders because of the attraction of the predators due to the increase in cumulative nest density [5]. Factors

commonly identified to explain aggregations are the spatial availability of food and defense against predators [6-8]. Other studies suggest that ectoparasitism and abiotic factors (Ex. Precipitation) affect habitat quality and become a dominant force influencing aggregation behaviour in birds [9-12]. The response of wild populations to their resources is not always predictable because of the outcome of the number of interacting factors, which may go since a single until multiple factors [13]. Food scarcity often leads to foraging in distant areas, which may result in formation of small colonies [14]. Strong seasonal peaks in food resources may limit breeding to a single season of the year and cause

synchronized breeding of the population. In these cases large colonies are formed and intense competition occurs for food [6]. Competition might be lessened by a strategy of fine scale temporal and spatial segregation in the use of habitats among species with similar feeding habits [9,15]. Anderson [16] suggested vertical stratification is believed to partition resources and thereby reduce competition among co-existing species.

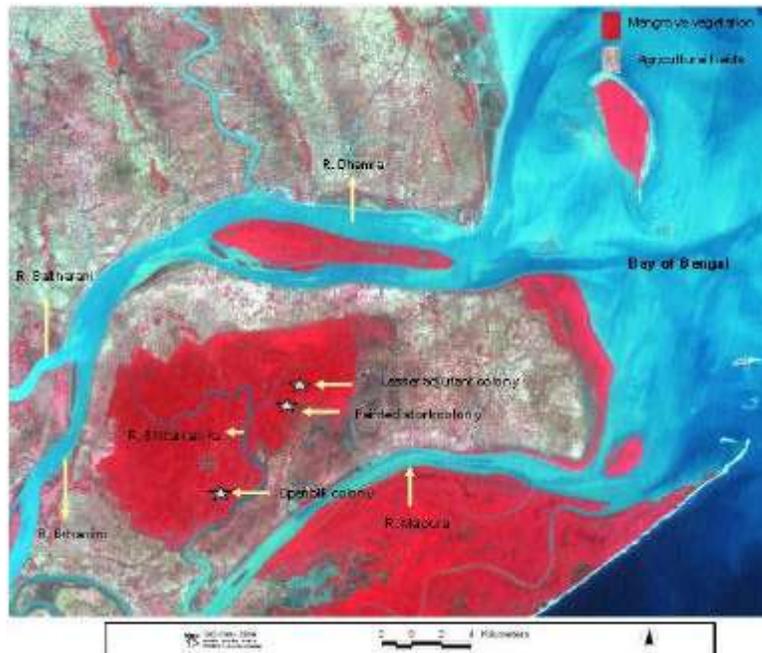
Habitat Selection and Nesting Association: The environment of most animal species is heterogeneous at different spatial and temporal scales for various characteristics that can directly affect components of fitness. The process of habitat selection is thus likely to be under strong selective pressures [17, 18]. Animals can use variety of physical cues to assess environmental suitability [19-21]. More parsimoniously, they can use some integrative cue such as the presence and activities of conspecifics [22-25]. Gulls and Terns breed colonially due to similar habitat preferences, mutual advantages provided by better predator avoidance and the possibility of exchange of information for food acquisition [26-29]. On the other hand, colonial birds may compete for resources and colonies may attract predators [30-32]. Multiple factors drive colony site dynamics in waterbirds, depending on habitat quality [33-36]. Habitat composition around nesting sites has been so far the most studied [37, 38]. Since reproduction is a time of high energy demand, availability of suitable foraging sites will directly influence colony location, colony size and reproductive parameters [39].

Temporal Segregation: Custer and Osborn [40] found asynchronous nest building phases in north Carolina. Maxwell and Kale [41] found Florida Caerulea, started to breed later than other colony species. Frederick and Callopy [42] showed a strong difference for the nesting chronology of four species (*Casmerodius albus*, *Egretta tricolor*, *Egretta caerulea*, *Edocimus albus*) in florida. Maxwell and Kale [41] and Jenni [43] found that nests of *Egretta thula* and *Bulbulcus ibis* showed an average nest height from 2.04 - 2.59 m. result of this work support the notion that species overlap temporally in breeding, also segregate vertically in nest placement within the colony.

Central-Periphery Distribution of Nests: Breeding success may differ between centre and edge nests [44 - 46], but it is not always attributable to predation [47, 48]. Nest defence against potential predators has long been suggested as an important force in the evolution of

coloniality in birds [49, 50]. Nests located in the more densely populated areas of the colonies are more sheltered from predation more than those at the periphery [30]. In the context of the relationship nest density and predation, the central - periphery distribution hypothesis was first proposed by Coulson [47] in his study of colony of Kittiwakes (*Rissa tridactyla*), where he found birds breeding in the central area were of better quality and had higher reproductive success than those nesting in the periphery. Moreover subsequent studies showed that this population is regulated by the availability of central sites [51] and that birds breeding in the centre have a higher survival rate [52]. The variation in survival arises because central individuals are less accessible to predators [53, 54]. Central - Periphery distribution hypothesis is generally accepted explanation for nest dispersion patterns in sea bird colonies [30, 55 and 56]. However there are some examples where this hypothesis is not fulfilled. Ryder and Ryder [57] found a colony of ring billed gulls (*Larus delawarensis*) in which there was no variation in reproductive success between central and peripheral areas, while in another colony, Pugsek and Diem [58] observed that reproductive success were determined by different spatial distributional of age groups. Scolaro *et al* [59], in a study on a colony of the South American tern (*Sterna hirundinacea*), found that birds nest site selection is at first random and then uniform but not in the central - periphery pattern. In a study on behavior of Kittiwake recruits in a colony in North shields, Porter [60] found that first time breeders prefer more densely populated sites, with poorer quality birds being regulated to peripheral zones. Danchin *et al.* [61] reported that recruits are directly attracted by successful sites and they visit these sites during the prospecting season. It's widely assumed that edge or fringe nesters should have a lower breeding success compared to central nesters [30]. Several authors have reported that edge or fringe nesters show higher levels of failure than more central nesters and that the centre advantage increases as colony size increases [46, 62 and 63]. Furthermore, several studies have shown preference by males for establishing territories with in the centre of colonies (Kittiwake, *Rissa tridactyla*, [44] and least terns [64]).

The heronries play a vital role in the life cycle of the birds of family Ardeidae, Ciconiidae, Threskiornithidae and Phalacrocoracidae. In mixed species heronries, such diverse groups congregate in large numbers to breed and raise their progeny. Different species occupy certain space in the heronry at certain times.



