

NILE CROCODILE NESTING ECOLOGY UNDER VARYING HUMAN DISTURBANCE INTENSITIES ALONG LOWER RIVER TANA, KENYA

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Abstract

*The Nile crocodile (*Crocodylus niloticus*, Laurenti, 1768) supports important ecological and socio-economic functions; however, its survival in most of its ranges in Africa continues to be threatened by anthropogenic activities. Here, we compared selected attributes of Nile crocodile nests (abundance, clutch size, distance from water, and presence or absence of eggs, tending and predation) across three human disturbance regimes (low, intermediate and high), indexed by coverage of cropland and settlement, along lower River Tana, Kenya. We conducted a crocodile nest survey in January 2019 and overlaid the resultant data on the most recent land cover map of a 1-km wide strip on both sides of the river, segmented into the different disturbance regimes using remote sensing and geographical information system techniques. The low, intermediate and high disturbance regimes comprised combined cropland and settlement coverage of 2%, 9% and 15%, respectively, and covered 28%, 27% and 47% of the surveyed river segment. We counted a total of 99 nests, with 45, 34 and 20 nests located in low, intermediate and high disturbance regimes, respectively. Nests were 56% less frequent than expected under high disturbance, whereas they were 69% more frequent than expected under low disturbance and showed expected frequency under intermediate disturbance. In addition, nests were 56% and 41% less frequent under high disturbance compared to low and intermediate disturbance, respectively. However, nest abundance was statistically similar between the latter two regimes. No significant differences were observed in other assessed attributes across disturbance regimes. Our study underscores the importance of minimizing land conversion in such human-dominated landscapes for enhanced sustainable utilization and conservation of crocodiles.*

*Keywords: *Crocodylus niloticus*, human disturbance, human-dominated landscapes, land conversion, land cover*

1. INTRODUCTION

Globally, crocodiles support critical ecological and socio-economic functions. Specifically, as apex predators with wide dietary breadth, crocodiles contribute significantly to the maintenance of the structure and function of many aquatic and riparian ecosystems (Thorbjarnarson, 1992; van der Ploeg et al., 2011). In addition, crocodiles provide various products for the human society, including food (meat and eggs) and skins for the leather fashion industry (Hoffman et al., 2000; Dzoma et al., 2008; Pooley, 2016). Furthermore, these products are usually produced in crocodile ranches, which employ local community members to harvest for them crocodile eggs from the wild, thereby enhancing the livelihoods of such community members (Convention on International Trade in Endangered Species of Wild Fauna and Flora [CITES], 2010; Manolis and Webb, 2016; Jyrwa et al., 2020; Than et al., 2020).

The Nile crocodile (*Crocodylus niloticus*, Laurenti, 1768) is one of the crocodylians with great ecological and socio-economic values. This species is endemic to Africa and is quite widespread throughout the sub-Saharan region (Eaton et al., 2010; Fergusson, 2010). Although the species is currently assessed as “Least Concern” in the IUCN Red List, human-induced declines in its population have been reported in many parts of Africa (Isberg et al., 2019). River Tana in Kenya is one such ecosystem in which the Nile crocodile population has been declining over time. For instance, it was recently reported that the Nile crocodile population along a 500-km stretch of this river decreased by more than 40% (i.e., from 18,000 to less than 10,800 individuals) over a 5-year period (Gari, 2015).

Human-induced disturbance is one of the major causes of Nile crocodile population declines in many parts of Africa (Salem, 2013; Aust et al., 2009; Isberg et al., 2019). One of the major ways in which humans negatively influence Nile crocodile populations is land conversion into croplands and settlement areas, which results into loss of suitable habitat for these reptiles. In particular, such activities can impair the ability of these crocodiles to find suitable nesting sites and guard their nests against predators (Somaweera et al., 2013; Somaweera and Shine, 2013; Somaweera et al., 2019; Utete, 2021). Ideally, crocodiles nest on shaded ground to protect their eggs from overheating (Combrink et al., 2016, 2017; Murray et al., 2020). In addition, they nest near water for ease of nest guarding during the incubation period, safety and cooling needs of brooding female crocodiles, and reduced vulnerability of new hatchlings to predation (Cott 1961; Modha 1967; Wallace and Leslie, 2008; Refsnider, 2016; Calverley and Downs, 2017).

Understanding the influence of human-induced disturbance on Nile crocodiles nesting ecology is fundamental for development of strategies and programmes aimed at enhancing sustainable utilization and conservation of this species in human-dominated riparian landscapes. Many studies have evaluated the effects of human disturbance on Nile crocodiles and other crocodylian species in general (Combrink et al., 2011; Salem, 2013; Evans et al., 2016; Bhattarai et al., 2022). However, there is still inadequate knowledge regarding the specific influence of increasing human disturbance intensity on the nesting ecology of these reptiles in many human-dominated landscapes, and especially in Africa. Understanding how crocodiles respond to different intensities of human disturbance is particularly vital for determining disturbance thresholds that should never be exceeded if we are to better maintain crocodile populations in such landscapes.

In this study, we aimed to assess the effects of intensifying human disturbance (indexed by coverage of cropland and settlement) on the nesting ecology of the Nile crocodile in lower River Tana, Kenya. Specifically, we compared selected ecological attributes of crocodile nests (frequency or abundance [number of nests], clutch size [number of eggs per nest], distance from water, and presence or absence of eggs, predation and tending), among three (high, intermediate and low) human disturbance regimes. We hypothesised that nests will be less frequent than expected under high disturbance, whereas this pattern will disappear or be reversed under low disturbance regimes. In addition, we hypothesized that the measured biophysical attributes of nests will be less favourable under high disturbance than under lower disturbance regimes.

2. MATERIALS AND METHODS

2.1 Study area

We conducted the study in the lower River Tana basin in Tana River County (0° 0'53"30" and 2° 0'41" South and 38°30' and 40°15' East) in southeast Kenya (Figure 1). This region hosts one of the largest populations of the Nile crocodile and is the main crocodile egg collection zone in Kenya

(Crocodile Specialist Group [CSG], 2003; Kyalo, 2008a; Odhengo et al., 2014). We focused on the egg collection zone allocated to Galaxy Croc Farm (hereafter referred to as Galaxy, a 335-km long segment stretching from Mbalambala to Mnazini (Figure 1).

