Water depth, vegetation height, and offshore distance are critical factors in nest-site selection for Grey Crowned Crane at Lake Ol' Bolossat, Kenya

Wanyoike Wamiti[1], Nathan Gichuki[2], Dorcas Sigana[2], Peter Njoroge[1], Kerryn Morrison[3], George Ndung'u[4], and Juan Rubalcaba[5]

[1]National Museums of Kenya
[2]University of Nairobi
[3]Endangered Wildlife Trust
[4]Crane Conservation Volunteers
[5]McGill University

October 5, 2020

Abstract

Grey Crowned Crane Balearica regulorum is described as an icon of Africa's wetlands and grasslands and is listed as Endangered on the IUCN Red List of Threatened species. Conservation efforts are partially hindered by lack of information on factors influencing breeding productivity, such as nest-site selection. Factors influencing nest-site selection were investigated at Lake Ol' Bolossat, a 43.3 km2 wetland located in the central Kenya from 30 paired nests. Generalized Linear Mixed-Effects Models were used to analyse the relationship between factors influencing nest-site selection by cranes and variables that were predicted to have a compelling influence on nest-site selection besides i) food and nesting materials availability i.e. the offshore distance of the nest and water depth, and ii) nest concealment and susceptibility to predation i.e. vegetation height and grazing intensity. Results show that variables which had a significant influence on nest-site selection were: water depth (p=0.005), the offshore distance from the nest (p=0.037), and vegetation height (p=0.035). Cranes located their nests in water points above 50 cm deep, vegetation height of 60-90 cm, and preferably 100 m offshore. A minimum of 103 territorial pairs, both breeding and non-breeding cranes, were recorded. The middle section of the lake had the highest number (52), while north and south had 32 and 19 pairs respectively. The mean distance between any two pairs was 302.53±17.02 (SE) meters. This study sheds some light on the understanding of characteristics of Grey Crowned Crane's nesting sites that will facilitate manipulation and management of breeding sites. Lake Ol' Bolossat is consequently a critical breeding site with a substantial role in the species' population recovery and survival. A wetland management option that aims at achieving sustainable use of lake's resources by local communities without compromising needs of wildlife is highly commended.

INTRODUCTION

Knowledge of environmental features that determine habitat quality is critical to developing effective strategies for preserving and restoring natural areas (Hobbs, 2003). Nest-site selection is an integrative behavioural process that evolved to maximize reproductive success (Catlin et. al., 2019). Therefore, understanding what key variables influence nest-site selection in a species is the first step towards its effective management and conservation (Hobbs, 2003; Swaisgood et. al., 2017; van de Loock, 2019).

Nest-site selection involves the specific choice of a site to build a nest from all possible sites (Burger, 1985). This choice must: avoid or reduce risks of predation (Holway, 1991; Götmark, Blomqvist, Johansson & Bergkvistv, 1995), or increase offspring survival (Kolbe & Janzen, 2002). Nest-sites are hence an important part of an animal's niche (Gould, 2008), and a major determinant of reproductive success for many organisms since the quality of a nest-site is often linked to a species breeding success (Hatchwell, Russell, Fowlie & Ross, 1999). It is also a fundamental factor in the survival of a species through generations and is often a poorly understood component of many organisms' reproductive investment (Baden, 2018). The choice of a nest-site determines the available resources and threats that the animal and its offspring encounter, making it an important fitness-related decision (Tolvanen et. al., 2018).

While information on the breeding behaviour of most of the 15 extant species of cranes is available, it is cited as lacking for Grey Crowned Crane *Balearica regulorum* . Walkinshaw (1964) wrote on taxonomy of this species where he identified one genus (*Balearica*), two species (*B. regulorum, B. pavonina*) and four races, two in each species. Standing at 100-110 cm, adults appear similar in plumage but the male is larger (Figure 1; Walkinshaw, 1964; Archibald & Meine, 1996). The species occupies a mixture of wetlands and open grasslands or savanna, and human-modified habitats such as cropland and irrigated fields (Archibald & Meine, 1996; Austin, Morrison, & Harris, 2018). They are omnivores feeding on seeds, fresh tips of grasses, insects and small vertebrates (Pomeroy, 1980; Archibald & Meine, 1996). The cranes population at Lake Ol' Bolossat share the marshes with several avian groups such as herons, ducks, geese and ibises.

Grey Crowned Crane is a solitary bird (living as a pair or a family unit) during the breeding season whereas the non-breeders congregate in foraging fields forming flocks. In eastern Africa, cranes breed all year round (Archibald & Meine, 1996). Mating for life, the nesting behaviour starts with courtship dance with the male as the aggressor (Walkinshaw, 1964). They nest in moist habitats preferring those with a standing water of 80-180 cm deep with knee- and shoulder-high sedges where the nest platform is usually constructed over a mound of heaped aquatic vegetation collected around the nest-site by both sexes (Walkinshaw, 1964). A clutch of 1-4 bluish-white eggs that turn brownish through the 28-30 days incubation period are laid, with an average of 2.53 and a mode of 3 eggs (this study). In Kenya, breeding cranes have been reported from across where they occur. At Lake Ol' Bolossat, the breeding season variably start between April and August into the dry season in March-February, and may last over 12 months in years with good precipitation.

Although still Africa's most abundant crane species, its population has been described as declining over the years. Urban (1988) estimated a population of 100,000 individuals, and a decade later, at 85,000-95,000 (Urban, 1996). Other estimates have been 50,000-64,000 (Beilfuss, Dodman, & Urban, 2007), and 26,500-33,500 (Morrison, 2015). The Kenyan population too has declined from 35,000 (Urban, Fry & Keith, 1986), 10,000-12,500 (Morrison, 2015) and 8,000-10,000 (Wamiti et al., 2020). As such, this species is listed as Endangered on the IUCN Red List of Threatened Species. This is as a result of continued population declines attributed to habitat loss and fragmentation, and illegal removal of birds and eggs from the wild for food, traditional use, domestication and international illegal trade market (BirdLife International, 2020).

