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Source: Waterbirds, 34(4) : 448-456

Published By: The Waterbird Society

URL: https://doi.org/10.1675/063.034.0407

Foraging Ecology of the Painted Stork (*Mycteria leucocephala*): A Review

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Abstract.—The value of foraging studies in developing conservation strategies for storks is important because their breeding is often limited by food distribution. The foraging behavior and trophic specializations of the Painted Stork (*Mycteria leucocephala*), a flagship of wetlands and listed as near threatened, is reviewed here. Trophic adaptations among *Mycteria* and other storks, the importance of prey capture by tactolocation and various aspects of foraging behavior including diet, prey size**,** foraging and nesting correlates, variations in foraging activity, nocturnal foraging and kleptoparasitism are examined. Also, an account of the foraging behavior of a close congener, Milky Stork (*M. cinerea*), and the manner in which the foraging activities of Painted Stork, particularly biomass removal by predation and enrichment of the waters by droppings impact the ecosystem, is included. Since nesting of Painted Stork and other species of colonial waterbirds is closely linked to the performance of the monsoon, the primary driver triggering their food cycles, points for further studies are listed. *Received 29 April 2011, accepted 19 July 2011.*

Key words.—Ecology, foraging behavior, India, Milky Stork, *Mycteria*, Painted Stork.

Waterbirds 34(4): 448-456, 2011

In storks, breeding is limited by food availability (del Hoyo *et al.* 1992) and studies on foraging ecology are crucial for developing conservation strategies. The Painted Stork (*Mycteria leucocephala*), a colonially nesting species found across south and south east Asia, with a stronghold in India and Sri Lanka, is a flagship of wetlands. Its congeners, distributed across three continents are, Milky Stork (*M. cinerea*) in south east Asia, with whom it often co-occurs and sometimes hybridizes (Li *et al.* 2006), Yellow-billed Stork (*M. ibis*) in Africa and Wood Stork (*M. americana*) in the southern USA, Mexico and parts of south America (del Hoyo *et al.* 1992; Hancock *et al.* 1992). Across much of Asia, stork habitats are being rapidly lost to land encroachment, pollution and other factors, pushing the species into the near threatened category (Birdlife International 2001). Since the production of fish, the principal prey, is strongly influenced by the monsoon rains which, it is postulated, are being impacted by global climate change (Lal *et al.* 2001; Qui 2008), studies on stork foraging ecology assume greater significance.

While the foraging ecology of Wood Stork has been well studied (Kahl 1964; Ogden *et al.* 1976; Coulter and Bryan 1993; Gonzalez 1997) other stork species have received scant attention. In this paper, I review the trophic specializations and foraging behavior of the Painted Stork, along with a comparative study of Mycteria, particularly with respect to the closely related Milky Stork. Also, some longstanding questions on trophic adaptations in storks (Kushlan 1978) are revisited.

Trophic Adaptations in *Mycteria* and Other Storks

In the context of foraging, the bill is of primary importance, although it may have other functions such as nest construction and a weapon against rivals (Urfi and Kalam 2006). An adult Painted Stork's bill is large (>24 cm length), waxy yellow in color with a curvature at the tip (Fig. 1). The bird does not hold its bill completely horizontal to the ground while standing, thus giving an impression that it is strongly decurved. Actually, the bill is straight for most of its length but approximately 18.5 cm from the mouth there is a decurvature of approximately 11°. Also, a gap of less than one mm is observed between the mandibles in a locked position. The line along which the mandibles are locked is sinuous, with an elevation and depression in the distal and proximal portions, respectively. Thus, the inter-mandibular gap is variable and at several points along the length of the bill, the inner surfaces of mandibles are more or less horizontally placed in relation to each other. The functional morphology of down curving bills of waders has been the subject of