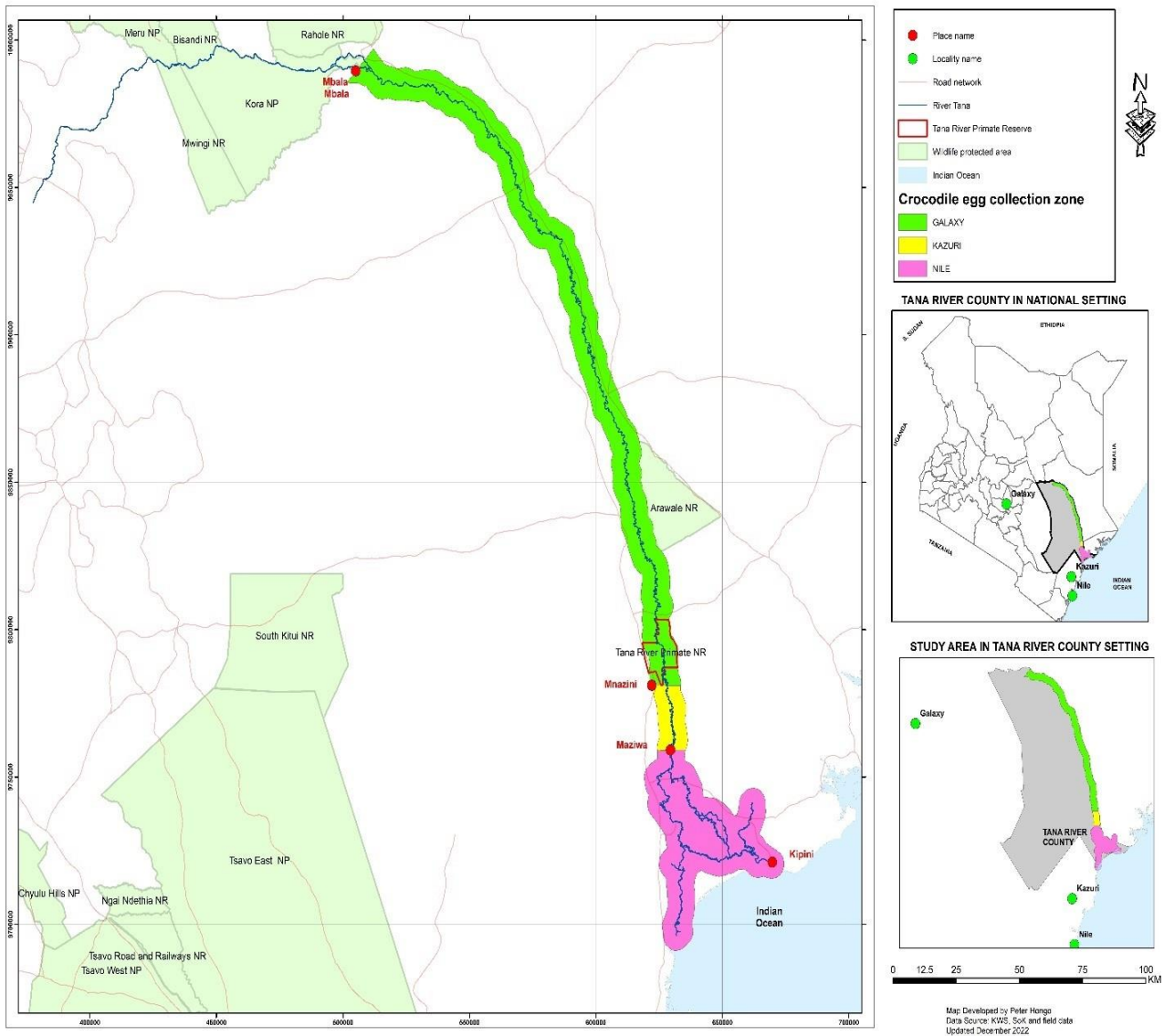


Figure 1. Map of lower River Tana showing the egg collection zones for Galaxy and other crocodile ranches in the region

Tana River County receives an annual rainfall ranging from 400 to 750mm, concentrated in two seasons; the long rainy season from March to May and the short rainy season from October to December (Mohamed, 2015; Government of Kenya [GoK], 2018). January, February, March, July, August and September are generally relatively dry (GoK, 2018). Notably, however, rainfall in this region exhibits considerable spatial and temporal variability. The region is characterized by frequent droughts and floods. The mean annual temperature ranges from 23° to 33°C. January,

February and March are generally the hottest months, with maximum daily temperatures of up to 41°C (GoK, 2018).

The natural vegetation in the study region consists of a mosaic of riverine forests, bushlands, woodlands and grasslands. Some of the common woody plant species include *Acacia reficiens*, *A. tortilis*, *A. bussei*, *A. mellifera*, *Cadaba glandulosa*, *Commiphora candidula*, *C. campestris* and *Salvadora persica* (Maingi, 1998; Njoroge et al., 2009). Some of the common grass species include *Echinochloa haploclada*, *E. staginina*, *Sporobolus helvolus*, *Panicum maximum* and *Cynodon dactylon*. The region is home to some of the most endangered, endemic and range-restricted animals including the Tana River red colobus (*Colobus badius rufomitatus*), the Tana River Crested Mangabey (*Cercocebus galeritus*), the hirola antelope (*Beatragus hunter*), and cheetah (*Acinonyx jubatus*), and provides habitats for many other animal species (GoK, 1996; Butynski, 2000; Njoroge et al., 2009; Ministry of Environment and Natural Resources [MENR], 2012; Odhengo et al., 2014). Notably, the region hosts two government-protected wildlife conservation areas, namely, Tana River Primate National Reserve (TRPNR) and Arawale National Reserve, which is located in Garissa County on the eastern side of the river (Figure 1).

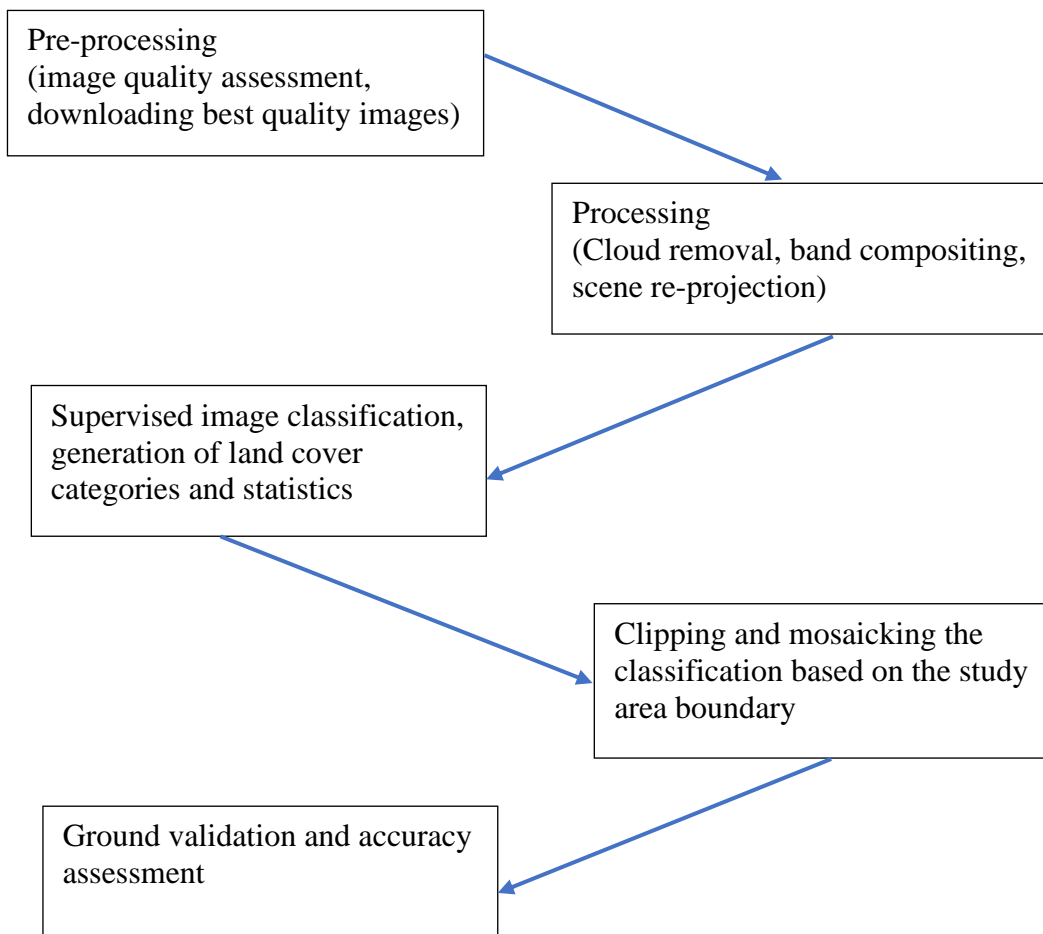


Figure 2. Flowchart showing the process used in image analysis (adapted from Briem et al., 2002; Cheruto et al., 2016; Rotich et al., 2022)

Tana River County has a human population of 314,710, based on the national census conducted in 2019 (Kenya National Bureau of Statistics [KNBS], 2019). Due to the arid conditions in the county, human settlements are commonly located in close proximity to the river. The study region is mainly occupied by the Pokomo, Orma, Wardei, Watta and Ilwana ethnic groups. The main socio-economic activities in the region include farming, livestock keeping, fishing and sand harvesting (GoK, 2018). Farmers in the county mainly rely on rain-fed and flood recession farming systems (Terer et al., 2004).

2.2 Land Cover and Human Disturbance Mapping




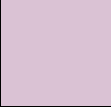
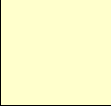


We assessed land cover types along the river segment using SENTINEL-2 satellite images of 2018 with 10 metres spatial resolution (European Space Agency, 2020). The total width of the segment assessed was 2 km (i.e., 1 km on both sides of the river), which is considered a core zone for Nile crocodile nesting (Shacks, 2006). We downloaded and processed these images using the Environment for Visualising Images (ENVI) software (Bailey et al., 2016). Our classification scheme consisted of seven land cover categories; namely, “forestland”, “open grassland”, “cropland”, “settlement”, “water bodies” and “other land” (bare soil and rock) (Supplementary Table 1). We used Earth Resources Data Analysis System (ERDAS) software to generate statistics for the different land cover types (Alam et al., 2019). Further details on the image analysis and classification process are presented in (Figure 2 and Table 1).