On 4^{th} July 2018, an area of 147 km^2enclosing the lake and a riparian zone was gazetted as a Protected Wetland Area under Section 42(2) of the Environmental Management and Coordination Act (EMCA), No. 8 of 1999 [Revised 2012]. Prior to this, operative management of the lake's diverse resources has been largely absent. This has been the main cause of habitats degradation that affects many species including Grey Crowned Crane. This declaration provides for, among others, development of a comprehensive management plan (process near conclusion) and regulation on sustainable use of resources. The lake was designated as an Important Bird Area in March 2008 following confirmation of globally-threatened birds (Wamiti et al., 2008). Despite Morrison (2015) having not listed it as one of Kenya's fundamental sites for the Grey Crowned Crane, recent research has given away that the lake is indeed a population stronghold, ranking second in the country (Wamiti et al., 2020). Except for a few studied breeding sites (e.g. Gichuki, 1993), information on the number of breeding pairs in different parts of Kenya is currently unavailable. This study makes a substantial attempt to contribute to this knowledge gap.

A literature exploration on Grey Crowned Crane's published material in Google Scholar and WorldWideScience implied that bulk of this has been on conservation (e.g., Meine & Archibald, 1996; Beilfuss, Dodman, & Urban, 2007) and population and ecology (e.g., Gichuki, 1993; Amulike, Fuller, Houlihan Griffin, 2020) while that on breeding densities is largely lacking. Morrison (2015), describing the Grey Crowned Crane as an icon of Africa's wetlands and grasslands, has listed factors influencing breeding productivity as an essential knowledge gap that hinder effective implementation of the species management and conservation actions. The purpose of this study was, therefore, to contribute to this knowledge gap.

Specifically, we investigated the critical factors influencing nest-site selection of the Grey Crowned Crane at Lake Ol' Bolossat. We measured variables at the nests that are known to have compelling biological influences on the choice of a nest-site location based on i) food and nesting materials availability, and ii) nest concealment and susceptibility to predation. We hence hypothesized that cranes select sections of the lake with higher water depth (as a proxy of the availability of macro invertebrates and small aquatic vertebrates – e.g. Baumgärtner, Mörtl & Rothhaupt, 2008), while avoiding flooding areas close to the shore. They also choose nest-sites that are inaccessible and concealed from terrestrial predators (e.g. Jobin & Picman, 1997; Jedlikowski, Brambilla & Suska-Malawska, 2014). Therefore, the preference for a nest-site is predicted to be positively related to both water depth and offshore distance from the nest. Moreover, factors that reduce the complexity of vegetation structure around the nest such as grazing might impede cranes to hide their nests from predators. Therefore, nest-site selection is predicted to be negatively affected by grazing intensity and positively affected by vegetation height. The number and distribution pattern pairs occupying territories were also estimated. This study's information will be important for the conservation and management of key breeding sites of this endangered species in Kenya and other range States across Africa.

METHODS AND MATERIALS

Study area

This study was carried out at Lake Ol' Bolossat (0°5'24.84"S, 36°25'4.77"E; elevation 2330 m above sea level, Figure 2) from December 2017 to October 2019. This lake is a 43 km^2 inland lacustrine wetland located in the central highlands of Kenya in Nyandarua County. It has characteristic features of Rift Valley lakes such as being shallow and narrow (stretches for c.30 km oriented in a north-south direction). The diversity of vegetation creates a mixture of habitats and microhabitats – ranging from open water to perennial marshes. The open water occupies c.23 km^2 from the central part towards the south, where the lake is wider (c.4 km) and deeper (1.5-2.5 m). The rest of the area (c.20 km^2) is comprised of marshes, dominated by sedges, for example *Cyperus*sp., *Papyrus* sp. (only found in the extreme northern end), and*Typha* sp., and this is the available habitat for waterfowl such as Grey Crowned Crane that use them for foraging, roosting, nesting and rearing chicks.

The lake basin and riparian grasslands are heavily intruded by humans for quarrying, settlements, crop farming and livestock grazing. Grazing happens throughout the year, with the number of livestock increasing during the dry season (from December to March) in most years. The study area falls within an equatorial type of climate receiving a bimodal rainfall pattern as described by Brown & Britton (1980). However, this pattern is no longer predictable due to the effects of climate change as experienced from field observations during the study period. For example, the 2017/2018 breeding season, whose commencement is marked by nest construction and egg-laying, lasted between July and February (8 months), compared to 13 months (April 2019 – April 2020). Romírez et. al. (2018), reporting climate change as an emerging issue in waterfowl communities (and wetlands) conservation, predicts that it will affect them in different ways depending on their life-history strategies, with resident species (like Grey Crowned Crane) being affected more than seasonal visitors. There are over 120 man-made or natural wetlands around the lake ranging in size from 420m^2 to 211 ha that are also used by cranes for feeding, roosting and nesting, but none was included in this study due to a few accessible nests and their ecological features variability compared to the lake.

The shoreline was divided into 17 sections to identify critical cranes breeding sites described using village names: Ziwani, Mairo-Inya, Githungucu, Kanguyo, Ngurumo, Makereka, Iria-Ini, Gakoe, Kirima, Mugathika, Mukindu, Bahati, Karandi, Fuleni, Gatumbiro, Kanguu and Kianjata. These sites were grouped into three by dividing the lake into 3 parts (north, middle and south; Figure 2) each of c.10 km long. These sections helped to identify critical areas for cranes.