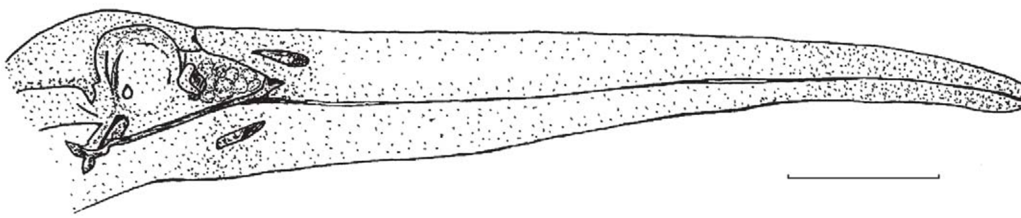

Figure 1. Skull and bill of an adult Painted Stork of unknown sex based on a specimen obtained from the Delhi region in ca 2004. Scale bar equals 50 mm

several investigations (Kushlan 1977; 1979; Owens 1984; Davidson *et al.* 1986; Bildstein 1993) and the explanations proposed are straightforward. Compared to a hypothetical straight bill, the points of contact between the mandible and prey are more extensive in the case of a curved bill (Fig. 2), resulting in a stronger grip on the prey. The pincer like tip is an adaptation for obtaining purchase and preventing prey from slipping. Fish produce powerful jerks (Bone 1978) but once captured by the Painted Stork do not escape easily, unless dropped.

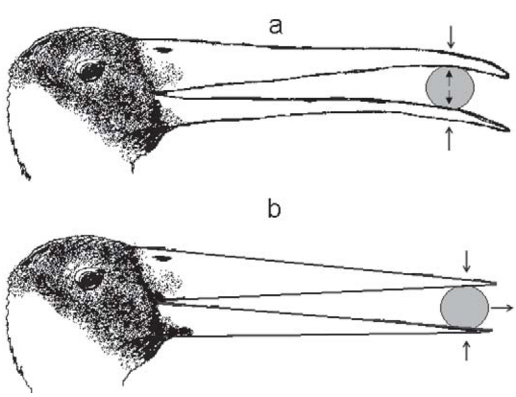

Figure 2. Model to explain the functional morphology of a Painted Stork bill (a) Diagram to show a Painted Stork holding a prey item at the tip of the bill. As the mandibles press the fish, being soft it will get flattened and a larger surface of it will come in contact with the bill. Due to the curved shape of the bill, the mandibles will be more or less parallel to each other, thereby permitting greater contact with the prey. (b) Depicts the situation in a hypothetical straight bill. As the mandibles press against each other the resulting pressure will tend to push the prey forward and it may fall off. Also a much lesser surface area of the mandibles comes in contact with the prey and so the grip will be weak. Source: Urfi 2011.

Among storks, the decurved bill is a characteristic of the genus *Mycteria* and all the four species are primarily piscivorous, foraging in muddy waters where capturing fish by using visual cues is exigent. However, all *Mycteria* take other types of prey opportunistically, as and when encountered, probably by employing visual cues. For example, the Wood Stork consumes crayfish, amphibians, insects, small snakes and even baby alligators (del Hoyo *et al.* 1992). The Painted Stork has been recorded swallowing a snake (Urfi 1988). In contrast, members of the tribes *Ciconiini* and *Leptoptilini* have straight bills. *Ciconia* have a characteristic visual foraging method and a catholic diet comprising vertebrate and invertebrate organisms. Some species, such as the White Stork (*Ciconia ciconia*), are long distance migrants and exhibit considerable variations in their diets between nesting and wintering grounds. *Ephippiorhynchus* have straight, thick, though slightly upturned, bills. These storks are primarily fish eaters and catch prey by walking in the shallows and stabbing the bill repeatedly in water. However, the Saddlebill (*E. senegalensis*) can be observed foraging in muddy waters, catching prey by tactolocation in a manner similar to *Mycteria* (del Hoyo *et al.* 1992) and the Black-necked Stork *(E. asiaticus*) is also known to employ tactile foraging. Fish captured are generally brought to dry ground and then swallowed (Maheswaran and Rahmani 2002) which is in contrast to *Mycteria* who complete all foraging in the water. *Leptoptilos* have straight, thick and slightly upturned bills and forage visually, on fish and a variety of other items, including offal at garbage dumps (Hancock *et al.* 1992).

