Tanzania Journal of Science 45(2): 131-143, 2019 ISSN 0856-1761, e-ISSN 2507-7961

Kleptoparasitism of Shoebills *Balaeniceps rex* by African Fish Eagles *Haliaeetus vocifer* in Western Tanzania

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Abstract

Kleptoparasitism is a specialised form of foraging interference occurring throughout the animal kingdom and especially is well documented among birds including African fish eagle *Haliaeetus vocifer*. However, only one record is reported between fish eagle and shoebill *Balaeniceps rex* despite their habitat overlap and it remains undescribed. This paper documents kleptoparasitism of shoebills by fish eagles in Malagarasi wetlands, western Tanzania. Kleptoparasitism was highly seasonal occurring in the dry season, especially at low floods. Both adults and non-adult eagles stole prey from shoebills, with non-adults initiating attacks at shorter distances than adults perhaps because of the lack of experience. The shoebill preys were comparatively larger than those from fish eagle own fishing and required long preparation time which provided the opportunities to kleptoparasites. Shoebill's long prey handling time (6.90 ± 4.48 min) may have provided benefits to fish eagles as all kleptoparasitism attempts (n = 138) were successful. Moreover, it seemed likely that an attacking fish eagle posed significant danger to the shoebill and given the fact that shoebill lacks structures such as pointed bill to defend from kleptoparasitic attack it opted not to retaliate. Perch availability and habitat openness in the study sites could also have facilitated kleptoparasitic behaviours.

Keywords: *Balaeniceps rex*, *Haliaeetus vocifer*, handling time, kleptoparasitism, Malagarasi-Muyovozi Ramsar Site

Introduction

Kleptoparasitism is a specialised form of foraging interference (Perrins and Birkhead 1983) occurring throughout the animal kingdom (Iyengar 2008), and especially is well documented among birds (Brockmann and Barnard 1979). It is particularly common in waterbirds (Furness 1987) and in Accipitridae (Morand-Ferron et al. 2007) especially eagles; notably the African fish eagle *Haliaeetus vocifer* (Sumba 1989, Kasoma 1995) and bald eagles *Haliaeetus leucocephalus* (Dekker et al. 2012).

Several studies have suggested ecological conditions that relate to the evolution of kleptoparasitism; they include habitat openness (Paulson 1985), large concentrations of hosts (Brockmann and Barnard 1979), large/visible food items or prey (Brockmann and Barnard 1979, Dekker et al. 2012) and shortage of food from self-foraging (Oro 1996). Moreover, age of kleptoparasites and hosts as well as the distance between them; have also been hypothesized to play significant roles in avian kleptoparasitism (Broom and Ruxton 1998, Dekker et al. 2012). Distances between the hosts and kleptoparasites not only affect the chances of observing kleptoparasitic opportunities but also increases the cost of attempting kleptoparasitism as kleptoparasites expend energy when travelling to the hosts. This could be more important for raptorial kleptoparasites such as fish eagles that perch on top of trees or emergent vegetation overlooking hosts.

Kleptoparasitised individuals may challenge or retaliate, escape with food to cover, reduce handling time (including switching to smaller prey) or remain passive (Stillman et al. 1997). Stillman et al. (1997) hypothesized that kleptoparasitism should be flexible, with aggression only occurring when benefits of this action outweigh the costs. Sirot (2000) suggested that kleptoparasitism and aggressiveness should increase when food patches are harder to locate. Using ideal free distribution (IFD) model, Hamilton (2002) found that kleptoparasitism increases with increasing difference in searching efficiency, increasing difference in fighting ability, increasing handling time while decreases with increasing resource input rates, increasing ownership advantage and increasing fighting time. In general, when payoff for kleptoparasitism is low, individuals switch to searching for prey (Stillman et al. 1997, Smith et al. 2002).

This paper both qualitatively and quantitatively describes kleptoparasitic interactions between shoebills *Balaeniceps rex* and fish eagles. The two are large waterbirds in sub-Saharan Africa where in some large wetlands (e.g., in Sudan, Tanzania, Uganda and Zambia) they share habitats (Brown et al. 1982). However, despite the habitat overlap between the two species, there is no mention of kleptoparasitism in Balaenicipitidae family (Gould 1851, Hagey et al. 2002), of which shoebill is the only member, in published reviews (Brockmann and Barnard 1979, Morand-Ferron et al. 2007, Iyengar 2008) and in shoebill foraging studies in Sudan, Uganda and Zambia (Guillet 1979, Möller 1982, Mullers and Amar 2015). The most recent extensive review of kleptoparasitism in birds being that of Morand-Ferron et al. (2007) where 33 families were noted to be involved in interspecific kleptoparasitism. Moreover, Nahonyo and Msuya (2008) registered one incidence of kleptoparasitism on a shoebill by fish eagles in Malagarasi wetlands but the interaction remains undescribed. Specifically, in addition to documenting this kleptoparasitic interaction, this research hypothesized that; (1) the rate of kleptoparasitic attack would be higher in driest months when fish eagles may be precluded from catching prey and it is during this period when shoebills become restricted to fewer and wetter locations which may attract kleptoparasites, and (2) the prey size and handling time would differ between hosts foraging under pressure of kleptoparasites and those that foraged in areas without kleptoparasites.

