**African Openbill Stork distributional response to rice paddy prey availability driven by crop-stage and competitor abundance – implications for bio-control of schistosomiasis gastropod vectors**

**Abstract**

Rice paddy-fields have become increasingly important worldwide as reliable alternative foraging sites for many wading birds due to the rapid loss or degradation of their natural wetland habitats. While assemblage and dispersal patterns of these birds are influenced by spatial distribution of their food resources, foraging activities of some species contribute significantly to natural suppression of some organism harmful to agriculture or human health. This 4-month study investigated how paddy-field management practices influence spatial and temporal linkage between African Openbill Stork distribution and abundance to that of its gastropod mollusc prey resources at Ahero Rice Irrigation Scheme, western Kenya. Regression models predicted African Openbill Stork abundance’s positive response to gastropod prey abundance, but negative response to conspecific competition abundance. Stork abundance also increased in response to rice-crop stage, with highest abundances at mid-crop stages, though only marginally due to field-flooding. Contrarily, gastropod abundance increased progressively with rice-crop phases, peaking at transplanting before reducing to stabilization towards crop maturity and harvesting. Paddy-field-block size showed no effect on abundances either Openbill Stork or gastropods. However, paddy block size predicted positive effect on Openbill Stork abundance when interacted with rice growth stage, and with gastropod abundance. Conversely, abundance of competing waterbirds, when interacted with gastropod abundance or rice-crop stage, predicted lower stork abundance, reaffirming negative impact of conspecific competition for stork assemblage. The findings demonstrate the significant role of gastropod food resources in overall distribution and assemblage of African Openbill Stork, impact of conspecific competition, and the crucial indirect influence of anthropogenic field management in shaping these dynamics through agronomic practices especially field flooding control and rice production cycles generally. The results are applicable in designing rice-fields as attractive alternative habitats for Openbill Stork and other waterbirds, to harness their potential contribution to bio-regulating the gastropod vectors of schistosomiasis.

***Key words****:* Rice, African Openbill, vertebrate predator, intermediate host; ecosystem service, One Health

**Introduction**

African Openbill Stork *Anastomus lamelligerus* Temminck, 1823, is a medium-sized Ciconnid wading bird that is endemic to the tropical sub-Saharan African including the island state of Madagascar (BirdLife International, 2025). It frequents many kinds of freshwater shallow wetlands, whether artificial or natural, large or small (del Hoyo et al. 1992). These include swamps, marshes, bogs, lake edges, rice fields, river deltas but also ponds and seasonal streams (Kahl 1971, BirfdLife International 2025). Like other stork species, African Openbill exhibits considerable periodic movement in flocks, but these are usually only localized and often take the form of intra-African migration at the very widest, often returning to same sites each season (Gula et al. 2022, BirdLife International 2025). Like its Asian counterpart *Anastomus oscitans,* the African Openbill utilizes rice paddy-fields important foraging sites year round (Anam et al. 2016; Zainul-Abidin et al. 2017). The species breeds mainly when there are abundant supplies of molluscs, its main primary prey resource (Hancock et al. 1992; del Hoyo, 1992, Pramanik et al. 2014), or other aquatic invertebrates. Within rice paddy-field, such fluxes in abundance of invertebrate food are driven by annually cyclic patterns of field agronomic operations that are entailed in the general rice production system (Anam et al. 2016, Bertolero and Navarro 2017; Horgan 2018). Thus, during periods of high invertebrate resource abundance in such rice fields, African Openbill Storks may forage more frequently or in larger flocks than at other times of the years. Such high food abundances often also attract other generalist wetland avian invertivores, some of which also feed on gastropod molluscs (Anam et al. 2016, Bertolero and Navarro 2017; Hara et al. 2018) and may thus produce competitive pressure (Matthysen, 2005, Sundar, 2006, Cheng et al. 2020, Guillaument et al. 2022).

Understanding factors that influence patterns of assemblage, dispersal and foraging performance by waterbirds in such natural wetlands in response to spatio-temporal distribution of their food resources, their interspecific interactions, as well as anthropogenic processes that drive such dynamics, is important for informing management decisions that will support conservation as well as maximization of ecosystem services provisioned by such birds (Peracuellos and Telleria 2004, Otieno et al. 2014). For instance, where they occur in frequent large flocks, Africa Openbill Stork’ specialist diet focus on gastropod molluscs represents significant potential for harnessing this top-down trophic linkage towards bio-regulation of these molluscs, which are recognized for their role as intermediate hosts of parasites that cause schistosomiasis in humans (Woodhall et al. 2013, CDC 2024)

The aim of this study was to I evaluate the inter-linkage between abundance and distribution of African Openbill Stork and their gastropod food resources, how this varies across rice paddy-field-blocks (spatial) and across rice growth phases (temporal). Specifically, we aimed to: 1) assess abundance of African Openbill Stork and its gastropod prey resources in across the various rice paddy agronomic management systems; 2) formulate models to for predicting African Openbill Stork’s abundance response to that of its gastropod prey resources; 3) identify paddy-field management variables that best predict African Openbill Stork and gastropod abundance patterns across the rice-fields

We hypothesized that: a) African Openbill Stork abundance patterns directly mirror those of its gastropod prey regardless of agronomic management patterns; b) African Openbill Stork and its gastropod prey resources increase in abundance during the more flooded periods of rice paddy-field management

