*Title*: Predatory bird cues structure avian communities and affect nesting behavior across a savanna shrub-encroachment gradient

*Running head*: Predatory bird effects on savanna birds

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**Abstract**

Land-cover change is restructuring animal communities worldwide, but the proximate mechanisms of community reassembly are largely unproven. Effectively predicting land-cover change effects on vertebrate communities is limited by this lack of understanding. We manipulated a shrub-cover gradient by providing cues of predatory birds associated with shrub encroachment to determine if predatory birds are driving community change in shrub-encroached savanna. We surveyed bird abundance, breeding behavior, and nesting across the gradient and treatment condition, testing for treatment effects and treatment X shrub cover interactions using hierarchical abundance models (Robust design abundance models… for the survey data; zero-inflated Poisson and zero-inflated negative binomial for models for the nest and breeding behavior data). We found that several species were more abundant in treatment plots and others less; species showed patterns of breeding behaviors and nesting consistent with this result. Likewise, bird abundance differed between bands 0-50 and 51-100 m from treatment plot centers but not control plot centers. These results show that predatory species can play an important role in determining community assembly under land-cover change. We speculate that the effects we observed were primarily driven by drongos, which are both predators and sentinels in savannas— raiding nests, killing adult birds, but also aggressively chasing off raptors and loudly warning (sometimes falsely) of a predator’s approach.

**Introduction**

Shrub encroachment in savannas is restructuring animal communities worldwide by changing vegetative cover and associated species interactions. Whether species interactions are driving community assembly associated with shrub-encroachment is largely unknown, making projections for the composition of future communities uncertain.

Changes in predator-prey interactions can rapidly and profoundly restructure animal communities (e.g., Hairston et al. 1960, Paine 1974). This is because predators exert strong direct and indirect effects on prey which in turn can determine whether prey species will coexist (Holt 1977).

Predators exhibit three important general effects on prey community structure. First, predators can increase prey species richness promoting coexistence (). This is because predators prefer common species, allowing rare species to persist (). Second, prey-switching with changes in prey relative densities promotes species evenness and selecting prey imperfectly can enhance this effect (Ryabov et al. 2015). Finally, predators can promote spatial turnover in prey communities by selecting different prey traits in different habitats ().

Prey responses to predator cues should be dependent on available cover, which may attenuate or intensify prey responses depending on prey traits. Relevant prey traits include physical attributes such as wing loading as well as life-history traits such as fecundity and longevity. In both cases, interactive effects of predator cues and cover on species composition are likely because escape and predator avoidance strategies differ among species.

We predicted that cover was interacting with predatory bird cues and re-structuring savanna bird communities across shrub-encroachment gradients. Since predatory bird abundance increased across a shrub gradient, we also tested the hypothesis that changes in predatory bird abundance have been driving bird community composition in shrub-encroached savannas.

Can predation maintain functional diversity and reproduce a suite of species interactions characteristic of shrub-encroached savanna?

We hypothesized that increasing cues of predatory birds would affect bird abundance and breeding effort in a manner similar to that associated with increasing shrub cover. We tested these hypotheses by repeatedly surveying bird communities during a field experiment where we randomly applied auditory cues of several predatory birds that prey on other birds at all life-history stages across a shrub-encroachment gradient.

**Methods**

Study Area

We studied the effects of predatory bird cues on avian community structure on the Mbuluzi and Mlawula game reserves in Swaziland’s Lowveld savanna (26.15 S, 31.78 E). The region is a moist subtropical savanna (AUTHOR DATE; mean annual precipitation: XXX mm; mean annual temperature: XX C), and breeding activity peaks for most birds during a summer rainfall period (November-January; Sirami and Monadjem 2012). Shrub encroachment is extensive in the region, and the reserves where we worked are embedded in a land-use mosaic comprised of subsistence farming, communal rangelands, and commercial agriculture (Sirami and Monadjem 2012).

Experimental design

We sampled bird occurrence, abundance, and breeding behavior on 24 plots of 100m radius from 21 October – 15 December 2015 (nest searching from ~20 Dec- ~12 Jan), when migrants were settling and local breeders were selecting nest sites (Sirami and Monadjem 2012).

We identified a set of 24 plots from 44 candidate sites visited 4 times from 4 December 2014-15 March 2015, paired for similar shrub cover and proximity (<7 km apart) that did not experience clearing or burning during the study. We randomly assigned one of each pair to a predatory bird cue addition treatment or a procedural control where we placed dummy boxes that were manipulated in the same manner as treatment gear. Each plot was >250m from any neighboring plot and each plot was >100 m from visible edges, i.e. abrupt changes in shrub, tree, and grass cover. We did not attempt to remove predators or protect prey species from predation events.