Survey and mapping of territorial pairs

Mapping of crane pairs occupying territories was carried out to determine the number and positions (distribution) of most (if not all) of the cranes utilising the lake as a nesting site. The entire 80 km long shoreline enclosing the lake was accessed at suitable locations that were 1-2 km apart from which pairs of cranes were comprehensively searched for presence/absence in the marshes using a pair of 10x42 binoculars and a telescope. Since cranes occupy territories with high vegetation cover during the breeding period, pairs are difficult to detect in their breeding territories. Therefore, performing a regular survey protocol (e.g., systematic sampling of equally sized plots around the shoreline) might require a higher sampling effort. Instead, walking or driving in motorable areas along the shoreline in a non-systematic way ensured substantial coverage of the sections to warrant that no pairs were undetected. Searching was made easier because of the visibility of the cranes due to their large body size and white wing patches. Vegetation height may however have affected detection of pairs as this varied across the lake. When a pair was present, the location was marked with a GPS and its relative position inside the wetland approximated in Google Earth Pro. The narrow (120-450 m) width of the lake, a contracted fringe of marshes between the shoreline and the open water, and sometimes absence of emergent macrophytes, improved detection of cranes.

According to Hinde (1956), a territory is 'any defended area', and is an outcome of two distinct, independent tendencies, i.e. site attachment and (intraspecific) hostility (Tinbergen, 1957). A crane territory was hence considered as having been occupied by a pair if either or all of the following observations were made: i) gathering nesting material, building a nest or pair present in a site with a complete or incomplete nest ii) seen lying on the nest hence contemplated as incubating), iii) rearing a flightless chick(s), and to a lesser extent iv), pair was recorded present more than once in a specific site and showed some intimate courtship behaviour such as standing face to face with bills touching, head bobbing or copulating.

Mapping and confirmation of pairs was carried within a week during the peak of the breeding season of 2017/2018 season in December 2017 to detect number of pairs that had occupied territories. Subsequent, infrequent visits continued throughout the study period to monitor breeding activities, detect new nests that were accessible for measuring, and to collect data for other objectives of a broader study. Since the study population was unmarked, observations across time pertain to site re-use or its continued use by the same or different individuals. Breeding season was contemplated as the period between laying of the first egg and fledging of the last chick, the duration of which was not uniform in the two seasons. Pairs taking up territories (e.g. late breeders) after the initial one-week survey were not included as these could have been previously located pairs changing positions as this may have exaggerated the minimum number of territorial pairs. Accessible nests were however measured throughout the study period to increase the sample size and provide for seasonality.

Nest searching and nest-site measurements

Understanding habitat features necessary for cranes to choose a site to locate a nest in the marshes necessitated nests access after mapping of territorial pairs. This was carried out between December 2017 and October 2019, thus traversing three breeding seasons. Location of nests was discerned from cues such as nesting pair behaviour when an individual was going for a nest relief. A pair of 10x42 binoculars and a telescope were additionally used to scan marshes for incubating cranes. Collecting data on nesting waterfowl however involves potential disturbance to nesting birds, through direct (e.g., handling of eggs) or indirect (e.g., walking near birds on nests) effects (Austin & Buhl, 2008). Grey Crowned Crane nests are also difficult to locate from the ground (Morrison & Bothma, 1998). With these considerations, nests were not actively searched as this would have possibly resulted to trampling on vegetation in the breeding habitats, cause disturbance to nesting birds and expose clutches and chicks to egg poachers. Nests were thus visited once to record measurements.

Measurements of variables at an active nest-site (i.e. a nest having an egg and/or chick) and at the random nest-sites followed Dwyer & Tanner (1992) and Wu, Zhu, Zhang & Yang (2009). A random nest-site for each active nest was selected to compare characteristics of active nests (presence, scored as 1) with those of randomly-selected sites (unused areas or absent nests, scored as 0). The random nest-sites were placed at 15-25m in any direction of the actual nest to avoid territory overlap with neighbouring nests (this study established a minimum distance of 47 m), and to ensure this random location was within the marshes (for nests located very close to the shoreline). Random nest-sites were not necessarily sites that cranes might never, or have never used before, but were unused sites during that specific season. Each pair of nests (active and randomly-selected) were then coded and included as a random factor in the mixed-effect models to control for possible non-independence between pair of nests. Some of the measurements recorded were: nest dimensions, mean water depth and vegetation height (over four samples taken at 1.5 m from centre of the nest in each cardinal point), offshore distance of nest, distance to the nearest active nest, distance of nearest homestead, and grazing (from livestock or wildlife) intensity that was assessed around the nest and recorded as either 0 (no faecal remains, vegetation intact, no spoors), 1 (low: scattered faecal, slight grazing, scattered spoors), 2 (medium: faecal remains evident, vegetation grazing more evident) or 3 (high: faecal remains around the nest, dense spoors and intensive grazing).

Data analyses

Generalized Mixed-Effects Linear Models were chosen assuming binomial family and logit link function to investigate how the selection of a nest-site (1, presence of nest *vs* 0, absence of nest) was influenced by four of the variables measured. These were: water depth, vegetation height, offshore distance of the nest, and grazing intensity. The identity of the pair of nests was included as a random intercept in the models to control for potential non-independence of paired nests. Test for multi-collinearity (using the Variance Inflation Factor, VIF) and over-dispersion (computing the parameter Φ) were performed in all models, and predictor variables were log-transformed for normalization.

An information-theoretic approach was used to examine the importance of each predictor variable (Burnham & Anderson, 2002). The full model including the four variables (i.e., water depth, vegetation height, offshore distance of the nest and grazing intensity) was compared against simpler models with all possible combination of predictor variables (random factor and intercept always included) using the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). Interaction and quadratic terms were not included in the analyses because no prior hypotheses justify including these terms, and the small sample size limits the capacity of inferring complex interactions between predictor variables. The significance values of the predictor variables in the best candidate model (i.e., the one with the lowest AICc) were then computed using Type III Wald chi-square test. Wald test helps to find out if explanatory variables in a model are significant (i.e. if they add something to the model) (Glen, 2020). Mixed-effect models were fitted using the R package *blme* (Chung et al., 2013) in R v3.5.3 (R Core Team, 2019).

