

**Occupancy pattern and food-niche partitioning
among sympatric kingfishers in Bhitarkanika
mangroves, Orissa**

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SUMMARY

Eight species of kingfishers, Common, Collared, White-throated, Pied, Stork-billed, Black-capped, Brown-winged and Rudy, - coexist in the mangrove forests of Bhitarkanika along the east coast of India. Sympatric species with similar resource requirements need to have niche partitioning as a strategy to avoid competition in order to coexist together. To understand the mechanisms underlying such species coexistence, it is vital to know about the food requirements, foraging habitat preference, and how the resources are shared between these sympatric species. The present study attempted to understand the potential mechanisms that might play a role in food-niche differentiation and examined the occupancy patterns of four sympatric kingfishers i.e. Common, Collared, Black-capped and Brown-winged kingfisher in Bhitarkanika mangroves.

I conducted field study from January to May, 2011 in Bhitarkanika mangroves. The creeks were categorized as primary, secondary and tertiary creeks based on the branching pattern. A total of 16, one km trails were selected in the intensive study area. Each 1km trail was further divided into 10, 100 m segments for sub-sampling. During the survey only seven among the 10 segments of each 1 km trail were surveyed which were selected randomly with replacement. A total of 160 creek segments of 100 m length were surveyed for six times during the study period and relevant habitat variables were recorded. For foraging behaviour observation, point count method was used i.e., an individual bird was followed till it captured a prey and relevant foraging variables were recorded. A total of 53 independent prey captures were recorded for the four species of kingfishers. Focal animal sampling method was used and observations were made opportunistically for time budget observation.

Detection histories were constructed for each segment for bird survey and all relevant covariates. The two model parameters i.e., the probability that a segment is occupied by the

species (ψ) and the detection probability (p) were estimated and analysed in the occupancy framework. For foraging behaviour and time budget analysis, different parametric and non-parametric tests were used.

Occupancy analysis confirmed that Collared and Black-capped Kingfisher occur seasonally in Bhitarkanika mangroves; Collared being more abundant in summer and Black-capped in winter. For all the four sympatric species river/creek width had a negative association with detection probability. Habitat type also affected the detection probability of all the species except Collared Kingfisher. The detection probability of Common and Black-capped Kingfisher decreased with the increase in depth whereas it did not affect the detection probability of Collared and Brown-winged Kingfishers. Water current and turbidity were negatively associated with the occupancy of Common and Brown-winged Kingfisher. However for Collared and Black-capped Kingfisher, it differed with vegetation layer.

Perch height and foraging distance differed significantly among the four species of kingfishers. All the prey characteristics i.e., prey type, prey size and foraging substrate differed significantly among the four species of kingfishers. This study reveals that each of the four species of kingfishers in Bhitarkanika mangroves occupy foraging niches corresponding to their respective body sizes. The occupancy pattern and foraging behaviour of the smallest species, i.e., Common Kingfisher and the largest species, i.e., Brown-winged Kingfisher is more similar. As, both mostly forage in water to catch fish, their occupancy is also determined by water current. They segregate in terms of prey size, which is reflected by the respective body sizes. On the other hand, the foraging behaviour of Collared and Black-capped Kingfisher is similar in terms of prey characteristics.

1. INTRODUCTION

Kingfishers are a cosmopolitan group of stockily built birds with characteristic colourful plumage, short neck and dagger like bills. They are members of the family, Alcedinidae, and the order Coraciiformes which also includes the bee eaters, rollers and hornbills (Knowles and Nitchen 1995). This large and wide spread family consists of 93 species worldwide with 12 residents and one vagrant species in India (Rasmussen and Anderton 2005). The largest concentration of the family is known to occur in New Guinea and adjacent islands (26 species). Kingfishers originated in the rain forests of South East Asia and the nearby pacific islands, centred on New Guinea (Fry 1980). Kingfishers are fairly similar in appearance but vary greatly in size, from the tiny genus *Ceyx* (approximately 10 cm in length), to the genus *Cerylinae*, which includes the largest member *Megaceryle maxima* of Africa with a body size of 48 cm (Knowles and Nitchen 1995). Kingfishers inhabit rain forests, deciduous woodlands, savannahs, arid areas, mangrove swamps, freshwater swamps, lakes, sea shores, river valleys and estuaries. Their food varies from small fish and water crustaceans to small vertebrates, insects and arachnids. Several species of kingfishers are known to coexist in a given space and hence they are a good group to study resource partitioning. Kingfishers are diurnal, highly mobile, wide ranging and are relatively easy to observe.

Populations of aquatic birds are highly sensitive to changes in the extent/quality of habitat and therefore can serve as ideal indicators of habitat quality (Castelletta *et al.* 2000). They have been shown to track environmental variations, at short (months) and long (years) temporal scale at both species and community level (Amat and Green 2010). Kingfisher is at the end of the food chain and is thus exposed to any contamination which may affect the water from which it obtains its prey (Morgan and David 1977). For example, a study on Pied Kingfisher (*Ceryle rudis*) (Douthwaite 1982) revealed that spraying of organochlorine insecticide endosulfan for controlling the tse tse fly, affected the feeding rate of Pied

Kingfisher. The study also demonstrated some of the advantages of using predatory aquatic species to indicate effects of spraying on prey. Kingfishers are easier to observe than fish and their hunting behaviour can clearly show the location and duration of the acute effects as well as help to identify the victims.

Mangroves, located at the confluence of land and sea are highly complex as well as fragile ecosystems (McLeod and Salm 2006). It is regarded as the nursery ground as it supports high densities of juvenile fishes (Sasekumar *et al.* 1992). Mangroves play an important role in functioning of the whole ecosystem by filtering and trapping pollutants, stabilizing the coastal land by trapping sediments and protecting it against storm damage (McLeod and Salm 2006). Although mangrove ecosystems have tremendous economic and ecological value for coastal communities and associated species, coverage and quality of the mangroves are declining at an alarming rate (Duke *et al.* 2007). Over the last 50 years, about one-third of the world's mangrove forests have been lost (Alongi 2008). So, from a conservation perspective, the value of understanding the mechanisms structuring the diverse sympatric species assemblages in this unique ecosystem can help in making informed management decisions.

Ecological studies on kingfishers in India are very scanty and are limited to casual observations. The nesting ecology of the White-breasted Kingfisher (*Halcyon smyrnensis*) was studied in Cauvery Delta of Tamil Nadu, Southern India by Ali *et al.* (2010). Asokan *et al.* (2009) studied the dietary composition of the White-breasted Kingfisher along with two other insectivorous species, the Small Bee-eater (*Merops orientalis*) and the Black Drongo (*Dicrurus macrocercus*) in Nagapattinam District, Tamil Nadu, by analyzing regurgitated pellets. The analysis revealed that the White-breasted Kingfisher preys mainly on arthropods (83.40%) and less on vertebrates. They also identified seven orders of insects with Coleoptera, Hemiptera, Hymenoptera and Orthoptera being predominant. There has been no other ecological study of

kingfishers in Indian mangroves. A study carried out on the status and density of eight different kingfisher species of Sundarbans mangroves of Bangladesh (Reza *et al.* 2003) revealed that the overall occurrence of the various kingfisher species in different habitats varied significantly. Among the eight species, Common Kingfisher (*Alcedo atthis*) was found to have highest density (5.69 individuals/km²) whereas Ruddy Kingfisher (*Halcyon coromanda*) had the lowest density (0.15 individuals /km²).

Bhitarkanika mangroves harbour a high diversity of kingfishers *viz.*, Common, Collared (*Todiramphus chloris*), Pied, White-throated, Black-capped (*Halcyon pileata*), Stork-billed (*Pelargopsis capensis*), Brown-winged (*Pelargopsis amauroptera*) and Rudy Kingfisher. Among these, Brown-winged Kingfisher has been listed under the near threatened category in IUCN Red Data Book and the rest have been kept in the least concern category. Till date there exists limited knowledge on the ecology of these species in this fragile habitat. In order to fill this gap, this study attempted to investigate how these sympatric species partition the habitat and foraging-niche. The study focussed on four species which are relatively common among the eight sympatric species of kingfishers, i.e, Common, Collared, Black-capped and Brown-winged.

1.1. Literature Review

1.1.1 Resource partitioning

Understanding the mechanisms of resource partitioning, - which allow coexistence of related species have been a central theme in ecology (Schoener 1974, Roughgarden 1976, Smith 1982, Walter 1991, McClean *et al.* 1998, Dolédec *et al.* 2000). The concept of resource partitioning is derived from the theory of limiting similarity—i.e., the limit of similarity among the competing species to coexist together. This theory presumes that there is an evolutionary

limit (L), to the similarity of two coexisting species such that if two species are more similar than L, a third intermediate species will converge towards the nearer of the pair and if two species are more different than L, a third intermediate species will diverge from either toward a phenotype intermediate between the two (MacArthur and Levins 1967). Resource partitioning among species reduces the effect of competition by decreasing the amount of overlap between the competing species and allows related sympatric species to coexist in the same area. The concept of resource partitioning originally developed as the evolutionary change in species in response to selection pressures generated by inter-specific competition (Walter 1991). Currently it is referred simply to differences in resource use between species regardless of the origins of the differences. To understand these mechanisms which facilitate such coexistence, it is important to assess how sympatric species share the available resources. In such cases, competition theory predicts that related species should differ in habitat or food types, or foraging strategies, or should show divergence in major morphological features to avoid competitive elimination (MacArthur and Levins 1964). Animals partition resources along three axes which are habitat, food and time (Schoener 1974). Partitioning habitat is one of the principal relationships which permit species to coexist (Rosenzweig 1981). Habitat selection can be a result of both prevailing environmental conditions and constraints in evolutionary terms. Apart from inter-specific competition, many other factors such as morphology, behaviour, ability to obtain food and shelter (ultimate factors), and structural features of the landscape, foraging and nesting opportunities (proximate factors) may influence habitat selection (Cody 1985). These factors may act independently or synergistically in a complex manner to achieve co-existence in the same area.

1.1.2. Food-niche partitioning

Food partitioning is considered to play an important role in facilitating co-existence of sympatric species. Three main factors that could be the potential mechanisms of food partitioning among sympatric species are the abundance of food, the body size of each species and their breeding system (i.e., the degree of territorial behaviour) (Garcia and Arroyo 2005). Abundance of food affects the potential levels of depletion and exploitative competition between individuals. So, the overlap of food-niche among the sympatric species decreases with the decrease of resource as it increases the cost of overlap (MacArthur and Levins 1967). Body size influences the energy requirement of each species, and ultimately the outcome of aggressive interactions (Garcia and Arroyo 2005). Species with larger body size has to obtain larger prey or more food resources as it requires more energy comparing to one with small body size but on the other hand it might get the advantage in inter-specific agonistic encounters (Robinson and Holmes 1984). So, food size could be one aspect of differentiation among congeneric or heterogeneric species that differ in body size (Garcia and Arroyo 2005). Finally, the breeding system influences the extent of monopolization of foraging areas through territorial behaviour (Schoener 1983), which in turn may allow species to segregate. Therefore, comparisons between sympatric species with similar ecology but different body size and social behaviour can be helpful in assessing the influence of energy needs or dominance on foraging strategies and food partitioning (Fedriani *et al.* 2000).

1.1.3. Food-niche partitioning among Avifauna

Resource partitioning have been studied in a wide range of bird species, including songbirds (Moskát and Fuisz 2002), raptors (Garcia and Arroyo 2005), and waterfowl (Frederick and Bildstein 1992). It has been analysed in terms of the segregation of both habitat and food.

Pianka (1974) proposed a related concept called the “niche overlap hypothesis”, which says that maximum tolerable niche overlap should be lower in communities where inter-specific competition (i.e., diffuse competition) is intense than in environments where competition is weak. It has been reported that average niche overlap decreases with the number of species in the guild and average niche overlap is greater when resources are more abundant (Rusterholz 1981). Therefore, seasonal changes in niche overlap among sympatric species can be most likely a strategy to avoid inter-specific competition for limited food resources (Alatalo 1982). Waterfowls have been mostly reported to partition both food and habitat (Paine *et al.* 1982). The study by Weimerskirch *et al.* (1988) provided evidence for the hypothesis that, separation of feeding zones is one of the mechanisms of resource partitioning in albatross communities and populations. Another study by Garcia and Arroyo (2005) revealed that both the size of prey and foraging behaviour can be another strategy to achieve coexistence among sympatric species.