Materials and Methods

Study sites

Field work was conducted between June 2011 and February 2012 within the central drainage of the Malagarasi-Muyovozi Ramsar Site (3–6°S, 30–32°E), and largely within a swamp located in southern part of Lake Nyamagoma around the village of Kasisi (5°03'05"S, 30°57'14"E) (Figure 1). The water levels in the lake and adjacent floodplains can fluctuate widely on an annual basis depending on rainfall and inflow (Nkotagu and Ndaro 2004); annual flooding beginning in November and peaking between April and May. Large and small open water channels around this lake variously open and close depending on currents and water volume. The vegetative swamp surrounding the edges of the lake is largely comprised of grasses and sedge species.

At Kasisi village, the miombo *Brachystegia* woodland which is mixed with Borassus palm (*Borassus aethiopum*) (Figure 2a, b) bordering the swamp on one side. In between the tall vegetative swamp and woodland, there are extensive open glades of short vegetation dominated by *Eleocharis-Leersia* plant species forming dense floating vegetation platforms (John and Lee 2012). These floating platforms sometimes contain small natural surface water openings (pools), which are supplemented by those made by humans and the antelope Sitatunga (*Tragelaphus spekii*). These ‘pools’ are used by shoebills to hunt for air-breathing fish that become sparse, especially as water recedes.

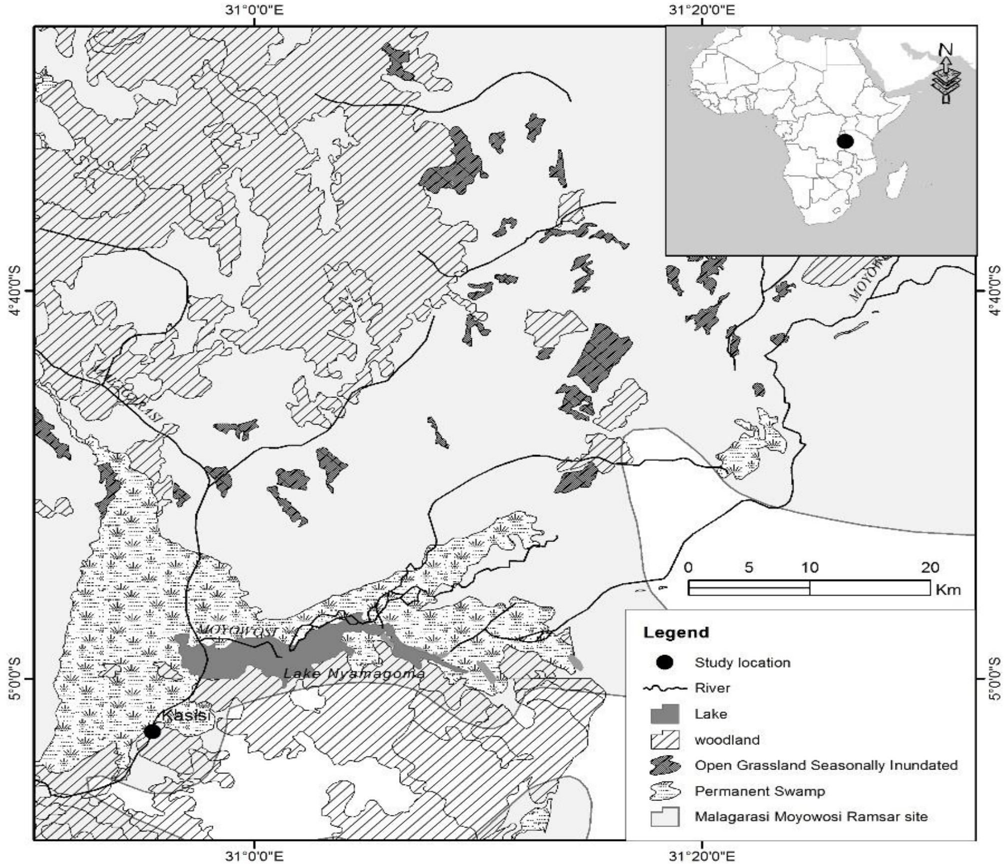

Figure 1: Map showing the study area at Kasisi Village, South of Lake Nyamagoma, within Malagarasi-Muyovozi Ramsar Site.