In a study on the reflex action of the mandibles in the Wood Stork, Kahl and Peacock (1963) demonstrated that the lower mandible snaps shut extremely rapidly (approximately 25 ms) as soon as it meets any object. The *Mycteria* bill has some tacto-receptors, whose exact location is not clear. The Wood Stork is able to forage in total darkness by tactolocation and, assuming that the basic mechanisms are the same in all *Mycteria,* this may explain why the system is so effective in muddy waters and why the Painted Stork should also have no difficulty foraging in darkness. However, while successfully explaining many aspects of tactile foraging in *Mycteria,* the bill snap reflex model leaves some important questions unanswered (Kushlan 1978). For example, while foraging in a vegetated area, it would be impossible to avoid the mandibles meeting some object accidentally, yet we do not see the bill needlessly snapping shut. Additionally, when moving through tangled vegetation, the bird does not seem to get confused between fish and plants. Fish over three cm are taken preferably; so, clearly, this is a system which is at least partly selective (del Hoyo *et al.* 1992). However, how this can happen in a system based on tactolocation is unclear.

Foraging and nesting correlates

The food availability-nesting time hypothesis (Perrins and Birkhead 1983) suggests that the nesting season of birds has evolved to coincide with periods of maximum food availability in the environment. In *Mycteria,* the foraging mode appears to be well suited to this situation because tactile foraging works best if the density of prey, and correspondingly the encounter rate, is high. High prey densities can result from either the concentration or production of fishes. In the case of Wood Stork, essentially a dry season nester, this effect results when water bodies evaporate and fish become concentrated. Densities of fish in drying pools of Florida have been recorded to be as high as 8,000 fish/m^2 (del Hoyo *et al.* 1992). In contrast, in the Indian subcontinent, the similar effect results from the glut of fish due to spawning activity after the monsoon. In one study at Keoladeo Ghana National Park (KDGNP) in northern India, nearly 336 fish fry were recorded in a plankton net of 1 m^2 , operated for 85 s. Thus, an estimated 8,600,000 fish fry were entering the park in a day (Ali and Vijayan 1983). However, at some sites, notably Kokkare Bellur in southern India, Painted Stork are believed to nest in the dry season (Bhat *et al.* 1991), seemingly taking advantage of fish which become concentrated as water bodies dry up. However, environmental factors producing abundances of prey locally and the timing of Painted Stork nesting at such sites remains to be properly studied.

Foraging Behavior of Painted Stork

The general pattern of tactile foraging in *Mycteria* is that the foraging individual inserts its partially open bill in the water, eyes above the watermark, and walks forward (Kushlan 1978). Sometimes the bill is moved from side to side and foot stirring, as also recorded in egrets (Willard 1977; Erwin *et al.* 1985; Master *et al.* 1993) is employed. Along with wing flashing, foot stirring is presumably used to startle concealed fish. Since the water in which the birds forage is muddy or hazy, the birds probably cannot see their prey clearly. Also, the Painted Stork sometimes pivots around a point, in the manner of ibises (Bildstein 1993). Although this behavior is recorded more frequently in vegetated habitats (Kalam and Urfi 2008) its functional significance is unclear. The typical manner of Painted Stork foraging can be termed as 'active tactolocation', i.e. the foraging bird walks in the water with its head immersed. However, sometimes the bird stands stationary, seemingly waiting for fish to make contact with the mandibles. Such, so-called 'passive tactolocation' would be expected to occur more at lotic sites but has been recorded equally at lentic sites (Kalam and Urfi 2008).

Water depth has an important influence on the distribution and foraging behavior of waders (Nagarajan and Thiyagesan 1996). The Painted Stork, being restricted to the littoral zone, forages in areas which are less than 25 cm deep. Typically, their foraging activity is in bouts of varying duration, followed by periods of inactivity when the bird either stands on one leg or hunched up, or sits on bent tarsi on the shore. The periods of inactivity could be due to the bird being satiated. Alternatively, these periods could be dictated by factors linked to prey availability and accessibility, such as differences in the activity patterns of fishes (Jhingran 1982). However, through the day, the oxygen content of the water fluctuates in relation to surface temperature and has an effect on fish behavior. Thus, during early morning, when the dissolved oxygen content of waters is low, fishes may come to shallow areas or close to the surface or make more frequent trips to the surface for gulping air and in the process become vulnerable to capture (Kushlan 1978). At other times of the day, fish may go into deeper areas, out of the reach of storks.