We visually assessed the resultant land cover map and segmented the river into areas of “high”, “intermediate” and “low” disturbance regimes. This segmentation was based on eye estimation of the joint coverage of cropland and human settlement relative to the coverage of all other land cover types (water, forestland, shrubland and grassland). Consequently, for each disturbance regime, we used ERDAS software to estimate the absolute and relative area covered by each land cover type.

2.3 Crocodile Nest Survey

We assessed a suite of ecological attributes of crocodile nests, namely, frequency (number of nests), presence or absence of eggs, clutch size (number of eggs per egg-containing nest), presence or absence of predation, presence or absence of tending female and distance from water. To assess these attributes, we conducted a crocodile nest survey along the river in January 2019, which coincided with an active egg collection season. We conducted the survey along the Galaxy egg collection zone’s 335-km long river segment, excluding the 25-km segment between Sala and Nanighi (Figure 3), which we could not access due to security and safety concerns. We conducted the survey through a combination of motor boat and foot searches. The nest survey team comprised of one of the investigators, a research assistant, two crocodile egg collectors and one agent from Galaxy. We relied on the knowledge and experience of the egg collectors and ranch agent in locating crocodile nest sites. We identified potential nest sites using a combination of cues, including the sight of a fleeing crocodile, signs of soil disturbance, excavation, and crocodile footprints (Champion and Downs, 2017) (Figure 3). We used a hand-held global positioning system (GPS) unit to record the geographical location of each identified nest site (Combrink et al., 2011).

Table 1. Definition of land cover categories

Land cover class	Description	Code	Colour
Forestland	Forestland according to Kenya’s definition (Kenya Forest Service [KFS], 2013) refers to ‘ <i>areas occupied by forests and characterised by tree crown cover $\geq 15\%$, an area ≥ 0.5 ha and a tree height ≥ 2m. It also includes areas managed for forestry where trees have not attained 2m height but with potential to do so, and areas that are temporarily destocked</i> ’. In the study area, forestlands mostly include the riverine vegetation which contains woody vegetation that is consistent with the national forest definition.	1	
Open grassland	This refers to rangelands and pasture land that is not considered as cropland. It includes grasslands without trees and are areas that mostly support pastoralism in the study area.	2	
Cropland	This category refers to land that is purposely managed for agricultural activities. It includes areas with annual herbaceous crops where crops grow in one or more seasons in a year and at times are bare due to tillage. It also includes agro-forestry systems which were, however, not mapped in this study.	3	
Settlement	Settlement includes all developed land, including transportation infrastructure and human settlements of any size, unless they are already included under the other categories.	4	
Other land	This includes any unidentified land. It could be bare soil, rock, and all unmanaged land areas that do not fall into any of the other categories at a specific time.	5	
Water bodies	This refers to either water bodies or vegetation found in wetlands. Water bodies refer to areas covered or saturated by water that is observable by remote sensing including lakes, oceans, dams, reservoirs, and rivers. Vegetated wetland contains the vegetation associated with these water bodies including papyrus and reeds and riverine trees. In this study, only the water bodies were mapped within this category, while wetland vegetation was mapped as a vegetation category.	6	
Shrubland	Shrubland was mapped as areas with vegetation that fall below the thresholds applied to the forestland category and are not expected to exceed the threshold defined in the forestland definition. The areas mainly consist of a combination of trees, shrubs and grasses. The biomass content here is very different from the open grassland and due to the canopy closure of the woody component; it is possible to differentiate these areas from the open grasslands.	7	

For covered (unexcavated) nests, we used a steel rod to probe into each nest in order to establish the precise location of eggs (Figure 3) in accordance with Champion and Downs (2017). Consequently, to determine the number of eggs in each nest, we carefully excavated the nest to access and count the eggs. Notably, since the survey coincided with egg harvesting for ranching, we placed all the

counted eggs in Styrofoam boxes containing nest substrate in readiness for transportation to the ranch's incubation units. For nests that were found empty (i.e., devoid of eggs), we attempted to establish whether the eggs had already been taken by the assigned egg collectors, taken by other people, damaged by people, eaten by predators, (mainly by monitor lizards), or overrun by floods. Information on whether eggs were taken by designated egg collectors or not was obtained from the egg collectors and ranch agent. Eggs were deemed to have been damaged by humans when they appeared to have been deliberately destroyed using a tool such as a machete and the shells were not scattered. Eggs were considered to have been depredated by monitor lizards when egg shells were scattered around the excavated nests. A nest was considered to be tended when a female crocodile was observed on or around the nest site, and when there were visible signs of soil disturbance, excavation, and crocodile footprints around the nest.

We measured the shortest distance of each nest to water (to the nearest one metre) using a flexible 30-m long measuring tape. However, where the vegetation was too thick to allow direct measurement, or for distances greater than 30 metres, we took a GPS waypoint at the nest and another at the water edge and calculated the distance between the two points using a coordinate distance calculator in accordance with Calverley and Downs (2017).



Figure 3. Locating a crocodile egg nest. (a) Crocodile claw marks visible in the foreground. (b) Egg collectors probing an area identified as a crocodile nesting site to identify the location of a nest using steel rods. (c) Crocodile egg nest with top nest substrate removed

2.4 Data analysis

We overlaid crocodile egg nest GPS locations on the land cover and human disturbance map to visualise the distribution of nest sites among the different human disturbance regimes; low, intermediate and high (Figure 3). Consequently, we used Chi-square goodness of fit test to determine whether the observed frequencies of nests across the different disturbance regimes differed significantly from the expected frequencies. The expected nest frequency was calculated for each disturbance regime based on its proportional coverage of the total area surveyed. We determined the effect size of the discrepancy between observed and expected nest frequencies using Cohen's ω (Cohen, 1988). Specifically, we divided the χ^2 value by the square root of the total number of observed nests (n), and compared the result with 0.1, 0.3 and 0.5, the thresholds for small, medium and large effect sizes, respectively. We determined whether the discrepancy between observed and expected nest frequencies within each disturbance regime was statistically significant by computing a standardized residual as the difference between observed and expected frequencies divided by the square root of the expected frequency, and comparing the resultant value against ± 1.96 , the critical value for the 95% confidence level. Additionally, we conducted *post hoc* pairwise comparisons between disturbance regimes, minimizing Type I error rate using the Bonferroni adjustment method.

We compared nest distance to water among the different disturbance regimes using one-way ANOVA. We used a generalized linear model (GLM) with Poisson error distribution to test the effect of disturbance regime on clutch size. We used binary logistic regression to test the effect of disturbance regime on the presence or absence of eggs, nest tending and predation. We performed all these analyses in the Statistical Package for Social Sciences software (SPSS, Version 20; International Business Machines Corporation [IBM], 2011).

3. RESULTS AND DISCUSSIONS

Overall, shrubland (51%) and forestland (32%) constituted the most extensive land cover types, followed by cropland (9%) (Figures 4 and 5a). All other land cover types were considerably less extensive, with each covering less than 3% of the surveyed river segment. These patterns were generally similar for individual disturbance regimes, except that both absolute and relative areas covered by both cropland and settlement increased with increasing disturbance level (Figures 4, 5b-d and 6a). Segments delineated as having low, intermediate and high disturbance levels had a combined settlement and cropland cover of approximately 2%, 9% and 15%, respectively (Figure 5b-d). The low, intermediate and high disturbance regimes covered approximately 28%, 27% and 46% of the total area of the surveyed river segment, respectively (Figure 6b).

