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Camera-trapping forest–woodland wildlife of western Uganda reveals how gregariousness biases estimates of relative abundance and distribution

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ABSTRACT

Camera traps are increasingly used to estimate relative abundance and distribution of wildlife. These methods are powerful and efficient ways to inventory multiple species simultaneously and count rare, secretive individuals across landscapes. However the estimation methods demand assumptions about relative capture probability that may not hold well for gregarious animals. We present results from the first systematic, camera-trap study in forest–woodland, western Uganda. Within a landscape of seven protected areas with globally important biodiversity, we detected >36 species of large mammals and birds in 8841 camera-trap days. Species photographed in groups of two or more individuals produced higher estimates of relative abundance and wider distribution than species photographed as single individuals. We propose these findings reflect higher detectability for animals that forage or travel in groups. We discuss how capture–recapture theory should be adapted to account for both non-independence among individuals in groups and for the interaction between individual and temporal variation in capture probability. We also identify several species that deserve greater conservation attention in Uganda and beyond. Among them, leopards were unexpectedly rare, especially when compared to the sympatric African golden cat. We recommend against a recent policy on leopard trophy hunting, at least in western Uganda.

1. Introduction

Monitoring multiple wildlife species across a wide area can be prohibitively costly in time, personnel, and resources (Field et al., 2005; Gompper et al., 2006; Long et al., 2007; Manley et al., 2004). Thus automatic cameras triggered by motion or body heat are increasingly being applied to species inventories, abundance estimation, and evaluation of conservation efforts (Balme et al., 2009; Mccarthy et al., 2008). Such "camera traps" may also reveal humans or associated threats to habitats and wildlife (O'Brien et al., 2003; van Schaik and Griffiths, 1996). Therefore the data from camera traps can help conservation planners to assess progress toward conservation goals and to target and design interventions (O'Brien et al., 2010; Wegge et al., 2004).

Camera traps are especially useful if conditions preclude direct observation or efficient indirect surveys. Wild animals using rugged topography, dense vegetation, or nocturnal conditions and those wary of humans have all been successfully photographed using camera traps (Larrucea et al., 2007; Maffei et al., 2004; Mccarthy et al., 2008; Silver et al., 2004). Camera traps provide precise estimates of the number of species of large (>1 kg), terrestrial mammals and birds (O'Brien et al., 2003; Tobler et al., 2008) and allow estimation of abundances based on individual identification for some species (Henschel and Ray, 2003; Karanth et al., 2004; Silver et al., 2004; Wegge et al., 2004). Abundance estimates from camera-trap surveys have also been validated by calibration with other methods with some caveats (Balme et al., 2009; O'Brien, 2008; O'Brien et al., 2003; Wegge et al., 2004). However, estimates of abundance and distribution from camera-trap studies must be treated with caution given the major potential bias arising from differential detectability of individuals or species.

Relative detectability is expected to correlate positively with time spent near camera sensors. The duration and also the frequency of visits may increase under several common conditions. If animals are large-bodied, slow-moving, or if wildlife is attracted to the cameras by novelty, lure or bait, then they may linger and produce numerous photos in one visit (Larrucea et al., 2007; Tobler et al., 2008; Zug, 2009). Commonly researchers avoid this by discarding photos of the same species within a set time interval such as 0.5 h (O'Brien et al., 2003). Similarly, the frequency of visits to camera-trap stations may increase if animals prefer microsites selected and accessible by researchers using camera traps (e.g., terrestrial vs. arboreal), if the animals have small home ranges, or if

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the wildlife habituate to signs of people (Larrucea et al., 2007; O'Brien et al., 2003). By the same logic, we predict that detectability may also increase with gregariousness and site fidelity as follows. Gregariousness may increase detectability in a number of ways. For a single source with descriptions of how diverse animals move in groups (see Boinski and Garber, 2000). Social facilitation occurs if one group-member draws the attention of others to an object; it has been demonstrated in studies of visual attention to associates and studies of foraging behavior in gregarious primates and birds (Treves, 2000; Vickery et al., 1991). Social facilitation could increase the number of different individuals photo-captured in the same group and thereby elevate the probability of recapturing a particular, marked individual. Furthermore, repeat visits over intervals of minutes to hours might occur if groups meander back and forth during foraging more than singletons. Gregarious animals that forage on small arthropods and concentrated fruits are noted for such meandering and return visits over various intervals (Robinson, 1986; Waser, 1981). Site fidelity such as territoriality or central place foraging (Larrucea et al., 2007; Waser and Wiley, 1979) would also tend to increase the frequency of revisits to a few camera stations. Differences between species in the duration of visits to foraging patches and the frequency of their revisits have been documented for many species (Boinski and Garber, 2000). In addition to increasing photo-captures at one or a few stations, gregariousness could increase the apparent spatial distribution of a species. Large groups tend to travel further than small groups within many species (Wrangham et al., 1993), hence larger groups may cross a greater number of different camera stations. Finally, species with nomadic movements or large numbers of dispersers might produce many scattered photos of the same individuals especially if cameras are distributed along habitual travel routes such as human-made paths (Maffei et al., 2004; Wegge et al., 2004). Social organization and individual differences in the costs and benefits of gregariousness underlie many of these predictions as short-term associations (e.g., mating associations), seasonal fluctuations in grouping, and behavior within groups produce differential patterns of association among individuals and among species. In short, complex, temporal and spatial variations in social behavior may affect the number of photos collected in a camera-trap survey and the temporal and spatial distribution of such photos.