Map 1. Map of Bhitarkanika Wildlife Sanctuary and location of the heronry inside the National Park

Strong site fidelity has been observed among birds as this is advantageous to them. As the birds become familiar with the area, it enhances their foraging success, predator avoidance, defence and other behaviours, which contribute to reproduction performance [65]. This manuscript documents about the patterns of nest spacing and the factors that determine such patterns. Nest tree preference, species association and disassociation patterns, species preference of nest trees and vertical stratification of nesting species are dealt in detail in this manuscript.

Study Area: The field study on the heronry was conducted in the Bhitarkanika Wildlife Sanctuary, Orissa. Bhitarkanika mangroves, located on the east coast of India (between 20°04'-20°08'N and 86°45'-87°50'E) represent one of the finest remaining patches of mangrove forests in India (Map. 1). The general elevation above mean sea level is between 1.5 to 2 meters. Higher ground extends to 3-4 meters. The field study in Bhitarkanika commenced in March 2004 and culminated in February 2007.

Location: The Bhitarkanika Mangroves are located in the deltaic region of Brahmani and Baitarani rivers in the Kendrapara district of Orissa. The Bhitarkanika Wildlife sanctuary is situated near the former port, Chandabali, which is about 50 km from the Bhadrakh railway station.

The sanctuary is bounded by rivers Dhamara to the north, Maipura to the south, Brahmani to the west and the Bay of Bengal in the east. The 35 km coast line from the mouth of river Maipura till Barunei forms the eastern boundary of the sanctuary. The annual rainfall ranges from 920 to 3000 mm.

The Bhitarkanika Heronry: This is the one of the oldest and largest mixed species colony in India [66]. Over 30,000 birds breed every year in this heronry, a single unbroken patch with an approximate area of less than 5 ha area comprising 3800 - 4200 trees are used for nesting. Birds use five species of mangrove trees for nesting which include *Excoecaria agallocha* (Guan), *Heritiera fomes* (Bada Sundari), *Cynometra iripa* (Singada), *Hibiscus tiliaceus* (Bania), *Tamarix troupii* (Jagula) for nesting in the heronry. The breeding birds in this mixed species colony are Asian openbill stork, Great Egret, Intermediate Egret, Little Egret, Cattle Egret, Grey Heron, Purple Heron, Black-crowned Night Heron, Little Cormorant, Darter and Black-headed Ibis. The Asian Openbill is the most abundant species nesting in the heronry (66%) and the least abundant being the little egret (0.8%). Abundant food resources in and around the heronry and the minimal disturbance due to the remoteness of the area are speculated to be the principal factors for this large congregation of breeding birds [67-70].

MATERIALS AND METHODS

Field Methods: With such a large congregation of breeding birds in a small area it would be interesting to learn how these birds share the available limited resources. Parameters such as type of materials used for nesting, nest height in a tree, type of branch in the tree used for nesting, direction of the nest, distance from the nearby foraging areas and food habits were collected to study the resource partitioning among breeding birds in the heronry. Nest constituents were visually identified and types of tree species used for nesting were noted. Since the average height of the trees in the heronry are around 5-6 m (personal observation), nest height was approximately estimated using one meter graded pole [71]. In case of exceptionally tall trees the tree height was visually estimated. Nearest neighbour distance was measured both vertically and horizontally using a measuring tape for all the species. To study the species association dissociation patterns all species in the selected nest tree will be recorded. The heronry census was carried out in the last week of August, just after the hatching process of all the birds were over. Since the nests of different bird species are not uniformly distributed in this heronry, sample count of nests would give biased information on the total number of breeding birds. Hence, a total count of nest trees was carried out in the heronry. The entire nesting colony was subdivided into smaller subunits and based on the natural boundaries. All the trees in the subunits were then marked numerically in increasing order by paint. Parameters like, tree species, tree height, Girth at breast height (GBH), species nesting on the tree, no of nests, nest height were recorded. Nest height and tree height were visually estimated. GBH was measured with an inch tape. The nest of the bird species was identified by looking at the species guarding the nests and during the absence of both the parents, the nest design and nest materials were used to identify the species nesting. To determine the nest location in the trees, the entire tree height was divided in to five strata i.e. Upper canopy, upper middle, lower middle, lower and lowest canopy.

Analytical Methods

Relationship Between Tree Height and No. Of Nests: Since the scatterplot showed a non-linear association, non-linear regression was performed. The relationship was found to follow quadratic model. ($r = 0.54$, F Significance < 0.01).

Species Preference of Nesting Trees: We developed a simple and straightforward preference index (PI) for investigating the nesting tree preference by the water birds.

$$PI = -1 * [1 - F (\text{observed}) / F (\text{expected})]$$

Where

F (obs) = Observed number of nests on the given tree species

F (exp) = Expected number of nests calculated as the relative proportion of the number of tree species

The final value ranges from $-\infty$ to $+\infty$, where 0 refers to random selection. Increasing values on positive scale indicate preference while the negative scores point to avoidance. For the sake of clarity, we predefine the index value of 1 to ≥ 3 as zone of preference and -1 to ≤ -3 as zone of avoidance. The scores ranging between -1 to $+1$ are treated as evidence for the random choice of the nesting tree.

Spatial Association / Co-occurrence of Nesting Species in the Heronry: Pearson's Chi-square Statistic # $P > 0.05$ (indicating spatial independence of nests) was carried out to understand the association between nesting species in the heronry.

All statistical analysis were carried out using the statistical package SPSS 8.0.

RESULTS

Nest Tree Usage: Birds used five species of mangrove trees; *Excoecaria agallocha* (Guan), *Heritiera fomes* (Bada Sundari), *Cynometra iripa* (Singada), *Hibiscus tiliaceus* (Bania), *Tamarix troupii* (Jagula) for nesting in the heronry. A total of 3843 nest trees were counted inside the heronry. A majority of 77.9% nest trees were *Excoecaria agallocha* followed by *Heritiera fomes* (18.7%), *Cynometra iripa* (2.8%), *Hibiscus tiliaceus* (0.9%) and only one tree of *Tamarix troupii* was used for nesting. Maximum numbers of 79.6% nests were recorded in *Excoecaria agallocha* followed by *Heritiera fomes* (17.4%), *Cynometra iripa* (2.2%), *Hibiscus tiliaceus* (0.9%) and only two nests were found on *Tamarix troupii* (Fig. 1).