Google Earth Pro was used to approximate distances between any two neighbouring territorial pairs within a group of nests in each of the three sections of the lake.

RESULTS

Factors influencing nest-site selection

Correlations among predictor variables (water depth, vegetation height, offshore distance of the nest and grazing intensity) were first considered to test for multicollinearity. The VIF values were low (<1.3), and models did not show evidence of overdispersion (Φ [?] 1), and therefore all predictor variables were included in the model without correcting for multicollinearity or overdispersion. The model selection procedure yielded a single best model (ΔAICc <2) with the predictor variables i) water depth, ii) vegetation height, and iii) offshore distance of the nest (Table 1). These variables had a significant influence on nest-site selection: water depth (p =0.005), offshore distance of the nest (p =0.037), and vegetation height (p =0.035) (Table 2).

A total of 30 nests out 63 active nests and an equal number of randomly selected nest-sites, were measured. These nests were distributed in all the three sections of the lake (north 14, middle 9, south 7), thus were a representative of crane's nesting-sites. The nests were located in the lake's marshes with varying levels of standing water, the mean water depths being north (35.76 cm), middle (55.76 cm) and south (64.86 cm), and a range of 14.2–123.63 cm. Cranes located their nests in water points above 50 cm deep, vegetation above 60-90 cm, and preferably 100 m offshore (Figure 3).

Distribution and number of territorial pairs

Lack of adequate detection probability data limited computation of pair densities since systematic sampling was not adopted. However, the distribution pattern was described. Territorial pairs in the lake mostly occurred in clusters (clumped) in local sites such as Kianjata, Makereka, Kirima and Fuleni (Figure 2). In other parts of the lake, pairs were randomly distributed in a linear manner where the marshes breadth was narrow (100-500 m wide) such as between Ziwani and Kanguu (Figure 2). A total of 103 pairs were mapped during the 2017/2018 breeding season (Figure 2). However, only 61% attempted breeding (i.e. a pair was observed as at least incubating). The highest number of pairs were found in the middle section (52) followed by the southern section (32) while 19 were in the north.

The mean distance between any two neighbouring crane pairs (breeding or territorial) was 302.53±17.02 (SE) m, and a minimum and maximum of 47 m and 759 m respectively. Majority of the pairs' (n =20) positions were in the range of 201-280 m (Figure 4). These distances were however observed to vary in different clusters of nests in the north, middle and south sections of the lake, and would be expected to vary in different breeding seasons as new pairs take up territories and conditions in the breeding habitat change.

DISCUSSION

Factors influencing nest-site selection

This study has established that there are three principal variables (i.e., water depth, vegetation height and offshore distance from the nest) that Grey Crowned Cranes consider in the choice of a wetland to locate a nest-site as discerned from the active nests accessed during this study. Although the small sample size could be a drawback in our study, the results provide key insights into features of the species' nesting habitat i.e. it prefers wetlands with a standing water of at least 50 cm deep surrounded by a vegetation of 60-90 cm tall, and place their nests at least 30-100 m inside the wetland from the shoreline. These results complement observations made by Urban, Fry & Keith (1986) and Walkinshaw (1964) of a nest-site preference with knee and should-high (1 m) of emergent vegetation and a standing water depth of 80-180 cm. Although some nests observed were in areas without an emergent vegetation cover, these were inaccessible due to a water depth beyond 1.5 m. In such cases, water depth was among the critical factors considered in choosing them. Water depth is described as an important predictor of invertebrate abundance (Smith & Smith, 1988), which forms a larger proportion of parental adult cranes diet (Gichuki, 2000). Inability to access all active nests due to danger of wading (muddy lake bed and deep ditches) and presence of hippopotamus, may however have biased our results.

Nesting cranes were observed to be somewhat sensitive to humans and dogs approaching nesting-sites and whenever they had unfledged chicks. However, breeding pairs were confirmed utilising smaller man-made wetlands around the lake that are within areas dominated by an influx of human activities such as water abstraction, grazing, and crop farming. This use of small wetlands could be an indication of deterioration of traditional and principal breeding site, hence cranes are desperate for suitable breeding sites. Accessible nests were visited once to reduce disturbances. Considering this is an endangered species, counting and mapping of territorial pairs was done rapidly, and this may have biased estimation of density of number of pairs occupying territories.

Although our results did not detect a significant effect of grazing in choice of a nest-site by cranes, it is very likely that they may avoid such sites due to disturbance arising from livestock especially the feral dogs. Grazing from livestock can degrade crane's breeding habitats and contribute to nest failure (Ivey & Dugger, 2008), and is known to affect waterfowls in several ways such as number of breeding pairs, nesting densities and nesting success (Kirsch, 1969). Vegetation height may also be related to concealment from terrestrial predators (Muheebwa-Muhoozi, 2001; Olupot, 2016) and could lead to succession of vegetation composition and a structure that is less suitable to Grey Crowned Cranes (Morrison, 2015).

While this study identifies features of nest-sites, it is important to note that the chemical and physical parameters of wetlands changes rapidly over time (Shelly, Mirza & Bashir, 2011). This was corrected by sampling nests across two breeding seasons (2017/2018, 2018/2019) which gave us a fair distribution of wetland conditions. Census and mapping of pairs was done in December, a time considered as the peak of this specific breeding season. At this time, pairs were at different breeding stages ranging from nest-building and incubation (for late breeders) to feeding flightless chicks, and hence most territorial pairs had taken positions. However, it is important to note that except for years with an extended drought, cranes of Lake Ol' Bolossat nests throughout the year, an observation also reported in Uganda by Pomeroy (1980) and Archibald & Meine (1996). It is thus quite challenging to determine the exact number of territorial pairs in such an expansive site like Lake Ol' Bolossat.