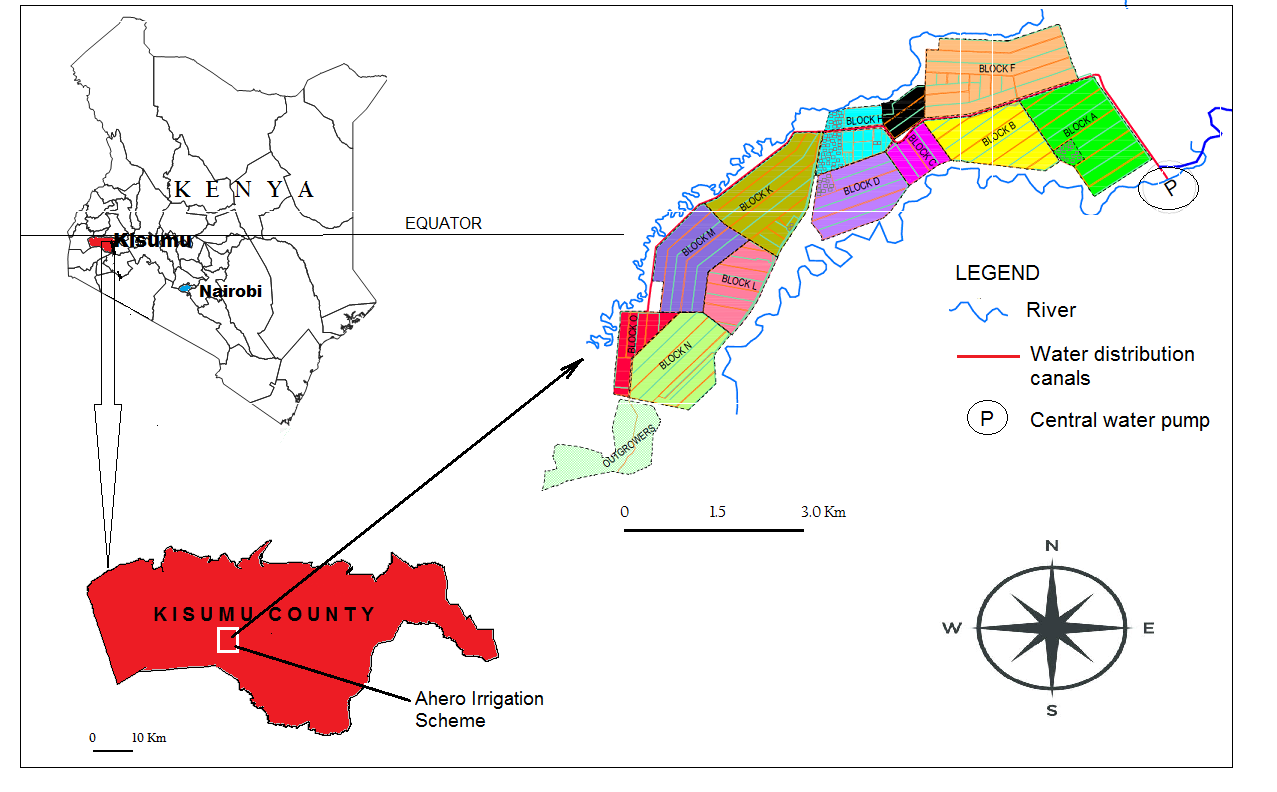
**Materials and methods**

**Study area**

The Ahero Rice Irrigation Scheme is located in the Kano Plains towards the eastern edge of the Winam Gulf of Lake Victoria, 20 Km east of Kisumu City in the western Kenya county of Kisumu as illustrated in Fig. 1 (Bukhari *et al.* 2011). The scheme is specifically located at 00° 09’ 14.31’’ S, 34° 59’ 49.16’’ E, covers 8.80 km2 and is supplied with water from the adjacent perennial River Nyando as illustrated in Fig. 1 (Bukhari *et al.* 2011, National Irrigation Board 2019). The mean annual rainfall in the region is 1082 mm with a high peak in March and a lower one in November while mean annual temperatures range from 17oC to 32oC, with average relative humidity at 65% (Bukhari *et al.* 2011, National Irrigation Authority 2019).

**Site description**

The rice irrigation scheme consists of 12 main irrigation blocks, ranging from 0.31-1.15 km2 in which rice is grown by a total of 533 contracted farmers. While main blocks differ in the numbers of farmers, each farmer is consistently allocated a paddy field of 1.6 ha (0.016 km2 or 4 acres), regardless of which main block it is located in (Bukhari et al. 2011). The paddy-field-blocks themselves ranged in sizes from 31-115 hectares (Table 1).Water is pumped into the main blocks through a main inlet and flows southwestwards under gravity along inter-block irrigation channels then into smaller secondary channels, which than flow into the paddy fields. Two crops of rice are grown each year, planting being timed to coincide with periods of local rainfall while harvesting takes place in July and January. The paddy fields initially receive moderate flooding from the time of ploughing to nursery establishment. Flooding is then maximized (to a depth of about 30 cm) from the time of transplantation (four weeks after ploughing) to the second period of weeding (two months after planting) before being gradually reduced (by about 10 cm weekly) until total discontinuation at crop maturity (after about three months) (Table 1). The site hosts large regular populations of resident and annually wintering birds comprising passerine and wading species (Zimmerman et al.2020).

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**FIGURE 1**. Map of study area showing various rice paddy-field-blocks where sampling was conducted. (Adopted from the National Irrigation Board, 2019)

**Sampling strategy and field protocol**

*Paddy-field-block selection and characterization*

The study was carried across all the 12 main blocks during the rice crop season spanning from November until February the following. Preceding actual field sampling, paddy-field-block characteristics were recorded using information from personnel at the Ahero Rice Research Centre, including paddy-field-block names, locations, sizes and prevalent stages of rice growth (Table 1).

**TABLE 1.** The 12 field-blocks comprising the rice-field paddies where the study was conducted. For each block, the number of farmers is not necessarily equivalent to the number of paddies because most farmers are allocated multiple paddies across the blocks

|  |  |  |  |
| --- | --- | --- | --- |
| Field-block | Block size  (Acres) | Block size (Hectares) | Number of  paddy-fields |
| A | 285.5 | 115.6 | 180 |
| B | 209.5 | 84.8 | 168 |
| C | 77.87 | 31.5 | 63 |
| D | 187.0 | 75.7 | 133 |
| F | 231 | 93.6 | 185 |
| G | 203.0 | 82.2 | 153 |
| K | 149.6 | 60.6 | 58 |
| L | 122.3 | 49.5 | 85 |
| M | 131.2 | 53.1 | 99 |
| N | 237.87 | 96.3 | 169 |
| O | 84.5 | 34.2 | 73 |
| P | 248.0 | 100.4 | 190 |
| 12 | 2167.3 | 877.7 | 1556 |

Information from Ahero Rice Research Centre,

Within paddy-field-blocks, rice growth stages and management operations correspond to specific field conditions (centrally-controlled flooding intensity) and are staggered and overlapped such that within the entire irrigation scheme, individual field-blocks are at different stages at any one time except after full crop harvest (Pers obs). However, within each individual block, all paddy-blocks are maintained at the same rice growth stage, and this is to facilitate ease of timing and execution of mechanized operations.

*Bird surveys*

Birds were surveyed in a total of five sampling periods – three times in December and twice in the following February, with 4-6 days separating each of the periods so as to maximize temporal randomization effects (Gotelli and Ellison 2013). Surveys were conducted in the mornings from 0630-0930 hrs. capturing the peak birds’ feeding activity (Bibby et al*.* 2000), with the use of 8 x 32 magnification binoculars. Observers worked in pairs with an experienced Ornithologist making the observation and a partner working as a data recorder. The total census was achieved through walking at slow steady paces along inter-block roads separating paddy fields and observing on either side of the road to record any birds detected. Attempts were made to maintain a distance of at least 60 m from birds to minimize disturbance (Bibby et al. 2000). All waterbirds observed in the main paddy fields, field margins, levees of irrigation channels within each main block, were considered to be utilizing it and therefore included while any birds observed flying in from behind were excluded from the counts in order to minimize chances of multiple counts (Bibby et al*.* 2000; Sutherland, 2006). Similarly, birds observed flying overhead without perching in the field being sampled were not included. On detection, birds were identified and recorded to species as well as whether or not they were potential competitors with African Openbill Stork for gastropod prey resources. Records were also taken of paddy-field-block names, crop growth stage, and general state of soil water (flooded, moist or dry)

*Gastropod prey sampling*

African Openbill Stork’s gastropod prey resources sampling was conducted twice during each of the field seasons from 10 selected paddy-fields in each field-block. The paddies were selected systematically by taking each every second paddy along a diagonal line from the east-facing towards the west-facing corner of the field-block (Sutherland 2006). The actual sampling was undertaken using a dipnet of 305 mm x 254 mm, 600 mm depth attached to a 1-m long handle (Zickovich and Bohovak 2007, Turner and Montgomery, 2009). **Holding the handle vertically,** one hand near net and the other up the handle and using strong strokes, a sampler swept through the water three successive times towards his leg before scooping up and transferring the contents through a fine white cotton cloth into a plastic bucket (Hafner and Fasola 1992). The contents were then transferred into labeled jars with 95% ethanol for preservation for subsequent later sorting and identification. In each of these paddy fields, four replicate dipnet samples were taken, with a fifth one drawn from the adjacent irrigation inlet/drainage channel (Sutherland 2006). For paddy-fields that were not flooded at the time of sampling, gastropod samples were collected using 4 1x1 m quadrats placed systematically along a diagonal line from one corner of the field to the opposite one, and a fifth quadrat thrown randomly into the adjacent water channel. Records were also taken of paddy-field-block names, crop growth stage and the general state of soil water (flooded, moist or dry)