We recorded a total of 99 crocodile nests; 45%, 34% and 20% of these were located in low, intermediate and high disturbance areas, respectively (Figure 7). Overall, there was a significant discrepancy between observed and expected frequencies of crocodile nests across the different human disturbance regimes ($\chi^2(2) = 28.29, p < 0.001$; Figure 7). The effect size of this discrepancy was large as evidenced by a Cohen's ω value of 0.53 against 0.5, which is the threshold for large effect size. Analysis of standard residuals revealed that the observed crocodile nest frequency was 56% lower than expected (standardized residual = -3.7) under high disturbance, whereas it was 69% higher than expected (standardized residual = 3.5) under low disturbance (Figure 7). However, under intermediate disturbance, there was no significant difference (standardized residuals = 1.3) between observed and expected nest frequencies. Further, Bonferroni-adjusted *post hoc* pairwise comparisons showed that nest frequency was 41% and 56% lower ($p < 0.001$) under high than in

intermediate and low disturbance regimes, respectively, whereas it did not differ ($p=0.541$) between the latter two disturbance regimes (Figure 7).

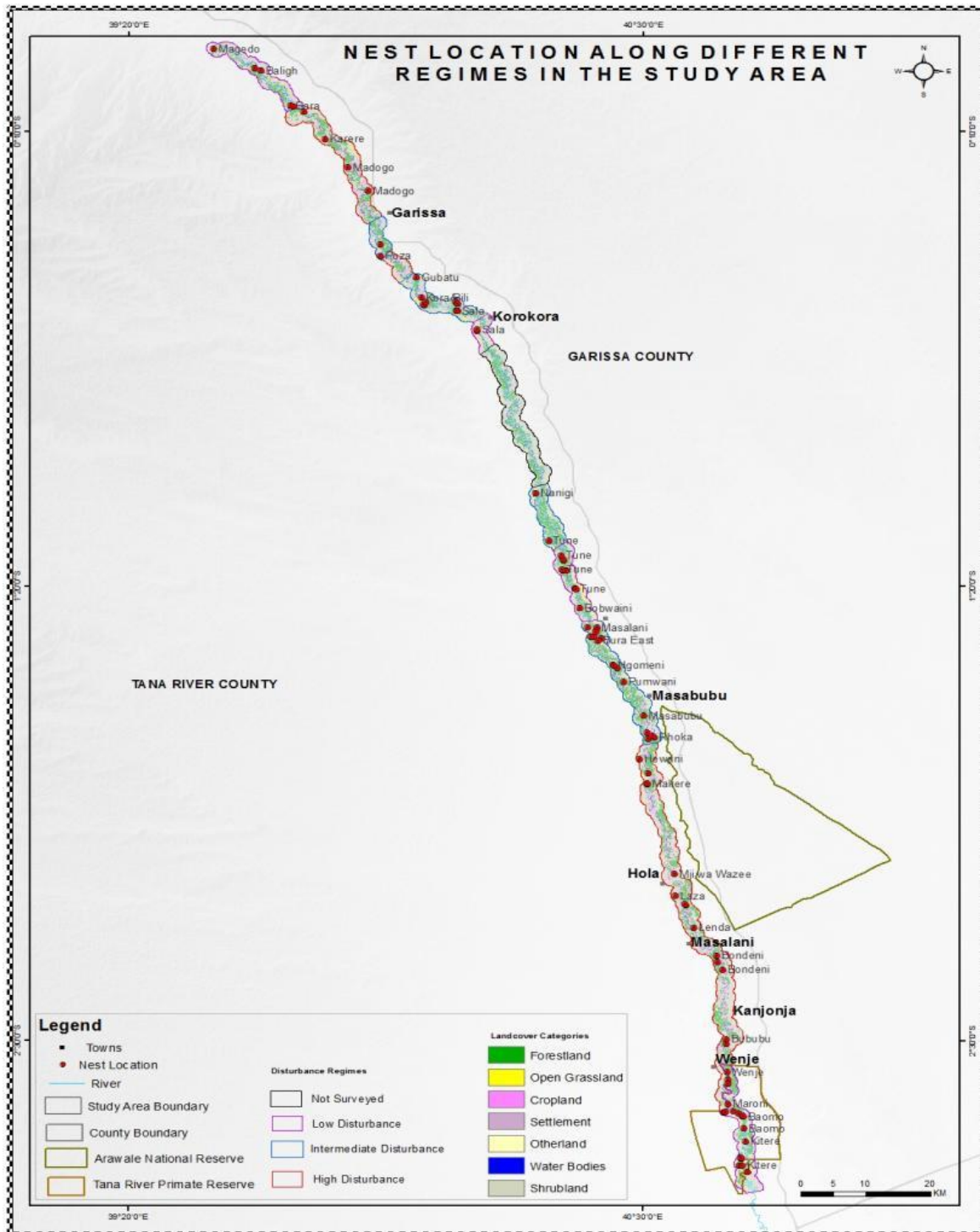


Figure 4. A map showing land cover types, human disturbance regimes and distribution of crocodile egg nests in lower River Tana

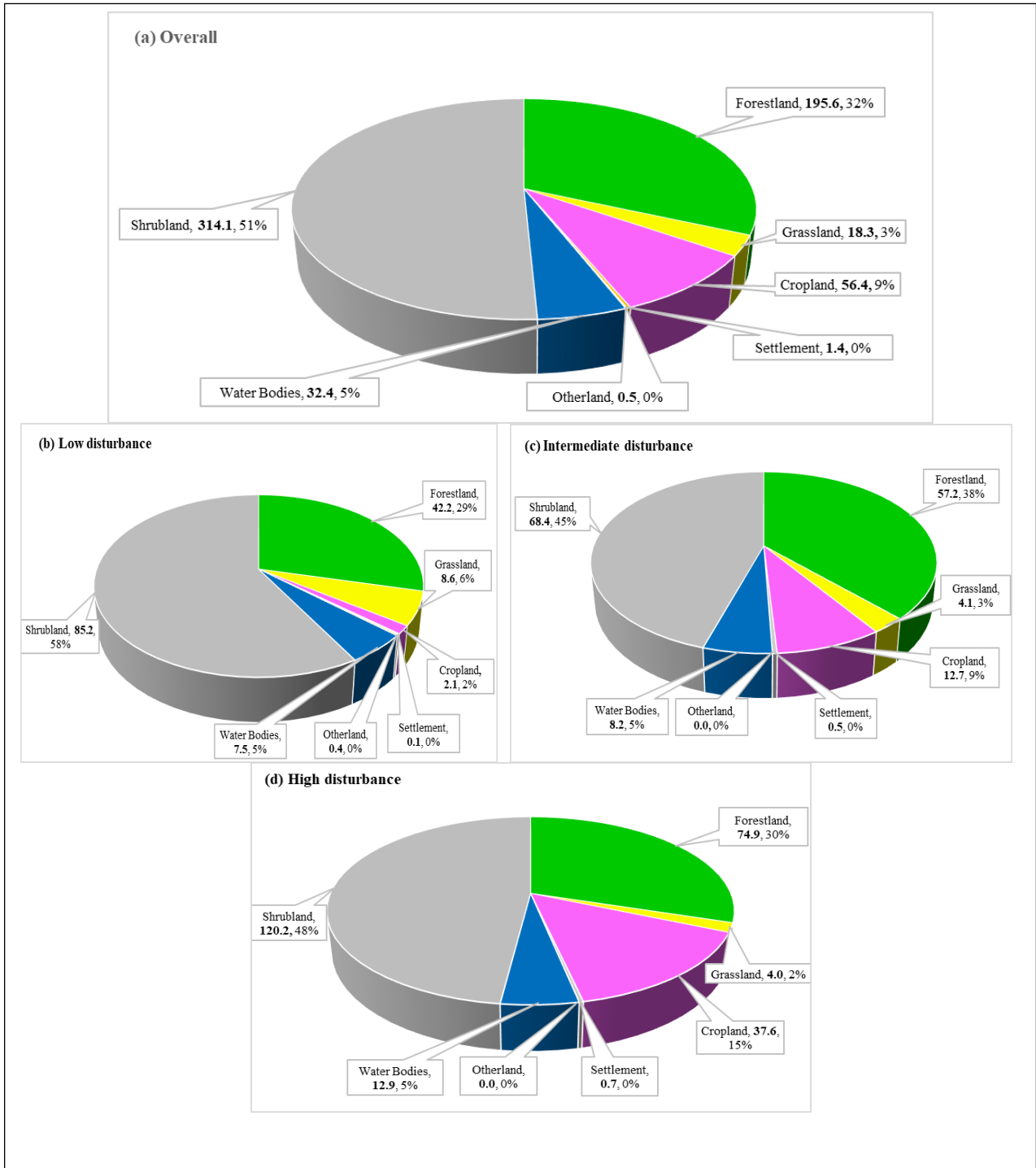


Figure 5. Area (km²; in bold fonts) and percentage cover of different land cover types across the whole of the surveyed area (a), and within disturbance regimes (b, c and d).