Distribution and number of territorial pairs

The distribution of territorial pairs across the lake could be an insinuation of availability and abundance of food resources, a factor described as probably stable in perennial wetlands (Brown & Britton, 1980), and may also suggest non-variation of lake's conditions. This study has also shown that other factors are also important in determining pair densities and distribution. The number of pairs observed is also expected from the vastness of the marshes that occur across the entire stretch of the lake. Such a high number might moreover be a suggestion of degradation of alternative breeding habitats and increased disturbances from humans (e.g. poaching, vegetation harvesting, fishing etc.) that coerce cranes (and other birds) to seek and congregate in a few 'safer' sites that may result to competition for resources (Goss-Custard, Triplet, Sueur & West, 2006; Watson, Bolton & Monaghan, 2014).

Pairs occupied territories all around the lake except for a 4 km stretch on the south-western shores (Figure 2). This section is characterised by a complete lack of marshes, a steep shoreline and a dense cover of a 1 m tall *Pennisetum spacelata* tussock grass unsuitable for cranes due to poor visibility and associated high risk of terrestrial predators, such as feral dogs, and poachers. Some sections of the lake such as at Gatumbiro have extensive marshes but a low occupation by cranes. This could perhaps be due the high traffic of fishermen on canoes, and a quarry in the heavily encroached and settled riparian grassland. Kianjata marshes are spread out and stable in terms of vegetation - useful as nest substrates, and provision of cover and shelter from wind. However, these marshes are frequented by a large number of livestock, fishermen, and poachers and were recently subdivided into small (50'x100') land parcels with upcoming homesteads and barbed wire fences presenting an unfavourable landscape.

CONCLUSIONS & RECOMMENDATIONS

The results of this study provided critical information towards understanding some of the basic characteristics of wetlands that Grey Crowned Crane require for nesting. They may thus be utilised as a basis for modification and management of wetlands with an aim of making them suitable for cranes. In degraded wetlands, a weir could be constructed or raised to ensure that the water held back reaches at least 50 cm in-depth in the shallow end. Low-level grazing or exclusion of large herbivores (such as buffalos, elephants, cattle, donkey etc.) would naturally allow vegetation to regenerate and flourish on its own to reach desired height of over 60 cm. This can be achieved by fencing off small to medium-sized wetlands, natural spring marshes or parts of extensive wetlands with a chain-link (or an electric fence in conservation areas). Besides, this information can be adopted in legal documents such as Integrated Management Plans, National Wetlands Policy and International Single Species Action Plans.

Given its outstanding significance as a key breeding site for Grey Crowned Crane alongside the presence of other globally-threatened bird species, we commend a full implementation of the gazette notice declaring the wetland as a Protected Wetland Area and effective implementation of a management plan that should give room for managing the wetland for the good of local communities and wildlife. A candid management of the wetland, such as exclusion of livestock during the peak of the breeding season, would be expected to reduce human and livestock disturbances to nesting birds. Law enforcement should cross the line too to control activities that impact negatively on crane's breeding performance such as trapping (poaching) and collection of eggs and chicks, and to halt further encroachment on the riparian land.

Similar studies in Kenya and across the species range are recommended to identify and protect key breeding sites for the species. In eastern Africa, where the population is still described as rapidly declining, it is paramount that efforts are made to understand the activities surrounding known and/or potential breeding sites and address these challenges, if any, at the local level. There are over 120 satellite wetlands around Lake Ol' Bolossat reported in this study and their role in cranes and waterfowl conservation should be investigated.

ACKNOWLEDGEMENTS

This research received funding from African Bird Club (Conservation Award), Leiden Conservation Foundation (African Fund for Cranes courtesy of the International Crane Foundation/Endangered Wildlife Trust Partnership) and benefited from activities of a CEPF-funded project to Crane Conservation Volunteers. The first author was granted an in-kind support of field equipment from IdeaWild (Denver, CO., USA), Werner Schröder (NABU, BirdLife Germany), Dr. Günter Nowald (Crane Information Centre, Germany) and Ted & Darcy Thousand (Baraboo, WI, USA). Dr. George Archibald and Betsy Didrickson (International Crane Foundation) availed selected literature. We are grateful to Kenya Wildlife Service for authorizing this research (Permit No. KWS/BRM/5001), and to the National Museums of Kenya and the University of Nairobi for its endorsement. We thank Dickens Odeny (NMK) for assistance with production of the study area map.

CONFLICT OF INTEREST

None

DATA ACCESSIBILITY

Nests and territorial pairs location data will be uploaded (as supplementary material) to DRYAD.

REFERENCES

Amulike, B.B., Fuller, T.K., Houlihan, P.W. & Griffin, C.R. (2020). Seasonal variation in grey crowned crane (*Balearica regulorum*) abundance in the Ngorongoro Crater, Tanzania. *African Journal of Ecology* , 00:1-7. DOI: 10.1111/aje.12738.

Archibald, G.W. & Meine, C.D. (1996). Family Gruidae (Cranes), In: del Hoyo, J., Elliott, A. & Sargatal, J. (Eds.) *Handbook of the Birds of the World, Volume 3: Hoatzin to Auks* , pp. 60-89. Lynx Edicions, Barcelona.