Study species

The African fish eagle is a widespread raptor in Africa occurring at many water bodies containing fish except in arid areas (Brown et al. 1982). As its name suggests, it chiefly feeds on fish, although other prey such as rodents, waterbirds and reptiles are occasionally consumed (Stewart et al. 1997). It is, however, the most known kleptoparasitic raptor in Africa (Sumba 1989, Kasoma 1995). The shoebill has a narrow and disconnected distribution along major water basins in eastern sub-Saharan Africa from Sudan to Zambia (Feduccia 1977, Hancock et al. 1992) and therefore classified as ‘vulnerable’ by IUCN (BirdLife International 2019). Most of the shoebill habitats are treeless remote floodplains and permanent swamps (Hancock et al. 1992). The shoebill is a rare (e.g., < 500 mature individuals survive in Tanzania) wetland specialist large bird (John et al. 2012). The shoebill has extremely long toes (Gould 1851) to support its weight (≈ 7 kg) when walking on floating vegetation platform unlike other large wetland birds which have to wade. The foraging behaviour of the shoebill resembles that of many Ardeidae, i.e., 'stand-and-wait' and 'walk slowly' (Guillet 1979, Mullers and Amar 2015), but in shoebill this is usually followed by a pronounced ambushing of surfacing prey, a phenomenon that Guillet (1979) described as 'collapsing' (Figure 2c). The shoebill is a non-social forager (Möller 1982) but may form loose groups at good foraging sites.