1.1.4. Kingfishers and food partitioning

Several factors have been found to influence kingfisher habitat use, including perch height (Monadjem *et al.* 1994), diet (Libois and Laudelout 2004), water quality (Douthwaite 1982), river depth (Monadjem 1996), river width and river speed (Peris and Rodriguez 1996). Johnston (1989) reported a significant difference in habitat use between the sexes during breeding season. Brooks *et al.* (1987) observed the habitat selection by breeding Belted Kingfishers (*Ceryle alcyon*) along sections of streams in Pennsylvania and Ohio. They found that differences in population density of kingfishers along streams appeared to be caused by differences in the number of suitable foraging sites rather than availability of nest sites. Bonnington *et al.* (2008) studied the habitat niche segregation among four kingfisher species in Southern Tanzania. The study reported niche segregation between Giant (*Megaceryle maxima*)

and Pied Kingfishers and Half-collared (*Alcedo semitorquata*) and Malachite Kingfishers (*Alcedo cristata*) with Giant and Pied Kingfishers favouring foraging areas with higher perch-sites and deeper and wider river stretches, and Half-collared and Malachite Kingfishers preferring lower perch-sites near shallower, narrower river stretches. Kasahara and Katoh (2008) studied the foraging ecology of sympatric Common Kingfisher and the Greater Pied Kingfisher (*Ceryle lugubris*) in the breeding seasons and concluded that the realized food-niches of the two kingfisher species reflect their respective body sizes.

1.1.5. Background of present Study

The present study focuses on the occupancy patterns of four sympatric kingfishers and food-niche partitioning among them in Bhitarkanika mangroves. These species are distributed widely (Fig. 1) and show variation in their morphological and ecological attributes (Table 1)

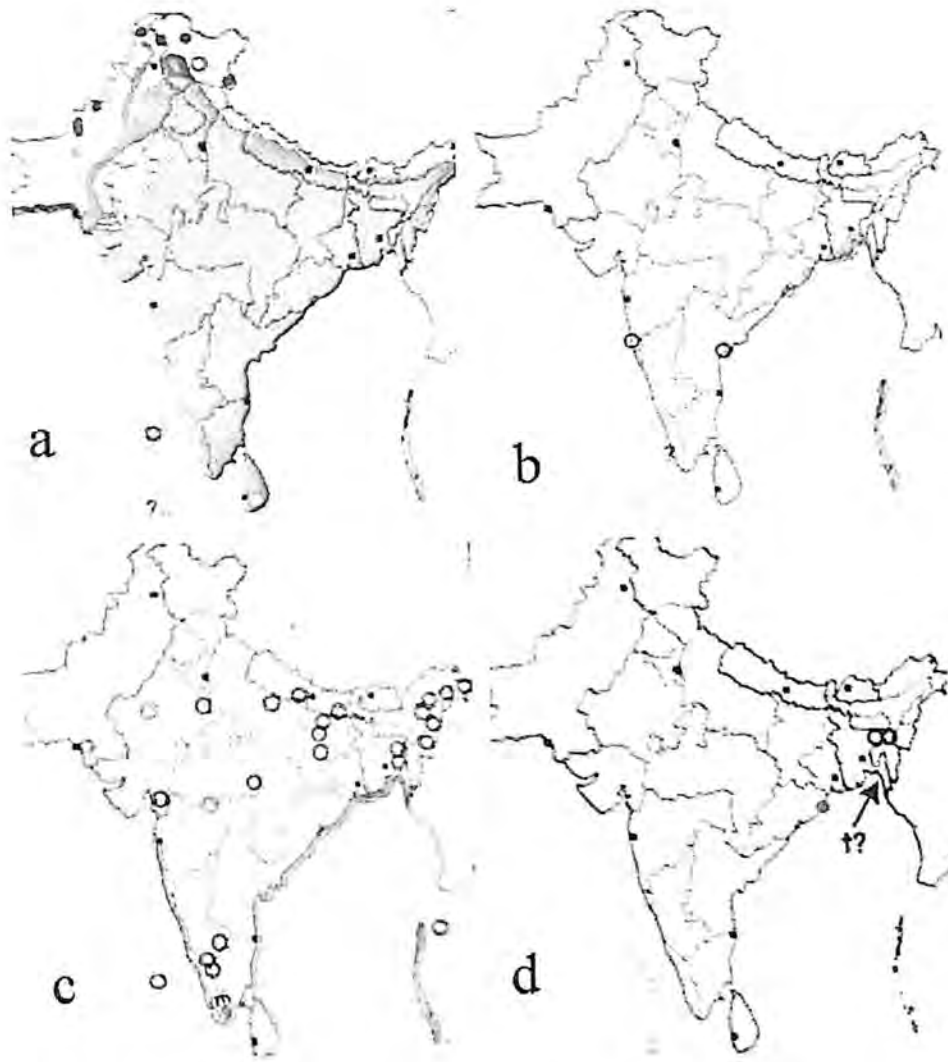


Figure 1. Distribution of the four studied kingfisher species across India (Rasmussen and Anderton 2005) a- Common Kingfisher, b- Collared Kingfisher, c- Black-capped Kingfisher, d- Brown-winged Kingfisher.

Table1. Summary of important ecological characters of the four species of kingfisher*

Attributes	Common Kingfisher	Collared Kingfisher	Black-capped Kingfisher	Brown-winged Kingfisher
Body Size	17 cm	24 cm	30 cm	36 cm
Wing length	68- 76 mm	90-107 mm	127 -133 mm	141-160 mm
Bill length	42-46 mm	40-47 mm	57-65 mm	70- 82 mm
Tarsus length	8-10 mm	15 mm	15 mm	18-19 mm
Tail length	30-37 mm	62-65 mm	83-88 mm	86-98 mm
Habitat type	open water ways of freshwater	along intertidal creeks	mangrove areas and estuaries, grass land and paddy field.	along coastal areas, saltwater tidal creeks,mangrove swamp
Type of prey	small fish, tadpoles, aquatic insects, ants, crickets and other land insects.	crabs, mudskipper, fish, insects	variety of insects, sometimes small fish and crabs.	mainly fish, also takes crustaceans, frogs, lizards and insects.
Nest	excavated hole in a steep river bank away from the water edge.	termite's nest, hole in a tree trunk near water	excavated hole in a river bank	excavated hole in a river bank, Termite's nest, Rotten tree trunk
Territoriality	territorial during winter months, defends territory on a stretch of river aggressively	very aggressive during breeding season	territorial	territorial
Breeding season	Apr-Aug	Apr-May	Sep-Jan	Mar- Apr

* Source: (Ali 1961)

1.1.6. Objectives

In order to gather ecological information on sympatric species of kingfishers in Bhitarkanika mangroves, Orissa, this study was carried out with the following objectives-

1. To assess the occupancy patterns of sympatric kingfishers and the factors influencing them
2. To determine patterns of food-niche partitioning among the sympatric kingfishers in terms of foraging behaviour and
3. To determine the allocation of time for different activities in each kingfisher species.

The study has addressed the following research questions-

1. What are factors that affect occupancy and detection probability of the sympatric species?
2. What are the inter-specific variations in the foraging behaviour of the sympatric kingfishers?
3. Is there any difference in the time spent for different activities among the sympatric species?

1.1.7. Hypotheses tested

- i) As preliminary observations during earlier studies in Bhitarkanika mangroves revealed that Black-capped and Collared Kingfishers show seasonal movement (Dr. Bivash Pandav, Wildlife Institute of India, personal communication), so it was hypothesized that there is a seasonal variation in occurrence of these two of the sympatric kingfishers.
- ii) According to the 'tidal-coupling hypothesis' (Zamon 2003), energy flow to piscivorous predators is strongly associated with tidal phase as fishes aggregate to feed in times or places corresponding to tidal fluctuation and these aggregations in turn attract the piscivorous

predators. Therefore, feeding activity in piscivorous predators is predicted to be strongly coupled to the daily tidal cycle (Wolanski and Hammer 1988). So, it was hypothesized that tidal condition might influence kingfisher occurrence along the creeks.

iii) Literature review reveals that kingfisher species with smaller body size hunts in narrow channels with less current and water depth. In contrast, the larger species tends to choose wider river stretches and sites with more current and depth (Bonnington *et al.* 2008). So river/creek width, water depth and current were hypothesized to have significant influence on the occupancy and detection probability of kingfishers.

iv) Collared Kingfisher is reported to be a generalist and may not be closely tied to variability in forest composition (Steadman and Franklin 2000). It is an ambush hunter of insects and small vertebrates in the forest understorey (Mayr 1945). It has been described as a bird of edges or fairly open forest (Freifeld 1999). As the breeding season of Collared Kingfisher started from March onwards in the study area, they began to nest in tree holes along the creeks. Therefore, though it is a generalist, availability of nesting and foraging sites might influence the occurrence of this species in a particular site during breeding season. So, it was assumed that number of vegetation layers and dominant tree species along the creeks to affect their occupancy.

v) Previous studies (Ashmole 1968, Padilla *et al.* 2007, Costa *et al.* 2008, Kasahara and Katoh 2008) have shown that the prey size is determined by the body size of the sympatric species. So the sympatric kingfishers of different body sizes in Bhitarkanika were expected to show similar pattern in determining prey size. Apart from this there might be other inter-specific variation in foraging behaviour reflecting the influence of body size, e.g. perch height, foraging distance, depth of water in foraging site.

2. STUDY AREA

2.1. General Description:

The study was carried out in Bhitarkanika National Park (Fig. 2). It is located in the deltaic region of Brahmani and Baitarani rivers in the Kendrapara district of Orissa (between 20° 30' - 20° 48' N latitude and 86° 45' - 87° 03' longitude). In 1975, the mangrove forests and the adjacent land of Bhitarkanika were declared Wildlife Sanctuary encompassing an area of 672 km², with a core area of 145 km². The core area was notified as a National Park on Sep 16, 1998. The coastline stretches 35 km along its eastern side which also constitutes the Gahirmatha Marine Sanctuary. Bhitarkanika National Park, Bhitarkanika Wildlife Sanctuary and parts of the Gahirmatha Marine Sanctuary together with 336 villages and adjacent cultivated agricultural lands within the BWS, constitute the Bhitarkanika Conservation Area (3000 km²). Bhitarkanika was also declared a Ramsar site in 2002 because of its international importance as a waterfowl habitat. It is the second largest existing mangrove ecosystem in India. The sanctuary is bounded by rivers Dhamara to the north, Maipura to the south, Brahmini to the west and the Bay of Bengal in the east. The annual rainfall ranges from 920 to 3000 mm.

Bhitarkanika National park harbours a rich diversity of mangrove floras in the country. This mangrove forest and the associated coast harbour the highest diversity of Indian mangrove flora and fauna (Gopi and Pandav 2007). About 63 species of mangroves and their associated vegetation are known to occur in this area. Occurrence of three species each of *Avicennia*, *Heritiera*, *Sonneratia*, *Rhizophora* and *Xylocarpus* and four species of *Bruguiera* is significant for this forest. Moreover, these mangroves constitute the preferred habitat for endangered reptiles such as the saltwater crocodile (*Crocodylus porosus*), Indian Python (*Python molurus*), King cobra (*Ophiophagus hannah*), water monitor (*Varanus salvator*) and the Olive ridley sea

turtle (*Lepidochelys olivacea*) (Patnaik *et al.* 1995). It also harbours one of the largest heronries and an important refuge for migratory waterfowl (Gopi and Pandav 2011).

2.2. The creek system:

Bhitarkanika mangrove presents a salt tolerant, complex and dynamic eco-system that occurs in tropical and subtropical inter-tidal regions. It lies in the estuarine region of Brahmani and Baitarani comprising mangrove forests, rivers, creeks, estuaries, back water, accreted land and mud flats. The intensive study area consists of four forest blocks, *viz.*, Bhitarkanika, Dangamal, Mahinsmada and Ragadapatia blocks with an area of about 40 km². The main river flowing through the area is Bhitarkanika. Numerous creeks of different sizes are located all along the river which are mainly fed by the tidal water and so are very dynamic in nature. Some of the tiny creeks completely dry out during low tide. The vegetation along the creeks mainly consists of tree species such as *Heritiera fomes*, *Sonneratia apetala*, *Avicennia officinalis* and *Excoecaria agallocha*. Among shrubs, *Brownlowia tersa* is the most abundant species all along the creeks.

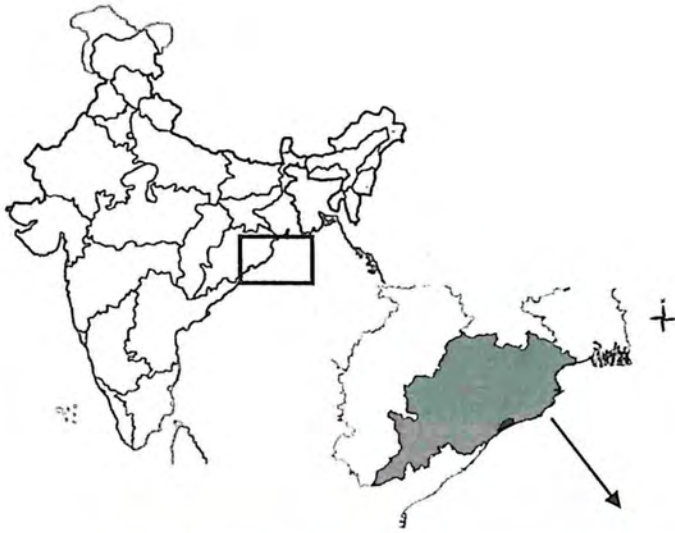


Figure 2. Location of Bhitarkanika N.P, Orissa. Bhitarkanika NP is located in the deltaic region of the rivers Brahmini and Baitarani, along the north eastern part of Orissa coast.