Tree Composition in the Heronry: Although *E. agallocha* was the most numerous in the heronry, *H. fomes* was found to be the tallest and stoutest tree species in

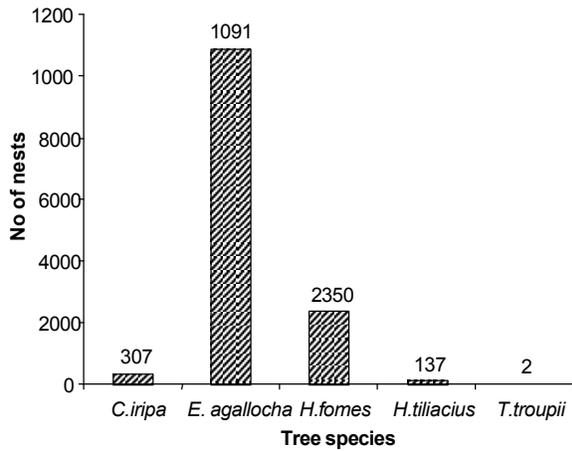


Fig. 1: Number of nest w.r.to tree species. *Excoecaria agallocha* is the most abundant tree species in the heronry and maximum nests were recorded in this tree species

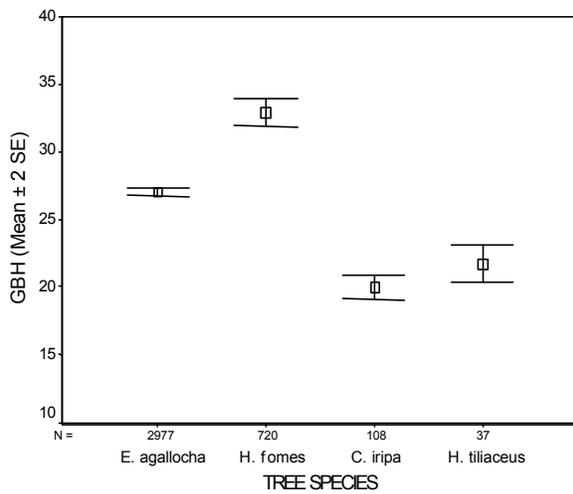


Fig. 2a: Relationship between tree species and GBH

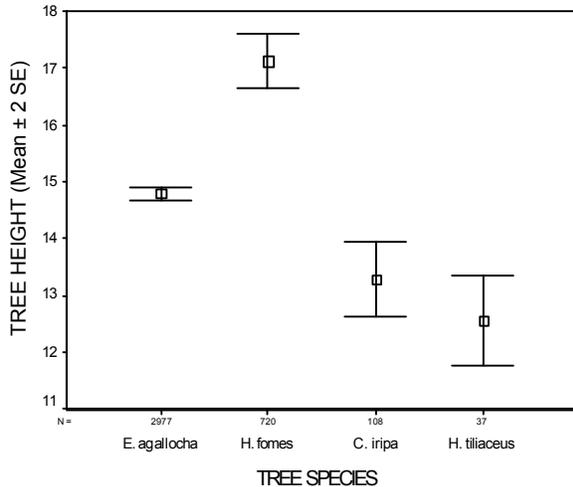


Fig. 2b: Relationship between tree species and tree height

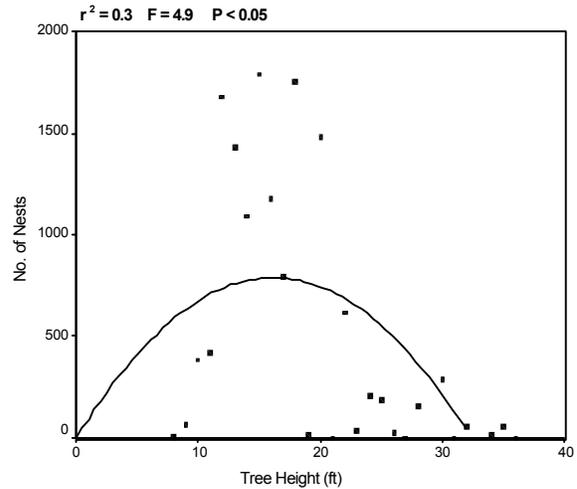


Fig. 3a: Relationship between tree height and no of nests

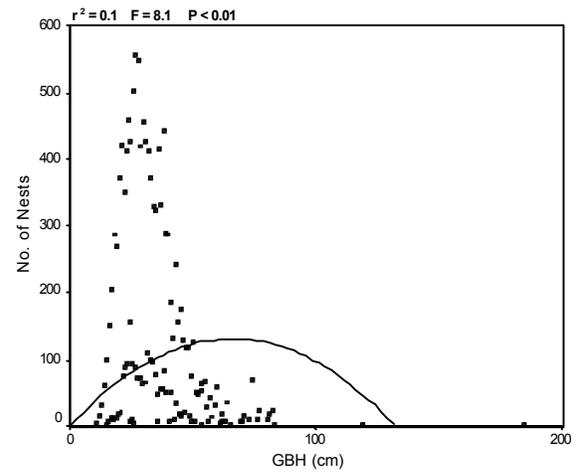


Fig. 3b: Relationship between GBH and no of nests

the heronry (Fig 2a and 2b). Asian openbill nests extensively on *E. agallocha* trees and most of these trees are located in the centre of the heronry. Continued nesting of openbill has damaged the top portions of the trees resulting in a stunted growth of *E. agallocha* in the heronry. This in turn has given a saucer shape to the heronry.

Relationship Between Tree Height/Gbh and No. Of Nests:

The relationship was found to follow the quadratic model which means that the number of nests increase with increasing GBH/tree height up to a certain value after which it starts to decline. This is because the tall and old growth trees occupy the periphery of the heronry but the water birds prefer the interior trees for nesting which are shorter and thinner compared to the peripheral ones (Fig. 3a and 3b).

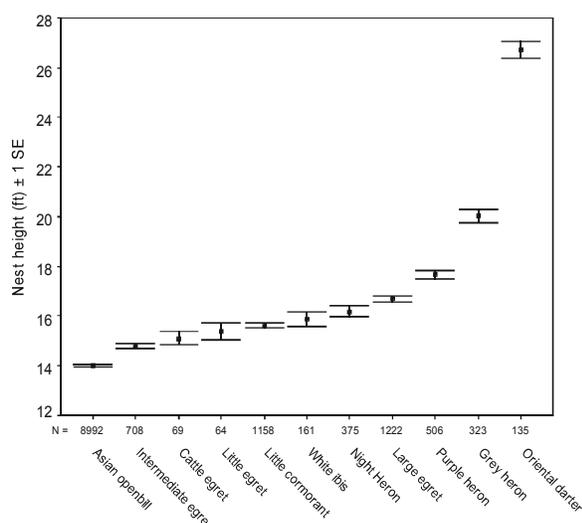


Fig. 4a: Mean nest height of nesting species

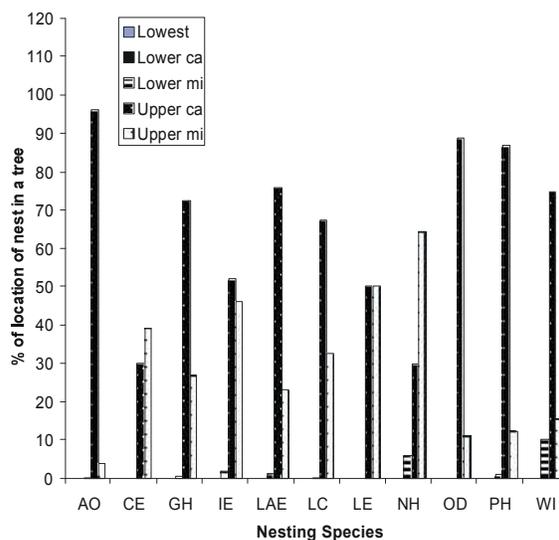


Fig. 4b: Nest location in the nesting trees

Table 1: Spatial association / co-occurrence of nesting species in the heronry: Pearson's Chi-square Statistic # P > 0.05 (indicating spatial independence of nests)