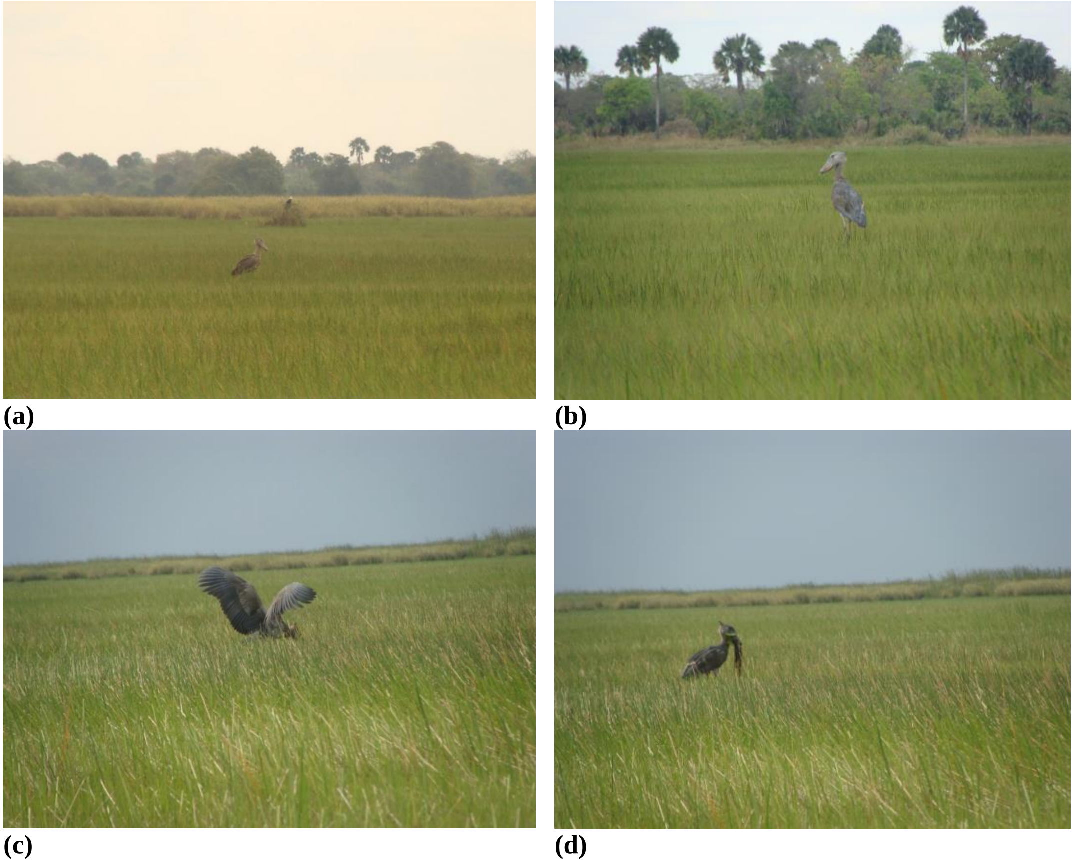

Figure 2: (**a**) An adult African fish eagle (*Haliaeetus vocifer*) perched on tall sedge clump attending the shoebill (*Balaeniceps rex*) for food stealing, (**b**) A Shoebill in floating mats, in the background is the Miombo woodland intermixed with Borassus palms which provided perches for African fish eagles when attending shoebills for kleptoparasitism, (**c**) The shoebill plunging for prey, a process described as 'collapsing' by doing this it is likely to attract kleptoparasites to prepare for attack, (**d**) The Shoebill with a prey accompanied by herbage debris which is likely to increase prey preparation time before swallowing.

Data collection

Host-kleptoparasite interaction

Host-kleptoparasite interaction was studied by using a method described by Mock and Mock (1980), whereby several birds (i.e., the entire study system; 1-10 for hosts, 1-6 for kleptoparasites) were kept under simultaneous and continuous observations for several hours up to 9 hours between sunrise (06:30 h) and sunset (19:30 h). Shoebills foraging (prey capture) bouts are longer (Möller 1982) and use in-between periods for resting (Mullers and Amar 2015) and thus foraging events for < 2 birds could be studied by a continuous watch. We used binoculars (Bushnell: 8 x 42 FOV430') for studying birds.

Although the study birds appeared not to be disturbed by human presence up to a distance of 70 m, observers, nonetheless, used neighbouring woodland and tall *Miscathidium* grass as natural blinds. The distance between original perches of kleptoparasites and shoebills was visually estimated by a single observer throughout the study period. Age classes of both the host and kleptoparasites were grouped into adults and non-adults based on plumage types according to Buxton et al. (1978) for shoebills and Brown and Cade (1972) for fish eagles (non-adults, < 4years). Total number of both hosts and kleptoparasites for each species was estimated by averaging the number of birds present at start and end of each observation. Rates of attacks in each continuous observation were estimated by dividing the number of attacks by total observation time (h).

A total of 777.2 observation-hours were conducted over 100 days (7-13 days/month) with a mean range of 6.22-9.54 h/day of observation. Observation time period from June 2011 to January 2012 did not vary significantly (Kruskal-Wallis H test: $H = 12.44$, $df = 7$, $P = 0.087$), less time (56 h) was spent in February 2012 because shoebills became scarce and, when present, they changed foraging locations frequently and quite often disappeared from the observers' view.

Independent foraging birds

A search for fish eagles and shoebills foraging independently was conducted after the break of the host groups and reduction of kleptoparasitic attacks in January and February. This part intended to establish the prey type and size consumed by both fish eagles and shoebills and handling time for shoebill in order to compare with those that foraged in areas with kleptoparasites. Prey items were identified whenever possible to species level and the size of prey was estimated in relationship to the length of the beak for shoebill (beak length; 22 cm, Brown et al. 1982, Hancock et al. 1992, Collar 1994) and tarsus for fish eagle (tarsus; 8.5 cm, Brown et al. 1982). Fish eagles use talons to fish and/or carry their prey to safe points usually in top of the trees. Capture success for each species was determined by dividing the number of successful strikes or collapsing (shoebill) by the total number of strikes/collapsing.

Statistical analysis

Data were managed using Microsoft Excel and SPSS for Windows Release 16.0 (SPSS Inc., Chicago, Illinois). Data are reported as mean and standard deviation (mean ± SD). Mann-Whitney U test was used to determine differences between means for prey size for both eagles and shoebills. Mann-Whitney U test was also used to compare the distances attained by non-adults and adult kleptoparasites during kleptoparasitic attacks. Spearman rank correlation was used to determine the effect of the group size of kleptoparasites and hosts on attack rates over the study period, and the dependent correlation coefficients (r) between eagles, shoebills and attack rates were tested by using t-statistics (Chen and Popovich 2002) where critical value was obtained from Natrella (2012). Results were considered significant at $P < 0.05$ (all two tailed).