Since Painted Stork are colonial nesters they would be expected to be flock foragers, since nesting colonies also serve as information centers about the location of food patches (Brown and Brown 2001). However, foraging group size is variable (Kalam and Urfi 2008). In the nesting season flock sizes are smaller than in the non-breeding season, probably because as the ponds and wetlands dry up in summer, birds tend to concentrate on the few remaining ones. Age and season specific differences in the foraging abilities of different individuals in a population have also been observed. For example, juvenile birds in the non-breeding season had a lower foraging success, though not significantly different, compared to adults (Kalam and Urfi 2008). Such could be due to lack of experience in the young birds. The capture rate of adult Painted Storks in the breeding season was estimated to be nearly two and half times higher than in the non-breeding season, indicative of varying energetic demands at different times of the year.

DIET AND PREY SIZE

Two studies from the Delhi region have reported in detail on the diet of Painted Stork (Table 1). In the first, eleven species of fish, mostly of commercial significance, were identified through gut content analyses (Desai *et al.* 1974). In the other, a video study, although accurate identification of fishes captured by Painted Stork was not possible in most cases, tilapia were observed to be part of the diet (Kalam and Urfi 2008). Tilapia is an exotic fish which was introduced in India in 1952 (Jhingran 1982) and has since become a major invasive species (Khan and Panikkar 2009). The absence of tilapia in the diet of Painted Stork in the mid-1960's and occurrence in the later study could be indicative of fluctuations in its relative abun-

Table 1. Fishes recorded in the diet of Painted Stork from two studies in the Delhi region.

Species[1]	Numbers recorded[2]	
	1966-71[3]	2004-06[4]
Wallago *Wallago attu* (Bloc and Schneider 1801)	4	3
Stinging Catfish *Heteropneustes fossilis* (Bloch 1794)	1	
Giant River-catfish *Sperata seenghala* (Sykes 1839)	2	
Scarlet-banded Barb *Puntius amphibius* (Valenciennes 1842)	3	
Catla *Catla catla* (Hamilton 1822)	3	
Mrigal Carp *Cirrhinus cirrhosus* (Bloch 1795)	2	
Rohu Labeo *Labeo rohita* (Hamilton 1822)	1	
Spotted Snakehead *Channa punctata* (Bloch 1793)	2	6
Striped Snakehead *Channa striat*a (Bloch 1793)	1	
Bronze Featherback *Notopterus notopterus* (Pallas 1769)	1	
Clown Knifefish *Chitala chitala* (Hamilton 1822)	1	
Tire Track Eel *Mastacembelus armatus* Hora 1924	—	1
Mozambique Tilapia *Oreochromis mossambicus* (Peters 1852)	—	3

[1]English and scientific names from *FishBase (2011)*.
Species not reported in the gut content analysis (second column) are indicated by —. Species whose presence or absence in the diet could not be ascertained (third column) are represented by blank cells.
[3]Desai *et al.* (1974).
[4]Kalam and Urfi (2008).

dance over the years. Besides ubiquitous fin-fish, items such as fragments of plant fiber and other plant material, including leaves, small stones, aquatic insects and a frog have been reported in the diet of the Painted Stork (Ali and Ripley 1987). Since storks are almost all exclusively carnivorous, plant material found in their guts is likely taken incidentally while foraging and unlikely to be of dietary significance. At Kokkare Bellur, adults were observed feeding nestlings with frogs, crabs, large insects and grasshoppers (Sridhar *et al.* 2002). While Black-necked and Adjutant Storks (*L dubius*) have been recorded catching birds (Pandey 1974) nothing so dramatic has been reported for the Painted Stork. At coastal sites in India, Painted Stork have been observed foraging on crustaceans and invertebrates common to such waters (Parasharya and Naik 1990; Urfi 2002). Visual foraging should be expected more often in such situations.

The relationship between prey size and handling time (*ht*) was investigated in the Painted Stork by using video techniques (Kalam and Urfi 2008). As shown in Fig. 3a, since small prey is easily swallowed, negligible time is spent in handling but with increasing prey size, *ht* increases exponentially. Thus, beyond a point, large prey become unprofitable (Fig. 3b), even though they may have a high calorific value. Also to be considered is the fact that different species of fishes have different calorific values (Love 1980) and, hence, their nutritional content may vary considerably. Regardless, fish larger than 20 cm were rarely captured and most of the prey ranged between one to 12 cm. Of note, there are instances of Painted Stork dropping very large fish after capturing them (Sankhala 1990). While this could be due to energetic factors (low profitability), the possibility that large fish can have sharp structures in their fins, which may injure the predator, could also be an explanation.