**Statistical analyses**

We used analyses of variance to compare African Openbill Stork and gastropod abundances across rice paddy-fields in terms of 6 broad rice growth stages (ploughing and rotavation; transplanting; first-weeding; second-weeding to flowering; maturity to harvest; post-harvest) as well as across the three levels of paddy-field flooding – flooded, moist and dry. To test habitat variables that best explained African Openbill Stork and gastropod abundance distribution across the paddy-fields, distance based linear modeling (DistLM) were employed in PRIMER-E, by running the tests on the log(X+1) transformed Bray-Curtis resemblance matrices of stork and gastropod abundance data, and on Euclidean distance-based normalized similarity matrices of habitat factors (Anderson et al. 2006). Since each of the two taxa had only one general identity (i.e. African Openbill Stork, and ‘Gastropods’) with no sub-divisions, we used each of the 5 field survey sessions as species IDs in column headings in the respective abundance resemblance matrices (PREMIER-E 2019). Models were run stepwise through 9999 permutations and selection of the best ones was based on Akaike Information Criterion adjusted for small sample size (AICc). Variables that best explained assemblage dissimilarities (abundance turnovers) were identified at p≤0.05) and ordination plots subsequently produced in PRIMER-E (PRIMER-E 2019).

Generalized linear mixed models (GLMM) were used to determine predictive responses of African Openbill Stork or gastropod abundances to the various explanatory variables separately. Here we used the *glmer* function in the *multcomp* and *lme4* packages of *R v4.4.1* (White 2009, Bates, 2010, R Core Team 2023), fitting Poisson error probability distributions and log-likelihood link function for bird species richness, using paddy-block name as random factor and the explanatory variables as fixed effects (Bolker et al. 2009). A similar procedure was used for testing stork and gastropod responses to interactive effects of the explanatory variables (Aiken et al. 1991). These tests were run subsequent to testing data for overdispersion, using the *AER* package (Bolker et al. 2009), and for normality using the Shapiro-Wilk test in the *mvShapiroTest* package of *R*. Selected models were those with lowest scores of the Akaike Information Criterion adjusted for small samples (∆AICc) as outlined by Barton (2023). The *interactions* and *ggplot* functions in the *ggplot2* package were subsequently used for graphical plots of significantly predicted effects

**Results**

**General distribution of African Openbill Stork and its gastropod prey resources**

Results from PERMANOVA modelling, African Openbill Storks were most commonly recorded during the rice cropping period from transplanting to a peak in second weeding and to flowering, but in lowest numbers during the earliest stage at ploughing and field rotavation (Fig 2A, Table 2). Their abundance appeared to be notably influenced by the level of potential competition posed by other wading bird species (Table 2), which were also most abundant at transplanting and first weeding, but least abundant at postharvest stages, even though the highest species richness of these competitors were observed at the second weeding to flowering stages (Fig 2A). African Openbill Stork abundance was also significantly influenced by paddy-field soil water conditions (Table 2) but was not affected by paddy-field-block size itself (Table 2). On the other hand, African Openbill Stork’s gastropod food resource abundance was linked to crop stage, reaching a peak at transplanting before subsiding through the first weeding to the lowest level at the flowering stage (Fig 2B, Table 2). This distribution was additionally influenced by paddy-field soil water condition (Table 2), but there appeared no influence of paddy-field-block size (Table 2).

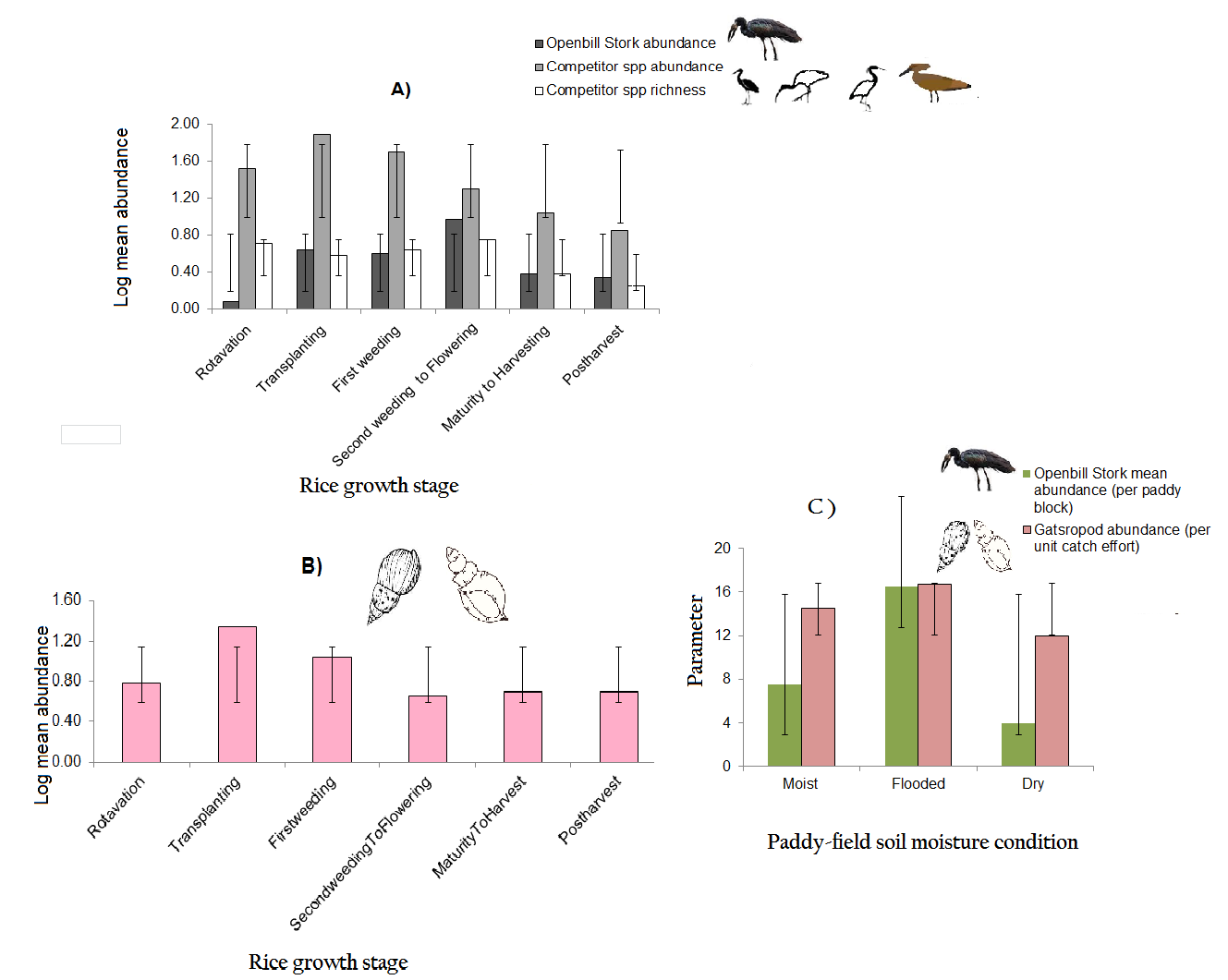
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Figure 2A) Abundance distribution across the various phases of rice crop growth for African Openbill Stork in comparison to abundance and species richness of other potentially competing wader waterbird species; B) Abundance distribution across the various phases of rice crop growth for gastropod molluscs; B) the role of paddy-field flooding in influencing abundance distribution of African Openbill Stork and gastropod molluscs. Means are derived by averaging abundances of the five survey episodes (N=434).