Results

Food stealing

A total of 234 and 359 independent observations were made on fish eagles and shoebills, respectively. During the study period, shoebills made a total of 317 strikes for prey of which 295 (93%) were successful and yet of these successful strikes, 138 (47%) were stolen by eagles. Fish eagles swooped down with their feet extended forward and talons outstretched and landed within 5 m to give time for shoebill to relinquish its prey. Most prey (fish) were disabled during the shoebill strikes and were therefore unlikely to escape the kleptoparasitic eagles; the dense floating vegetation platform also reduced the probability of the fish sliding back into water. In all kleptoparasitic events the shoebill did not retaliate; typically, it would move a few steps away from the relinquished prey and continue to preen and stretch its wings (these were however, common behaviours after any 'collapsing' whether successful or not). Thereafter it changed hunting location by either stalking or making short flights. On one occasion a shoebill tried to evade a fish eagle by flying with prey dangling in its beak but it was too slow for an adult eagle. Non-adult shoebills were rare (n = 19, ≈ 5%) and when present did not stay at one point unlike adults which lurked at water openings for longer periods.

Stolen food items were consumed by fish eagles on the ground presumably because the floating vegetation would entangle within the fish eagle's talons making it difficult to fly with the prey. Over 50% of the stolen prey items were either intra-kleptoparasitised or shared by a group of two or more fish eagles, which sometimes involved fierce contests and chases but non-adult fish eagles were usually tolerated. Non-adult eagles joined the food stealing from September onwards; this was suspected to be a post breeding period of fish eagles in the area. Fish eagles, irrespective of their age classes, were 100% (n = 138) successful in stealing food items from shoebills. Despite the fact that other large fish-eating wading birds were occasionally foraging near the kleptoparasitised shoebills (Table 1) fish eagles did not attempt to steal prey from them. However, non-adults eagles attended the host or initiated attacks at a shorter distance (103.79 ± 57.41 m) than did adults (441.67 ± 250.81 m) (Man-Whitney U test: $U_{29,48} = 89.50$, $P < 0.0001$). Adult kleptoparasites usually perched either in the top of tall emergent trees or tall grass/sedges adjacent to the floating platform while non-adults used floating vegetation platforms as close as 20 m from the shoebill (Figure 2) and were usually in a group of at least two. Even at this close proximity to a kleptoparasite, the shoebills did not attempt to escape or change hunting spots once established and continued to try to hunt.

Table 1: Large fish-eating birds that foraged near the kleptoparasitised shoebills but fish eagles did not attempt to steal prey from them

Species	Distance (m) from kleptoparasitised shoebill	Frequency of Prey strikes
Black-headed heron (*Ardea melanocephala*)	127.86 ± 98.60	21
Saddle-billed stork (*Ephippiorhynchus senegalensis*)	132.50 ± 127.44	24
Grey heron (*Ardea cinerea*)	150.50 ± 107.63	20
Great egret (*Ardea alba*)	175.00 ± 140.64	14
Goliath heron (*Ardea goliath*)	179.44 ± 137.44	14

Overall, the rates of food piracy were significantly correlated with the number of hosts present; Spearman rank correlation: r_s = 0.577, and kleptoparasites, r_s = 0.382 (all P values < 0.0001). The increase of shoebills at the study sites attracted more fish eagles (r_s = 0.275, n = 100, P = 0.006). The dependent correlation coefficients with rate of attack were significantly higher for hosts than kleptoparasites (t-statistic: $t_{Difference}$ = 2.0165, df = 97, $P < 0.05$). For pooled monthly data, the rate of food pirating and number of hosts showed a bell-shaped pattern over the study months increasing from July peaking around October-November (end of dry season), and declining afterwards (Figure 3). Figure 3 shows a pronounced bell-shaped pattern with shoebills (polynomial 2nd order equation: r^2 = 0.8076, $y = –0.277x^2 + 2.6116x – 0.9038$) and the rate of attack (r^2 = 0.7841, $y = –0.019x^2 + 0.1908x – 0.1848$) than in fish eagles ($r^2$ = 0.7948, $y = –0.0954x^2 + 1.1233x – 0.2345$). Shoebills dispersed to shallower areas as the swamp started to flood during the rainy season from December to February, but this did not cause a sharp decline in fish eagles because territorial eagles did not move.

