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ORIGINAL RESEARCH

Cameras replace human observers in multi-species aerial counts in Murchison Falls, Uganda

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Abstract

Wildlife counts in Africa and elsewhere are often implemented using light aircraft with 'rear-seat-observer' (RSO) counting crews. Previous research has indicated that RSOs often fail to detect animals, and that population estimates are therefore biased. We conducted aerial wildlife surveys in Murchison Falls Protected Area, Uganda, in which we replaced RSOs with high-definition 'oblique camera count' (OCC) systems. The survey area comprises forests, woodlands and grasslands. Four counts were conducted in 2015–2016 using a systematic-reconnaissance-flight (SRF) strip-transect design. Camera inclination angles, focal lengths, altitude and frame interval were calibrated to provide imaged strips of known sample size on the left and right sides of the aircraft. Using digital cameras, 24 000 high-definition images were acquired for each count, which were visually interpreted by four airphoto interpreters. We used the standard Jolly II SRF analysis to derive population estimates. Our OCC estimates of the antelopes – hartebeest, Uganda kob, waterbuck and oribi – were, respectively, 25%, 103%, 97% and 2100% higher than in the most recent RSO count conducted in 2014. The OCC surveys doubled the 2014 RSO estimate of 58 000 Uganda kob to over 118 000. Population size estimates of elephants and giraffes did not differ significantly. Although all four OCC buffalo estimates were higher than the RSO estimates – in one count by 60% – these differences were not significant due to the clumped distribution and high variation in herd sizes, resulting in imprecise estimation by sampling. We conclude that RSO wildlife counts in Murchison have been effective in enumerating elephants and giraffe, but that many smaller species have not been well detected. We emphasize the importance of 60 years of RSO-based surveys across Africa, but suggest that new imaging technologies are embraced to improve accuracy.

Introduction

Wildlife surveys over large and remote wilderness areas in Africa, America and Australia are often conducted using light aircraft with 'rear-seat-observer' (RSO) crews who count within defined 'strip-transects' (Caughley 1977; Norton-Griffiths 1978; Grimsdell and Westley 1981; Gasaway et al. 1986; PAEAS, 2014), or record distance of animals from the aircraft path in the 'line-transect' method (Burnham et al. 1985; Pollock and Kendall 1987; Samuel et al. 1987; Hone 1988; Buckland et al. 2004). It has long been recognized that RSOs may fail to detect animals, resulting in negatively biased population estimates (Caughley 1974; Cook and Jacobson 1979; Pollock and Kendall 1987; Graham and Bell 1989; Jachmann 2002; Tracey et al. 2008; Jacques et al. 2014; Lee and Bond 2016). Animals might not be detected either because they are 'unavailable for detection', being for example hidden in dense vegetation cover or underwater (Bayliss and Yeomans 1989; Marsh and Sinclair 1989; Jachmann 2001; Mackie et al. 2013; Jacques et al. 2014) or because they available but 'overlooked' by the RSOs (Fleming and

Tracey 2008). RSO detection of 'available' animals depends on a range of 'environmental factors' such as animal size, group size, vegetation cover, species coloration, reaction to the aircraft, occurrence in multi-species assemblages; 'survey factors' such as flying height, counting strip-width and sun angle; and 'observer factors' such as experience and level of fatigue (Caughley et al. 1976; Anderson and Lindzey 1996; Jachmann 2002; Melville et al. 2008; McConville et al. 2009; Wal et al. 2011; Ransom 2012; Griffin et al. 2013; Jacques et al. 2014; Strobel and Butler 2014; Lubow and Ransom 2016; Schlossberg et al. 2016; Schlossberg et al. 2017).

For the last 60 years in East Africa, the RSO-based 'systematic-reconnaissance-flight' (SRF) strip-transect technique, coupled with the 'Jolly II analysis for unequal sized sample units' (Jolly 1969), has been the standard procedure for counting wildlife and livestock at the local and the national level (Andere 1981; Ottichilo et al. 2000). In the traditional SRF technique, the aircraft follows a systematic flight pattern of transects, usually aligned to a spatial grid-system, while RSOs count animals within sample strips defined on each side of the aircraft (Jolly 1969; Norton-Griffiths 1978; Gasaway et al. 1986). In Kenya, a national programme of surveys using 'SRF-Jolly II', launched in 1977, has provided a unique 40-year record for determining trends in wildlife and livestock populations (Ogutu et al. 2016). In Tanzania where the SRF technique was developed in the late 1960s for mapping seasonal distributions of wildlife in Serengeti (Maddock 1979; Norton-Griffiths 1981), SRF surveys inform policymakers of the status of wildlife populations, and particularly of elephants (TAWIRI, 2010b). At the continental scale, SRF results are compiled to determine the overall population status of the African elephant (Thouless et al. 2016).