Accordingly, ordination using distance-based linear modelling indicated African Openbill Storks selecting paddy-field-blocks with the higher levels of soil flooding (Fig 3A) while generally avoiding those with the highest levels of potential competitive pressure (Fig 3B-C) but that although gastropod turnover was predominantly in the wetter soil blocks, their overall abundance distribution was much more widespread across the various paddy-soil soil water conditions ((Fig 3D).

Table 2: Results of one-way analysis of variance (ANOVA) models for comparison of mean abundances of African Openbill Stork and gastropods across the various levels of habitat factors. For the purpose of the ANOVA procedure, field size was derived into three classes as Small, Medium or Large; paddy soil water condition as Dry, Moist or Flooded; and presence of African Openbill Stork’s potential competitor species into three categories of intensity as Low, Moderate or High. *Df*= degrees of freedom

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Dependent variable | Response variable | F | P≤0.05 | df |
| Gastropod abundance turnover | Rice growth stage | 2.125 | **0.041** | 5 |
| Paddy-field size class | 0.867 | 0.602 | 2 |
| Paddy-field soil water condition | 2.125 | **0.003** | 2 |
| Openbill-Stork abundance turnover | Rice growth stage | 2.225 | **0.035** | 5 |
| Paddy-field size class | 0.569 | 0.988 | 2 |
| Paddy-field soil water condition | 2.092 | **0.027** | 2 |
| Level of potential competition | 2.158 | **0.039** | 2 |

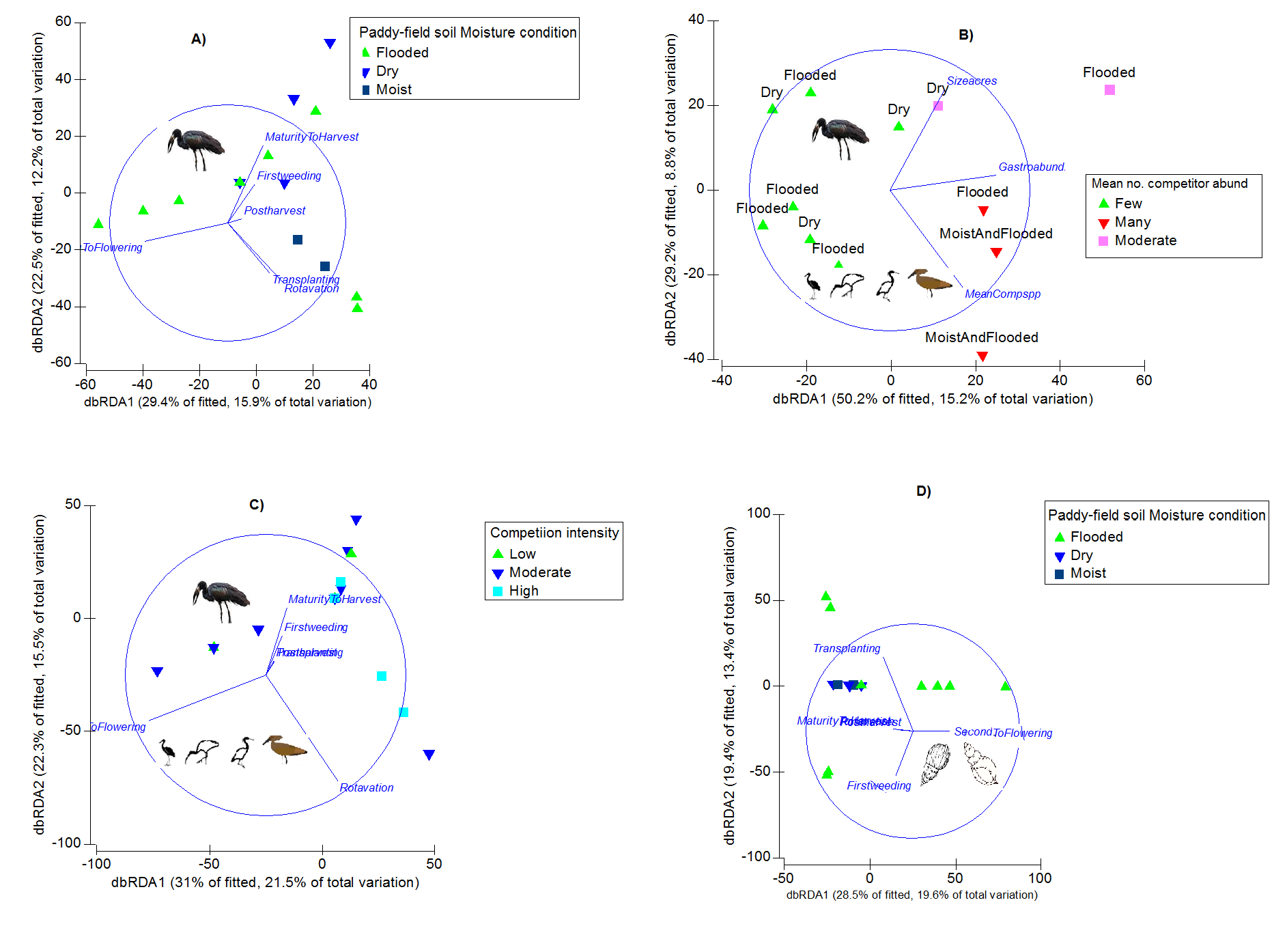


Figure 3. Distance-based Linear Model (DistLM) ordination plots showing African Openbill Stork abundance distribution in relation to A) rice growth stage and across the various levels of field flooding; B) field flooding across various levels of potential competition pressure; and C) competition pressure across the various rice growth stages; D) Gastropod abundance distribution in relation to rice growth stages across the various levels of field flooding. The DistLM models are based on (LogX+1) transformed resemblance matrices of Bray Curtis similarities for abundance distribution

**Predictive models of African Openbill Stork and gastropod abundance responses to habitat variables**

***Independent responses to effects of habitat variables***

General linear mixed modeling predicted an increase in Openbill Stork abundance with higher abundance of gastropods but a decrease in African Openbill Stork with increase in competitive pressure from other wading bird species (Table 3, Fig 4C-D). It also predicted higher African Openbill Stork abundance from the early to mid-stages of rice growth especially at second weeding (Table 3, Fig 4A), but only a marginal direct effect of paddy-field soil water condition, while paddy block size was not expected to have any effect (Table 2, Fig 4B). Abundance of gastropod was also predicted to increase with paddy flooding, particularly at the initial stages following field ploughing and rotavation, with only minimal response to flooding condition itself, but just like the case for storks’ abundance, no response to paddy block size (Table 3, Fig 4E-F).