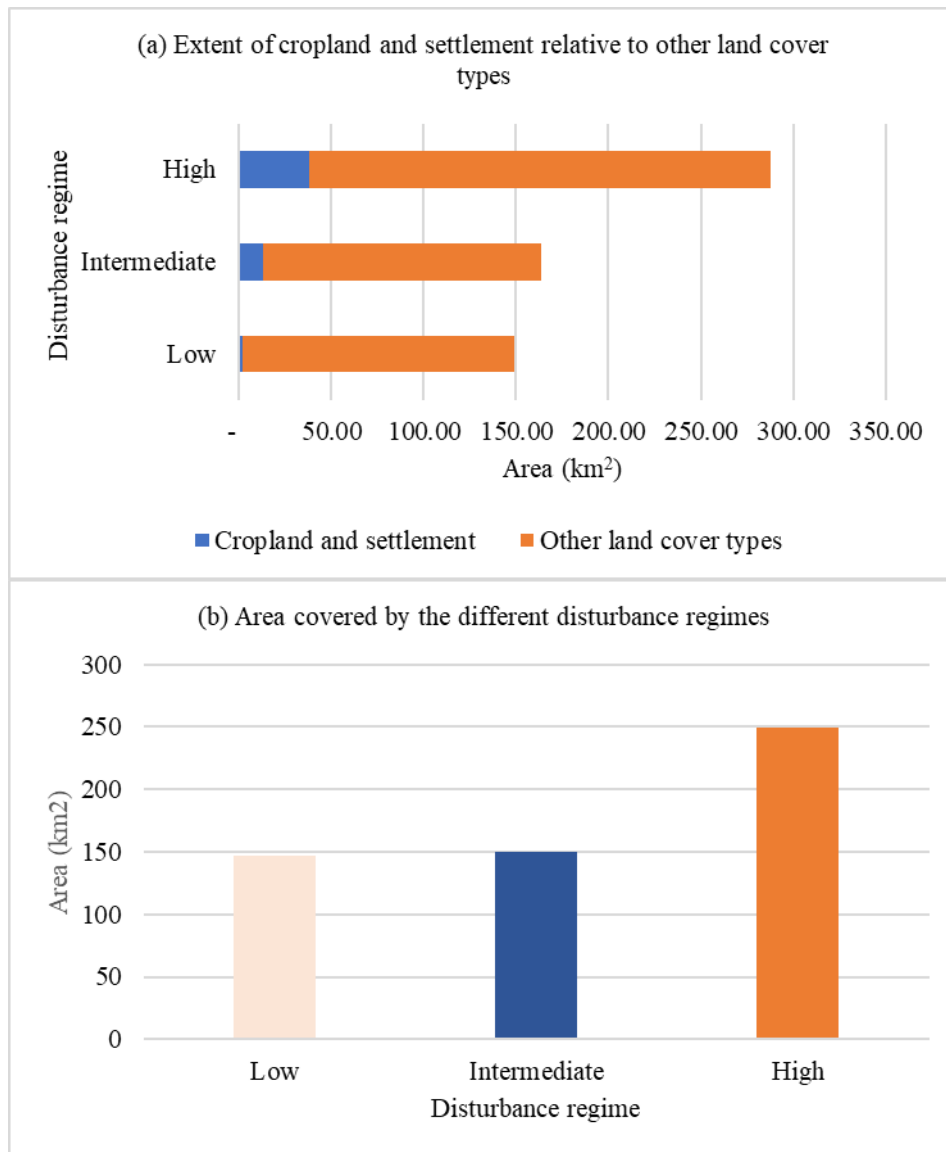


Figure 6. Area covered jointly by cropland and settlement versus natural land cover types- water, forestland, shrubland and grassland (a), and area covered by the different human disturbance regimes (b).

Of the located 99 nests, 82% contained eggs, 85% were tended by females and 8% had been predated upon. Overall, we counted a total of 3,254 eggs and obtained an overall average clutch size of 40.2 ± 1.0 eggs per nest across all disturbance regimes combined. Clutch size averaged 41.0 ± 2.2 eggs, 40.8 ± 2.1 eggs and 39.3 ± 1.4 eggs in high, intermediate and low disturbance regimes, respectively. The effect of human disturbance regime on clutch size was not statistically significant (Wald $\chi^2(1) > .007$, $p > 0.36$; Table 2). Likewise, the effects of disturbance regime on the presence or absence of eggs, nest tending and predation were all not significant (all Wald $\chi^2(1) < 0.1$, $p > 0.999$). The overall mean distance of nests from water across all the three disturbance regimes (low, intermediate and high) was $10.0 \text{ m} \pm 0.8$ (SE). Nest distance from water averaged $7.6 \text{ m} \pm 1.3$,

10.8 m ± 1.4 and 10.5 m ± 1.4 under high, intermediate and low disturbance regimes, respectively. However, this attribute did not differ among disturbance regimes ($F(2, 96) = 1.06, p = 0.350$).

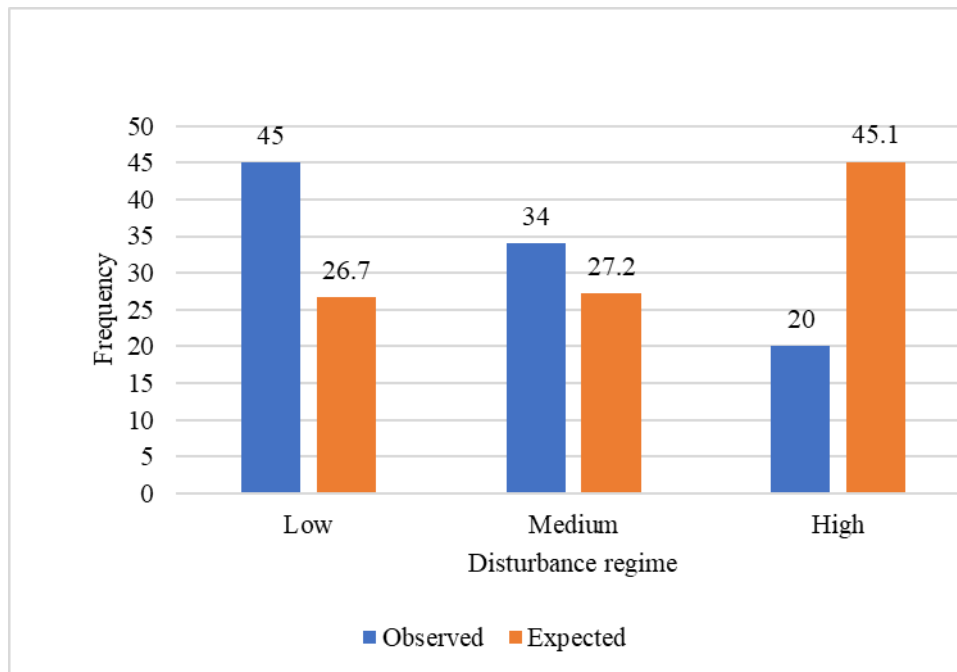


Figure 7. Observed and expected frequencies of crocodile nests across different human disturbance regimes

Our study demonstrates that increasing coverage of cropland and settlement within 1 km of the river to 15% (high disturbance) from 9% (intermediate disturbance) and 2% (low disturbance) diminished the number of Nile crocodile nests by approximately four-tenths and more than half, respectively. Furthermore, our findings indicate that the number of crocodile nests becomes more than half lower than expected under high disturbance, more than two-thirds greater than expected under low disturbance, and does not differ from the expected count under intermediate disturbance. These findings were generally in agreement with our hypothesis that the number of crocodile nests would be lower than expected under high disturbance but not under lower disturbance regimes. However, contrary to our hypothesis, our study shows that several other measured nest attributes (i.e., distance from water, clutch size, tending, presence of eggs, and depredation incidents) are not statistically responsive to changes in disturbance intensity.