Austin, J.E. & Buhl, D.A. (2008). Responses of nesting Sandhill Cranes to research activities and effects on nest survival. *North American Crane Workshop Proceedings.* Retrieved from http://digitalcommons.unl.edu/nacwgproc/156

Austin, J.E., Morrison, K.L. & Harris, J.T. (Eds.) (2018). *Cranes and Agriculture: A global guide to sharing the landscape* . International Crane Foundation, Baraboo, WI, USA, 303pp.

Baden, A.L. (2018). A description of nesting behaviours, including factors impacting nest site selection, in black-and-white ruffed lemurs (*Varecia variegata*). *Ecology & Evolution* , 9: 1010-1028.

Baumgartner, D., Mortl, M. & Rothhaupt, K. (2008). Effects of water-depth and water-level fluctuations on the macroinvertebrate community structure in the litoral zone of Lake Constance. Hydrobiologia, 613: 97-107. https://doi.org/10.1007/s10750-008-9475-0

Beilfuss, R.D., Dodman, T. & Urban, E.K. (2007). The status of cranes in Africa in 2005. *Ostrich* 78(2): 175-184. doi: 10.2989/OSTRICH.2007.78.2.11.91

BirdLife International. (2020). Species factsheet: *Balearica regulorum* . Retrieved from http://www.birdlife.org.

Brown, L.H. & Britton, P.L. (1980). *The Breeding seasons of East African Birds* . East African Natural History Society, Nairobi.

Burger, J. (1985). Habitat selection in temperate marsh nesting birds. In: M.L. Cody (ed.) *Nest-site Selection in Birds* , pp 253–281. Academic Press, New York.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* . Springer.

Catlin, D., Gibson, D., Friedrich, M.J., Hunt, K.L., Karpanty, S.M. & Fraser, J.D. (2019). Habitat selection and potential fitness consequences of two early-successional species with differing life-history strategies. *Ecology & Evolution* , 9: 13966-13978. DOI: 10.1002/ece3.5834

Chung, Y., Rabe-Hesketh, S., Dorie, V., Gelman, A. & Liu, J. (2013). A non-degenerate penalized likelihood estimator for variance parameters in multilevel models. *Psychometrika* , 78: 685-709.

Dwyer, N.C. & Tanner, G.W. (1992). Nesting Success in Florida Sandhill Cranes. *The Wilson Bulletin* , 104(1): 22-31. Retrieved from http://www.jstor.org/stable/4163113.

Gichuki, N.N. (1993). Factors affecting the reproductive success of the Grey Crowned Cranes. PhD Thesis, Cambridge University. pp 196.

Gichuki N.N. (2000). Influence of breeding on foraging behaviour and diet of crowned cranes. *Ostrich* , 71: 74-79.

Glen, S. (2020). Wald test: definition, examples, running the test from StatisticsHowTo.com: Elementary statistics for all us! https://www.statisticshowto.com/wald-test/

Gotmark, F., Blomqvist, D., Johansson, C.F. & Bergkvistv, J. (1995). Nest site selection: a trade-off between concealment and view of the surroundings? *Journal of Avian Biology* , 26(4): 305-312.

Gould, J.L. (2008). Cognition and Behavioural Ecology. In: S.E. Jorgensen & B.D. Fath, (Eds). *Encyclopedia of Ecology* , pp.668-672. Academic Press.

Goss-Custard, J.D., Triplet, P., Sueur, F & West, A.D. (2006). Critical thresholds of disturbance by people and raptors in foraging wading birds. *Biological Conservation* , 127(1): 88-97. https://doi.org/10.1016/j.biocon.2005.07.015

Hatchwell, B.J., Russell, A.E., Fowlie, M.K. & Ross, D.J. (1999). Reproductive success and nest-site selection in a cooperative breeder: effect of experience and a direct benefit of helping. *The Auk* , 116(2): 355-363.

Hinde, A. (1956). The biological significance of the territories of birds. *Ibis* , 98(3): 340-369. https://onlinelibrary.wiley.com/doi/10.1111/j.1474-919X.1956.tb01419.x

Hobbs, R.J. (2003). Ecological management and restoration: assessment, setting goals and measuring success. *Ecological Management & Restoration* , 4(Supplement), S2-S4.

Holway, D.A. (1991). Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. *The Condor,*93(3): 575-581.

Ivey, G.L & Dugger, B.D. (2008). Factors influencing nest success of Greater Sandhill Cranes at Malheur National Wildlife Refuge, Oregon. *Waterbirds* , 31(1): 52-61.

Jedlikowski, J., Brambilla, M. & Suska-Malawska, M. (2014). Finescale selection of nesting habitat in Little Crake *Porzana parva* and Water Rail *Rallus aquaticus* in small ponds. *Bird Study* , 61(2): 171-181. DOI: 10.1080/00063657.2014.904271

Jobin, B. & Picman, J. (1997). Factors affecting predation on artificial nests in marshes. *The Journal of Wildlife Management,* 61(3): 792-800. doi: 10.2307/3802186

Kirsch, L.M. (1969). Waterfowl production in relation to grazing. *Journal of Wildlife Management* , 33(4): 821-828.

Kolbe, J.J. & Janzen, F.J. (2002). Impact of nest-site selection on nest success and temperature in natural and disturbed habitats. *Ecology* , 83(1): 269-281. DOI: 10.2307/2680137.

Morrison, K.L. & Bothma, J.P. (1998). Wetland nesting sites of wattled and grey crowned crane on the Steenkampsberg Plateau, South Africa.*South Africa Journal of Wildlife Research* , 28(4): 110-170.

Morrison, K. (2015). (Ed.) International Single Species Action Plan for the Conservation of the Grey Crowned Crane *Balearica regulorum* . AEWA Technical Series No. 59. https://www.unep-aewa.org/sites/default/files/publication/ts59_issap_ggc_final_complete.pdf

Muheebwa-Muhoozi, J. (2001). The status of the Grey Crowned Crane,*Balearica regulorum* in Uganda, with special reference to breeding. *Ostrich Supplement* , 15: 122-125.