We broadcast a mix of vocalizations from the 6 predatory bird species that comprised >95% of the predatory bird community in Swaziland’s shrub-encroached Lowveld savanna on all treatment plots: Burchell’s coucal, *Centropus burchelli*;fork-tailed drongo, *Dicrurus adsimilis*;grey-headed bushshrike, *Malaconotus blanchoti*; southern boubou, *Laniarius ferrugineus*; southern yellow-billed hornbill, *Tockus leucomelas*;and woodland kingfisher, *Halcyon senegalensis* (Stanton et al., unpublished data). Collectively, these species prey on other birds at all life-history stages, and most species have been documented killing both nestlings and adults (Hockey et al. 2005). We broadcast vocalizations of these species because (1) we were interested in how the collective effects of predatory birds in savanna bird communities were moderated by shrub cover, and (2) what proportion of the variance between open and shrub-encroached savanna can be explained by the effects of increased cues of this suite of predatory birds.

We rotated one playback station among three locations in each 100m radius plot twice weekly to reduce habituation to playback conditions. Each playback station consisted of a functional station or dummy gear. Each functional station consisted of a SanDisk Clip Sport (location) MP3 player and a RACPower 3150 mAh lithium-ion battery inside an EcoExtreme [model#] (location) 3 amp speaker powered by three 2100 mAh AA batteries (brand, location) suspended 0.5-2.3 m above ground level in a shaded spot to prevent overheating. Dummy stations consisted of a plain black dry case (Make, Model, Location) placed and moved in the same manner as treatment stations. We focused on procedural controls that did not include sound because control vocalizations can have unknown effects. However, we ran a follow-up experiment on 12 plots from DATE-DATE comparing the effects of 6 silent stations to 6 stations where we broadcast pink noise and noted no effects of sound addition ([presumed, analysis required]).

We prepared 3 playback files for use in predator cue treatments by drawing 2-3 recordings per playback file from a set of available exemplars (McGregor et al. 1992, Kroodsma et al. 2001), totaling ≤4 individuals of any species. [I listened to everything with the focal species in the foreground and rated A or B quality by xeno-canto.org users and selected all that I deemed useable as-is or with very simple editing, e.g., truncating a non-target species from the end of a recording in program Audacity. I also added recordings of 3 southern boubou groups and 1 grey-headed bushshrike group that I recorded in Swaziland; I did not broadcast these in the same place they were recorded. I also listened to everything in the Florida museum collection but nothing was suitable because the recordings were noisy. I have a spreadsheet with notes on all manipulations done to recordings. The vocalizations are mostly songs but include calls, including one drongo mimicking something. I excluded alarm calls. I am inclined to leave these details out in lieu of providing the playbacks files as a data supplement]). We determined how many vocalizations to include in each file and each day based on previous field experience and acoustic monitoring data (unpublished). We provided 564 total vocalizations per playback file and day comprised of 48, 216, 48, 180 … vocalizations of Burchell’s coucal, fork-tailed drongo, grey-headed bushshrike, southern boubou, southern yellow-billed hornbill, and woodland kingfisher, respectively, representing their relative frequency of detection in shrub-encroached savanna in Swaziland (unpublished data). We played vocalizations each day from dawn to twilight.

We surveyed each plot for bird occurrence, abundance, and breeding behaviors12 times during 6 focal periods throughout the experiment to disentangle changes in species detectability from species abundance [and identify patterns of occupancy dynamics] (e.g. Hua et al. 2013; i.e., “closure” *sensu* Rota et al. [20XX]). We also searched for nests for 6 hrs per plot from DATE to DATE.

We predicted that [natural history and several life-history and functional traits] would predict how species responded to predatory bird cues and how those responses would be moderated by shrub cover. [i.e. I expect to see cue X cover interactions among species consistent with antipredator behavior predicting species response to shrub encroachment]. [Add details].

We also predicted that overall bird community structure would change across the shrub-encroachment gradient in qualitatively similar ways when predatory bird cues were added [a figure might help, but I since I am hypothesizing that predation risk is the strongest effect of encroachment, I expect to see an additive effect when looking at a gradient at the community level].