Species	Asian Openbill	Little Cormorant	White Ibis	Oriental Darter	Large Egret	Intermediate Egret	Little Egret	Cattle Egret	Grey Heron	Purple Heron
Asian Openbill										
Little Cormorant	444.1P<0.0001									
White Ibis	140.6P = 0.753	182.1P<0.0001								
Oriental Darter	204.4P<0.0001	57.8P = 0.886	0.673P > 0.999							
Large Egret	1761.3P<0.0001	1236.3P<0.0001	378.8P < 0.0001	205.3P<0.0001						
Intermediate Egret										
Little Egret	585.1P<0.0001	1441.2P<0.0001	197.8P< 0.0001	60P = 0.114	710.2P< 0.0001					
Cattle Egret	56.8P = 0.008	424.9P<0.0001	0.710P > 0.999	0.886P>0.999	199.7P< 0.0001	195.7P< 0.0001				
Grey Heron	240.5P<0.0001	921.3P<0.0001	11.6P = 0.995	28.3P = 0.24	239.1P< 0.0001	840.1P< 0.0001	23.2P=0.001			
Purple Heron	723.9P<0.0001	81.8P = 0.009	6.15P >0.999	5417.6P<0.0001	267.4P< 0.0001	118.1P< 0.0001	10.8P = 0.541	20.1P=0.322		
Night Heron	628.0P<0.0001	987.9P<0.0001	5.47P> 0.999	157P< 0.0001	1108.5P< 0.0001	297P< 0.0001	126.1P< 0.0001	156.2P< 0.0001	59.8P=0.118	
	278.3P<0.0001	648.1P<0.0001	10.5P > 0.999	4529.1P< 0.0001	1052P< 0.0001	116.8P< 0.0001	124.8P<0.0001	31.6P = 0.06	4911.1P< 0.0001	1341.4P<0.0001

Species Wise Nest Height and Nest Location in the Heronry: Oriental darter, Grey heron and Purple heron showed a higher nest height compared to other species since they preferred the tall *Heritiera fomes* to nest (Fig 4a). Asian openbill storks showed affinity to nest in the top canopy and their mean nest height was 14 ft. They nest extensively on *Excoecaria agallocha*, which had a mean tree height of 14.5 ft. Most of the nesting species showed affinities to nest in the upper and upper middle canopy; however White ibis and Night herons showed preference for nesting in the lower middle canopy also (Fig 4b). None of the species showed evidence to nest in the lower and lowest canopy since the branching of the trees started only from the lower middle canopy.

Spatial Association / Co-occurrence of Nesting Species in the Heronry: White Ibis showed strong

dissociation with other colonial species except for Large and Intermediate egrets and tends to nest forming sub colonies inside the heronry. Grey heron and Purple heron showed lesser evidence of nesting together and similar trend was also seen between Night heron and cattle egret. Darters also showed dissociation with Little cormorants, Intermediate, Little and Cattle egrets (Table 1).

Species Preference of Nesting Trees: Asian openbill, Little cormorant, White ibis, Little egret, Cattle egrets showed a preference to nest in *Excoecaria agallocha*, where as Darter, Grey heron, purple heron and night herons showed a preference to nest in *Heritiera fomes*. White Ibis, Little cormorant, Darter, Intermediate egret, little egret and cattle egret tends to avoid nesting in *Hibiscus tiliaceus*. (Fig 5a, b and c)

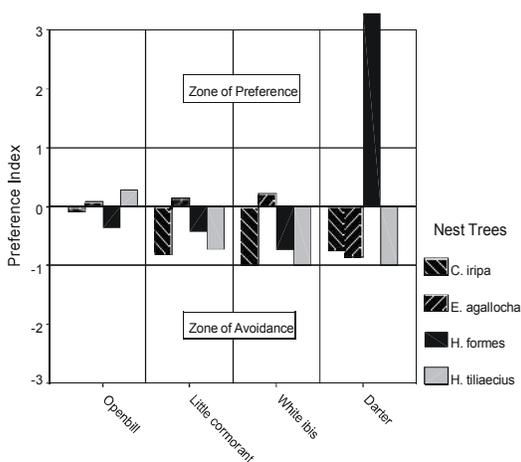


Fig. 5a: Nest tree preference of Openbill, Little cormorant, White ibis and Darter. Darter showed a strong preference to nest in *Heritiera fomes*.

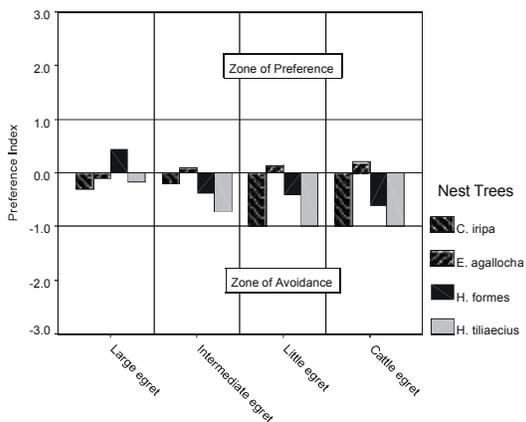


Fig. 5b: Nest tree preference of Large egret, Intermediate egret, Little egret, Cattle egret.

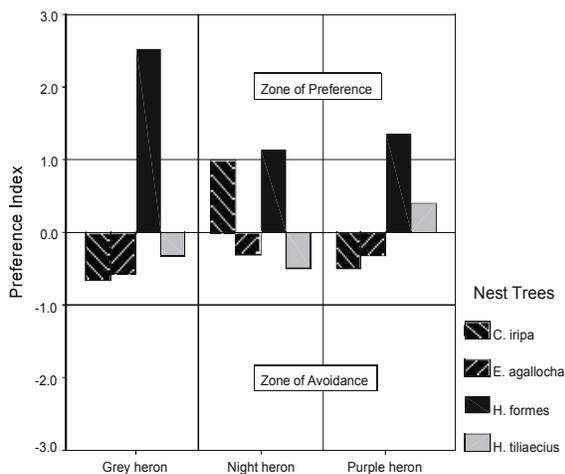


Fig. 5c: Nest tree preference of Grey heron, Purple heron and Night heron. All the three species showed a strong preference of *Heritiera fomes*.