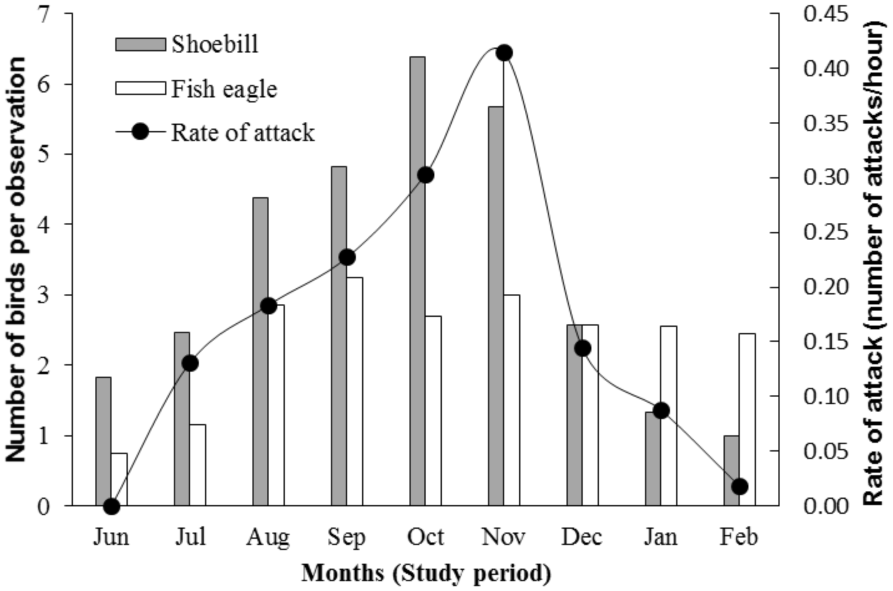

Figure 3: Monthly trends of host-kleptoparasite interaction from June 2011 to February 2012 in the Malagarasi wetlands.

Prey type, size and handling time

Shoebills preyed on two species of fish but predominantly on the African lung fish, *Protopterus aethiopicus* (> 60%) while fish eagle preyed on six species of fish but largely on *C. gariepinus* and tilapia (*Tilapia rendalli*) (x^2 = 37.000, df = 5, $P < 0.0001$, Figure 4). Shoebills foraged on larger prey than fish eagles (shoebill prey; 41.800 ± 19.39 cm, 11-99 cm, fish eagle prey; 28.42 ± 14.26 cm, 8.5-68 cm, $U_{32,35}$ = 354.000, P = 0.009, Figure 5). Kleptoparasitic pressure did not affect the prey size consumed by shoebills as prey size of shoebills foraging in areas with fish eagles (39.33 ± 17.75 cm) did not differ significantly ($U_{35,146}$ = 2373.500, P = 0.506) from those preyed by shoebills foraging in areas without fish eagles (41.800 ± 19.39 cm). Large prey

(> 60 cm) were usually cut into sections by shoebills and swallowed at intervals. The entire process from scooping to swallowing ranged from 2 to 30 minutes (6.90 ± 4.48 min) depending on the size of the prey. Prey handling time by shoebill increased with prey length (in areas without kleptoparasites; $r_s = 0.673$, $P < 0.0001$, with kleptoparasites; $r_s = 0.582$, $P < 0.0001$) and handling time did not differ for shoebills foraging with and without the kleptoparasitic pressure ($U_{35,146} = 2260$, $P = 0.285$).

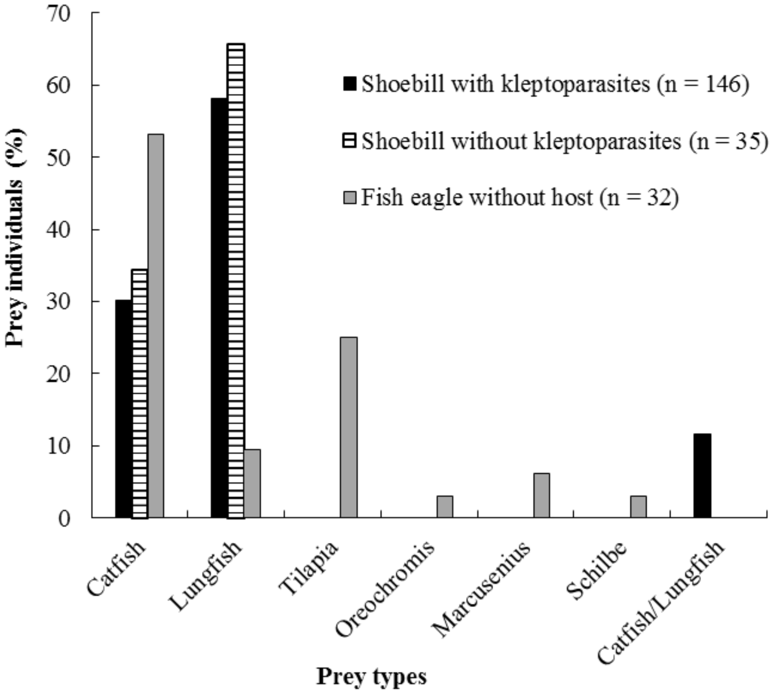

Figure 4: Diet prey compositions for shoebills and fish eagles. In addition to lungfish and catfish, fish eagles fed on *Tilapia rendalli*, *Schilbe mystus*, *Marcusenius stanleyanus* and *Oreochromis* sp.