Olupot, W. (2016). Grey Crowned Crane threat assessment around the wetlands of eastern Uganda. *Ostrich* , 87(3): 263-270. DOI: 10.2989/00306525.2016.1214931

Pomeroy, D.E. (1980). Aspects of the ecology of Crowned Cranes*Balearica regulorum* in Uganda. *Scopus* , 4: 29-35.

R Core Team. (2019). *R: A language and environment for statistical computing* . Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Shelly, S.Y., Mirza, Z.B. & Bashir, S. (2011). Comparative ecological study of aquatic macroinvertebrates of Mangla Dam and Chashma Barrage wetland areas. *Journal of Animal & Plant Sciences* , 21(2): 340-350.

Smith, B. & Smith, W.P. (1988). Environmental criteria for nest site selection by Mississippi Sandhill Cranes. *Proceedings of the Annual Conference of Southeast Association of Fish and Wildlife Agencies* , 42: 431-442.

Swaisgood, R.R., Nordstrom, L.A., Schuetz, J.G., Boylan, J.T., Fournier, J.J. & Shemai, B. (2017). A management experiment evaluating nest-site selection by beach-nesting birds. *Journal of Wildlife Management* , 82(1): 192–201.

Tinbergen, N. (1957). The functions of territory. *Bird Study* , 4(1): 14-27. https://doi.org/10.1080/00063655709475864

Tolvanen, J., Seppanen, J-T, Monkkonen, M., Thomson, R.L., Ylonen, H. & Forsman, J.T. (2018). Interspecific information on predation risk affects nest site choice in a passerine bird. *Evolutionary Biology* , 18: 181. https://doi.org/10.1186/s12862-018-1301-3

Urban, E.K. (1988). Status of cranes in Africa. In: Backhurst, G.C. (ed). *Proceedings of the 6th Pan-African Ornithological Congress* , Francistown (Botswana). pp 315–329. Sixth PAOC Organizing Committee, Nairobi, Kenya.

Urban, E.K. (1996). Status of cranes in Africa, 1994. In: Beilfuss, R., Tarboton, W. & Gichuki, N. (eds) *Proceedings of the 1993 African Crane and Wetland Training Workshop* , Maun, Botswana. Pp 53–59. International Crane Foundation, Baraboo, Wisconsin, USA.

Urban, E.K., Fry, C.H. & Keith, S. (1986). *The Birds of Africa* . Vol. II. Academic Press, London.

van de Loock, D. (2019). Life-history strategies of a facultative cooperative breeder in a fragmented Afrotropical cloud forest. PhD Dissertation. Antwerp, Belgium.

Walkinshaw, L.H. (1964). The Afrian Crowned Cranes. *The Wilson Bulletin* , 76(4): 355-377.

Wamiti, W., Malaki, P. & Mwangi, A. (2008). Birds of Conservation Concern Upgrades Lake Ol' Bolossat Status to Kenya's 61st Important Bird Area. In: Harebottle, D.M., A.J.F.K. Craig, M.D. Anderson, H. Rakotomanana & M. Muchai (Eds.) *Proceedings of the 12th Pan-African Ornithological Congress* . Cape Town.

Wamiti, W., Mwangi, J., Fox, D., Bakari, N., Schroder, W., Nowald, G., Walter, B., Ndung'u, G., Bii, E., Wanjala, M., Nekesa, V., Waiguchu, G. & Kimani, D. (2020). Kenya's first countrywide census of Grey Crowned Crane *Balearica reguloram* : February-March 2019. *Bulletin Africa Bird Club,* 27(2): 210-218.

Watson, H., Bolton, M., & Monaghan, P. (2014). Out of sight but not out of harm's way: Human disturbance reduces reproductive success of a cavity-nesting seabird. *Biological conservation* , 174(100): 127–133. https://doi.org/10.1016/j.biocon.2014.03.020

Wu, H., Zha, K., Zhang, M. & Yang, X. (2009). Nest site selection by Black-necked Crane *Grus nigricollis* in the Ruoergai Wetland, China. *Bird Conservation International* , 19: 277-286.

FIGURE LEGENDS

Figure 1 : A family of the monogamous Grey Crowned Crane*Balearica regulorum* [Bennette, 1834] in a typical grassland habitat, Lake Ol' Bolossat. Sexes of adult breeding pairs are alike, except the male (C) is slightly larger than the female (A). Young cranes (B, D) attain full adult features at c.24 months of age (Pomeroy, 1980). ((c) GN Muigai).

Figure 2: Map showing the location of Lake Ol' Bolossat and distribution of territorial pairs during the 2017/2018 breeding season in each of the lake's sections.

Figure 3: Relationship between nesting probability and the three most important predictor variables. Points indicate either presence (1) or absence (0) of crane nests, and lines and shaded areas are, respectively, fitted values and standard errors.

Figure 4: Number (frequency) of Grey Crowned Crane territorial pairs and their distribution at different distances from each other.

TABLES

Table 1: Results of the model selection. Each row represents a candidate model, including parameter estimates for the predictor variables: offshore distance of the nest (OSD), vegetation height (VH), water depth (Wd), Grazing intensity (Gr) and the identity of the pair of nests, which was included as a random factor (RF) in the models.