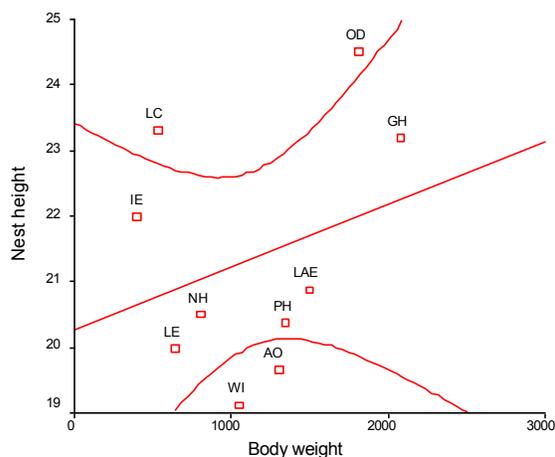


Fig. 6: Body mass Vs Nest height:

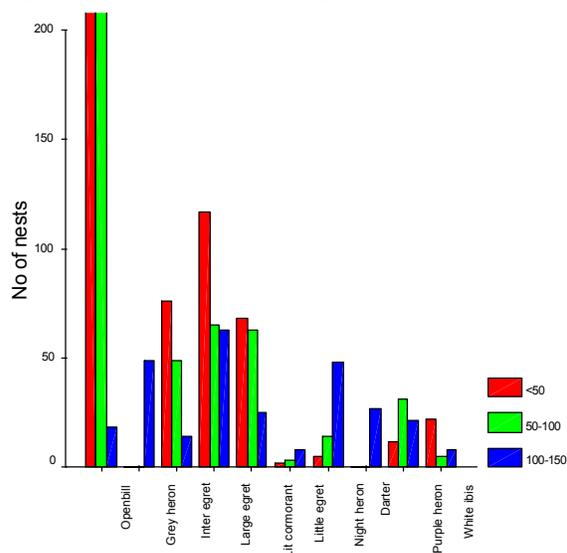


Fig. 7: Radial distribution of nests:

Competition for space in waterbird colonies is known to be mitigated through habitat partitioning. Both vertical and horizontal associations among the nesting waterbirds in the heronry were studied. It was observed that Asian openbill (*Anastomus oscitans*), Large egret (*Ardea alba*), Intermediate egret (*Egretta intermedia*), Little cormorant (*Phalacrocorax niger*) and Little egret (*Egretta garzetta*) were associated more frequently than they would be expected at random. There was a significant avoidance trend between Grey (*Ardea cinerea*) and Purple (*Ardea purpurea*) herons and between Darter (*Anhinga rufa*) and Asian openbill. Interestingly, Black-headed ibis (*Threskiornis aethiopica*) was observed to nest away from most of the species within the heronry forming sub-colonies on its own.

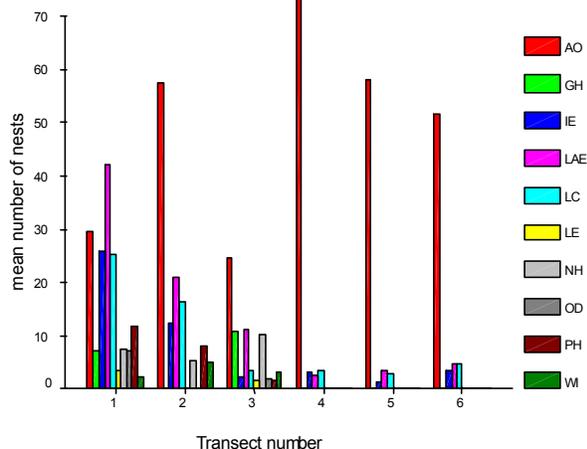


Fig. 8: Sector wise distribution of nests

Results of our analysis on vertical alignment of nests did not support the body mass-nest height hypothesis which postulated a direct positive correlation between body weight and nest height among colonial waterbirds (Fig.6). There was a significant radial zonation of species in the heronry with Asian openbill storks preferring the central portion of the heronry (KW $\chi^2=8.54$, $P<0.05$) whereas Darter and Grey heron nests were observed more towards the periphery of the heronry (KW $\chi^2=6.40$, $P<0.05$) (Fig.7). On the other hand, nests of Little egret (KW $\chi^2=11.11$, $P<0.05$), Purple heron (KW $\chi^2=11.53$, $P<0.05$) and Night heron *Nycticorax nycticorax* (KW $\chi^2=10.61$, $P<0.05$) were found to have clumped distribution being restricted to select blocks of the heronry (Fig.8).

Reproductive Success in Relation to Spatial Location Of Nests (Core vs Edge): Since breeding success was known to differ between center and edge nests [44 -46] the reproductive success was compared between edge nests and core nests which revealed no difference in success rate, thus indicating reproductive success was random at both space and time immaterial of their spatial location (Tables 2 and 3).

It is widely assumed that edge or fringe nester should have a lower breeding success compared to centre nesters [30]. Several authors have reported that edge or fringe nesters show higher levels of failure than more central nesters and that the centre advantage increases as colony size increases [46, 62, 63]. Further more several studies have shown preferences by males for establishing territories within the centre often colonies (Kittiwake, *Rissa tridactyla*, [47]; Least Terns, Burger [64]. The study clearly supports the hypothesis that edge nests suffer

Table 2: Comparative Asian openbill hatching success in central and edge nests:

Nesting Variable	Mann-whitney U	n	p-value
Clutch size	32.5	18	0.550
Clutch mass	24.0	18	0.189
Hatching success %	34.0	18	0.010
Fledgling success %	34.0	18	0.010

Table 3: Comparative Large egret hatching success in central and edge nests:

Nesting Variable	Mann-whitney U	n	p-value
Clutch size	56	25	0.231
Clutch mass	45	23	0.257
Hatching success %	55	25	0.013
Fledgling success %	55	25	0.013

higher level of predation and demonstrates that the highest level of predation occur in the periphery. The “selfish herd” hypothesis predicts aggregative behaviour because edge individuals are at high risk. Wittenburger and Hunt [30] suggest that as a general rule, the proportion of nests lost to predators will decrease with increasing colony size once the colony is large enough to “swamp” all the predators.