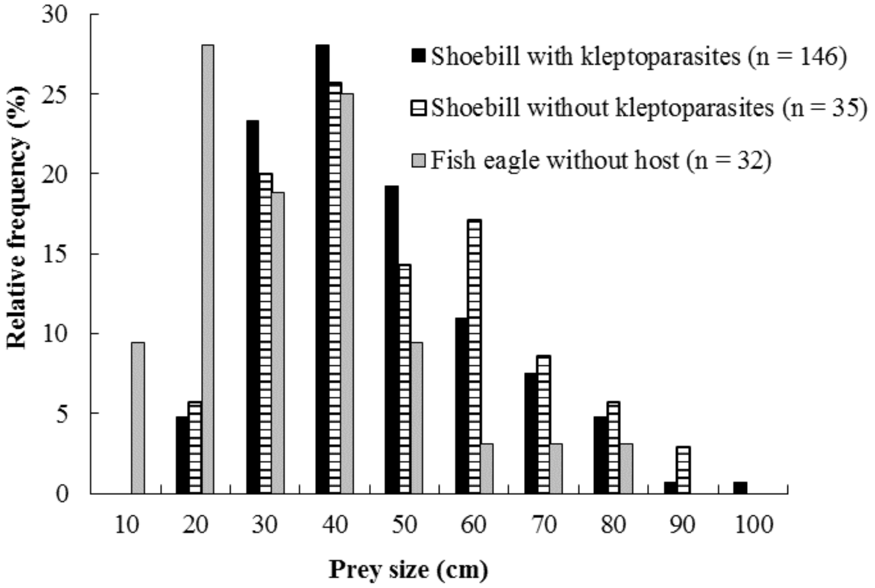

Figure 5: Distribution of fish total length in the diet of shoebills and fish eagles.

Discussion

Food stealing

Kleptoparasitism in African fish eagles is well documented whereby it steals food mainly from egrets and storks (Sumba 1989, Kasoma 1995). However, this is the first time a detailed ecological investigation on fish eagles stealing food from shoebills is described. The environmental characteristics in the study area were unique and likely important in facilitating kleptoparasitic behaviour in this eagle species. For example, the dense floating platforms of vegetation, which prevented fish eagles from hunting, made it more accessible for them to steal prey captured by their hosts, the shoebill. Unlike in the Malagarasi-Muyovozi Ramsar Site, habitat openness and presence of perching locations for avian kleptoparasites that favour food piracy (Paulson 1985) are usually lacking in most shoebill habitats (Hancock et al. 1992). Openness provided two benefits to facilitate kleptoparasitism (see also Paulson 1985): (1) several shoebills could be under continuous surveillance by fish eagles from high perches, (2) shoebill ‘collapsing’ events, a potentially learned behaviour of fish eagles that prey was likely captured by their hosts, were visible from a long distance. These habitat qualities may explain why pirating from shoebills is not common elsewhere.

What is surprising in this study is the large (150 cm tall) stork-like bird, the shoebill, did not retaliate nor escape when attacked by the fish eagles. This could be due to the lack of particular physical traits such as pointed beak (shoebill has a huge shoe-like bill) which could inflict pain to the fish eagles and was not agile enough to chase an eagle when it escaped with a prey. It is therefore not surprising that other large waterbirds with spear-like bill were not kleptoparasitised by fish eagles. Sumba (1989) reported that in Uganda saddle-billed storks and goliath herons defended their prey successfully against fish eagles and in fact saddle-billed stork could stab a fish eagle with its bill to death (Mock and Mock 1980). It could also be that shoebills may be expending much energy during ‘collapsing’ and may be temporarily exhausted immediately after collapsing events putting it at a disadvantage of winning the contest and so deciding to be passive.

Non-adult fish eagles appeared at the study swamp during post breeding and participated in food stealing. These non-adults were tolerated by adult fish eagles unlike other adults joining the meal where fierce contests always occurred. It is assumed that these non-adults were related to the adults (territory owners) and thus tolerance may have been related to familial relationship. Familial tolerance has also been reported in other raptor species such as crested caracara *Polyborus plancus* (Rodríguez-Estrella and Rivera-Rodríguez 1992). Fish eagles are territorial and adult tend to remain resident in their breeding areas but some proportion of the young disperse (Brown and Cade 1972, Brown and Hopcraft 1973). Non-adults, which may include progeny of the resident eagles as well as dispersing from elsewhere were probably less efficient than adults in obtaining food independently and so they compensated for this by robbing prey from shoebills (see Fischer 1985 for Bald eagles *H. leucocephalus*). This was also reflected in the shorter approach distances attained by non-adult fish eagles as compared to adults when stealing food from shoebills.