Table 3Results of generalized linear mixed models for responses of African Openbill Stork and gastropod abundance to individual effects of the agronomic system factors across the study area. \*p<0.05; \*\*P<0.01; \*\*\*p<0.001; Significant effects are in bold face; *Coeff*=Estimated parameter coefficient; *Resid df*= Residual degrees of freedom; *AIC*= Value of Akaike information criterion for the selected model.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Response variable | Predictor variable | Coefficient estimate | Standard error | N | AIC |
| Mean abundance of Open-bill Storks | Rice crop stage | **0.034\*\*\*** | 0.967 | 78 | 502.7 |
| Paddy-field-block size | -0.045 | 0.079 |
| Paddy-field soil water condition | -0..105 | 0.036 |
| Abundance of gastropods | **0.079\*** | 0.038 |
| Number of potential competitor species | **-0.044\*** | 0.034 |
|  |  |  |  |  |  |
| Mean gastropod abundance | Rice crop stage | **1.949\*\*\*** | 0.381 | 57 | 510.6 |
| Paddy-field-block size | -0.005 | 0.005 |
| Paddy-field soil water condition | 1.702 | 0.950 |

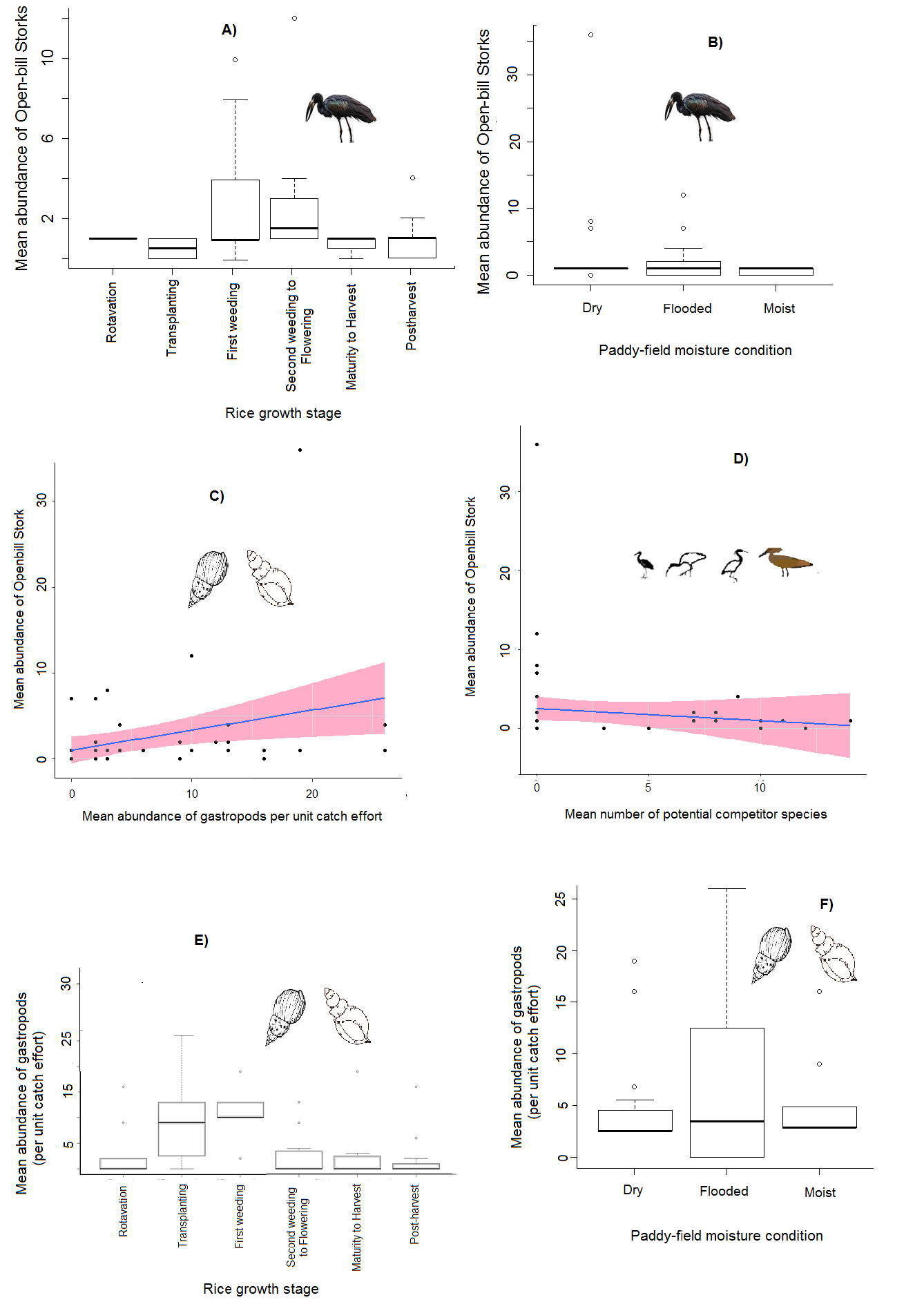


Figure 4**.** Boxplots and regression graphs from GLMM modeling, showing significant predicted responses of African Openbill Stork to effects of A) rice growth stage and B) paddy flooding. Regression plots showing predicted effects of C) gastropod abundance and a, D) waterbird competition pressure on African Openbill Stork abundance. Boxplots showing predicted response of gastropod abundance to A) Rice growth stage and F) paddy0-field flooding.

***Response to interactive effects of habitat variables***

Although rice paddy block size had no predicted independent effect on African Openbill Stork abundance, it showed a positive effect when combined with gastropod abundance and also in combination with rice growth stage, specifically at first weeding and at maturity stages (Table 4, Fig 5A, 5C). The number of African Openbill Stork’s potential competitor species was also important in combination with either rice growth stage (period between rotavation to first weeding) or gastropod abundance, in predicting reduced African Openbill Stork abundance across the rice paddies (Table 4, Fig 5B, 5D).