DISCUSSION

Resource partitioning studies generally deal with food [72, 73], but the partitioning of space to avoid competition is least studied. Actually aggression is the most precise mechanism for such partitioning. Since large species largely win over smaller species by occupying the preferred nest sites independent of their arrival and settlement patterns of the birds to the heronry [1]. In heronries with mixed tree species, the larger species tend to select particular types of vegetation and while in homogenous vegetation heronries with no physical difference, species might divide the available space among themselves. The Darters and Grey herons were the first to arrive at the heronry and they chose to nest only in the peripheral tall *Heritiera fomes* trees and the Asian openbill storks which are the dominant nesting birds in the heronry chose to nest only in the central location of the heronry. The Oriental white ibis, though arrives last in the heronry, they also tend to nest in the central location by displacing already established nests of small birds like large egrets, intermediate egrets and little egrets. One other major factor to partition the space is by nest tree preference. The oriental darters, Grey herons, Purple

heron and Night herons showed a strong preference to the *Heritiera fomes* trees. Night herons also showed preference to the *Cynometra iripa* trees. Night herons are usually shy species and love to nest in thick canopy trees with plenty of shade and this might be the reason for them to choose the peripheral location of the heronry dominated by *Heritiera fomes* and *Cynometra iripa*. Species like White Ibis, Asian openbills, little cormorant, Intermediate egret and Cattle egret showed a strong preference to nest in the *Excoecaria agallocha* trees. Asian openbill stork have a propensity to clip the apical leaves while nest building and renovation, which is why openbills prefer to nest in the small and tender *Excoecaria agallocha* trees whose apical leaves could be easily clipped by openbills in comparison to the hard and sturdy *Heritiera fomes* and *Cynometra iripa* trees. White ibis tend to form subcolonies i.e. many individuals group together and occupy an entire tree and nest either vertically or horizontally with all the nests touching each other. *Excoecaria agallocha* trees structures are perfect for supporting these sub colonies and this would be the reason white ibis showing preference to nest in *Excoecaria agallocha* trees. Certain species showed strong association patterns and whereas certain species tend to avoid each other, for example White Ibis showed strong dissociation with other colonial species except for Large and Intermediate egrets and tends to nest forming sub colonies inside the heronry. Grey heron and Purple heron showed lesser evidence of nesting together and similar trend was also seen between Night heron and cattle egret. Darters also showed dissociation with Little cormorants, Intermediate, Little and Cattle egrets. The relationship was found to follow the quadratic model which means that the number of nests increases with increasing GBH/tree height up to a certain value after which it starts to decline. This is because the tall and old growth trees occupy the periphery of the heronry but the water birds prefer the interior trees for nesting which are shorter and thinner compared to the peripheral ones. Oriental darter, Grey heron and Purple heron showed a higher nest height compared to other species since they preferred the tall *Heritiera fomes* to nest. Asian openbill storks showed affinity to nest in the top canopy and their mean nest height was 14 ft. They nest extensively on *Excoecaria agallocha*, which had a mean tree height of 14.5 ft. Most of the nesting species showed affinities to nest in the upper and upper middle canopy; however White ibis and Night herons showed preference for

nesting in the lower middle canopy also. None of the species showed evidence to nest in the lower and lowest canopy since the branching of the trees started only from the lower middle canopy. Both vertical and horizontal associations among the nesting waterbirds in the heronry were studied. It was observed that Asian openbill (*Anastomus oscitans*), Large egret (*Ardea alba*), Intermediate egret (*Egretta intermedia*), Little cormorant (*Phalacrocorax niger*) and Little egret (*Egretta garzetta*) were associated more frequently than they would be expected at random. There was a significant avoidance trend between Grey (*Ardea cinerea*) and Purple (*Ardea purpurea*) herons and between Darter (*Anhinga melanogaster*) and Asian openbill. Interestingly, Black-headed ibis (*Threskiornis melanocephalus*) was observed to nest away from most of the species within the heronry forming sub-colonies on its own.

It has been proposed that within homogenous vegetation, nesting herons align themselves vertically in direct relation to body length, with larger species at higher levels. This was attributed mainly to arrival times and to aggressive dominance by the larger species [74,75]. This pattern has been confirmed in some studies [76] but not in others [4] and a large variation exists between colonies, because herons adapt to the available vegetation [77]. However results of our analysis on vertical alignment of nests did not support the body mass-nest height hypothesis which postulated a direct positive correlation between body weight and nest height among colonial waterbirds. This observed pattern might be due to two reasons: 1. Occurrence of heterogeneous vegetation which makes different birds chooses different nest trees according to biological requirements and 2. Larger birds might tend to nest lower in the nest tree to conceal their large nests and attain greater protection from the aerial predators.

There was a significant radial zonation of species in the heronry with Asian Openbill storks preferring the central portion of the heronry (KW $\chi^2=8.54$, $P<0.05$) whereas Darter and Grey heron nests were observed more towards the periphery of the heronry (KW $\chi^2=6.40$, $P<0.05$). On the other hand, nests of little egret (KW $\chi^2=11.11$, $P<0.05$), Purple heron (KW $\chi^2=11.53$, $P<0.05$) and Night heron *Nycticorax nycticorax* (KW $\chi^2=10.61$, $P<0.05$) were found to have clumped distribution being restricted to select blocks of the heronry.

CONCLUSION

It was observed that Asian openbill stork, Large egret, Intermediate egret, little cormorant and little egret were associated more frequently than they would be expected at random. There was a significant avoidance trend between Grey heron and Purple heron and between Oriental Darter and Asian openbill stork. Interestingly, White Ibis was observed to nest away from most of the species within the heronry forming sub-colonies on its own. Results of our analysis on vertical alignment of nests did not support the body mass-nest height hypothesis which postulated a direct positive correlation between body weight and nest height among colonial waterbirds. There was a significant radial zonation of species in the heronry with Asian Openbill storks preferring the central portion of the heronry, whereas Oriental Darter and Grey heron nests were observed more towards the periphery of the heronry. On the other hand, nests of little egret, Purple heron and Night heron were found to have clumped distribution being restricted to select blocks of the heronry. These foretold patterns might have been responsible for reducing the interspecific aggression and thereby enhancing the interspecific resource partitioning.

ACKNOWLEDGEMENTS

This manuscript is an outcome of the research project “Ecological reconnaissance of colonial nesting waterbirds at Bhitarkanika mangroves, Orissa” of the Wildlife Institute of India (WII). We are grateful to the Director and Dean, Wildlife Institute of India, for fund support infrastructure and facilities. We are deeply thankful to Mr Bijoy kumar Das, field assistant, for his extensive help, to the staff of the Orissa Forest Department who took care of our logistics and was very supportive during the field days. In, WII we would like to thank Rajah Jayapal for his valuable comments and suggestions.