In the Malagarasi wetlands, as water draws back into the main channels and ponds, food resources (especially fish) become concentrated in these places thereby influencing the distribution of animals that depend on them. In addition, human activities (fishing, grazing, burning and even excavation of aestivated lungfish) also intensify towards the end of the dry season (i.e., during the low floods) (Nahonyo and Msuya 2008). During this period, shoebills are forced to search for good foraging sites which unfortunately become limited resulting in the formation of loose groups at few locations. Aggregated hosts may imply good conditions for kleptoparasitism (Brockmann and Barnard 1979, Vickery and Brooke 1994), for instance because of short flight distance to hosts (Thompson 1986). Increased human activities in open waters (fish eagles can only fish in open waters) during the dry season, may have, encouraged kleptoparasitism. Studies have shown that kleptoparasites often steal food during poor conditions for foraging (Oro 1996, Varpe 2010) which explains the increased rates of kleptoparasitic attack during low flood period. As the swamp became flooded from January following the onset of rains in October, fish eagles altered their behaviour towards active hunting independently, perhaps due to their increased foraging sites/success and the difficulties of accessing shoebills. Shoebills changed from ‘stand-and-wait’ to ‘walking slowly’ foraging strategy following flood rise (see also John and Lee 2012).

Prey type, size and handling time

The shoebill’s chief food, African lung fish and catfish, are both piscivorous, air breathers and also show a degree of cannibalism (Smith 1931, Willoughby and Tweddle 1978, Guillet 1979, Möller 1982, van der Valk 2012, Mullers and Amar 2015) which may reduce abundance of smaller fish in shoebill foraging sites especially in dense floating vegetation platforms with few surface openings. Moreover, the larger prey favours kleptoparasitism as they require long processing periods (Kushlan 1978, Mock and Mock 1980). This can also explain why fish eagle did not attempt to steal prey from other waterbirds (such as egrets and herons) around because they prey on smaller food items than shoebills (Kasoma 1995). For example the largest of all, goliath heron feeds mostly on prey of ≈30 cm while those of > 50 cm are voluntarily rejected (Mock and Mock 1980). Smaller prey items are usually consumed rapidly and provide little reward for kleptoparasitism (Barnard et al. 1982, Kellner and Cooper 1998). The Shoebill prey size and handling time were not affected by kleptoparasitic pressure from fish eagles because the shoebill does not have the chance to select prey. Instead, it feeds by ambushing any surfacing organisms and then scooping of prey includes intake of dead herbage debris (Figure 2d). As a result, this probably reduces the chances for smaller prey to slip back into water, but it would increase prey preparation time because smaller prey may sometimes be difficult to separate from vegetation debris. The difference in diet composition between shoebills and fish eagles is a result of prey behaviours. For example, preys hunted by fish eagles (Figure 4) tend to feed in open waters where they form schools at water surface (Bruton 1979, Stewart et al. 1997).

Conclusion

Although this study was not able to estimate the sizes of the prey stolen by fish eagles, there is little doubt that they were as large as those taken by shoebills and hence provided incentives for theft. The habitat characteristics in the study area, non-retaliatory behaviour of shoebills, and large prey that require long handling time also favoured kleptoparasitism. Moreover, the shoebill inhabits inaccessible and often remote swamps. Thus there is a possibility that kleptoparasitism, in addition to being seasonal, may have gone unnoticed. Kleptoparasitism is likely to increase and interfere with the foraging of the shoebills if human activities in wetlands are not controlled or regulated. In future, kleptoparasitic interactions between shoebills and fish eagles will also be influenced by the changing climate due to changes in flooding cycles.

Acknowledgements

Ministry of Natural Resources and Tourism provided research permit. Financial support came from Mohamed bin Zayed Species Conservation Fund Project No. 0925790, Tampa’s Lowry Park Zoos and SNU-Environmental Leadership Program Alumni Scholarship. Field logistical support was greatly offered by O. Msangi, I. Nkuwi, C. Nahonyo, A. Lameck, F. Mwalle and the Kasisi village government. Authors are also indebted to all the field assistants and S. Knappe for English translation of the German shoebill article. IdeaWild provided additional field equipment. Stephen Clark and W.D. Newmark commented on earlier drafts of this manuscript.

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