The effects of anthropogenic activities on crocodiles have been previously reported in many ecosystems globally (Shacks, 2006; Calverley and Downs, 2017; Somaweera et al., 2019; Mazzotti et al., 2022). However, our study additionally demonstrates the extent to which intensifying human disturbance can reduce the number of Nile crocodile nests in human-dominated landscapes such as the lower River Tana. Our observation of lower than expected nest count under high disturbance, and vice versa, generally compares to previous findings from other regions indicating greater negative responses of Nile crocodiles and other crocodylian species to increasing human disturbance intensity (Nordkvist, 2015; Nyirenda, 2015; Amoah et al., 2021; Pereira et al., 2022).

We attribute the observed lower crocodile nest count under the high disturbance (compared to intermediate and low disturbance regimes) to intensified expansion of agricultural activities and

settlements into crocodile nesting habitat. Specifically, we posit that intensified land conversion directly led to a dramatic reduction in the availability of suitable nesting sites for crocodiles, similar to findings in a southern African riparian landscape (Gibson, 2014). Despite evidence that crocodiles can select suitable patches within highly disturbed landscapes for nesting (Amoah et al., 2021), our study demonstrates that their ability to do so greatly diminishes when 15% of their natural habitat is converted to cropland and settlement.

In addition, increased human encroachment through cultivation and settlement is typically accompanied by the intensification of various human activities such as fishing, sand harvesting, water fetching, livestock grazing and vegetation harvesting, resulting in an overall increase in human presence within crocodile habitat (van der Ploeg et al, 2011; Salem, 2013; Than et al., 2020). Consequently, the lower than expected number of crocodile nests in the high disturbance regime can be partly attributed to increased intensity of these activities and the associated greater physical presence of humans in crocodile habitat, which can negatively affect breeding and nesting activities of crocodiles (Shacks, 2006). Breeding crocodile females usually situate their nests in hidden locations, away from areas accessible to humans (Bourquin, 2007). Therefore, it would be expected that such concealed locations would be far much less available under high levels of disturbance, further explaining our observed lower number of nests across the high disturbance regime.

Crocodiles exhibit a preference for nesting in close proximity to water to enhance nest-guarding against predators and increased hatchling survival (Salem, 2013; Refsnider, 2016; Calverley and Downs, 2017). Our observed mean nest distance from water (10 m) compares well to those reported for Nile crocodiles in other regions (Champion and Downs, 2017; Swanepoel et al., 2000). The overall mean clutch size (40 eggs) observed in our study is well within the normal range of Nile crocodile clutch size of 20-60 eggs (Kyalo, 2008b), and is generally comparable to mean clutch sizes (37-48 eggs) reported for this species in parts of southern Africa (Swanepoel et al., 2000; Khosa et al., 2012). Notably, however, the mean clutch size observed in the current study is remarkably higher than the mean (25 eggs) previously reported for Nile crocodiles in our study region in 2007 (Kyalo, 2008b). This apparent temporal increase in mean clutch size could be attributed to the advanced age of breeding female crocodiles as older females tend to produce larger clutches (Cott, 1961). However, the observed lack of differences in nest distance from water, clutch size, and presence or absence of eggs, nest tending and predation across disturbance regimes suggests that, under the conditions of our study, these attributes are relatively less sensitive to varying human disturbance intensity.

4. CONCLUSIONS

Our study demonstrates that an increasing level of human encroachment, characterised by the expansion of cultivation and settlement negatively affects the Nile crocodile nesting ecology, primarily leading to reduced nest abundance. Among all attributes assessed in this study, nest abundance appears to be the most sensitive and important attribute for tracking the impacts of intensification of human disturbance on crocodile nesting ecology. Furthermore, our findings emphasize that the magnitude of land conversion to farmland and settlement areas should be kept minimal and should not exceed 9% of the total crocodile habitat area to enhance crocodile conservation in such human-dominated landscapes. We recommend the establishment of riparian buffer zones within 1 km from the river in such landscapes to minimize human encroachment into crocodile nesting habitat. In addition, strategic restoration of heavily disturbed crocodile nesting areas should be prioritized in such landscapes.

5. ACKNOWLEDGEMENTS

This research was conducted under the auspices of the National Commission for Science, Technology and Innovation (NACOSTI, Permit Number NACOSTI/P/19/11428/2775) and the Egerton University Research Ethics Review Committee (EUREC, Approval Number EUREC/APP/083/2019). We express our gratitude to the IUCN Crocodile Specialist Group for partially funding the project through the Student Research Assistance Scheme Project 18/28. We extend our appreciation to Dr. Norah Mose and Benson Ibrahim for logistical support. Thanks to Mercelyne Ojwala, Robert Kimutai, Faith Muchiri and Peter Hongo for technical assistance on remotely sensed images and ground-truthing and Calvince Ngaji for support in data analysis. Our sincere thanks to Galaxy egg collectors, ranch supervisors and Kenya Wildlife Service officers for their support during the crocodile nest survey. The support of Dr Kirsten Davies through the International Support Network for African Development (ISNAD-Africa) is greatly appreciated.

6. REFERENCES

- Alam, A., Bhat, M. S., Maheen, M. (2019). Using Landsat satellite data for assessing the land use and land cover change in Kashmir Valley. *GeoJournal*, 85, 1529-1543. Retrieved March 31, 2020, from <https://doi.org/10.1007/s10708-019-10037-x>
- Amoah, E., Danquah, E., Perran Ross, J. (2021). Nesting ecology of west African dwarf crocodiles in a heavily disturbed landscape in Chirehin, Ghana. *International Journal of Ecology*, 2021, e8871631. Retrieved September 10, 2023, from <https://doi.org/10.1155/2021/8871631>
- Aust, P., Boyle, B., Fergusson, R., Coulson, T. (2009). The impact of Nile crocodiles on rural livelihoods in Northeastern Namibia. *South African Journal of Wildlife Research*, 39(1), 57–69. Retrieved April 12, 2020, from <https://doi.org/10.3957/056.039.0107>
- Bailey, K. M., McCleery, R. A., Binford, M. W., Zweig, C. (2016). Land-cover change within and around protected areas in a biodiversity hotspot. *Journal of Land Use Science*, 11(2), 154–176. Retrieved March 31, 2020, from <https://doi.org/10.1080/1747423X.2015.1086905>
- Bhattarai, D., Lamichhane, S., Pandeya, P., Bhattarai, S., Gautam, J., Kandel, R. C., Pokheral, C. P. (2022). Status, distribution and habitat use by Muggers crocodile (*Crocodylus palustris*) in and around Koshi Tappu Wildlife Reserve, Nepal. *Heliyon*, 8(8), e10235. Retrieved August 15, 2023, from <https://doi.org/10.1016/j.heliyon.2022.e10235>
- Bourquin, S. L., Leslie, A. J. (2012). Estimating demographics of the Nile crocodile (*Crocodylus niloticus* Laurenti) in the panhandle region of the Okavango Delta, Botswana: Nile crocodile population ecology. *African Journal of Ecology*, 50(1), 1-8. Retrieved January 8, 2020, from <http://doi.wiley.com/10.1111/j.1365-2028.2011.01285.x>
- Briem, G. J., Benediktsson, J. A., Sveinsson, J. R. (2002). Multiple classifiers applied to multisource remote sensing data. 40 (10), 2291–2299. *IEEE Transactions on Geoscience and Remote Sensing*, 40(10), 2291–2299.
- Butynski, T. M. (2000). *Independent evaluation of Hirola antelope *Beatragus hunteri* conservation status and conservation action in Kenya*. (pp. 1–200) [A Report for the Kenya Wildlife Service the Hirola Antelope Management Committee]. Retrieved April 30, 2023, from DOI: 10.13140/RG.2.1.1129.2246
- Calverley, P. M., Downs, C. T. (2017). The past and present nesting ecology of Nile crocodiles in Ndumo Game Reserve, South Africa: Reason for concern? *Journal of Herpetology*, 51(1), 19–26. Retrieved March 18, 2020, from <https://doi.org/10.1670/13-200>
- Champion, G., Downs, C. T. (2017). Status of the Nile crocodile population in Pongolapoort Dam after river impoundment. *African Zoology*, 52(1), 55–63. Retrieved January 8, 2020, from <https://doi.org/10.1080/15627020.2016.1238321>
- Cheruto, M. C., Kauti M. K., Kasingau, P.D., Kariuki, P. (2016). Assessment of land use and land cover change using GIS and remote sensing techniques: a case study of Makueni County, Kenya. *J. Remote Sensing and GIS*, 5: 175. Retrieved December 10, 2018 from doi:10.4175/2469-4134.1000175
- Convention on International Trade in Endangered Species of Wild Fauna and Flora. (2010). Ranching and trade in ranching specimens of species transferred from Appendix I to Appendix II. (Resolution Conf. 11.6 (Rev. CoP15)). Retrieved June 6, 2020, from <https://www.cites.org/eng/res/11/11-16R15.php>
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed). L. Erlbaum Associates.
- Combrink, X., Korrübel, J. L., Kyle, R., Taylor, R., Ross, P. (2011). Evidence of a Declining Nile crocodile (*Crocodylus niloticus*) population at Lake Sibaya, South Africa. *South African Journal of Wildlife Research*, 41(2), 145–157. Retrieved January 8, 2020 from <https://doi.org/10.3957/056.041.0201>