REFERENCES

1. Schoener, T.S., 1974. Resource partitioning in ecological communities. *Sci.*, **185**: 27-39.
2. Rosenzweig, M.L., 1981. A theory of habitat selection. *Ecol.*, **62**: 327-335.
3. Wiens, J.A., 1989. The ecology of bird communities. Volume 1. Foundations and patterns. Cambridge University Press. Cambridge, United Kingdom. pp: 540.
4. Burger, J. and M. Gochfield, 1990. The black skimmer: Social dynamics of a colonial species. New York: Columbia University Press.
5. Martin, T.E., 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist*. **141**: 897-913.
6. Emlen, J.T. and N.I. Demong, 1971. Adaptive significance of synchronized breeding in a colonial bird. A new hypothesis. *Sci.*, **188**: 1029-1031.
7. Birkhead, T. and M.P. Furness, 1985. Ecological adaptations for breeding in the Atlantic alcidae. In: The atlantic alcidae. D.N. Nettleship and T.R. Birkhead, (Eds). Academic press, New York, pp: 205-231.
8. Brown, C.R., B.J. Stutchbury and P.D. Walsh, 1990. Choice of colony size in birds, *Trends in Ecology and Evolution*. **5**: 398-403.
9. Hill, B.G. and M.R. Levin, 1989. Territory overlap and habitat use of sympatric chickadees. *Auk.*, **106**: 259-268.
10. Bollinger, E.K. and T.A. Gavin, 1989. The effects of site quality on breeding-site fidelity in Bobolinks. *Auk.*, **106**: 584-594.
11. Weins, J.A., 1992. An ontogeny of concepts and approaches. In *Ecological heterogeneity* ed. M.J. Hutchin, E.A. John and A.J.A Stewart. pp: 9-31.
12. Boulinier, T. and J.Y. Lemel, 1996. Spatial and temporal variations of factors affecting breeding habitat quality in colonial birds: some consequences for dispersal and habitat selection. *Acta. Oecologica*. **17**: 531-552.
13. Parrish, J.K., 1995 Influence of group size and habitat type on reproductive success in common murrens (*Uria alga*). *Auk.*, **112**: 390-401.
14. Arengo, F and G.A. Baldassare, 1995. Effects of food density on the behaviour and distribution of non-breeding American flamingos in Yuctan, Mexico. *Condor.*, **97**: 325-334.
15. Murray, Jr. B.G., 1971. The ecological consequences of interspecific territorial behaviour in birds. *Ecol.*, **52**: 414-423.
16. Anderson, M., 1980. Nomadism and site tenacity as alternating reproductive tactics in birds. *Journal of Animal Ecol.*, **49**: 175-184.
17. Cody, M.L., 1985. Habitat selection in birds. *Physiological ecology*. Academic press, San Diego, California, USA,
18. Martin, T.E., 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist*. **141**: 897-913.

19. Buckley, F.G. and P.A. Buckley, 1980. Habitat selection and marine birds. In Behaviour of marine animals. J.Burger, B.L. Olla and H.E. Winn (Eds). Marine Birds. pp: 69-112. Plenum press. New York, 4: 69-112
20. Cody, M.L., 1971. Finch flocks in Mohave Desert. Theoretical population Biol., 2: 142-158.
21. Danchin, E. and R. Wagner, 1997. The evolution of coloniality: the emergence of new perspectives. Trends in Ecology and Evolution. 12: 342-347.
22. Keister, A.R., 1979. Conspecifics as cues: a mechanism for habitat selection in a Panamanian grass anole (*Anolis aeneus*). Behavioural Ecology and Sociobiol., 5: 323-331.
23. Shields, W.M., J.R. Crook, M. L. Hebblethwaite and S.S. Wiles-Ehmann, 1988. Ideal free coloniality in the swallows. Pages 189-228 In: (Ed) C.N. Slobodchikoff, *The ecology of social behaviour*. Academic press, San Diego, California, USA,
24. Stamps, J.A., 1991. The effect of conspecifics on habitat selection in territorial species. Behavioural Ecology and Sociobiol., 28: 29-36.
25. Boulinier, T. and E. Danchin, 1997. The use of conspecific reproductive success for breeding path selection in territorial migratory species. Evolutionary Ecol., 11: 505-517.
26. Erwin, R.M., 1979. Species interaction in a mixed colony of common tern *Sterna hirundo* and Black skimmers *Rynchops niger*. Animal Behaviour. 27: 1054-1062.
27. Burger, J. and M. Gochfield, 1990. The black skimmer: Social dynamics of a colonial species. New York: Columbia University Press.
28. Oro, D., 1998. Colonial seabird nesting in dense and small sub colonies: an advantage against aerial predation. Condor., 98: 848-850.
29. Rolland, C., E. Danchin and M. de Fraipont, 1998. The evolution of coloniality in birds in relation to food, habitat, predation and life history traits: a comparative analysis. American Naturalist. 151: 514-529.
30. Wittenberger, J.F. and G.L. Hunt, Jr, 1985. The adaptive significance of coloniality in birds. In: Avian biology. (Ed by D.S.Farner and J.R.King). San Diego: Academic Press. 8: 1-78.
31. Krebs, J.R. and N.B. Davies, 1987. An introduction in to behavioural ecology. Blackwell. Oxford.
32. Siegel-causey, D. and S.P. Kharitonov, 1990. The evolution of coloniality, In: *Current Ornithology* (Vol 7) (Power, D.M. ed.), pp: 285-330, Plenum press.
33. Kharitonov, S.P. and D. Siegel Causey, 1988. Colony formation in sea birds. Current Ornithol., 5: 223-272.
34. Fasola, M. and R. Alieri, 1992. Nest site characteristics in relation to body size in herons in Italy. Colonial Waterbirds, 15: 185-192.
35. Boulinier, T. and J.Y. Lemel, 1996. Spatial and temporal variations of factors affecting breeding habitat quality in colonial birds: some consequences for dispersal and habitat selection. Acta Oecologica. 17: 531-552.
36. Erwin, R.M., J.D. Nichols, T.B. Eyer, D.B. Stotts and B.R. Truitt, 1998. Modeling colony-site dynamics: a case study of Gull-billed Terns (*Sterna nilotica*) in coastal Virginia. Auk., 115:970-978
37. Fasola, M. and R. Alieri, 1992. Conservation of herony ardeidae sites in northern Italian agricultural landscapes. Biological Conservation. 62: 219 -228.
38. Baxter, G.S. and P.G. Fairweather, 1998. Does available foraging area, location or colony character control the size of multispecies egret colonies? Wildlife Res., 25: 23-32.
39. Drent, R.H. and S. Dann, 1980. The prudent parent: energetic adjustments in avian breeding. Ardea., 68: 225-252.
40. Custer, T.W. and R.G. Osborn, 1978. Feeding habitat use by colonially breeding herons, egrets and Ibises in North Carolina. Auk., 95: 733-743.
41. Maxwell, G.R and W. Kale, 1977. Breeding biology of five species of herons in coastal Florida. Auk., 94: 689-700
42. Frederick, P.C. and M.W. Collopy, 1989. The role of predation in determining nesting success of colonially-nesting wading birds in the Florida Everglades. Condor., 91: 860-867.
43. Jenni, D.A., 1969. A study on the ecology of four species of herons during the breeding season at lake alicia. Alachua County, Florida. Ecological Monograph. 39: 245-270.
44. Coulson, J.C., 1968, Difference in the quality of bids nesting in the center and on the edges of a colony. Nature. 217: 478-479.
45. Balda, R.P. and G.C. Bateman, 1972. The breeding biology of Pinon Jay. Living Bird., 11: 5-42
46. Brown, C.R. and M.R. Bomberger Brown, 1987. Group living in cliff swallow: as an advantage in avoiding predators. Behavioral Ecology and Sociobiol., 21: 97-107.
47. Coulson, J.C., 1968. Difference in the quality of bids nesting in the center and on the edges of a colony. Nature. 217: 478-479.