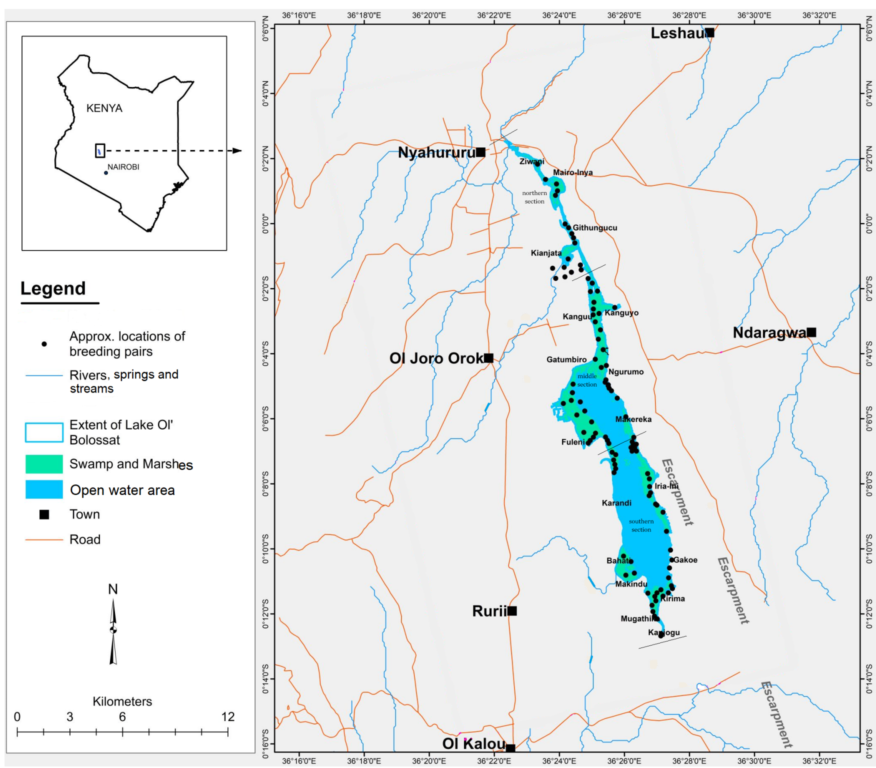
Intercept	Wd	Vh	OSD	Gr	RF	df	AICc	ΔAICc
-29.67	3.26	1.20	1.26		0.89	5	56.55	0.00
-26.82	2.98	1.06	1.20	-0.38	0.94	6	58.72	2.17
-21.96	2.95		1.45		0.67	4	59.18	2.62
-19.13	2.64		1.30	-0.73	0.74	5	59.22	2.67
-25.97	3.34	1.35			0.69	4	59.67	3.12
-21.70	2.88	1.13		-0.60	0.76	5	60.75	4.19
-12.72	2.43			-0.94	0.60	4	62.95	6.40
-15.62	2.82				0.50	3	66.11	9.56
-8.32		0.75	1.26	-0.80	0.70	5	69.26	12.71
-4.03			1.25	-0.94	0.62	4	69.91	13.36
-10.66		0.93	1.45		0.59	4	70.49	13.94
-5.77			1.51		0.51	3	73.91	17.35
-3.16		0.74		-1.07	0.54	4	74.72	18.17
0.98				-1.21	0.47	3	75.72	19.17
-6.03		1.10			0.40	3	81.73	25.17

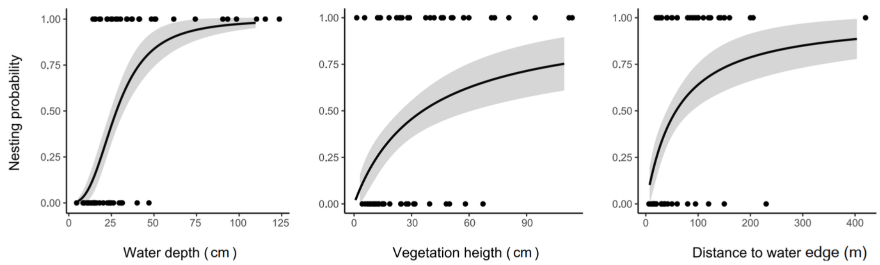
Table 2: Parameters and significance levels (Type III Wald chi-square test) of the best mixed-effect model that includes offshore distance (OSD), vegetation height (Vh), water depth (Wd), and the identity of the pair of nests as a random factor (RF).

	Estimate	**Std. Error**	**Tψπε III Ωαλδ χ$^2_1$**	***p* value**
Intercept	-29.67	9.26		

	Estimate	**Std. Error**	**Tψπε III Ωαλδ χ^2_1**	p **value**
RF	0.79	0.89		
Wd	3.26	1.16	7.95	0.005
Vh	1.20	0.57	4.45	0.035
OSD	1.26	0.61	4.35	0.037


A
B
C
D


KENYA
NAIROBI
Legend
Approx. locations of breeding pairs
Rivers, springs and streams
Extent of Lake Ol' Bolossat
Swamp and Marshes
Open water area
Town
Road
N
Kilometers
0
3
6
12
Leshau
Nyahururu
Ol Joro Orok
Ndaragwa
Rurii
Ol Kalou
Ziwani
Mairo-Inya
northern section
Githungucu
Kianjata
Kanguyo
Gatumbiro
Ngurumo
middle section
Mikereka
Fuleni
Karandi
southern section
Gakoe
Makindu
Kirima
Mugathika
Escarpment
Escarpment
Escarpment
36°16'0"E
36°18'0"E
36°20'0"E
36°22'0"E
36°24'0"E
36°26'0"E
36°28'0"E
36°30'0"E
36°32'0"E
0°6'0"N
0°4'0"N
0°2'0"N
0°0'0"
0°2'0"S
0°4'0"S
0°6'0"S
0°8'0"S
0°10'0"S
0°12'0"S
0°14'0"S
0°16'0"S



Hosted file

E&E Figure 4 - Histogram of Territorial Pair's Distance.pdf available at https://authorea.com/users/317648/articles/484825-water-depth-vegetation-height-and-offshore-distance-are-critical-factors-in-nest-site-selection-for-grey-crowned-crane-at-lake-ol-bolossat-kenya