Table 4Results of generalized linear mixed models for African Openbill Stork and gastropod abundance responses to interactive effects of the range of agronomic management system factors across the study area. \*p<0.05; \*\*p<0.01; Significant effects are in bold face; *Coeff*=Estimated parameter coefficient; *Resid df*= Residual degrees of freedom; *AIC*= Value of Akaike information criterion for the selected model.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| RESPONSE VARIABLE | Predictor  variable 1 | Predictor  variable 2 | Coeff | SE | Resid. df | AIC |
| African Openbill Stork abundance | Rice crop stage | Paddy-field-block size | **0.025\*** | 0.010 | 55 | 482.6 |
| Gastropod abundance | Rice crop stage | -0.123 | 0.099 | 46 | 264.1 |
| Gastropod abundance | Paddy-field-block size | **7.340\*** | 3.634 | 51 | 465.8 |
| Gastropod abundance | Paddy-field soil water condition | -0.166 | 0.102 | 51 | 336.2 |
| Paddy-field-block size | Paddy-field soil water condition | 8.087 | 4.919 | 56 | 225.6 |
| Rice crop stage | Number of potential competitor species | **-0.341\*\*** | 0.124 | 57 | 267.0 |
| Paddy-field-block size | Number of potential competitor species | 0.005 | 0.007 | 57 | 281.0 |
| Gastropod abundance | Number of potential competitor species | **-0.005\*** | 0.002 | 57 | 225.6 |
| Gastropod abundance | Rice crop stage | Paddy-field-block size | -**0.036\*\*\*** | 0.009 | 46 | 358.9 |
| Rice crop stage | Paddy-field soil water condition | NULL | NULL | NULL | NULL |
| Paddy-field soil water condition | Number of potential competitor species | **-0.030\*\*** | 0.010 | 51 | 553.8 |

Similarly, when combined with rice crop stage, the effect of paddy field size predicted increased abundance of gastropods especially at rotavation stage, but when combined with paddy soil water condition, the effect of paddy size predicted a reduction in gastropod abundance, specifically in the wetter paddy-fields (Table 4, Fig 5E-F).

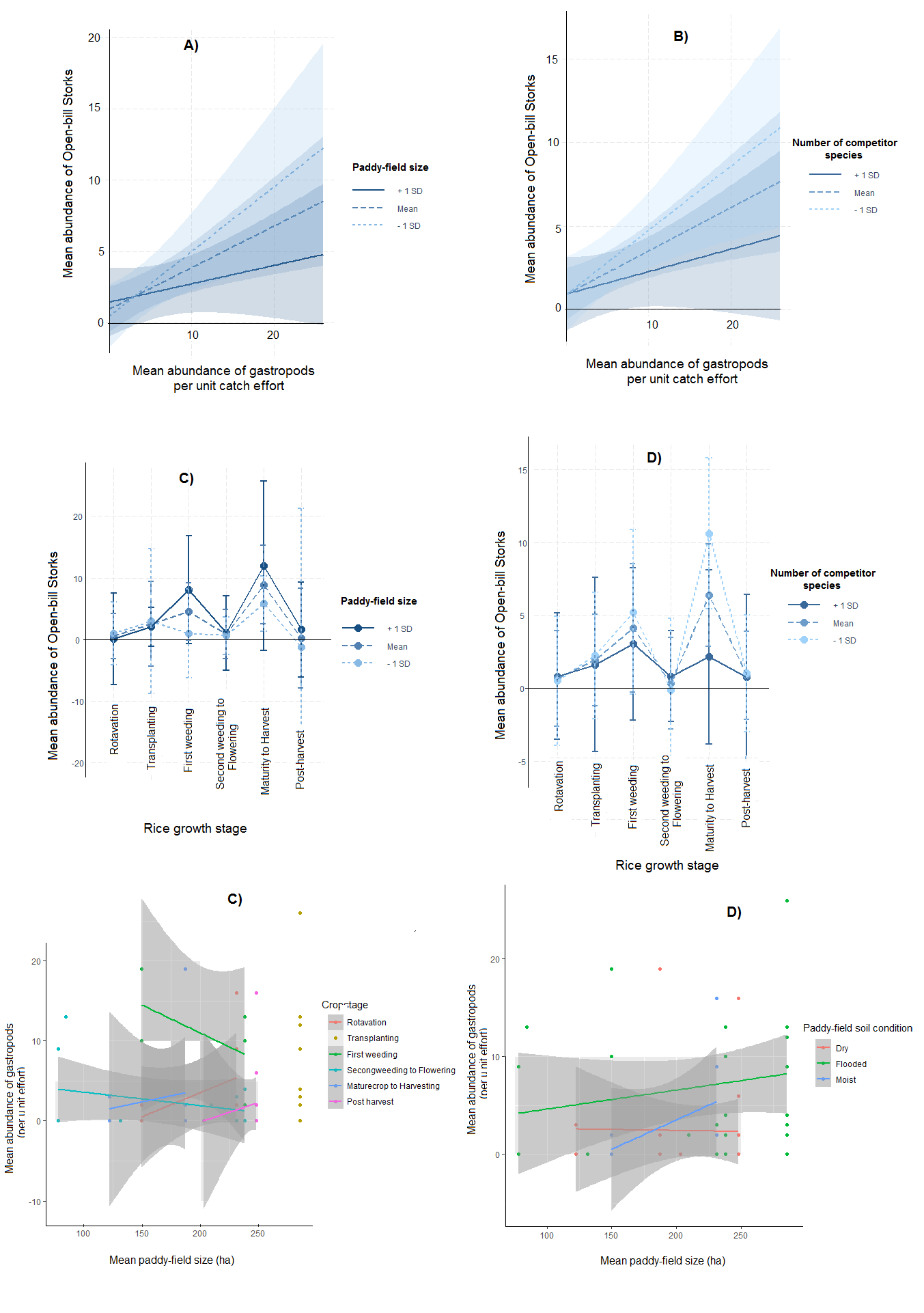


Figure 5. Regression model plots showing response of African Openbill Stork abundance response to interactive effects of A) gastropod food resource abundance with paddy-field-block size or B) gastropod food resource abundance with waterbird competition pressure, and C) rice growth stage with paddy-field-block size or D) gastropod food resource abundance with waterbird competition pressure; and also the response of gastropod abundance response to interactive effects of E) paddy-field-block size with rice growth stage or paddy field size with paddy flooding

**Discussion**

**Distribution of African Openbill Stork and its gastropod food resources**

General patterns of African Openbill Stork abundance distribution across the rice paddy-fields showed an important indirect relation to the state of paddy-field soil water, which was largely variant for each of the rice growth stages. Thus the stork was most commonly encountered during the flooded stages of paddy-field management, and this closely mirrored the general abundance of gastropod molluscs which are known to constitute primary prey food for Openbill storks (Kahl 1971, Anam et al. 2016, Tamang et al. 2024a). Similar patterns of the dual role of rice paddy-field flooding and gastropod abundance were reported from studies of Asian Openbill Storks *Anastomus oscitans* in Thailand (Sawangproh 2012) and in Malaysia (Zainul-Abidin et al. 2017). However, in the present study, this temporal abundance linkage was not necessarily linear. For instance, while the stork’s abundance appeared to peak around the mid-stage of rice growth at second weeding, that of gastropods reached a zenith much earlier at transplanting stage. This suggest that although gastropods are the stork’s main food resource and the bird’s spatio-temporal abundance is influenced by gastropod availability across the field (del Hoyo et al. 1992), additional proximate factors may be driving abundance of the stork across it wetland forging sites. One such possible factor is the presence of other wading waterbird species that potentially compete with African Openbill Stork for this prey resource. This explains why African Openbill Stork’s abundance was not observed at its peak at transplanting stage when gastropods were most numerous since this was the stage when the stork’s foraging conspecifics were also most abundant. Although they have often been observed to share colonial nesting or roosting sites with other large wading bird species (del Hoyo et al. 1992; Tamang et al. 2024b, Stalmans et al. 2025), African Openbill Storks often also forage exclusively as individuals, pairs or detached groups separated from those of other species (Kasoma and Pomeroy, 1987; del Hoyo et al. 1992). Furthermore, gastropod abundance was at its peak at transplanting stage and then remained fairly stabilized after first-weeding stage stages whereas for the case of Open bill Stork, abundance tended to vary across the rice growth stages in inverse consonance with that of the potential competitors, This further highlights the potential nugatory impact of the latter on the stork’s temporal distribution presumably due to interspecific competitive pressure (Guillaumet and Russell 2022). Even when encountered within flooded field-blocks, the stork preferred those paddies with fewer potential competitors. This finding is, however, contrary to those reported by Cheng et al. (2020) indicating that Oriental Stork’s Ciconia boyciana foraging intensity at feeding sites was enhanced by presence of its conspecific competitors.