3. STUDY DESIGN AND METHODS

A reconnaissance survey was conducted in Bhitarkanika mangroves from December 2010 to January 2011. During this survey get acquainted with the vegetation structure and nature of the surrounding wetlands (tidal marshes, big rivers, creeks etc). It was observed during reconnaissance that Rudy and Stork-billed Kingfishers were uncommon in the study area and Pied and White-throated Kingfishers primarily occurred along the periphery of mangrove forest. Therefore, the study focussed on the rest four kingfisher species, i.e., Common, Collared, Black-capped and Brown-winged Kingfisher for my study.

3.1. Occupancy estimation:

The study area was thoroughly surveyed to look at kingfisher's resource utilization pattern during the reconnaissance study. As kingfishers are mostly associated with water bodies, the study mainly focussed on the creeks and other surrounding wetlands. The creeks were categorized as primary, secondary and tertiary creeks based on the branching pattern. Only those creeks were selected for sampling which were accessible during both high and low tide conditions to examine if tidal condition affects the occurrence of the sympatric kingfishers. Trails of 1 km in each creek type were selected. A total of 16, one km trails were selected in the intensive study area (Table 2, Fig. 3). Each 1km trail was further divided into 10, 100 m segments for sub-sampling and marked (Fig. 4).

Table 2. Summary of sampled creek characters in Bhitarkanika mangroves (Jan-May, 2011).

Creek type	Creek name/ID	Total creek length (km)	Average width of sampled section (m)
Primary	Bhitarkanika-1	11*	76.8±6.5
	Bhitarkanika-2		69.95±9.2
	Bhitarkanika-3		103.6±11.3
	Bhitarkanika-4		134.85±23.4
Secondary	Balijore	2.5	18.2±3.9
	Bhamaramari	3	13.55±2.6
	Ganjeikhia	3	11.6±2.4
	Jaladhar	2.5	11±2.5
	Khola	3	24.6±3.3
	Mahinshamada	7	60.05±5.6
	Suajore	6	19.25±2.1
Tertiary	Thanupati	1.5	38.4±4.9
	Boro kathua	3.5-4	18±1.9
	Chintamoni Mohanty	2	19.2±3.6
	Junojore	1.5	19.85±2.4
	Shymsudin	2-3	16.65±1.7

*Pathsala mouth to Khola mouth



Figure 3. Map of the intensive study area in Bhitarkanika N.P showing the main river and its creeks with the sampled 1 km trails in each creek (Jan-May, 2011).

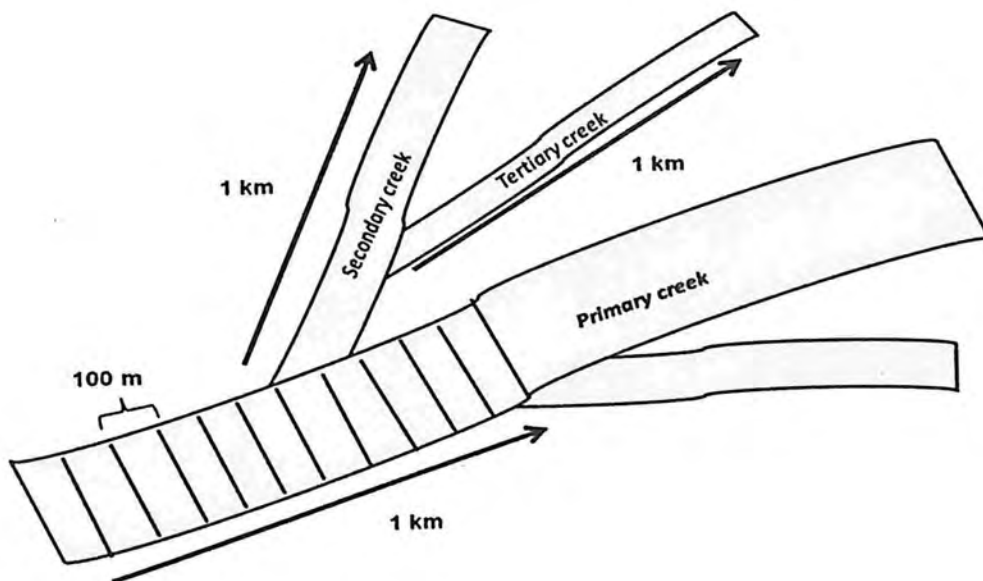


Figure 4. Graphical representation of the 10, 100 segments in each 1 km trail laid in the intensive study area in Bhitarkanika mangroves (Jan-May, 2011).

- **Habitat Characterisation:**

During the first month of field work, the entire habitat along the river/creeks was characterised by measuring relevant habitat variables in each segment on both side of the river/creek. As tidal condition of mangrove areas like Bhitarkanika is very much dependent on the lunar cycle and all other variables are also directly or indirectly correlated to tidal condition, efforts were made to record the variables within one lunar cycle (New Moon to Full Moon).

- **Bird Survey:**

Bird surveys were done from February 02 to April 30, 2011 and the trails in each type of creeks were surveyed by country boat. Spatial sub-samples were used as temporal replicates for estimation of occupancy within a season due to logistic constraints and also to estimate seasonal changes in occupancy for Collared and Black-capped Kingfishers. The 10 segments in every 1 km trail were considered as closed sessions for occupancy (MacKenzie and Royle 2005) and these were repeated six times during the entire study period. During each bird survey only seven among the 10 segments of each 1 km trail were surveyed. For the estimation of single season occupancy, these segments were selected randomly with replacement to remove the estimation bias and ensure spatial independence among the sampling sites (Kendall and White 2009). For example, if the following random numbers were picked among 10, 100 m segments- 1, 4, 6, 7, 4, 6 and 10, to implement these random draws , the 1st, 4th, 6th and 7th segment were surveyed first and then 4th and 6th segments were surveyed again for the second time; at last the 10th segment was surveyed. Detection histories were built specific to each species.

Surveys were carried out on sunny, calm days, as kingfishers are known to be most active when visibility is good (Douthwaite 1982). Whenever any kingfisher species was sighted during the survey, data on habitat variables were collected (Table 3).

Table 3: Habitat variables recorded during creek and bird survey for occupancy estimation in Bhitarkanika mangroves (Jan-May, 2011). During creek surveys, habitat variables were recorded at 5 m distance from potential perch sites for kingfishers. During bird survey, habitat variables were measured from the actual perch site.

Sl no	Variable name	Remarks
1	Veg layer	vegetation layers on both side of the creek; categorized as— i) tree, ii) shrub and tree and iii) grass, shrub and tree.
2	Habitat type	ranked as having dominant tree species on both side of the creek; rank 1- <i>H. fomes</i> , 2- <i>S.apetala</i> , 3- <i>A. officinalis</i> , 4- <i>E. agallocha</i> , and 5- others; the ranks were added for both sides of the bank in all segments.
3	Tidal magnitude	distance between water level and high tide line in meters; used as a measure of tidal fluctuation.
4	River/ creek width	distance in meters between the tree lines on both side of the banks were considered as width as water level fluctuates with tide.
5	Water current	measured in meter/second at 5 m distance from the potential perch site with the help of an empty plastic bottle tied to a rope of 2 m length. Current was calculated as the time taken by the bottle to cover that 2 m distance.
6	Water depth	measured in meters by a bamboo stick at 5m distance from the potential perch site.
7	Water turbidity	measured in cm with the help of a Secchi disk.

Analyses:

Identification of habitat covariates:

The relevant habitat covariates influencing the occurrence of kingfishers were identified with the help of literature survey and observation for each of the sympatric species. The measurable habitat covariates were divided into two broad categories-

- i) Habitat covariates related to tidal fluctuation- water depth, water current and water turbidity.
- ii) Habitat covariates related to bank structure along the creeks- vegetation layers, habitat type, and creek/river width.

Based on the *a priori* hypotheses, the response of each sympatric species to the relevant habitat covariates was predicted (Table 4).

Table 4: Predicted response of each of the sympatric Kingfisher species to the habitat covariates based on *a priori* hypotheses in Bhitarkanika mangroves (Jan-May, 2011); ψ , probability of occurrence; p , species detection probability.

Covariates	Common Kingfisher		Collared Kingfisher		Black-capped Kingfisher		Brown-winged Kingfisher	
	ψ	p	ψ	p	ψ	p	ψ	p
Veg lr	-	0	+	0	-	0	-	0
Current	-	0	0	0	0	0	-	0
Turbidity	-	0	0	0	-	0	-	0
Width	0	-	0	-	0	-	0	-
Depth	0	-	0	-	0	-	0	-
Dtree	0	0	0	0	0	+	0	0

‘+’ signifies a positive effect on the response variable, ‘-’ signifies a negative effect on the response variable and ‘0’ signifies that the covariate has no effect on the response variable. Veg lr, Vegetation layer; Dtree-dominant tree species.

Detection histories were constructed for each segment, where ‘1’ indicates detection of bird, ‘0’ indicates non-detection and ‘-’ indicates a missing observation. Detection histories of each segment for bird survey and all relevant covariates were constructed. For the site covariates, the mean values of the habitat characteristic data was used and for the sampling covariates the actual bird survey data was used. The two model parameters i.e., the probability that a segment is occupied by the species (ψ) and the detection probability (p) were estimated in

the occupancy framework (MacKenzie *et al.* 2002). This was then analysed using PRESENCE version 2.4 (Hines 2006).

A candidate set of variables was used to construct the global model for each species. Single species, multi season models were used for all the four species of kingfishers to assess their seasonal variation in occupancy. As the occurrence of two species of kingfishers, i.e., Collared and Black-capped Kingfishers was hypothesized to be seasonal, these were modelled on colonization (γ) and extinction (ϵ) probability with time respectively. The variables included in the global model were vegetation layer, water current, turbidity, creek width, water depth, dominant tree species, height of nearest tree.

Common Kingfisher: Ψ (vegetation layer+ water current +water turbidity), ϵ (time), p (creek width+ water depth+ dominant tree sp +height of nearest tree)

Collared Kingfisher: Ψ (vegetation layer+ water current +water turbidity), γ (time), p (creek width+ water depth+ dominant tree sp).

Black-capped Kingfisher: Ψ (vegetation layer+ water current +water turbidity), ϵ (time), p (creek width+ water depth+ dominant tree sp).

Brown-winged Kingfisher: Ψ (vegetation layer+ water current +water turbidity), ϵ (time), p (creek width+ water depth+ dominant tree sp).

Modelling effects of covariates on detection probability and occurrence:

A step-wise approach was used; the detection probability was first modelled by keeping the most complex model from the global model as a constant model and the best model for p

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was derived. Then ψ was modelled using the derived best model of p . All inferences were made using model averaged parameters (Burnham and Anderson 1998).

3.2. Prey sampling:

Efforts were made to have a broad estimate of prey availability in different strata to see whether the occurrences of the species of kingfishers across different habitat types correspond to prey abundance or not. A pilot survey was done to get an idea about the major prey groups as it was not possible to account for the wide range of prey species intensively due to logistics and time constraints. Sampling was done once in all three types of creeks during the study period for each group of prey except fishes. For fishes it was done once in every 15 days – so, all total five times during the entire study period.

- **Fish:**

As kingfishers primarily feed on surface swimming and shallow water fish species (Davis 1982), efforts were made to get estimate for this target group only. It was estimated by catching fish with the help of a cast net with small mesh size all along the creeks. The fishes were then emptied into a bucket, counted, measured and returned to the water. After each catch fish was identified, body length was recorded and later categorized as small, medium, large. The abundance was calculated as Catch per unit effort to quantify (CPUE) i.e., total number of individuals caught /number of times the net was casted.

- **Crustaceans:**

The same 100 m segments of each type of 1 km trail were sampled with a quadrat of 0.56m^2 made of wooden sticks. The frame was randomly placed once along the bank of creeks in every segment - i.e., 10 times in a 1 km trail. These were observed for 10 min after the

quadrate was placed and the number of crabs emerging from burrows within the quadrate was recorded. Crabs which went up and down a burrow several times were not recounted and those which entered the quadrate from outside were also not counted at all. As the crabs and their burrows get exposed only when the water level is low, the sampling was done during low tide.