Differences in sizes of prey captured during the breeding and non-breeding seasons have been recorded (Kalam and Urfi 2008). However, whether such differences are due either to active selection or more a reflection of seasonal changes in the abundance of certain prey size groups remains to be established. In the monsoon months, due to spawning activity, small fish predominate but in the summer months larger fish are abundant (Jhingran 1982). Prey sizes regurgitated by Painted Stork at the time when the nestlings were very small was significantly smaller from those regurgitated a few weeks later when the nestlings had grown (Kalam and Urfi 2008). If a fish larger than 20 cm was regurgitated in the nest it was ignored by the nestlings, suggesting a gape size constraint.

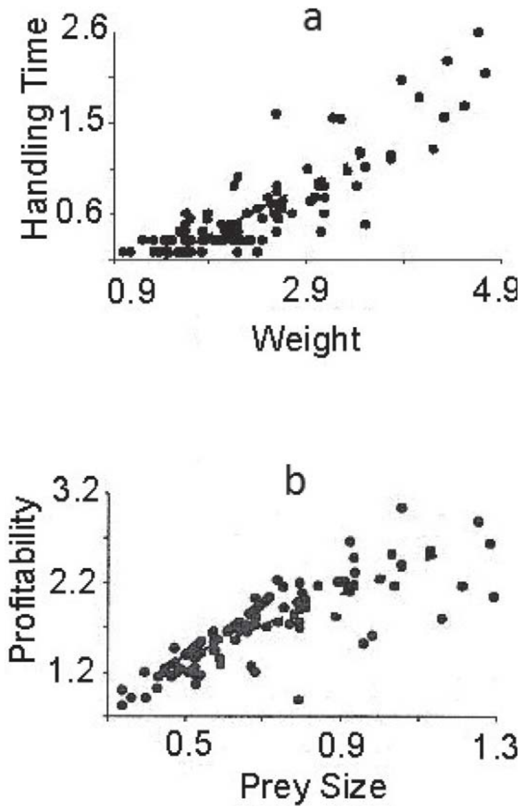

Figure 3. (a) Relationship between prey weight (mg) and handling time (s) and (b) prey length (cm) and profitability (mg/s). Note the scale is $\log_{10}$ in both graphs. Redrawn from Kalam and Urfi (2008)

Nocturnal foraging and Kleptoparasitism

Given that field observations on birds are generally made during the day, instances of nocturnal foraging may remain unnoticed.

Among the few cases on record, one is in the form of general observations made at Pulicat Lake in south India in July 2005 (Kannan and Manakadan 2007). Due to the activity of local fishermen, Painted Stork were disturbed and resorted to resting in nearby fields. However, after 19:00 h, when the disturbance had subsided, the birds were observed to return to the lake. In fact, Painted Stork were observed feeding at the lake between 19:00 to 23:00 h on several days. While these observations suggest that Painted Stork are capable of forging in darkness, they also suggest that they resort to it only when they are hungry. Since the above report is based on birds that had been disturbed, it would seem likely that the birds were 'time stressed' and making up for lost foraging time (Urfi *et al.* 1996).

Next to actively foraging, an alternative strategy is to steal food. While several bird species occur alongside the Painted Stork at foraging locations, among fish eating waders of a comparable body size, Grey Heron (*Ardea cinerea*) and Great Egret (*Casmerodius albus*) are the only birds from which a Painted Stork can steal prey. Mahindiran and Urfi (2010) recorded Painted Stork stealing fish from Little Cormorant (*Phalacrocorax niger*). However, the fish taken by the cormorant were relatively small, since it forages in shallow waters which are often near the shore. The Painted Stork is able to steal prey from other waders, except Blacknecked Stork, but, at the nesting site, it is unable to defend regurgitated fish from herons and egrets (Naoroji 1989).