Data collection

We collected data on plot-level bird community composition throughout the experiment using fixed-radius 10 min stationary point count surveys (30 mins before sunrise to 5 hrs after, 21 October-15 December). We surveyed each plot 12 times— twice-daily during 6 periods where we assumed population closure at each site during a single day and modeled closure over longer time periods. We alternated the sequence in which plots were visited in order to control for time-of-day effects on bird activity. We recorded each bird seen or heard and identified to species We also recorded all observations of breeding behaviors, i.e., carrying food or nesting material; nest building; incubation; and feeding chicks. RAS conducted all surveys. We did not survey when winds were >20 km/hr or in the rain. We recorded the time, temperature, wind speed, and cloud cover for each survey.

We searched for nests immediately after the conclusion of the experimental treatment. We searched for 6 hours per plot (144 hours total; XX Dec- 2015-YY Jan 2016) divided into 2-3 stints of 1-4 hrs per stint split among two time blocks: 30 mins before sunrise to 2 hrs after and all other times. We used behavioral clues to locate nests and focused our efforts on species that were recorded markedly more or less commonly on treatment plots than on controls.

We sampled vegetation structure twice at each plot, first from DATES during the pre-treatment year, then from DATES during the experiment. We described patch vegetation structure in each plot by measuring grass, shrub, and tree cover. We defined trees as woody plants >3 m and shrubs as woody plants ≤ 3m after Sirami and Monadjem (2012). We measured grass, shrub, and tree cover using the line intercept method with 3 replicates per point and a 50m tape (Tansley and Chipp 1926 in Bureau of Land Management 1999). We also recorded grass, shrub and tree height at 10m intervals along each line. We recorded the diameter at breast height (DBH) of each tree within 50m using a Biltmore stick. We recorded DBH and distance from the plot center (using a laser rangefinder [Bushnell Yardage Pro Sport, Location]) for all standing dead trees visible from each plot and classified them into functional categories based on the resources they may provide for birds (Maser et al. 1979 [tree data restricted to 2014 season; 100 m data collected in 2016 for grass and shrub cover]).

Finally, we sorted the initial 12 control plots by percent shrub cover and randomly divided them into 6 control and 6 pink noise treatments after nest searching had concluded in order to determine how much of the predator-cue treatment effects we observed were attributable to noise rather than species interactions. We broadcast intermittent pink noise from DATE to DATE during the same times of day as predator-cue treatments and surveyed for bird occurrence, abundance, and breeding behaviors once-daily from DATE to DATE using the same methods employed for the predator-cue treatments (sound file used available as a supplement).

Analytical methods

*Abundance estimation—*. We estimated abundance and detectability for each species from our survey data using robust-design hierarchical N-mixture models (after Hua et al. 2013). We used conventional models. We also used distance sampling to compare community composition within treatment and control plots near and far from plot centers.

*Functional group composition—.*We assigned each species to a foraging group, i.e. predator, nectarivore, frugivore, insectivore, or granivore, based on species accounts from Hockey et al. (2005). We classified as predators all species that Hockey et al. (2005) reported as taking other birds at any life-history stage. We classified all other species based on the predominant or main food items reported in Hockey et al. (2006).

*Life-history composition*—. We used data from Hockey et al. (YEAR) to assign each species life-history trait values.

*Breeding behaviors—.* We adapted the framework of Vickery et al. (1992) to treat breeding behaviors as an ordinal index of increasing likelihood of reproductive success, i.e., nest building, copulating, incubating, carrying food, feeding nestlings, and feeding fledglings.

*Nesting—.* We used the number of active nests located as a response variable.

*Analytical methods and models—.*  We used zero-inflated Poisson and negative-binomial models to test for treatment effects and treatment X shrub cover interactions within and among plots.

We computed several measures of plot-level vegetation structure from our sampling data. We calculated means and coefficients of variation for grass, shrub, and tree cover [other details on trees and snags].

We tested for differences in… using a priori linear contrasts ().

**Discussion**

Resource selection and activity in animals likely reflect trade-offs between foraging and predation risk, particularly for birds (Creswell 2008). This study will help determine how these trade-offs are shaping the structure and function of bird communities as savannas in southern Africa become increasingly shrub-encroached.

Maintaining biodiversity and ecosystem services in increasingly shrub-dominated savannas will require the sort of knowledge this study may offer. Our understanding of how the abundance and species diversity of functional group members contributes to ecosystem services is also quite limited. It will be possible to parameterize more realistic models of biodiversity-ecosystem service relationships by treating the survey data collected in this experiment as a measure of activity.

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