- **Mudskippers:**

The same 100 m segments of each type of 1 km trail were sampled with a quadrate of 0.56m² made of wooden sticks to get an estimate of mudskippers abundance. The frame was placed once along the bank of creeks in every segment-i.e., 10 times in a 1 km trail. These were observed for 5 min after the quadrate was placed and the number of mudskippers emerging from burrows within the quadrate was recorded. As mudskippers are very sensitive to any kind of disturbances, they came out of the burrows very rarely after placing the frame. Literature says that most of the mudskipper species are territorial (Al-Behbehani and Ebrahim 2010), so the number of burrows were expected to provide a good estimate of their abundance. Therefore, instead of individual counts of mudskippers, the burrows were counted to get the abundance estimate.

3.3. Foraging behaviour observation:

The data presented in this study were collected during 15 February- 02 May, 2011. Observation protocols were standardized after making ad-libitum observations in the field. Observations were done opportunistically. The creeks were surveyed by country boats and individuals of the target species were actively searched. Efforts were made to record foraging observation from all types of habitats. Point observation method was used i.e., an individual bird was followed till it captured a prey and relevant foraging variables were recorded (Table 5). To reduce the problem of pseudoreplication, after recording an observation, no further data

was collected on the same species within 500 m distance from that site. All the data were recorded in a dicta phone.

Table 5. Variables recorded during foraging behaviour observation of kingfisher species in Bhitarkanika N.P. (Jan-May, 2011).

Sl no	Variables.	Remarks
1	Kingfisher species	Common, Collared, Black-capped or Brown-winged Kingfisher.
2	Type of perch.	categorized as- i) plant, ii) dry log, iii) bank, iii) artificial pole
3	Perch height	height at which the bird perched while feeding - estimated visually in meters
4	Foraging distance	distance travelled to catch the prey- estimated visually in meters
5	Water depth	measured in meter at the visually determined point after the foraging individual flew away
6	Foraging substrate	the material from which food was taken ; categorized as i) water, ii) vegetation, iii) tree hole, iv) mud bank, v) air
7	Size of prey	estimated by comparing it with the bird's bill (as % of bill length) and categorized as i) small (lesser than the bill length of the smallest species Common Kingfisher, i.e., < 4 cm) ii) medium (all in between small and big category, i.e., 4-8 cm) iii) big (greater than the bill length of the largest species Brown-winged Kingfisher, i.e., > 8cm)
8	Type of prey	categorized as i) fish, ii) crabs, iii) insects, iv) mudskipper.
9	Vegetation cover	% foliage cover imagining a circular plot of 5 meter radius around the bird at 5 meter distance from the perch site of the bird.

Analyses:

Inter-specific variations in microhabitat variables were tested with parametric test (Zar 1998) and wherever it did not satisfy the assumptions for parametric test, non-parametric test (Siegel and Castellan Jr 1988) was used. Perch height, foraging distance and vegetation cover were tested using one-way ANOVA. Vegetation cover and foraging distance values were square root-arcsine and log (x+1)-transformed, respectively. Water depth was tested for Common and Brown-winged Kingfisher using independent samples t-test. For water depth,

Collared and Black-capped Kingfisher were dropped because it rarely captured prey from water during observations.

To test for differences in prey characteristics across species, non-parametric Fisher's exact test of probability was used as sample sizes were low. Other variables tested using a similar approach were prey type, prey size and foraging substrate. Correspondence analysis (McGarigal *et al.* 2002) was applied to visualize the kingfisher species on a multidimensional space in relation to the prey characteristics.

3.4. Behavioural sampling (time activity budget):

The data used in this study was collected from 01 March to 02 May, 2011. Focal animal sampling method was used and observations were made opportunistically. All observations were made by using a 10×42 binocular. Only one bird was observed at a time. When it was lost from sight, another one was selected. During sampling all observed activities of the individual were recorded with time.

Eight different categories of activities were sorted out and defined based on literature review-

- (1) Feeding - time spent by the birds in capturing the prey and handling it into buccal chamber. It is from the time the bird leaves a perch aiming at the target till it catches and feeds on it. If the attempt fails then the time ends when it goes back to previous or any nearby perch.
- (2) Flying - flying from one perch to another not aiming at any prey.
- (3) Vigilance/Scanning - birds perching in an upright position, looking around attentively, scanning their surroundings actively.
- (4) Comfort activities - all forms of comfort movements including the feather shaking, wing flapping, bill cleaning, bill scratching, body shaking and tail shaking so on and so forth,

defecating and taking bath, i.e., when it goes into water very frequently without scanning and every time it is followed by preening.

(5) Calling/ displaying - calling, displaying, i.e., moving its tail upwards and downwards, body elongated.

(6) Resting - perched, birds that were sleeping or dozing, with the head retracted and eyes closed.

(7) Nest attendance - going in and out of nest.

(8) Competition - chasing away other species.

Analyses:

As a measure of relative importance of the time devoted to each activity category during the total period of observation, the time-activity index (TAI) (Morrier and McNeil 1991) was calculated for each species,

$$\text{TAI (\%)} = \text{TTA} \times 100 / \text{TDO}$$

Where, TTA= total time (s) spent in a given activity category during the observation period, and TDO=total duration of observation for the species.

Frequency-activity index (FAI) was also calculated in the same way for each species.

$$\text{FAI (\%)} = \text{FA} \times 100 / \text{TFA}$$

Where, FAI=total frequency of a given activity category during the observation period, and TFA=total frequency of all activities during the observation of the species.

As the data was not normally distributed and some of the cells had values less than five, Kruskal-Wallis test for independent samples was used to test for any difference in time spent and frequency of each activity by the four species of kingfishers.

All analyses were performed using MS Excel 2007, SPSS ver. 16.0 (SPSS, Chicago, IL) and R (R Development Core Team 2009).

4. RESULTS

4.1. Occupancy estimates:

All total 112 creek segments of 100 m length were surveyed for six times during the study period from February to May 2011. Throughout the study period, a total of 425 sightings of the four species of kingfishers (Common-37, Collared-133, Black-capped-140 and Brown-winged-115) were recorded. The species detection rate across the six surveys decreased for Common, Black-capped and Brown-winged Kingfisher but increased for Collared Kingfisher (Table 6).

Table 6. Species detection rate (\pm SD) of the four species of kingfishers per every 1 km trail of the 16 sampled creeks across six bird surveys in Bhitarkanika mangroves (Jan-May, 2011).

Species	Survey 1	Survey 2	Survey 3	Survey 4	Survey 5	Survey 6
Common Kingfisher	0.5 \pm 0.51	0.4 \pm 0.51	0.4 \pm 0.50	0.1 \pm 0.25	0.3 \pm 0.44	0
Collared Kingfisher	0.2 \pm 0.40	0	0.6 \pm 0.50	0.6 \pm 0.51	1	0.9 \pm 0.25
Black-capped Kingfisher	0.9 \pm 0.34	0.9 \pm 0.25	0.9 \pm 0.34	0.6 \pm 0.51	0.4 \pm 0.50	0
Brown-winged Kingfisher	0.8 \pm 0.44	0.5 \pm 0.52	0.7 \pm 0.48	0.7 \pm 0.48	0.6 \pm 0.51	0.6 \pm 0.51

• Common Kingfisher:

The global model defined for Common Kingfisher was-

ψ (vegetation layer+ water current +water turbidity), ϵ (time), p (creek width+ water depth+ dominant tree sp +height of nearest tree).

Keeping the global model structure of ψ constant, covariates for p (Appendix B, Table 1) were varied and model structure p ($W+D+H$) was selected as the best model ($\Delta AIC=0.37$).

The final best model for ψ was assessed by using this p model structure. For Common Kingfisher,

$\psi(C), \varepsilon(t), p(W+D+H)$ was selected as the final best model with $\Delta AIC=0.40$ (Table 7)

The occupancy estimate of Common Kingfisher revealed that water current accounted for relatively higher AIC weight of 0.38 (Table 7), added from all the model structures with current as covariate; whereas turbidity had a total AIC weight of 0.32. Therefore, water current and turbidity were the most important determinants of occupancy of the species. The β coefficient values for different covariates, which were expected to influence the occupancy of Common Kingfisher were also examined (Table 8). These coefficient values/signs express the strength/direction of their expected influence (MacKenzie 2006). Water current and vegetation layer had a negative association with occupancy of Common Kingfisher (Fig. 5) as indicated by negative values associated with these covariates.

Similarly the covariates that influenced its detection probability were water depth (total AIC weight=0.89), habitat type (total AIC weight=0.55) and creek width (total AIC weight=0.52) (Appendix B, Table 1).

Table 7. Model selection results for occupancy estimation of Common Kingfisher from Bhitarkanika mangroves from February to May, 2011; No of sites = 16.

Model	AIC	ΔAIC	AIC wgt	Model		
				likelihood	no.Par.	-2*LogLike
$\psi(C), \varepsilon(t), p(W+D+H)$	275.62	0	0.27	1	11	253.62
$\psi(\cdot), \varepsilon(t), p(W+D+H)$	276.02	0.40	0.22	0.82	10	256.02
$\psi(T), \varepsilon(t), p(W+D+H)$	276.10	0.48	0.21	0.79	11	254.10
$\psi(Vlr), \varepsilon(t), p(W+D+H)$	277.27	1.65	0.12	0.44	11	255.27
$\psi(Vlr+T), \varepsilon(t), p(W+D+H)$	278.80	3.18	0.05	0.20	12	254.80
$\psi(Vlr+C), \varepsilon(t), p(W+D+H)$	278.85	3.23	0.05	0.20	12	254.85
$\psi(C+T), \varepsilon(t), p(W+D+H)$	279.51	3.89	0.04	0.14	12	255.51
$\psi(Vlr+C+T), \varepsilon(t), p(W+D+H)$	280.82	5.20	0.02	0.07	13	254.82

Covariates considered were water current(C), creek width (W), water depth (D), dominant tree sp (H), vegetation layer (Vlr), water turbidity (T).

Table 8. Model-specific β coefficient estimates and associated standard errors for covariates determining the occupancy of Common Kingfisher in Bhitarkanika mangroves from February to May, 2011; No of sites = 16.

Model	$\beta_0 (SE[\beta_0])$	$\beta_c (SE[\beta_c])$	$\beta_T (SE[\beta_T])$	$\beta_{Vlr} (SE[\beta_{Vlr}])$
$\psi (C), \varepsilon (t), p (W+D+H)$	0.54 (0.00)	-2.12 (0.00)	-	-
$\psi (.), \varepsilon (t), p (W+D+H)$	0.39 (0.00)	-	-	-
$\psi (T), \varepsilon (t), p (W+D+H)$	0.02 (0.00)	-	0.08 (0.00)	-
$\psi (Vlr), \varepsilon (t), p (W+D+H)$	1.59 (0.43)	-	-	-0.62 (0.69)
$\psi (Vlr+T), \varepsilon (t), p (W+D+H)$	0.90 (0.00)	-	0.26 (0.00)	-0.61 (0.00)
$\psi (Vlr+C), \varepsilon (t), p (W+D+H)$	1.34 (0.47)	-1.94 (0.37)	-	-0.39 (0.80)
$\psi (C+T), \varepsilon (t), p (W+D+H)$	0.46 (0.00)	-1.49 (0.00)	0.02 (0.00)	-
$\psi (Vlr+C+T), \varepsilon (t), p (W+D+H)$	0.81 (0.61)	-1.21 (0.50)	0.36 (0.82)	-0.67 (0.66)

Covariates considered were water current (C), creek width (W), water depth (D), dominant tree sp (H), vegetation layer (Vlr), water turbidity (T).

• **Collared Kingfisher:**

The global model defined for Collared Kingfisher was,

ψ (vegetation layer + water current + water turbidity), γ (time), p (creek width+ water depth+ dominant tree sp).

Keeping the global model structure of ψ constant, covariates for p (Appendix B, Table 2) were varied and model structure p (D) was selected as the best model ($\Delta AIC=1.64$). The final best model for ψ was assessed by using this p model structure. For Collared Kingfisher,

ψ (Vlr), γ (t), p (D) was selected as the final best model with $\Delta AIC= 0.09$ (Table 9)

The occupancy estimate of Collared Kingfisher revealed that, vegetation layer accounted for a relatively higher AIC weight of 0.44 (Table 9), added from all the model structures with vegetation layer as covariate; whereas turbidity and current had a total AIC weight of 0.43 and 0.41 respectively. Therefore, vegetation layer, water current and turbidity were the most important determinants of occupancy of the species (Table 9). The β coefficient values for

different covariates, which were expected to influence the occupancy of Collared Kingfisher were also examined (Table 10). Water current had a negative association with occupancy of Collared Kingfisher (Fig. 5) as indicated by negative values associated with these covariates. Similarly, the covariates that influenced its detection probability were water depth (total AIC weight= 0.75) and creek width (total AIC weight=0.32) (Appendix B, Table 2).