Comparisons with Milky Stork

In south east Asia, the Painted Stork is suggested to frequent fresh water habitats while the Milky Stork prefers the coast, so the two species separate ecologically (Li *et al.* 2006). Also, the Milky Stork is perhaps more likely to engage in nocturnal foraging (Hancock *et al.* 1992). A study from Sumatra reported Milkfish (*Chanos chanos*), Elongate Mudskipper (*Pseudapocryptes elongatus*), Giant Mudskipper (*Periaptholomodon schlosseri*), and mullet *Moolgarda* sp./*Chelon* sp., in the diet of Milky Stork (Iqbal *et al.* 2009). All of these prey being coastal or brackish water species, their availability in the inter-tidal zone is largely governed by the tidal cycle, rather than the diurnal cycle.

As for the Painted Stork, the Milky Stork also employs tactile foraging involving probing in the mud with a partly opened bill, drawing it in an arc from side to side and using foot stirring (Swennen and Marteijn 1987; Silvius and Verheugt 1988; Indrawan *et al.* 1993). Foraging individuals are spaced 50-100 m apart (Li *et al.* 2006) although single tight flocks have been observed (Indrawan *et al.* 1993). While searching for mudskippers, Milky Stork probe in holes, sometimes immersing the whole bill and head in the mud. Once inside the hole, the bill is pushed forward, opening up a groove in the mud and any prey which comes in contact is immediately captured as this method is entirely tactile (del Hoyo *et al.* 1992). Such specialized behaviors have not been recorded for Painted Stork.

Painted Stork and the Ecosystem Context

Among numerous ways in which birds impact their ecosystem, biomass harvesting and enrichment are most relevant in the present context. The former impacts energy flow in the ecosystem, the structure of aquatic communities (Hurlbert and Chang 1983) and facilitates the biomagnification of toxins, particularly pesticides. From India, only two estimates of fish harvested by Painted Stork predation appear on record. At KDGNP, birds from a colony of approximately 2,000 nests were estimated to consume approximately 90 mt of fish over a 90 day period (Ali 1953). At the Delhi zoo, Painted Storks from a colony of approximately 100 nests, were estimated to consume approximately 24 mt over a 150 day period (Desai *et al.* 1974). These estimates pertain only to the nesting season and, if a whole year is considered, then the harvesting figures must be considerably higher. At mixed species heronries, dropping of Painted Stork and other species greatly enrich the waters and contribute to the ecosystem dynamics. For example, at Vedanthangal Bird Sanctuary in south India where heronry birds breed in large numbers, a chemical analysis of the reservoir water, revealed approximately 0.4 mg/l of nitrite (NO_2), 0.2 mg/l of nitrate (NO_3) and 17.4 mg/l of phosphorus (P_2O_5) (Paulraj 1988).

Directions for Further Research

The monsoon govern Painted Stork nesting activity as follows: rainfall → plankton cycles → fish spawning → bird reproduction. Important side effects include the dispersal of food due to flooding and creation of islands which effectively isolate nesting colonies from ground predators (Ali and Ripley 1987; Urfi 2010). (1) The causal linkages between the monsoon rains and Painted Stork nesting merit more detailed investigation. (2) The location of nesting colonies in the vicinity of foraging grounds make the system amenable for testing simple patch models. Investigations on variability of load sizes, distances travelled between foraging and nesting sites are likely to open up new questions. (3) The bill is a highly plastic structure in waders (Hulscher 1996) and in the Painted Stork considerable variations in its shape and size are observed. Although many variations can be related to either age or sex differences, further studies on morphological variations of the bill will be useful. (4) Since information on the diet of Painted Stork mostly emanates from studies at inland fresh water sites, there is need to extend studies to include coastal sites. (5) The impacts of invasive fish species on the ecology of wetlands and their impacts on the diets of resident fish eating birds needs to be investigated. Also, loss of foraging habitats due to urbanization is a cause for concern and detailed studies on the foraging ecology of Painted Stork nesting in urban areas, such as the Delhi Zoo, are warranted (Urfi 2010a). (6) Improved understanding on predation pressure and enrichment of local waters can have an important role in ecosystem modeling studies.

Acknowledgments

I thank the University of Delhi for providing funds under its scheme to 'Strengthen R & D Doctoral Research Programme by providing funds to university faculty'. I thank R. Nagarajan and J. Kushlan for comments on the manuscript.

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