Here we present results of the first camera-trap study of the forests and woodlands of western Uganda (Fig. 1). We present species inventories from 8841 camera trap-days at 192 separate stations in seven protected areas (Table 1). We present measures of species richness for a landscape pool of 36 taxa and estimates of spatial distribution at three scales. We explore relative detectability as a function of two estimates of gregariousness taken from our own study, as well as female body mass, female home range size, and microsite use, all estimated from the literature. We end by calling attention to several species needing conservation attention including information for an ongoing debate about hunting leopards (*Panthera pardus*) in Uganda.

2. Methods

We placed camera traps in seven protected areas (PAs, Fig. 1). Three were national parks (NPs) and four were Forest or Wildlife Reserves (Reserves) but average size of NPs and Reserves was the same (Table 1: median test $X^2 = 1.0$, $df = 1$, $P = 0.31$). The two categories experienced different levels of protection and management attention in Uganda (Howard, 1991; Uganda Wildlife Authority, 2000). All camera-trap (CT) stations were in the northern Albertine Rift, which stretches from the northern tip of Lake Albert to Lake Tanganyika, Tanzania. The Albertine Rift is one of the most species-rich regions on earth (Plumptre et al., 2007a). Four of the PAs in this landscape have been noted for species richness or high numbers of endemic vertebrates and threatened species: Kibale NP, Bwindi NP, Rwenzori NP, and Kasyoha–Kitomi Reserve (Plumptre et al., 2007a). All the protected areas are ascribed to the Greater Virunga Landscape and adjoin densely settled areas or Virunga National Park, across the frontier of the Democratic Republic of Congo (Plumptre et al., 2007b; Treves et al., 2009).

We positioned CT stations (film Camtrakkers) in one of two ways. Where access was difficult (Kasyoha–Kitomi $n = 49$ CT stations, Maramagambo $n = 25$, and Kalinzu Reserves $n = 23$), we mapped transects by Systematic Segmented Trackline Sampling using DISTANCE software (Thomas et al., 2006). We then walked these transects, cut occasionally for access, and placed CT stations only where wildlife trails or sign crossed transects. In all other PAs, CT stations were placed along wildlife trails or within 6 m of a trail used by people or wildlife but no transects were cut because access was easier. No two CT stations were placed within 200 m of each other and most were 0.5–1 km apart, clustered in localities within PAs. The locations of individual CT stations are not necessarily discernible in our map due to scale but localities can be seen as clusters of CT station points (Table 1; Fig. 1). GPS locations of CT stations are available from the authors. Localities were distinguishable to the field teams by obvious habitat or topographical differences. Thus we adopted a stratified approach within each PA but the placement of CT stations was somewhat haphazard within the constraints of the criteria mentioned above. Indeed this study spanning a long period with two field team leaders (SI and PM) working at different PAs may include interobserver differences that add to or confound intersite and interannual variations. This raises the possibility that we under- or over-represented species that preferred the habitats accessible to us. This is a common bias in camera-trap studies – one alternative would have been to cut vegetation around camera traps to improve human access but that approach carries with it different biases.

We identified most wildlife photos to species (Appendix 1 for scientific names). However a few were difficult to distinguish or taxonomically unresolved so we pooled them at the level of genus or family (genets, mongooses, squirrels) but for simplicity we refer to them as species.

We followed common recommendations on sampling a wide area to capture far-ranging species and using many CT stations for long periods (O'Brien et al., 2010; Tobler et al., 2008). However, our mixed design for CT station placement over several years demands caution in interpreting differences in species richness between PAs. Differential use of wildlife trails could bias for and against some species and individuals (Harmsen et al., 2009; Larrucea et al., 2007; Maffei et al., 2004). Also the multi-year span of the study could confound temporal changes in species richness (turnover, colonization, local extinction, etc.) with differences between PAs.

Because we did not resample the same CT stations at successive seasons and within-seasons, we have no objective way to define resampling intervals. Hence our design did not meet the demands of occupancy analysis for two key reasons. First, robust and precise estimation of occupancy demands an appropriate model of detection probability as a prerequisite (Bailey et al., 2007). Our "model of detection probability" (which we call detectability) is based on rank correlations (i.e., relative between species) not an absolute probability of detection. Furthermore our data contain neither temporal replication between-seasons nor objective criteria for within-season replication, yet "occupancy estimators were generally less biased under designs that include temporal survey replication both within *and* among seasons…" (emphasis added, p. 289 Bailey et al., 2007). Although we might adopt an arbitrary interval to designate a temporal replicate, that could be biased by variable likelihood of photo-capture over time, e.g., trap shyness (Wegge et al., 2004). Our results on detectability can guide future efforts