Table 9. Model selection results for occupancy estimation of Collared Kingfisher from Bhitarkanika mangroves from February to May, 2011; No of sites = 16.

Model	AIC	Δ AIC	AIC wgt	Model likelihood	no.Par.	-2*LogLike
ψ (Vlr), γ (t), p (D)	590.51	0	0.24	1	9	572.51
ψ (T), γ (t), p (D)	590.60	0.09	0.23	0.96	9	572.60
ψ (C), γ (t), p (D)	590.67	0.16	0.22	0.92	9	572.67
ψ (Vlr+T), γ (t), p (D)	592.54	2.03	0.09	0.36	10	572.54
ψ (Vlr+C), γ (t), p (D)	592.76	2.25	0.08	0.32	10	572.76
ψ (T+C), γ (t), p (D)	592.78	2.27	0.08	0.32	10	572.78
ψ (Vlr+C+T), γ (t), p (D)	594.40	3.89	0.03	0.14	11	572.40
ψ (.), γ (.), p (D)	595.62	5.11	0.02	0.08	4	587.62

Covariates considered were water current (C), water depth (D), vegetation layer (Vlr), water turbidity (T).

Table 10. Model-specific β coefficient estimates and associated standard errors for covariates determining the occupancy of Collared Kingfisher in Bhitarkanika mangroves from February to May, 2011; No of sites =16

Model	β_0 (SE [β_0])	β_C (SE [β_C])	β_T (SE [β_T])	β_{Vlr} (SE [β_{Vlr}])
ψ (Vlr), γ (t), p (D)	-0.32 (0.00)	-	-	-0.01 (0.00)
ψ (T), γ (t), p (D)	-0.96 (0.00)	-	-0.29 (0.00)	-
ψ (C), γ (t), p (D)	-0.09 (0.00)	-0.80 (0.00)	-	-
ψ (Vlr+T), γ (t), p (D)	-0.28 (0.00)	-	0.34 (0.00)	-0.39 (0.00)
ψ (Vlr+C), γ (t), p (D)	0.17 (0.00)	-0.71 (0.00)	-	-0.12 (0.00)
ψ (T+C), γ (t), p (D)	-0.82 (0.00)	-0.76 (0.00)	0.29 (0.00)	-
ψ (Vlr+C+T), γ (t), p (D)	-0.19 (0.00)	-1.06 (0.00)	0.40 (0.00)	-0.42 (0.00)
ψ (.), γ (.), p (D)	0.38 (0.30)	-	-	-

Covariates considered were water current (C), water depth (D), vegetation layer (Vlr), water turbidity (T).

• **Black-capped Kingfisher:**

The global model defined for Black-capped Kingfisher was,

ψ (vegetation layer+ water current + water turbidity), ε (time), p (creek width+ water depth+ dominant tree sp).

Keeping the global model structure of ψ constant, covariates for p (Appendix B, Table 3) were varied and model structure p ($W+D+H$) was selected as the best model ($\Delta AIC=0.29$). The final best model for ψ was assessed by using this p model structure.

For Black-capped Kingfisher,

ψ (Vlr), ε (t), p (W+D+H) was selected as the final best model with $\Delta AIC=1.53$ (Table 11).

The occupancy estimate of Black-capped Kingfisher revealed that vegetation layer accounted for the highest AIC weight of 0.55 (Table 11), added from all the model structures with vegetation layer as covariate, whereas water current had a total AIC weight of 0.49. Therefore, vegetation layer and water current were the most important determinants of occupancy of the species. The β coefficient values for different covariates which were expected to influence the occupancy of Black-capped Kingfisher were also examined (Table 12). Water turbidity and vegetation layer had a negative association with occupancy of Black-capped Kingfisher (Fig. 5) as indicated by negative values associated with these covariates. Similarly, the covariates that influenced its detection probability were dominant tree sp (total AIC weight=0.77) water depth (total AIC weight= 0.69), and creek width (total AIC weight=0.44) (Appendix B, Table 3).

Table 11. Model selection results for occupancy estimation of Black-capped Kingfisher from Bhitarkanika mangroves from February to May, 2011; No of sites = 16.

Model	AIC	Δ AIC	AIC wgt	Model		
				likelihood	no.Par.	-2*LogLike
$\Psi(\text{Vlr}), \varepsilon(t), p(W+D+H)$	616.81	0	0.36	1	11	594.81
$\Psi(C), \varepsilon(t), p(W+D+H)$	618.34	1.53	0.16	0.47	11	596.34
$\Psi(C+T), \varepsilon(t), p(W+D+H)$	618.46	1.65	0.16	0.44	12	594.46
$\Psi(T), \varepsilon(t), p(W+D+H)$	619.02	2.21	0.12	0.33	11	597.02
$\Psi(\text{Vlr}+C), \varepsilon(t), p(W+D+H)$	619.41	2.60	0.10	0.27	12	595.41
$\Psi(\text{Vlr}+C+T), \varepsilon(t), p(W+D+H)$	620.07	3.26	0.07	0.19	13	594.07
$\Psi(\text{Vlr}+T), \varepsilon(t), p(W+D+H)$	622.37	5.56	0.02	0.06	12	598.37
$\Psi(\cdot), \varepsilon(\cdot), p(W+D+H)$	623.38	6.57	0.01	0.04	6	611.37

Covariates considered were water current (C), creek width (W), water depth (D), dominant tree sp (H), vegetation layer (Vlr), water turbidity (T).

Table 12. Model-specific β coefficient estimates and associated standard errors for covariates determining the occupancy of Black-capped Kingfisher in Bhitarkanika mangroves from February to May, 2011; No of sites =16.

Model	$\beta_0 (SE[\beta_0])$	$\beta_C (SE[\beta_C])$	$\beta_T (SE[\beta_T])$	$\beta_{\text{Vlr}} (SE[\beta_{\text{Vlr}}])$
$\Psi(\text{Vlr}), \varepsilon(t), p(W+D+H)$	1.85 (0.00)	-	-	-0.78 (0.00)
$\Psi(C), \varepsilon(t), p(W+D+H)$	-0.16(0.00)	1.63 (0.00)	-	-
$\Psi(C+T), \varepsilon(t), p(W+D+H)$	0.80 (0.00)	1.93 (0.00)	-0.34 (0.00)	-
$\Psi(T), \varepsilon(t), p(W+D+H)$	0.00 (0.32)	-	-0.00 (0.09)	-
$\Psi(\text{Vlr}+C), \varepsilon(t), p(W+D+H)$	1.05 (0.00)	0.49 (0.00)	-	-0.46 (0.00)
$\Psi(\text{Vlr}+C+T), \varepsilon(t), p(W+D+H)$	1.26(0.00)	1.66 (0.00)	-0.48 (0.00)	-0.03 (0.00)
$\Psi(\text{Vlr}+T), \varepsilon(t), p(W+D+H)$	0.76 (0.00)	-	-0.30 (0.00)	0.09 (0.00)
$\Psi(\cdot), \varepsilon(\cdot), p(W+D+H)$	0.56 (0.31)	-	-	-

Covariates considered were water current (C), creek width (W), water depth (D), dominant tree sp (H), vegetation layer (Vlr), water turbidity (T).

• **Brown-winged Kingfisher:**

The global model defined for Brown-winged Kingfisher was,

ψ (*vegetation layer + water current + water turbidity*), ε (*time*), p (*creek width + water depth + dominant tree sp*).

Keeping the global model structure of ψ constant, covariates for p (Appendix B, Table 4) were varied and model structure p (.) was selected as the best model ($\Delta AIC=0.58$). The final best model for ψ was assessed by using this p model structure. For Brown-winged Kingfisher, ψ (C), ε (t), p (.) was selected as the final best model with $\Delta AIC=0.25$ (Table 13)

The occupancy estimate of Brown-winged Kingfisher revealed that water current accounted for a relatively higher AIC weight of 0.40 (Table 13), added from all the model structures with current as covariate whereas turbidity had a total AIC weight of 0.37. Therefore, water current and turbidity were the most important determinants of occupancy of the species. The β coefficient values for different covariates which were expected to influence the occupancy of Brown-winged Kingfisher were also examined (Table 14). Water current and turbidity had a negative association with occupancy of Brown-winged Kingfisher as indicated by negative values associated with these covariates. Similarly, the covariates that influenced its detection probability were habitat type (total AIC weight=0.50) and creek width (total AIC weight=0.47) (Appendix B, Table 4).

Table 13. Model selection results for occupancy estimation of Brown-winged Kingfishers from Bhitarkanika mangroves from February to May, 2011; No of sites = 16

Model	AIC	Δ AIC	AIC wgt	Model		
				likelihood	no.Par.	2*LogLike
$\Psi(C), \varepsilon(t), p(.)$	595.54	0	0.28	1	8	579.54
$\Psi(T), \varepsilon(t), p(.)$	595.79	0.25	0.24	0.88	8	579.79
$\Psi(Vlr), \varepsilon(t), p(.)$	595.90	0.36	0.23	0.83	8	579.9
$\Psi(Vlr+C), \varepsilon(t), p(.)$	597.55	2.01	0.10	0.37	9	579.55
$\Psi(Vlr+T), \varepsilon(t), p(.)$	597.64	2.10	0.09	0.35	9	579.64
$\Psi(Vlr+C+T), \varepsilon(t), p(.)$	600.46	4.92	0.02	0.09	10	580.46
$\Psi(C+T), \varepsilon(t), p(.)$	600.57	5.03	0.02	0.08	9	582.57

Covariates considered were water current (C), vegetation layer (Vlr), water turbidity (T).

Table 14. Model-specific β coefficient estimates and associated standard errors for covariates determining the occupancy of Brown-winged Kingfisher in Bhitarkanika mangroves from February to May, 2011; No of sites =16

Model	$\beta_0 (SE[\beta_0])$	$\beta_C (SE[\beta_C])$	$\beta_T (SE[\beta_T])$	$\beta_{Vlr} (SE[\beta_{Vlr}])$
$\Psi(C), \varepsilon(t), p(.)$	1.12 (0.00)	-1.36 (0.86)	-	-
$\Psi(T), \varepsilon(t), p(.)$	1.53 (0.00)	-	-0.04 (0.00)	-
$\Psi(Vlr), \varepsilon(t), p(.)$	1.59 (0.00)	-	-	-0.08 (0.00)
$\Psi(Vlr+C), \varepsilon(t), p(.)$	0.76 (0.00)	-2.45 (0.00)	-	0.22 (0.00)
$\Psi(Vlr+T), \varepsilon(t), p(.)$	1.20 (0.00)	-	-0.25 (0.00)	0.31 (0.00)
$\Psi(Vlr+C+T), \varepsilon(t), p(.)$	0.72 (0.00)	-2.08 (0.00)	-0.37 (0.00)	0.69 (0.00)
$\Psi(C+T), \varepsilon(t), p(.)$	1.31 (0.00)	-2.34 (0.00)	-0.02 (0.00)	-

Covariates considered were water current(C), vegetation layer (Vlr), water turbidity (T).

River/creek width had a negative association with detection probability of all the four sympatric species i.e., detection probability decreased with increase of width (Fig. 6a). Water depth impacted the detection probability of the four species differently (Fig. 6b). The detection probability of Common and Black-capped Kingfisher went down with the increase in water depth whereas, it did not affect the detection probability of Brown-winged Kingfisher.

Based on the AIC weight of the covariates for each Kingfisher species, the variation of ψ across seasons was also examined when the occupancy was modelled on time. For Collared Kingfisher, estimated ψ increased across seasons (1- 0.31 ± 0.17 , 2- 0.29 ± 0.15 , 3- 0.47 ± 0.39 , 4- 0.56 ± 0.00 , 5- 0.79 ± 0.00 , 6- 0.82 ± 0.10). As the occupancy for this species was modelled on colonization probability, this increasing trend proved that it colonized the area over time.

Similarly, for Black capped Kingfisher the trend was inverse, i.e., the estimated ψ decreased across season (1- 0.68 ± 0.13 , 2- 0.58 ± 0.22 , 3- 0.48 ± 1.40 , 4- 0.45 ± 0.48 , 5- 0.36 ± 0.00 , 6- 0.29 ± 0.00) indicating that this species moved out over time. For the rest two species, i.e., Common and Brown-winged Kingfisher the estimated ψ values did not show any pattern.