48. Bunin, J.S. and J.S. Boates, 1994. Effects of nesting location on breeding success of Arctic Terns on Machias Seal Island. *Canadian J. Zool.*, **72**: 1841-1847.
49. Lack, D., 1968. Ecological adaptations for breeding birds. London: Methuen.
50. Gotmark, F. and T. Anderson, 1984. Colonial breeding reduces nest predation in common gull (*Larus canus*). *Animal Behaviour*. **32**: 485-492.
51. Porter, J.M. and J.C. Coulson, 1981. Long term changes in recruitment to the breeding group and the quality or recruits at a kittiwake *Rissa tridactyla* colony. *J. Animal Ecol.*, **56**: 765-790.
52. Aebischer, N.J. and J.C. Coulson, 1990. Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. *J. Animal Ecol.*, **59**: 1063-1071.
53. Hamilton, W.D., 1971. Geometry for the Selfish herd. *J. Theoretical Biol.*, **31**: 295-311.
54. Vine, I., 1971. Risk of visual detection and pursuit by a predator and the selective advantage on flock behaviour. *J. Theoretical Biol.*, **30**: 405-442.
55. Furness, R.W. and P. Monaghan, 1987. Sea bird colony. Blackie Glasgow.
56. Kharitonov, S.P. and D. Siegel Causey, 1988. Colony formation in sea birds. *Current Ornithol.*, **5**: 223-272.
57. Ryder, P.I. and J.P. Ryder, 1981. Reproductive performance of ring billed gulls in relation to nest location. *Condor.*, **83**: 57-60.
58. Pugsek, B.H. and K.L. Diem, 1990. The relationship between reproduction and survival in known aged California gulls. *Ecol.*, **71**: 811-817.
59. Scolaro, J.A., S. Laurenti and H. Galelli, 1996. The nesting and breeding biology of the South American tern in northern patagonia. *J. Field Ornithol.*, **67**: 17-24.
60. Porter, J.M. and Coulson, 1981. Long term changes in recruitment to the breeding group and the quality or recruits at a kittiwake *Rissa tridactyla* colony. *J. Animal Ecol.*, **56**: 765-790.
61. Danchin, E., B. Cadiou, J.Y. Monnat and R. Rodriguez estrell, 1991. Recruitment in longlived birds: conceptual framework and behavioural mechanisms. *Proceedings of the International Ornithological Congress*. **20**: 1641-1656.
62. Tenaza, R., 1971. Behaviour and nesting success relative to nest location in Adelie penguins (*Pygoscelias deliae*). *Condor.*, **73**: 81-92.
63. Spear. L.B., 1993. Dynamics and effect of western gulls feeding in a colony of the Gullimots and Brandis cormorants. *J. Animal Ecol.*, **62**: 399-414.
64. Burger, J., 1982. On the nesting location of cattle egret. *Bulbulcus ibis* in South African heronries. *American Midland-Naturalist*. **124**: 523-529.
65. Newton, I and I. Wyllie, 1992. Fidelity to nesting territory among European Sparrowhawks in three areas. *J. Raptor Res.*, **26**: 108-114.
66. Subramanya, S., 1996. Distribution, Status and conservation of Indian heronries. *J. Bombay Natural History Society*. **98**: 459-486.
67. Gopi, G.V. and Bivash Pandav, 2007a Conservation of Avifauna of Bhitarkanika Mangroves, India. *Zoosprint*. **22**(10): 2839-2847.
68. Gopi, G.V. and B. Pandav, 2007b. Observations on breeding biology of three stork species in Bhitarkanika mangroves, India. *Indian Birds*. **3**(2): 45-50
69. Gopi, G.V., 2007c. Bhitarkanika: A breeding haven. *Sanctuary Asia.*, **XXVII** (2): 48-51.
70. Gopi, G.V., 2008. Bagagahana - the hidden paradise of Bhitarkanika. *Hornbill.*, **3**: 29-31.
71. Datta, T. and B.C. Pal, 1993. The effect of human interference on the nesting of Openbill stork *Anastomus Oscitans* at the Raiganj Wildlife Sanctuary, India. *Biological Conservation*. **64**: 149-154.
72. Culver, D.C., 1974. Species packing in Caribbean and north temperate ant communities. *Ecol.*, **55**: 974-988.
73. Kaufmann J.H., 1974. Social ethology of the whiptail wallaby, *Macropus parryi*, in north-eastern New South Wales, Australia. *Animal Behaviour*. **22**: 281-369
74. Burger, J., 1978. The pattern and mechanism of nesting in mixed species heronries. In A. Sprunt, J.Ogden and S. Wickler (eds), *Wading birds* (Natl. Aud. Soc. Res. Ret. No. 7). National Audubon Society, New York, pp: 45-60.
75. Burger, J., 1982. The role of reproductive success in colony site selection and abandonment in Black Skimmers *Rynchops niger*. *Auk.*, **99**: 109- 115.
76. McCrimmon, Jr. D.A., 1978. The collection, management and exchange of information on colonially nesting birds. in wading birds (A. Sprunt IV, J.C. Ogden and S. Winkler, Eds). Natl Audubon Society research Report. No.7. New York, pp: 187-196 .
77. Beaver, D.L., R.C. Osborn and T. W. Custer, 1980. Nest site and colony characteristics of wading birds in selected Atlantic coast colonies. *Wilson Bulletin*. **92**: 200-220.