Trends in richness of potential competitors, however, appeared to have little influence on African Openbill Stork abundance, implying that the stork may be able to tolerate other species at foraging sites to a certain threshold of the latter’s assemblage density (Guillaumet et al. 2022, Naikatini et al. 2022). Thus, conditions that favour temporal or spatial availability of gastropods across the rice-fields may indirectly also determine abundance of African Openbill Stork and its conspecific competitors. Some of these conspecific competitors may also opportunistically utilize this gastropod prey resource when it occurs at periodically high concentrations (Horgan 2018). For instance, Glossy Ibis (*Plegadis falcinellus,* Threskiornithidae*)* were shown to be considerable consumers of apple snails (*Pomacea maculate*, Ampullaridae, Gastropoda) in rice-fields of northern Spain (Bertolero and Navarro 2018). Hamerkop (*Scopus umbretta*, Scopidae) and other species of ibis may also incorporate gastropod molluscs in their diet at these feeding sites (Marion 2013, Bertolero and Navarro 2018), Majority of the other competitors, however, compete with the stork for space primarily to exploit abundant alternative invertebrate prey resources since they are not as gastropod-specialist feeders as is the African Openbill Stork. The insignificant influence of paddy-field-block size in driving these stork-competitor-gastropod inter-linkages, however implies two possible scenario: first, the temporal dimension is superior to the spatial one in determining abundance of gastropods and thus this abundance strongly depends on anthropogenic agronomic operations including use of chemical farm inputs to boost soil and water nutrients, which results into enhanced gastropod reproduction. Secondly, abundance of gastropods, regardless of soil flooding status, is fundamentally patchy within individual paddy-blocks. Therefore, when a paddy block is in an agronomic operational state which presents conditions favourable for proliferation of gastropods and other invertebrates, such as during the early phases of rice growth when prey is also easier to detect and capture due to relatively low water levels (Zainul-Abidin et al. 2017), such a block constitutes a potential competition hot-spot for space between African Openbill Stork and other predatory waterbirds, regardless of the size of that paddy block. This is because of the established field management synchrony in the whole rice scheme such that at any one time, all constituent paddy-fields with a block are at the same agronomic operation as well as rice growth stage (National Irrigation Authority, 2019). Therefore for foraging waterbirds, dispersing to neighbouring blocks due to competitive pressure, or space delimitations, may not be of any benefit (Matthysen 2005, Guillaumet and Russell 2022) because such neighbouring blocks may at totally different flooding stages at that point in time. The observation of a fairly stable abundance distribution of gastropods across rice growth stages except for the apparent peak at around the early stages of rice growth suggests, however, that while actual field flooding may be important in boosting their populations on a rotational field management basis, the molluscs are largely persistent across rice crop cycles, including periods coinciding with termination of field flooding. A possible explanation is that majority of the gastropod species may continue to be supported by the remnant water or muddy sediments, soil and silt within adjacent water-dissemination channels even after flooding is discontinued (Natuhara 2033). Here they may remain in temporary dormancy or aestivation, waiting to disperse into and recolonize the paddies once flooding is resumed (Horgan 2018).

**Predicted African Openbill Stork and gastropod abundance response to habitat variables**

***Independent responses to effects of habitat variables***

Regression modeling confirmed the initial (rice transplanting to first weeding) and the terminal (second weeding to flowering) stages of field flooding to be characteristic of highest abundances of both the storks and the molluscs. On the other hand, although paddy-field flooding was a positive predictor of stork abundance, this factor showed, unlike the case for distribution, only a marginal effect on gastropod abundance. Thus while field flooding was of importance in overall distribution of both taxa, its direct value for determining actual gastropod abundance was not definitely linear. Nevertheless, the models predicted a direct linear link between gastropod and African Openbill Stork abundance the highlighting that like its Asian counterpart, this species’ foraging activity around the rice-fields involves tracking the mollusc prey items (Ajayan et al. 2016), even though abundance of potentially competing waterbirds pedicured reduced abundance of Openbill Stork. Yet, abundance peaks for both the stork and the molluscs occurred at different rice growth stages. Considering these facts together, it can be presumed that while field flooding is important for overall distribution across the rice scheme it is fundamentally of practical value to gastropods mostly for purposes of reproduction and early growth, subsequent to which the molluscs may remain as dormant adults withstanding drier conditions till the next flooding event (Merlo et al. 2016, Yesmin et al. 2018), or disperse to alternative paddy field with the right microhabitat conditions. Horgan (2018) showed that gastropod molluscs are well adapted for resilience and persistence in rice paddies due a range of favorable conditions obtaining in these artificial wetland and which closely mirror their ideal natural habitat, These include periodic flooding, warm temperatures, slow moving water, high salinity and nutrient concentrations that guarantee their abundance of their micro-nutritional needs, as well as rotational periods when the soil is drier to suit their aestivation requirements in preparation for successive stages of their life cycles. For this reason, the gastropods were observed at highest abundance during transplanting to first-weeding, which mark the onset of field flooding. Openbill Stork on the other hand, also prefer to feed on gastropods during the flooded-field phases, but may, however, be discouraged from focusing these foraging efforts at the early phases of rice growth (transplanting to first weeding) due to competitive pressure from the highest concentrations of other wading birds as discussed above. For such competitors, the proliferation in gastropod and other invertebrate biomass at this field phase may constitute an easy and opportunistic diet supplement (Bertolero and Navarro 2017, Barboza et al. 2022) since unlike African Openbill Storks, none of them is an obligate or specialist gastropod feeder. An alternative explanation is the possibility that African Openbill Storks, prefer to feed on gastropods at the terminal stages of field-flooding (second weeding to flowering) when the molluscs have grown larger, a strategy that might offer more efficient expenditure of foraging energy (Sotillo et al. 2019), while also minimizing competitive pressure from their opportunistic-feeding conspecifics. Many such competitors might also have departed their East African wintering grounds by this rice growth phase and migrated back to their breeding grounds in the northern hemisphere (Zimmerman et al. 2020).

***Response to interactive effects of habitat variables***

The predicted positive response of African Openbill Stork abundance to the interactive effects of field-block size and gastropod abundance, especially at first weeding and at rice maturity phases, serve to indicate that at these stages of rice growth and field management or field flooding, African Openbill Storks may need to range at wider spatial scales to optimize foraging efficiency. This would primarily be due to relatively lower abundance, more patchy distribution or reduced activity (and hence detectability) of their gastropod prey at the rice maturity characterized by reduced flooding. At the same time, it might owe to the need for the Openbill to disperse wider to reduce competitive pressure from other wading waterbirds that were shown above to be most abundant from the transplanting to the first weeding phases (Meganathan and Jeevanadham 2019).. This is particularly likely since the interactive effect of field-block size and gastropod abundance, as well as that between block size and rice growth stage, both predicted reduced abundances of African Openbill Stork especially at the initial flooding stages (rotavation through transplanting to first weeding).