- Combrink, X., Warner, J. K., Downs, C. T. (2016). Nest predation and maternal care in the Nile crocodile (*Crocodylus niloticus*) at Lake St Lucia, South Africa. *Behavioural Processes*, 133, 31–36. Retrieved March 10, 2020, from <https://doi.org/10.1016/j.beproc.2016.10.014>
- Combrink, X., Warner, J. K., Downs, C. T. (2017). Nest-site selection, nesting behaviour and spatial ecology of female Nile crocodiles (*Crocodylus niloticus*) in South Africa. *Behavioural Processes*, 135, 101–112. Retrieved March 3, 2020, from <https://www.sciencedirect.com/science/article/abs/pii/S0376635716304004>
- Cott, H. B. (1961). Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *The Transactions of the Zoological Society of London*, 29(4), 211–356. Retrieved April 5, 2020 from <https://doi.org/10.1111/j.1096-3642.1961.tb00220.x>
- Crocodile Specialist Group. (2003). *African Crocodile Survey Database*. UNEP and WCMC. Retrieved October 10, 2020, from www.crocsurveys.net/content/SurveyDetails/310
- Dzoma, B. M., Sejoe, S., Segwagwe, B. V. E. (2008). Commercial crocodile farming in Botswana. *Tropical Animal Health and Production*, 40(5), 377–381. Retrieved August 29, 2020, from <https://doi.org/10.1007/s11250-007-9103-4>
- Eaton, M. J., Manolis, S. C., Stevenson, C. (2010). *Crocodiles: Status Survey and Conservation Action Plan*. Crocodile Specialist Group of the Species Survival Commission. Retrieved October 20, 2020, from <http://www.iucnscg.org/pages/General-Crocodilian-Topics.html>
- European Space Agency. (2020). *About Copernicus Sentinel-2*. Copernicus Europe's Eyes on Earth. Retrieved May 1, 2023, from <https://sentinel.esa.int/documents/247904/4180891/Sentinel-2-infographic.pdf>
- Evans, L. J., Jones, T. H., Pang, K., Saimin, S., Goossens, B. (2016). Spatial ecology of estuarine crocodile (*Crocodylus porosus*) nesting in a fragmented landscape. *Sensors*, 16(9), 1527. Retrieved January 8, 2020, from <https://doi.org/10.3390/s16091527>
- Fergusson, R. A. (2010). *Nile crocodile (Crocodylus niloticus)* [Status Survey and Conservation Action Plan]. IUCN Crocodile Specialist Group. Retrieved March 3, 2020, from https://www.iucnscg.org/365_docs/attachments/protarea/15_C-cf25967f.pdf
- Gari, A. (2015, February 20). Under siege: Who is killing crocodiles in Tana River? *The Star Newspaper*. Retrieved August 19, 2023 from, <https://www.the-star.co.ke/sasa/lifestyle/2015-02-20-under-siege-who-is-killing-crocodiles-in-tana-river/>
- Gibson, M. (2014). *Preliminary investigation into anthropogenic and natural disturbance effects on the Nile crocodile (Crocodylus niloticus) in the Mutale River, Limpopo Province*. Master's thesis. Cape Town: University of the Witwatersrand. Retrieved March 22, 2020, from <https://wiredspace.wits.ac.za/items/a7f30f80-977d-49b8-a96c-fafeae46aa6e>
- Government of Kenya. (1996). *Tana River Primate National Reserve. Project Document*. [Project Document]. Kenya Wildlife Service.
- Government of Kenya. (2018). *Tana River County: Second County Integrated Development Plan: 2018-2022* [Budget and Fiscal Plan].
- Hoffman, L. C., Fisher, P. P., Sales, J. (2000). Carcass and meat characteristics of the Nile crocodile (*Crocodylus niloticus*). *Journal of the Science of Food and Agriculture*, 80(3), 390–396. Retrieved September 8, 2020, from [https://doi.org/doi.org/10.1002/1097-0010\(200002\)80:3%3C390::AID-JSFA540%3E3.0.CO;2-G](https://doi.org/doi.org/10.1002/1097-0010(200002)80:3%3C390::AID-JSFA540%3E3.0.CO;2-G)
- International Business Machines Corporation. (2011). *IBM SPSS Statistics 20 Brief Guide*. IBM Corporation. Retrieved December 12, 2022, from <https://www.manua.ls/ibm/spss-20/manual>
- Isberg, S., Combrink, X., Lippai, C., Balaguera-Reina, S. A. (2019). *Crocodylus niloticus: The IUCN Red List of Threatened Species 2019* [dataset]. International Union for Conservation of Nature. Retrieved August 20, 2023, from <http://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T45433088A3010181.en>
- Jyrwa, J. D., Joshi, B. D., Ghosh, A., Mayi, Y., Nipa, M., Anga, N., Pali, M., Thakur, M., Chandra, K., Sharma, L. K. (2020). Dimensions of changing perception towards wildlife conservation in East Siang district of Arunachal Pradesh, Eastern Himalayas. *Global Ecology and Conservation*, 24. Retrieved July 10, 2022, from <https://doi.org/10.1016/j.gecco.2020.e01265>
- Kenya Forest Service. (2013). *Key forest definitions*. Retrieved March 8, 2023, from http://www.kenyaforestservice.org/index.php?option=com_content&view=article&id=406&Itemid=563
- Khosa, P., Imbayarwo-Chikosi, V. E., Hamandishe, V. (2012). Comparative analysis of hatching rates and clutch sizes of Nile crocodile (*Crocodylus niloticus*) eggs collected on- and off-farm in Zimbabwe. *Tropical Animal Health and Production*, 44(4), 905–909. Retrieved August 21, 2020, from <https://doi.org/10.1007/s11250-011-9985-z>