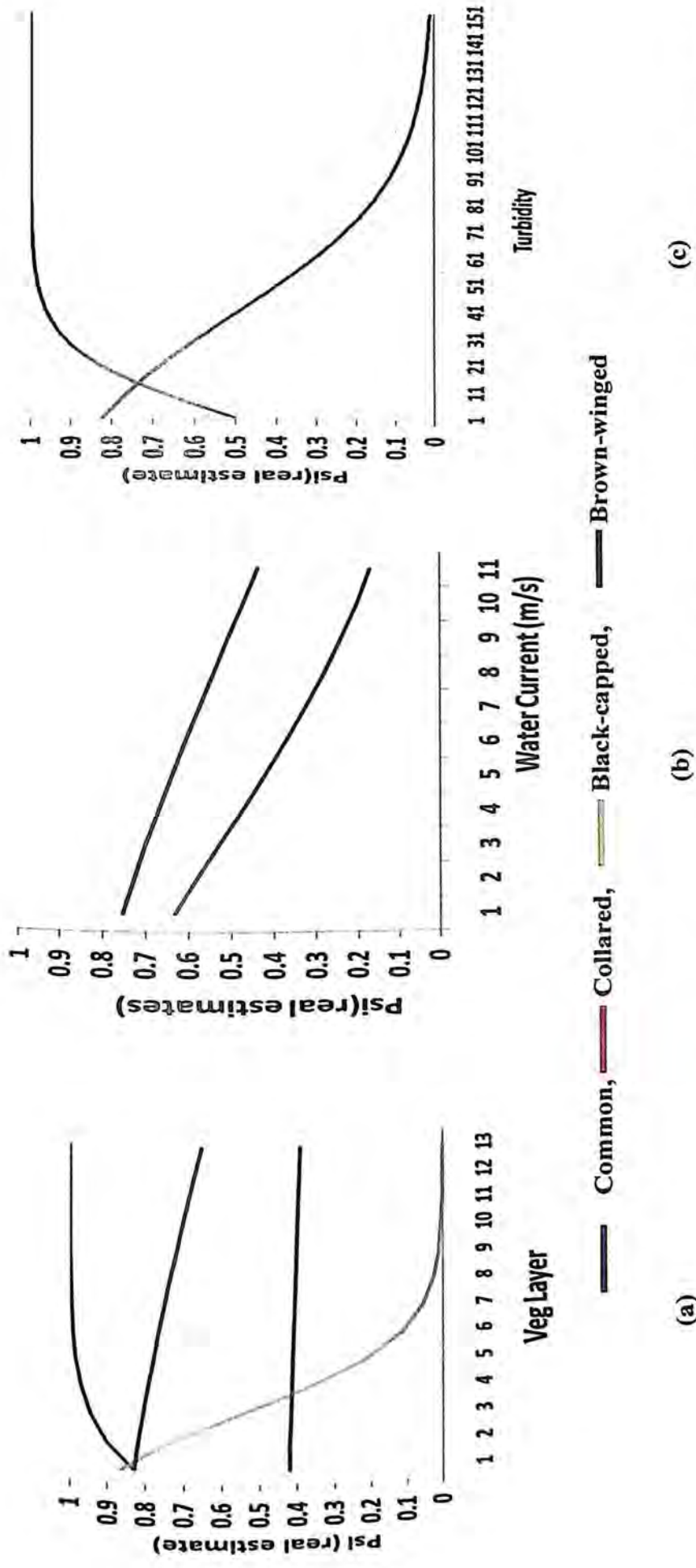


Figure 5. Variation of occupancy (ψ) of the four species of kingfisher with (a) vegetation layer (b) water current (m/s) and (c) turbidity (cm) in Bhitarkanika mangroves (Jan-May, 2011).

4.2. Foraging-niche segregation

A total of 53 independent prey captures were recorded for the four species of kingfishers (Table 15).

Table 15. Summary of microhabitat variables affecting the foraging behaviour of each species of kingfishers in Bhitarkanika mangroves (Jan-May, 2011). N ind-total no of total independent foraging observation.

Species	Microhabitat variables				N ind
	Perch ht	Vegetation cover	Foraging distance	Water depth	
Common	0.86±0.6	0.53± 0.2	1.98±1.1	0.41±0.4	9
Collared	2.31±1.5	0.54±0.2	3.78±1.8	0	9
Black-capped	3.29±3.6	0.52±0.2	8.44±6.6	0.06±0.2	17
Brown-winged	4.83±2.3	0.42±0.2	7.53±5.4	0.87±1.0	18
ANOVA, P	0.004	0.435	0.000	-	53
F	5.153	0.926	7.520	-	
df	3, 49	3,49	3,49	-	

Microhabitat variables:

Perch height differed significantly (ANOVA: $F [3, 49] = 5.153, P = 0.004$) among the four species of kingfishers with the mean perch height of Common Kingfisher being the lowest and Brown-winged Kingfisher being the highest (Fig. 7a). The foraging distance i.e., the distance covered by the four species to capture a prey also differed significantly (ANOVA: $F [3, 49] = 7.520, P = 0.000$). Difference in water depths used for capturing prey was tested only for Common and Brown-winged Kingfishers since the other two species did not pick any prey from water. It did not vary significantly between the two species (t-test, $t=0.539, df =25 p=0.594$). The vegetation cover used by the four species did not show any significant difference (ANOVA: $F [3, 49] = 0.926, p = 0.435$). Post-hoc tests revealed that the distance covered by Common and Collared Kingfisher for foraging is lesser than Black-capped and Brown-winged Kingfisher (Fig. 7b).

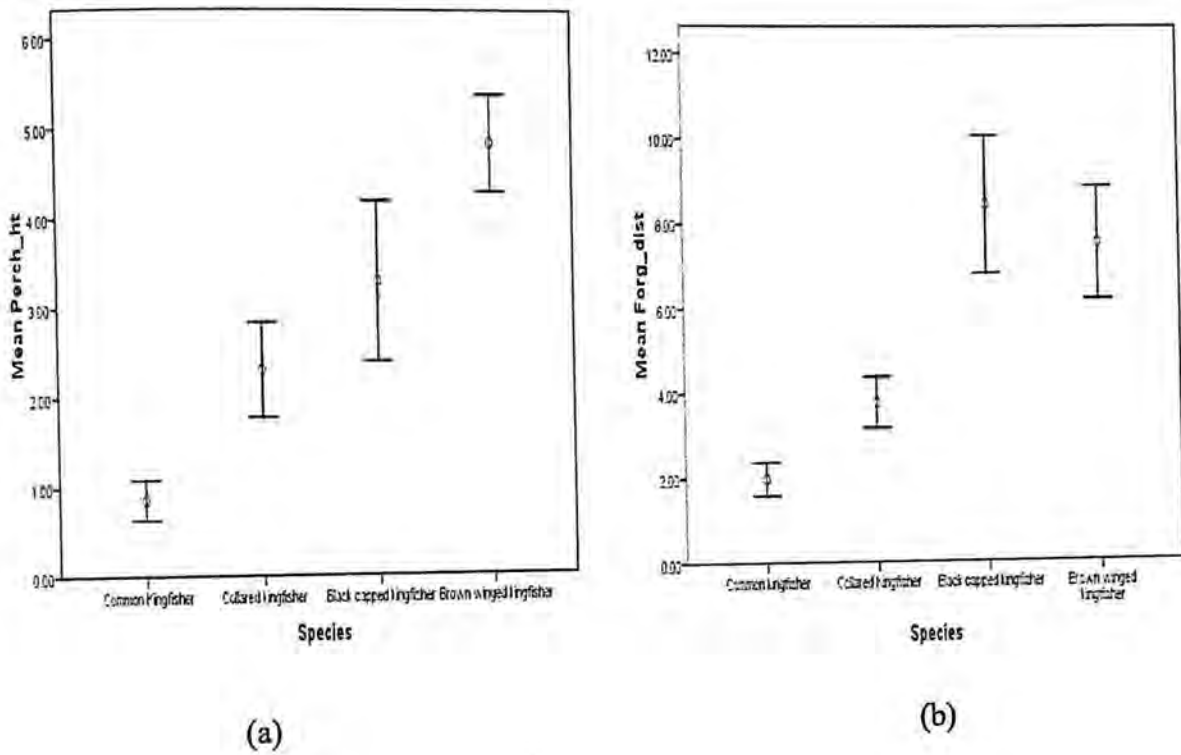


Figure 7. (a) Perch height (mean \pm 1 SE), (b) foraging distance (mean \pm 1 SE) used for foraging by the four species of kingfishers in Bhitarkanika mangroves (Jan-May, 2011).

All the variables were not used to visualize a multivariate niche as two species had no observation for one of the variables (water depth) and the four species did not differ significantly in the vegetation cover they used. In order to visualize the overall foraging niche-partitioning of the four species along the two variables which differed significantly across the four species (perch height and foraging distance), individual observations were plotted along these two axes (Fig. 8). Based on the biplot, it is evident that Common and Collared Kingfishers occupy relatively smaller foraging niches than Black-capped and Brown-winged Kingfishers in terms of perch height and foraging distance (Fig. 8).

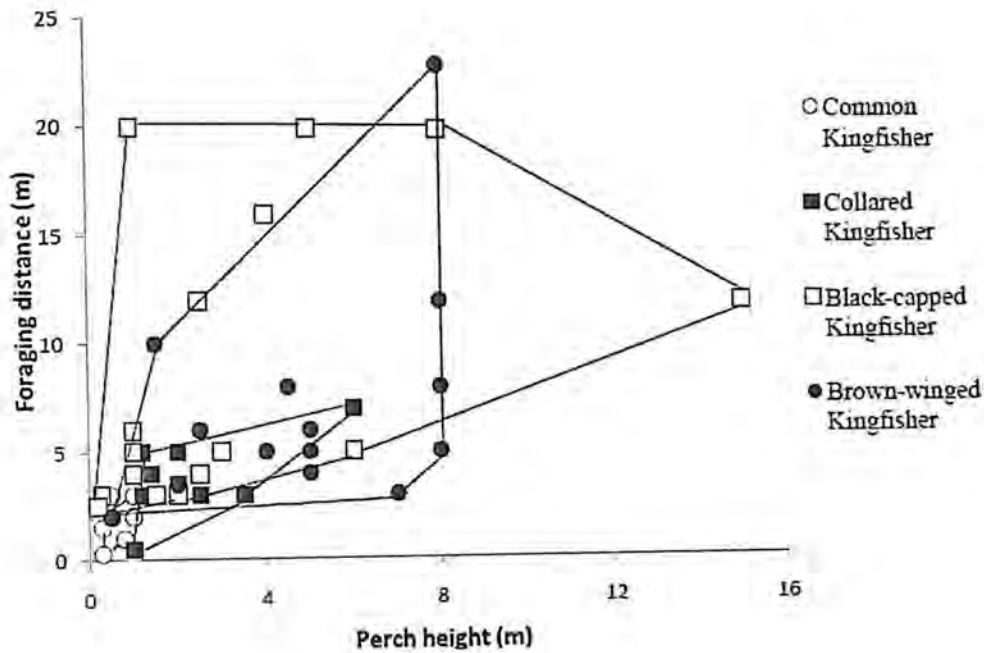


Figure 8. Foraging-niche of the four species of kingfishers in terms of perch height (m) and foraging distance (m) in Bhitarkanika mangroves (Jan-May, 2011).

Among the prey characteristics, prey type (Fisher's exact test, $p < 0.05$) differed significantly among the four species of kingfishers. Common and Brown-winged Kingfisher seemed to prefer fish more than other prey types (Fig. 9a). However, Brown-winged Kingfisher feeds on mudskipper and crabs as well. On the other hand, Collared and Black-capped Kingfisher's diet mainly consists of insects and crabs respectively. Size of prey foraged by each species also differed significantly (Fisher's exact test, $p = 0.005$) among the four species of kingfishers. Common Kingfisher was observed to forage on small and medium prey almost equally and very less large preys (Fig. 9b). Collared and Black-capped Kingfisher captured more, smaller prey than the rest of the two kingfisher species. Brown-winged Kingfisher foraged more on larger prey than the rest three kingfisher species. The use

of different foraging substrates among the four species of kingfishers also differed significantly (Fisher's exact test, $p < 0.05$). Common Kingfisher was seen foraging entirely in water (Fig. 9c). Brown-winged Kingfisher also preferred water as foraging substrate. In contrast, Collared Kingfisher mostly foraged in mud bank, vegetation and tree holes to some extent. Black-capped Kingfisher used four types of foraging substrate, mud bank most often and air, water and vegetation also.