**Implications for bio-control of schistosoma parasite’s intermediate host**

With regards to natural bio-regulation of populations of gastropod molluscs, the key intermediate hosts for the nematode parasites of schistosomiasis which is of considerable economic and public health importance in the region (Woodhall et al. 2013, CDC 2024), the results of this study demonstrate that rice-field management strategies for maximize African Openbill Stork’s contribution in provisioning this ecological service should involve considering one key agronomic action point: In light of the current management system of staggering the rice crop growth continuum with various field-blocks at different growth phases though year, there is need to maximize the number of blocks at flooding phase, especially those for which paddy-fields are timed to reach second-weeding to flowering around February to March. First, this will increase the number of paddy fields at transplanting stage early in the year during which African Openbill Storks face the highest competitive pressure for invertebrates from other waterbird species which occur at high abundances in the few blocks that are at this growth stage at this time, but most of which may do not significantly consume gastropods. The storks would thus more easily disperse to alternative blocks to minimize this competition for space. The additional benefit of this strategy would be that majority of the storks’ wintering competitors would have migrated back to their natural breeding grounds in the northern hemisphere thus easing up the local pressure for foraging space. Other resident waterbird species such as Hamerkop (Winkler et al. 2020) and ibises (Marion 2013, Bertolero and Navarro 2018), known to be considerable opportunistic consumers of gastropod molluscs would also more easily make more significant additional top-down contributions towards this ecological and public health service across these rice-fields.

**Conclusion**

The results of the study reaffirm the role of rice paddy-fields as significant alternative foraging habitats that serve to expend the forging ranges of the African Openbill Stork. The study has also demonstrated the significance of gastropod molluscs’ availability and distribution in shaping distribution of its prime avian predator, the African Openbill Stork, both in time and in space across its foraging grounds, in this case, rice paddy fields. Patterns of this trophic co-distribution are determined by local microhabitat factors, particularly the crop phases that are intimately linked to soil water regimes and perhaps soil nutrient fluxes. These habitat factors are themselves driven by periodic anthropogenic field management practices whose impacts are thus superimposed on the predator-prey responses to the local spatial microhabitat variables. A further temporal confounding variable is the impact of open bill’s other conspecific waterbird species competing for foraging space potentially for the gastropod prey resources during certain periods of the year. Notably, the study illustrated that the impact of such inter-specific competition constitutes the only factor that significantly disrupted a potentially perfect tandem distribution of African Openbill Storks and their gastropod food across the rice-fields, especially on the temporal scale. General anthropogenic disturbance appeared to be an insignificant factor in the Openbill’s foraging activity as the species was observed to be very tolerant of farmers’ agronomic field activities within the paddies during most of the survey sessions, which is consistent with earlier observations on the Asian Openbill (Dutta and Pal 1993; Tamang et al. 2024b).

To minimize impact of such competitive pressure, the storks seemed to adopt a strategy of shifting maximization of their foraging focus to a different crop growth phase when most of the competitors were either less abundant in the fields or presumably had access to a variety of other prey resource options.

**Study’s limitations and Research direction**

The study did not investigate the role that the paddy-field water quality during the flooded phases, such as due to agrochemical inputs, might play in influencing localized or field-scale distribution and abundance of gastropods to, in turn, driving African Openbill Stork foraging dispersal patterns. However, we presume that the impact of this variable is effectively controlled for due to the centralized overall-scheme management system whereby all the contracted paddy rice farmers conform to established field operational routines including common-source water distribution, type and quantity of agrochemical inputs, and clearly-defined cropping regimes at all growth phases thus guaranteeing environmental uniformity. Secondly, we did not make any direct estimation of the trophic off-take rate of gastropod prey by African Openbill Stork in comparison with its other potential opportunistic and non-specialist avian or other vertebrate competitors for this resource. As such the scope of this study is unable to provide a quantitative evaluation of the stork’s actual role in the natural bio-regulation of mollusc population across the farm, particularly the species that serve as vectors for schistosoma parasites. Thirdly, the fact that this study adopted a strong African Openbill Stork-to-gastropod mollusc trophic connection does not imply that these molluscs constitute the bird’s only prey option across the study area.

Finally, future research on this subject should also consider non-staggered rice cultivation systems in which all paddy fields are at the same growth stage at any one time, and hos these might influence African Openbill Stork assemblage and foraging dispersal patterns in relation to gastropod distribution with or in presence of other competing waterbirds or other vertebrate taxa.

*Acknowledgements*

We thank all of the landowners in the entire eastern region of Ahero where the study was carried out, for permitting access to their property on multiple occasions for purposes of the research. The National Museums of Kenya provided additional administrative logistical support for the project. The field work complied with the research regulatory framework of the laws of Kenya regarding handling of wild animals, and approval from the wildlife authorities at the time of the study.

**Funding**

This work was supported by a Waterbird Society grant to NEO under the Kushlan Research Award Scheme

**Authorship contributions**

NEO: Methodology, Formal analysis, Investigation, Data curation, Data analyses, Writing - original draft, Project administration.

DO, PA, CA and ASM: Field Investigation, Bird systematics and identification, Data collation; Draft manuscript approval

**Conflicts of Interest**

The authors decorate that there were no conflicts of interest

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**FIGURE LEGENDS**

**FIGURE 1**. Map of study area showing various rice paddy-field-blocks where sampling was conducted. (Adopted from the National Irrigation Board, 2019)

**FIGURE 2** A) Abundance distribution across the various phases of rice crop growth for African Openbill Stork in comparison to abundance and species richness of other potentially competing wader waterbird species; B) Abundance distribution across the various phases of rice crop growth for gastropod molluscs; B) the role of paddy-field flooding in influencing abundance distribution of African Openbill Stork and gastropod molluscs. Means are derived by averaging abundances of the five survey episodes (N=434).

**FIGURE 3.** Distance-based Linear Model (DistLM) ordination plots showing African Openbill Stork abundance distribution in relation to A) rice growth stage and across the various levels of field flooding; B) field flooding across various levels of potential competition pressure; and C) competition pressure across the various rice growth stages; D) Gastropod abundance distribution in relation to rice growth stages across the various levels of field flooding. The DistLM models are based on (LogX+1) transformed resemblance matrices of Bray Curtis similarities for abundance distribution

**FIGURE 4.** Boxplots and regression graphs from GLMM modeling, showing significant predicted responses of African Openbill Stork to effects of A) rice growth stage and B) paddy flooding. Regression plots showing predicted effects of C) gastropod abundance and a, D) waterbird competition pressure on African Openbill Stork abundance. Boxplots showing predicted response of gastropod abundance to A) Rice growth stage and F) paddy0-field flooding.

**FIGURE 5.** Regression model plots showing response of African Openbill Stork abundance response to interactive effects of A) gastropod food resource abundance with paddy-field-block size or B) gastropod food resource abundance with waterbird competition pressure, and C) rice growth stage with paddy-field-block size or D) gastropod food resource abundance with waterbird competition pressure; and also the response of gastropod abundance response to interactive effects of E) paddy-field-block size with rice growth stage or paddy field size with paddy flooding