- Kenya National Bureau of Statistics. (2019). *The 2019 Kenya population and housing census* (p. 38). Government of Kenya. Retrieved March 20, 2018, from <https://www.knbs.or.ke/?wpmpro=2019-kenya-population-and-housing-census-volume-i-population-by-county-and-sub-county>
- Kyalo, S. N. (2008a, November 17). *NDF Studies: The Status of and Trade in Nile Crocodile (Crocodylus niloticus) in Kenya* [Case Study]. International Expert Workshop on CITES Non- Detriment Findings, Cancun, México. Retrieved October 20, 2018, from https://cites.org/sites/default/files/ndf_material/WG7-CS1-P.pdf
- Kyalo, S. (2008b). Non-detriment finding studies on Nile crocodile (*Crocodylus niloticus*): The status of and trade in the Nile crocodile in Kenya. *NDF Workshop Case Studies, Workshop Case Studies*, 16. Retrieved March 23, 2023, from https://www.cites.org/sites/default/files/ndf_material/WG7-CS1.pdf
- Maingi, J. K. (1998). *Land Use and Vegetation Change in Response to River Basin Development in the Lower Tana Basin of Eastern Kenya*. Doctoral dissertation. Tucson: The University of Arizona.
- Manolis, S. C., Webb, G. J. W. (2016). *Best Management Practices for Crocodylian Farming*. Crocodile Specialist Group of the Species Survival Commission. Retrieved September 6, 2020, from https://www.iucnscg.org/365_docs/attachments/protarea/227c50b2e92bf796cbb1573bdd348b12.pdf
- Mazzotti, F. J., Balaguera-Reina, S. A., Brandt, L. A., Briggs-González, V., Cherkiss, M., Farris, S., Godahewa, A. (2022). Natural and Anthropogenic Factors Influencing Nesting Ecology of the American Crocodile in Florida, United States. *Frontiers in Ecology and Evolution*, 10, 1-10. Retrieved September 10, 2023, from <https://www.frontiersin.org/articles/10.3389/fevo.2022.904576>
- Ministry of Environment and Natural Resources. (2012). *Kenya wetlands atlas*. Government of Kenya and United Nations Environment Programme. Retrieved October 20, 2020, from https://na.unep.net/atlas/datlas/sites/default/files/Kenya_Wetlands.pdf
- Modha, M. L. (1967). The ecology of the Nile crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. *African Journal of Ecology*, 1967(1) 74-95. Retrieved August 23, 2020, from, <http://doi.wiley.com/10.1111/j.1365-2028.1967.tb00763.x>
- Mohamed, A. (2015). *Underlying causes of inter-ethnic conflict in Tana River County, Kenya*. Master's thesis. Winnipeg: University of Manitoba.
- Murray, C. M., Crother, B. I., Doody, J. S. (2020). The evolution of crocodylian nesting ecology and behavior. *Ecology and Evolution*, 10(1), 131–149. Retrieved March 22, 2020, from <https://doi.org/10.1002/ece3.5859>
- Njoroge, P., Yego, R., Muchane, M., Githiru, M., Njeri, T., Giani, A., Nuova, T. (2009). A survey of the large and medium sized mammals of Arawale National Reserve, Kenya. *Journal of East African Natural History*, 98(1), 119–128. Retrieved April 30, 2023, from <http://dx.doi.org/10.2982/028.098.0108>
- Nordkvist, M. (2015). *Anthropogenic disturbance along the Kinabatangan River in Borneo, Malaysia and the distribution and abundance of the saltwater crocodile (Crocodylus porosus)*. Minor Field Study 195. Uppsala: Uppsala University. Retrieved August 23, 2023, from <http://files.webb.uu.se/uploader/858/MFS-195nordkvistliten.pdf>
- Nyirenda, V. R. (2015). Spatial variability of Nile crocodiles (*Crocodylus niloticus*) in the lower Zambezi River reaches. *Herpetological Conservation and Biology*, 10(3), 874–882.
- Odhengo, P., Matiku, P., Nyangena, J., Wahome, J., Opa, K., Munguti, B., Koyier, G., Nelson, P., Mnyamwesi, E. (2014). *Tana River Delta Strategic Environmental Assessment*. Ministry of Lands.
- Pereira, A. C., Portelinho, T. C. G., Malvasio, A. (2022). Population Ecology and Human Disturbance Effects on Two Caiman Species in the Southern Brazilian Amazon. *South American Journal of Herpetology*, 23(1), 32–41. Retrieved September 10, 2023, from <https://doi.org/10.2994/SAJH-D-19-00110.1>
- Pooley, S. (2016). A cultural herpetology of Nile crocodiles in Africa. *Conservation and Society*, 14(4), 391. Retrieved March 7, 2020 from <https://doi.org/10.4103/0972-4923.197609>
- Refsnider, J. M. (2016). Nest-site choice and nest construction in non-avian reptiles: Evolutionary significance and ecological implications. *Avian Biology Research*, 9(2), 76–88. Retrieved March 26, 2020, from <https://doi.org/10.3184/175815516X14490631289752>
- Rotich, B., Kindu, M., Kipkulei, H., Kibet, S., Ojwang, D. (2022). Impact of land use/ land cover changes on ecosystem service values in the Cherangany hills water tower, Kenya. *Environmental Challenges*, 8 (2022) 100576
- Salem, A. H. I. (2013). Habitat Vulnerability for the Nile Crocodile (*Crocodylus Niloticus*) in Nasser Lake (Egypt). *Transylvanian Review of Systematical and Ecological Research*, 15(1), 19–32. Retrieved March 26, 2020, from <https://doi.org/10.2478/trser-2013-0003>
- Shacks, V. (2006). *Habitat vulnerability for Nile crocodile (Crocodylus niloticus) in the Okavango Delta, Botswana*. Master's thesis. Stellenbosch: University of Stellenbosch]. Retrieved August 28, 2023, from

<https://www.researchgate.net/publication/44138463> Habitat vulnerability for the Nile crocodile *Crocodylus niloticus* in the Okavango Delta Botswana

- Somaweera, R., Brien, M., Shine, R. (2013). The role of predation in shaping crocodylian natural history. *Herpetological Monographs*, 27(1), 23. Retrieved March 22, 2020, from <https://doi.org/10.1655/HERPMONOGRAPHS-D-11-00001>
- Somaweera, R., Brien, M. L., Sonneman, T., Didham, R. K., Webber, B. L. (2019). Absence of evidence is not evidence of absence: Knowledge shortfalls threaten the effective conservation of freshwater crocodiles. *Global Ecology and Conservation*, 20. Retrieved July 31, 2020, from <https://doi.org/10.1016/j.gecco.2019.e00773>
- Somaweera, R., Shine, R. (2013). Nest-site selection by crocodiles at a rocky site in the Australian tropics: Making the best of a bad lot: constraints on nest- site selection. *Austral Ecology*, 38(3), 313–325. Retrieved March 21, 2020 from <https://doi.org/10.1111/j.1442-9993.2012.02406.x>
- Swanepoel, D. G. J., Ferguson, N. S., Perrin, M. R. (2000). Nesting ecology of Nile crocodiles (*Crocodylus niloticus*) in the Olifants River, Kruger National Park. *Koedoe- African Protected Area Conservation and Science*, 43(2), 35–46. Retrieved March 3, 2020, from <http://dx.doi.org/10.4102/koedoe.v43i2.197>
- Terer, T., Ndiritu, G. G., Gichuki, N. (2004). Socio-economic values and traditional strategies of managing wetland resources in Lower Tana River, Kenya. *Hydrobiologia*, 527(1), 3–15. Retrieved July 16, 2023, from <https://doi.org/10.1023/B:HYDR.0000043332.9636.c5>
- Than, K. Z., Zaw, Z., Hughes, A. C. (2020). Integrating local perspectives into conservation could facilitate human–crocodile coexistence in the Ayeyarwady Delta, Myanmar. *Oryx*, 56(1) 82-90. Retrieved August 27, 2023, from <https://doi.org/10.1017/S003060532000037X>
- Thorbjarnarson, J. (1992). *Crocodyles: An Action Plan for Their Conservation* (p. 150). Crocodile Specialist Group of the Species Survival Commission. Retrieved April 5, 2020, from http://www.iucncsg.org/365_docs/attachments/protarea/d533f0e76d85cb061de6b7c8fff5766c.pdf
- Utete, B. (2021). A review of the conservation status of the Nile crocodile (*Crocodylus niloticus* Laurenti, 1768) in aquatic systems of Zimbabwe. *Global Ecology and Conservation*, 29, 2021 e01743, 1-20. Retrieved October 11, 2022, from <https://doi.org/10.1016/j.gecco.2021.e01743>.
- van der Ploeg, J., Cauillan-Cureg, M., van Weerd, M., Persoon, G. (2011). ‘Why must we protect crocodiles?’ Explaining the value of the Philippine crocodile to rural communities. *Journal of Integrative Environmental Sciences*, 8(4), 287–298. Retrieved October 11, 2022, from <https://doi.org/10.1080/1943815X.2011.610804>
- Wallace, K. M., Leslie, A. J. (2008). Diet of the Nile crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Journal of Herpetology*, 42(2), 361–368. Retrieved April 18, 2023, from <https://doi.org/10.1670/07-1071.1>