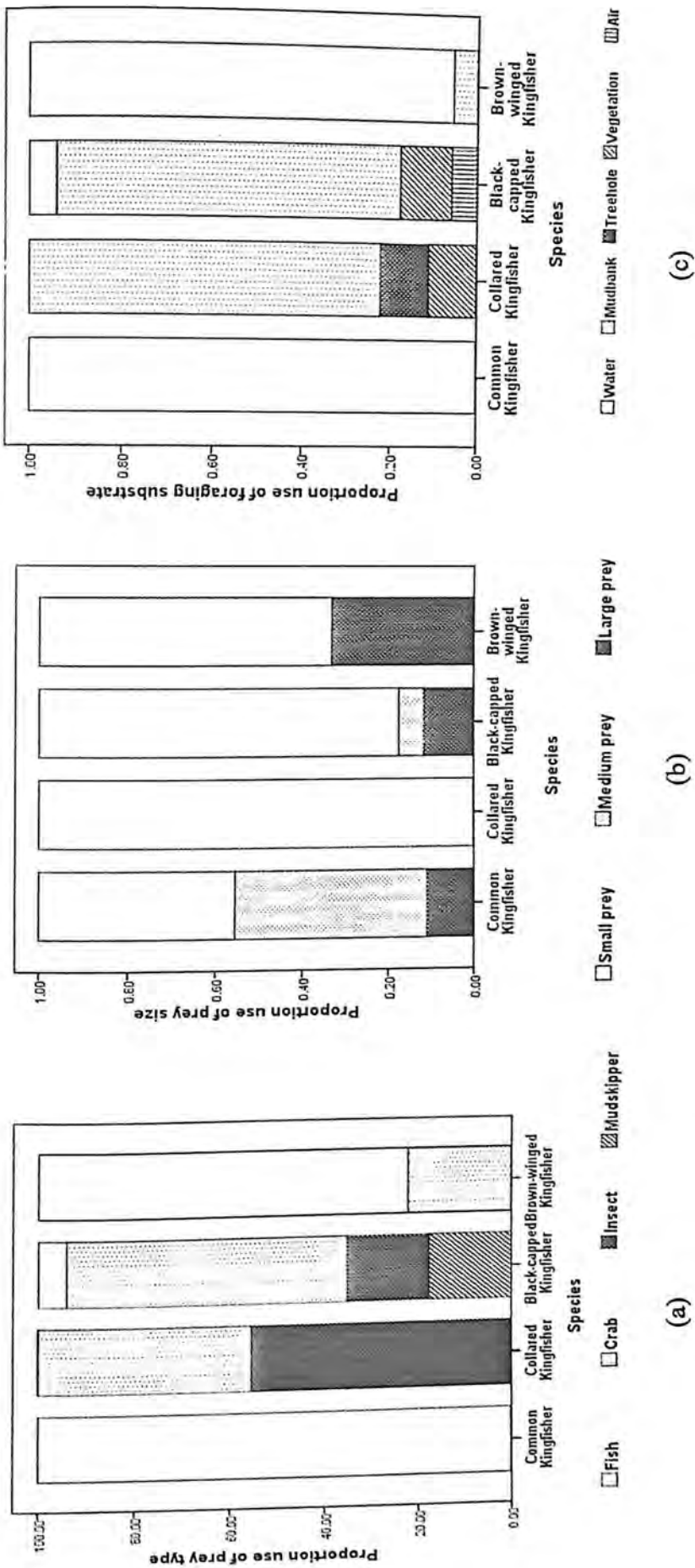


Figure 9. Proportional use of (a) prey type (b) prey size and (c) foraging substrate by the four species of kingfishers in Bhitarkanika N.P. i.e., Common Kingfisher (n=9), Collared Kingfisher (n=9), Black-capped Kingfisher (n=17), Brown-winged Kingfisher (n=18) (Jan-May, 2011).

Correspondence analysis of prey characteristics resulted in one dimension which explained 91.9% variation in the data (Table 16). The axis reflected change in prey type from fishes to insects to crabs and mudskippers as we move from the negative to the positive end. Similarly, the axis represents a gradient in prey size, with higher scores indicating intake of smaller prey. While the use of water as a foraging substrate is indicated by lower scores, increasing score is associated with greater use of mud bank. Therefore, the species on the negative side of the axis, i.e., Common and Brown-winged Kingfisher are more associated with capturing fish from water (Fig. 10) whereas species placed in the positive part, i.e., Collared and Black-capped Kingfisher have more association with intake of mudskipper, crab and small prey from mud banks.

Table 16. Respective scores of the one dimension for each category of prey characteristic variables in correspondence analysis for the four kingfisher species in Bhitarkanika mangroves (Jan-May, 2011).

Category	Scores
	Dimension 1
Fish	-1.79
Mudskipper	0.87
Crab	0.61
insect	0.30
Small prey	0.58
Medium prey	-0.16
Large prey	-0.43
Water	-2.07
Mud bank	1.64
Tree hole	0.06
Vegetation	0.26
Air	0.1

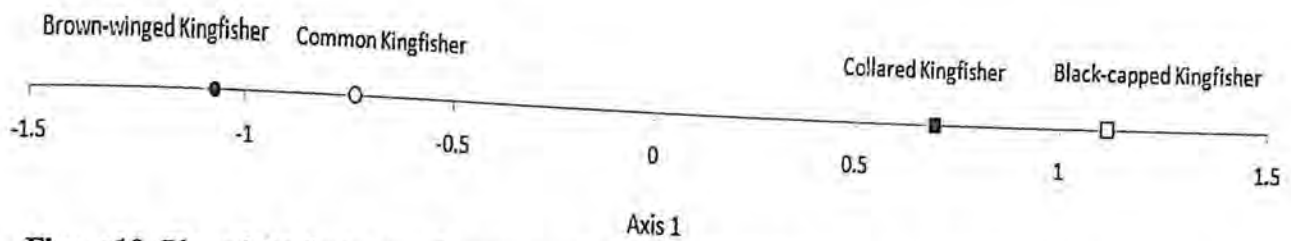


Figure 10. Plot of the first axis of correspondence analysis (CA) ordination (91.9% of the variation) based on prey characteristics in Bhitarkanika mangroves (Jan-May, 2011).

4.3. Time-Activity budget:

Total time spent in observing the birds amounted to 1.90 hrs for Common, 7.44 hrs for Collared, 7.02 hrs for Black-capped and 8.27 hrs for Brown-winged Kingfisher. Time spent in different activities by kingfishers did not show any significant difference (K-W test, $df = 3$, $p = 0.963$) among the four species. Again, the frequency of each activity in the four species also did not differ significantly (K-W test, $df = 3$, $p = 0.954$). Most of the time was devoted in vigilance/scanning in all the species. Common and Black-capped Kingfisher spent more time in feeding than the other two species. Except Collared Kingfisher no other species spent time in nest attendance and calling/displaying (Fig. 11). Again, vigilance/scanning occurred more frequently than any other activities in all four sympatric species. Resting occurred more frequently in Black-capped and Brown-winged Kingfisher than Common and Collared Kingfisher (Fig. 11).

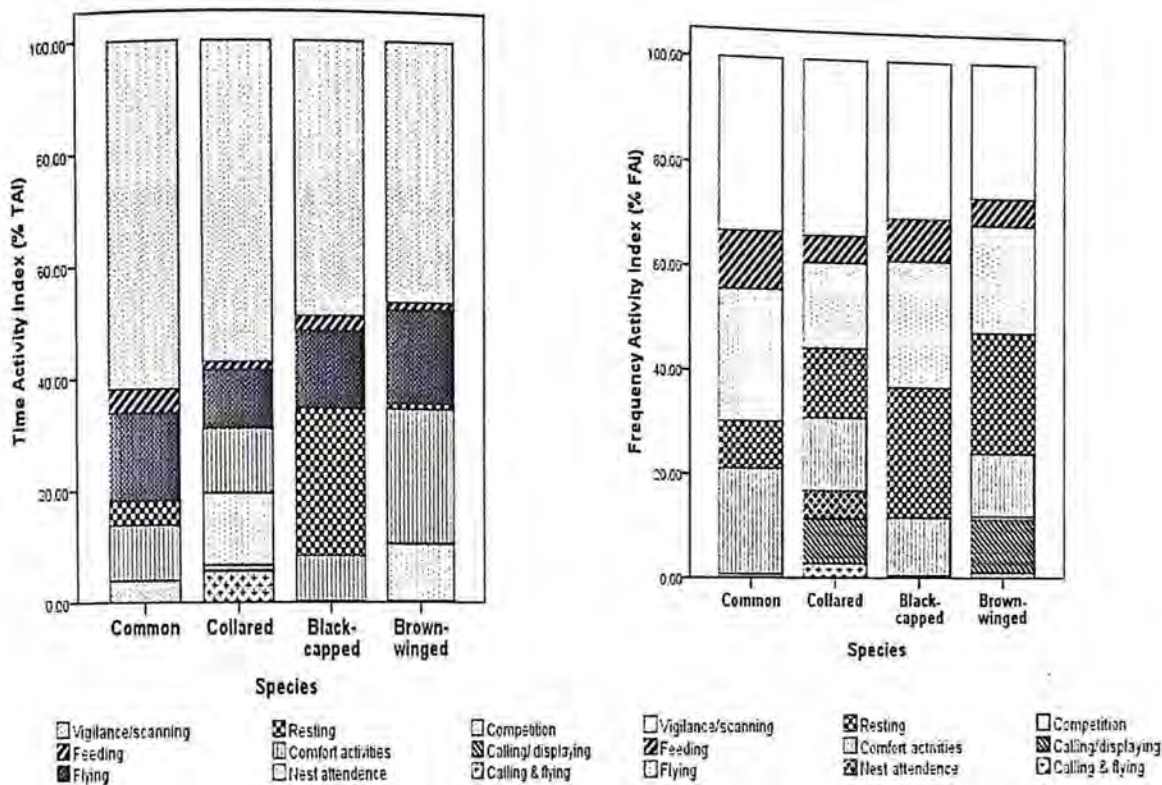


Figure 11. Time Activity Index (%TAI) and Frequency Activity Index (% FAI) of each of the four kingfisher species, i.e., Common Kingfisher (n=9), Collared Kingfisher (n=50), Black-capped Kingfisher (n=39), Brown-winged Kingfisher (n=63) in Bhitarkanika mangroves(Jan-May, 2011).

5. DISCUSSION

Occupancy pattern:

Occupancy analysis reveals that many covariates affect the detection probability of each species, e.g. creek width, water depth and dominant tree species. For all the four sympatric species river/creek width had a negative impact on detection probability. It is because the visibility on both sides of the bank went down with increase in creek width. So, it was more difficult to detect an individual in the main river or any larger creek than other narrower creeks. Dominant tree species also affected the detection probability of all the species positively except Black-capped Kingfisher (Appendix B).As it was a ranked covariate given on the basis of presence of dominant tree species on both side of the banks, it can

indicate the heterogeneity of habitat along the creeks. So, it is possible that Black-capped Kingfisher might be associated with homogenous habitat whereas the rest three species prefer more heterogeneity in nature.

Water depth also emerged as an important covariate affecting the detection probability of the four species. Water depth in an estuary like Bhitarkanika mangroves is always variable and it reflects the tidal fluctuation. The detection probability of Common and Black-capped Kingfisher went down with the increase in depth. This might be because Common Kingfisher is known to hunt mostly in lower water depth as it feeds on small fishes of shallow water (Kasahara and Katoh 2008). For Black-capped Kingfisher also, the pattern indicates that detection probability is mainly determined by its foraging behaviour. During this study, Black-capped Kingfisher seemed to feed primarily on crabs and mudskippers. During low tide, water depth decreases and both sides of the mud banks get exposed with crabs and mudskippers. Therefore availability of prey attracts them (Zamon 2003) to the bank side and ultimately influences detection probability. So, it supported our hypothesis that feeding activity of the kingfishers was influenced by tidal fluctuation in Bhitarkanika mangroves. Collared Kingfisher was less affected by depth than any other species as most of them were very vocal all the time because of breeding season. This made it easier to detect it even if it was far away. The detection probability of Brown-winged Kingfisher did not show any strong correlation with depth as being a larger species it can predate in deeper water also.

The occupancy estimates of the four species of kingfishers revealed that occupancy of Common and Brown-winged Kingfisher varied with water current and turbidity whereas for Collared and Black-capped Kingfisher it differed with vegetation layer. The occurrence of Common Kingfisher decreased with increase in water current as it is known to prefer habitat with shallow and stable water for catching small prey (Raven 1986, Kasahara and Katoh 2008). Water current did not affect the occurrence of Collared Kingfisher as, it may not be

dependent on water conditions for foraging as it is mainly insectivorous. Brown-winged Kingfishers was also less affected by current as being large enough it was capable of catching prey in fast-flowing water too.

Vegetation layer affected the occupancy of Collared and Black-capped Kingfisher differently. This might be because of availability of perch site as both need perch site to perch and hunt for prey. As vegetation layer increases (Tree → shrub+ tree → grass+ shrub + tree) perch site availability near water is expected to go down. Therefore increase in vegetation layer will negatively impact the occurrence of Black-capped Kingfisher. On the contrary, Collared Kingfisher was least affected. This is because, they mainly feed on insects and increase in vegetation layers might provide more diversity of prey for them. Brown-winged Kingfisher did not show any affect of vegetation layer in its occurrence. That is probably because even if there are more vegetation layers, Brown-winged Kingfisher might perch little away from water near the tree line and is still able to scan and catch prey.

This study also reports that two of the sympatric species, i.e., Collared and Black-capped have seasonal movement in Bhitarkanika mangroves, Collared being more abundant in summer and Black-capped in winter.

Inter-specific variation in foraging behaviour:

This study reports variation of foraging behavior among the four kingfisher species in terms of microhabitat variables and prey characteristics and it can be further related to the respective body size of each species. The mean perch height and foraging distance covered by the species showed positive association with body size. The size of the foraging niche of each species corresponds to their respective body sizes as well. The two smaller species i.e., Common and Collared Kingfisher occupy comparatively a smaller foraging niche than the bigger species i.e., Black-capped and Brown-winged Kingfisher. As being the smallest

species Common Kingfisher is able to catch small prey only, it prefers to perch in lower height than any other larger kingfisher species. On the contrary, the larger species i.e., Black-capped and Brown-winged need to catch larger prey to support their energy requirement and therefore they perch higher to cover a large area for prey. Moreover diving from a higher perch is advantageous to gain potential energy or momentum to dive into deep and/or rapid water for the larger species (Kasahara and Katoh 2008).

Similar pattern in foraging behavior and the body size of kingfishers has been documented in earlier studies. Monadjem *et al.* (1994) found that Giant (41-46 cm) and Pied (25 cm) kingfishers favoured perch-sites 2-4 m high, whereas the smaller species Half-collared Kingfishers (18 cm) favoured perches <2 m in height. Another study by (Bonnington *et al.* 2008) along a branch of the Kilombero River in Southern Tanzania revealed that Giant and Pied Kingfishers favoured foraging areas with higher perch-sites and deeper and wider river stretches, and Half-collared and Malachite Kingfishers (14 cm) preferred lower perch-sites near shallower, narrower river stretches. (Kasahara and Katoh 2008) also studied the food niche differentiation between Common Kingfisher (16 cm) and Greater Pied Kingfisher (41-43 cm) along the Chikuma River in central Japan and found that the smaller species, i.e., Common Kingfisher foraged frequently in small channels with shallow and calm water; on the contrary Greater Pied Kingfisher hunted mostly in the main channel where the water was deep and fast-flowing. This study is consistent with the findings of these previous studies.

This study reveals that each of the four species of kingfishers in Bhitarkanika occupy foraging niches corresponding to their respective body sizes. The occupancy pattern and foraging behaviour of the smallest species i.e., Common Kingfisher and the largest species i.e., Brown-winged Kingfisher is more similar. As, both mostly forage in water to catch fish, their occupancy is also determined by water current and turbidity. They segregate in terms of prey size which is reflected by the respective body sizes i.e., Common, the smaller species

feeding more on small and medium sized prey and the larger species, i.e., Brown-winged feeding on larger prey. However for Common Kingfisher, the pattern might not be actual representative because of smaller sample size. Further research is required to come to a valid conclusion.

Collared and Black-capped Kingfisher have been found to occur seasonally in Bhitarkanika mangroves; Black-capped Kingfisher being active in winter and Collared Kingfisher in summer. The foraging behaviour of these two species is similar in terms of prey characteristics. Both species feed on crab and insects from mud banks. Probably, being the larger species Black-capped explores other prey types as well, e.g. fish and mudskippers. Collared Kingfisher was seen preying entirely on small prey. A good portion of the diet of Black-capped Kingfisher also consisted of small prey. Therefore, it is possible that with so much similarity in both habitat association and foraging behaviour, these two species might actually replace each other over time. However, this is difficult to confirm from the results of the present study.

This study reports that, prey size partitioning between Common and Brown-winged Kingfisher leads to differentiation in prey type and microhabitat use in the same area. This segregation of prey size is probably associated with the requirements of each kingfisher species corresponding to their body sizes. Thus, foraging-niche partitioning can allow these two sympatric kingfisher species to co-exist in the same area.

Some of the major findings of this study are-

- Occupancy analysis confirmed that Collared and Black-capped Kingfisher occur seasonally in Bhitarkanika mangroves; Collared Kingfisher being more abundant in summer and Black-capped Kingfisher in winter.

- For all the four sympatric species river/creek width had a negative impact on detection probability. Habitat type also affected the detection probability of all the species

except Collared Kingfisher. The detection probability of Common and Black-capped Kingfisher decreased with the increase in depth whereas it did not affect the detection probability of Collared and Brown-winged Kingfishers.

- Water current and turbidity were negatively associated with the occupancy of Common and Brown-winged Kingfisher. However for Collared and Black-capped Kingfisher, it differed with vegetation layer.

- The size of the foraging niche of each species in terms of perch height and foraging distance corresponds to their respective body sizes. The two smaller species i.e., Common and Collared Kingfisher occupy comparatively a smaller foraging niche than the bigger species i.e., Black-capped and Brown-winged Kingfisher.

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7. APPENDICES :

APPENDIX A. GPS locations of the point 0 and point 10 of the sampled creeks in Bhitarkanika mangroves (Jan-May, 2011).

Sl no	Creek type	Creek name	Longitude	Latitude
1	Primary	Bhtrk-1_Point 0	86.86378	20.73386
2	Primary	Bhtrk-1_Point 10	86.85650	20.7275
3	Primary	Bhtrk-2_Point 0	86.85450	20.72742
4	Primary	Bhtrk-2_Point 10	86.84633	20.72500
5	Primary	Bhtrk-3_Point 0	86.87356	20.73456
6	Primary	Bhtrk-3_Point 10	86.87917	20.73242
7	Primary	Bhtrk-4_Point 0	86.87939	20.72764
8	Primary	Bhtrk-4_Point 10	86.87697	20.71828
9	Secondary	Balijore_Point 0	86.86664	20.74125
10	Secondary	Balijore_Point 10	86.85939	20.74422
11	Secondary	Bhamaramari_Point 0	86.87364	20.73628
12	Secondary	Bhamaramari_Point 10	86.87153	20.74214
13	Secondary	Ganjeikhia_Point 0	86.85547	20.71761
14	Secondary	Ganjeikhia_Point 10	86.86214	20.71731
15	Secondary	Jaladhar_Point 0	86.84733	20.72406
16	Secondary	Jaladhar_Point 10	86.84311	20.71736
17	Secondary	Junojore_Point 0	86.86258	20.73436
18	Secondary	Junojore_Point 10	86.85392	20.73608
19	Secondary	Khola_Point 0	86.83733	20.72086
20	Secondary	Khola_Point 10	86.83158	20.71728
21	Secondary	Mhnshmd_point 0	86.88903	20.73700
22	Secondary	Mhnshmd_Point 10	86.89594	20.74178
23	Secondary	Thanupati_Point 0	86.84331	20.74372
24	Secondary	Thanupati_Point 10	86.83906	20.73347
25	Tertiary	Bdkathua_Point 0	86.89297	20.74397
26	Tertiary	Bdkathua_Point 10	86.88389	20.74517
27	Tertiary	C_M_Point 0	86.84564	20.73914
28	Tertiary	C_M_Point 10	86.84047	20.73706
29	Tertiary	Shymsudin_Point 0	86.91419	20.74728
30	Tertiary	Shymsudin_Point 10	86.91606	20.74097
31	Tertiary	Suajore_Point 0	86.87225	20.70422
32	Tertiary	Suajore_Point 10	86.86917	20.70214

Bhtrk-Bhitarkanika ,C_M- Chintamony Mohanty, Bdkathua- Bodokathua

APPENDIX B.

Model selection results for detection probability estimation of the four species of Kingfishers in Bhitarkanika mangroves. Detection probability p was varied with associated covariates keeping the global model structure for ψ as constant to derive the best model structure for detection probability.

Table 1. Model selection results for detection probability estimation of Common kingfishers from Bhitarkanika mangroves from February to May, 2011; No of sites = 16.

Model	AIC	Δ AIC	AIC wgt	Model likelihood	no.Par.	- 2*LogLike
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H+W+D})$	280.24	0	0.24	1	13	254.24
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{D})$	280.61	0.37	0.20	0.83	11	258.61
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H+D})$	281.24	1	0.15	0.60	12	257.24
$\Psi(\text{vlr+C+T}), \varepsilon(t), p(\text{W+D})$	281.37	1.13	0.14	0.57	12	257.37
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H+D+W+ht})$	282.9	2.66	0.06	0.26	14	254.90
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H+D+ht})$	283.44	3.2	0.05	0.20	13	257.44
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{D+ht})$	283.92	3.68	0.04	0.16	12	259.92
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{W})$	284.38	4.14	0.03	0.12	11	262.38
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H+W})$	284.81	4.57	0.02	0.10	12	260.81
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H})$	286.08	5.84	0.01	0.05	11	264.08
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{W+D+ht})$	286.29	6.05	0.01	0.05	13	260.29
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{W+ht})$	286.42	6.18	0.01	0.05	12	262.42
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H+W+ht})$	286.84	6.60	0.01	0.04	13	260.84
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\cdot)$	287.07	6.83	0.01	0.03	10	267.07
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{ht})$	287.75	7.51	0.01	0.02	11	265.78
$\Psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H+ht})$	287.82	7.58	0.01	0.02	12	263.82

Table 2. Model selection results for detection probability estimation of Collared kingfishers from Bhitarkanika mangroves from February to May, 2011; No of sites = 16.

Model	AIC	Δ AIC	Model			
			AIC wgt	likelihood	no.Par.	-2*LogLike
$\Psi(VI_r+C+T), \gamma(t), p(D)$	594.40	0	0.38	1	11	572.40
$\psi(VI_r+C+T), \gamma(t), p(W+D)$	596.04	1.64	0.17	0.44	12	572.04
$\psi(VI_r+C+T), \gamma(t), p(D+H)$	596.42	2.02	0.14	0.36	12	572.42
$\psi(VI_r+C+T), \gamma(t), p(\cdot)$	596.68	2.28	0.12	0.32	10	576.68
$\psi(VI_r+C+T), \gamma(t), p(W)$	598.02	3.62	0.06	0.16	11	576.02
$\psi(VI_r+C+T), \gamma(t), p(W+D+H)$	598.10	3.70	0.06	0.16	13	572.10
$\psi(VI_r+C+T), \gamma(t), p(H)$	598.21	3.81	0.05	0.15	11	576.21
$\psi(VI_r+C+T), \gamma(t), p(W+H)$	599.70	5.30	0.03	0.07	12	575.70
$\psi(VI_r+C+T), \gamma(t), p(t)$	612.51	18.11	0	0.00	51	510.51

Table 3. Model selection results for detection probability estimation of Black-capped kingfishers from Bhitarkanika mangroves from February to May, 2011; No of sites = 16.

Model	AIC	Δ AIC	Model			
			AIC wgt	likelihood	no.Par.	-2*LogLike
$\psi(VI_r+C+T), \varepsilon(t), p(H+W+D)$	620.41	0	0.27	1	13	594.41
$\psi(VI_r+C+T), \varepsilon(t), p(H+D)$	620.70	0.29	0.23	0.86	12	596.70
$\psi(VI_r+C+T), \varepsilon(t), p(D)$	621.53	1.12	0.15	0.57	11	599.53
$\psi(VI_r+C+T), \varepsilon(t), p(H)$	621.60	1.19	0.15	0.55	11	599.60
$\psi(VI_r+C+T), \varepsilon(t), p(H+W)$	622.04	1.63	0.12	0.44	12	598.04
$\psi(VI_r+C+T), \varepsilon(t), p(W+D)$	624.47	4.06	0.04	0.13	12	600.47
$\psi(VI_r+C+T), \varepsilon(t), p(\cdot)$	624.83	4.42	0.03	0.11	10	604.83
$\psi(VI_r+C+T), \varepsilon(t), p(W)$	627.29	6.88	0.01	0.03	11	605.29

Table 4. Model selection results for detection probability estimation of Brown-winged kingfishers from Bhitarkanika mangroves from February to May, 2011; No of sites = 16.

Model	AIC	Δ AIC	AIC wgt	Model		
				likelihood	no.Par.	-2*LogLike
$\psi(\text{Vlr+C+T}), \varepsilon(t), p(\cdot)$	600.46	0	0.32	1	10	580.46
$\psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H+D+W})$	601.04	0.58	0.24	0.75	13	575.03
$\psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H})$	602.16	1.70	0.13	0.43	11	580.16
$\psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{W})$	602.52	2.06	0.11	0.36	11	580.52
$\psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H+W})$	602.53	2.07	0.11	0.36	12	578.53
$\psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{D})$	603.71	3.25	0.06	0.20	11	581.71
$\psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{H+D})$	606.37	5.91	0.02	0.05	12	582.37
$\psi(\text{Vlr+C+T}), \varepsilon(t), p(\text{W+D})$	607.01	6.55	0.01	0.04	12	583.01

Covariates considered were vegetation layer (Vlr), water current (C), water turbidity (T), dominant tree species (H), water depth (D), creek width (W).