The SRF technique is therefore ubiquitous, but concern is often raised that SRF-derived population estimates are not precise (have high margins of error), or fluctuate wildly, or differ significantly (usually being lower) with estimates derived from ground counts which are assumed to more accurately reflect the population (Grimsdell and Westley 1981; de Leeuw et al. 1998; Jachmann 2002; Ferreira and Van Arde 2009; Lee and Bond 2016; Greene et al. 2017; Reilly et al. 2017). In the context of SRFs, many studies have been conducted to improve RSO counting, from determining optimum flying heights and strip widths (Pennycuick and Western 1969; Caughley 1974), to RSO use of cameras for photographing large herds for later counting (Sinclair 1973; Norton-Griffiths 1974), to double-observation techniques with two RSOs on each side of the aircraft (Magnusson et al. 1978; Caughley and Grice 1982; Pollock et al. 2006; Griffin et al. 2013; Schlossberg et al. 2016). In recent initiatives to standardize procedures, guidelines have been developed that prescribe such fundamental aspects as eyesight and counting tests for RSOs and the maximum counting periods 'on-transect' (Frederick et al. 2010; Craig 2012; PAEAS, 2014). Studies to determine a 'probability of detection' for SRFs have largely focussed on comparisons with ground counts (Stelfox and Peden 1981; Jachmann 2002; Greene et al. 2017), but results are usually species and survey specific. Elsewhere, for example, in the US, such biases are also ascertained when marked or radio-tagged animals known to be within the viewing field of the RSOs were not detected (Rice et al. 2009; Wal et al. 2011; Jacques et al. 2014; Lubow and Ransom 2016), essentially the approach that 'we-know-they-are-there, but-you-did-not-see-them'. This requires the availability of many tagged animals for a meaningful sample, and there is no evidence that this approach has been tried in the context of an SRF survey in Africa.

SRFs over large areas are conducted using fixed-wing aircraft, since helicopters do not have the endurance for large surveys, and are usually unavailable or unaffordable. Aircraft must operate at speed well above the stall to remain safe, and hence ground speeds of 160–180 $km.hr^{-1}$ are usually prescribed (Craig 2012; PAEAS, 2014). At this speed, any particular component of the sample-strip scene – grassland, woodland, open glade, patch of wetland – remains in the RSO's view for no more than 5 seconds. In multi-species SRFs, within this short time, the RSO must detect the species (for example, wildebeest, zebra, gazelle); prioritize which species must be counted first; count the animals; possibly photograph the herd; 'subtize' (short-term memorize) the estimate and image number (Fleming and Tracey 2008); record both of these on voice recorder or call estimates to front-seat-observer (FSO, the 'recorder') (Craig 2012; PAEAS, 2014); repeat this process species for species 2 and 3 etc. Calling to the FSO might coincide with a call-out of the opposite RSO in the aircraft who has also seen animals, causing confusion and distraction to all parties. Observing is characterized by long periods of nothing (where the mind may wander), punctuated with bouts of frenetic counting where the observer may be overwhelmed with large herds or congregations of many species. Often multi-species counts are focussed on 1–3 priority species, for example, elephant, buffalo and giraffe; 'supplementary species', for example, the antelopes are added because program managers argue that "it costs us US $ 700 an hour to keep this plane in the air and we want to collect as much data as possible". Tired RSOs do not prioritize supplementary species, with the result that these count data are of low quality.

For many years researchers have suggested that to reduce bias, cameras could replace observers in large-area counts (Leedy 1948; Siniff and Skoog 1964; Caughley

1974). However, in early attempts using analogue camera systems for large-area surveys, the logistics of handling, geo-referencing, processing and interpreting huge volumes of analogue imagery inevitably proved challenging (Terletzky 2013). Early examples include oblique and 'aerial-point-sampling' (APS) surveys of wildebeest and buffalo in Serengeti, Tanzania, (Norton-Griffiths 1973; Sinclair 1973), and caribou in Canada (Couturier et al. 1994). The use of digital cameras has greatly enhanced the scope for large area surveys, but development has been relatively slow since, inevitably, this still requires the use of expensive aircraft and the visual interpretation of thousands of images. However, where the target wildlife population runs into millions, or survey areas are very remote, digital camera APS surveys are the only possible way to count; they are now periodically conducted in Serengeti (TAWIRI, 2010a; Hopcraft et al. 2015), with a recent further application in Mongolia (Norton-Griffiths et al. 2015).

High-resolution digital cameras are now cheap, available and small, and data storage media have a capacity for many thousands of images. It is now possible to test RSO performance with parallel digital camera systems that are inclined at the same angle as RSO-viewing, and image the same strip. Recent cross-comparisons in simultaneous RSO and OCC counting have been conducted for narwhal in Greenland (*Monodon monoceros*) (Bröker et al. 2019) and kangaroos in Australia (Lethbridge et al. 2019) where thermal image-based estimates of kangaroo density were 30% higher than RSO estimates. In Kenya, an RSO-based SRF was run concurrently with high-resolution camera systems in a multi-species count over a large protected area, and it was found that RSOs missed, for example, 60% of giraffe and 66% of the large antelopes (Lamprey et al. 2019).

In this paper, we report on the earliest known experiment in Africa in which an 'oblique-camera count' (OCC) system entirely replaced RSOs in a systematic reconnaissance flight (Lamprey 2016); the study established the later methods for the Kenya surveys indicated above. In Uganda's Murchison Falls Protected Area (MFPA), we tested the hypothesis that high-resolution camera systems, set up obliquely to replicate RSO strip-sample counting, would generate higher and more consistent population estimates than those derived from RSOs. To achieve this, we acquired continuous imagery along SRF transects, and interpreted this imagery for species and numbers in the laboratory. We then compared our estimates with those derived from recent RSO-based counts of MFPA.

In MFPA, Uganda kob (*Kobus kob* ssp. *thomasi*) provide a special case for investigating counting performance. The Uganda kob (pl. kob) is the national emblem species, being the main feature of the country's coat of arms and also the logo of the Uganda Wildlife Authority. Uganda kob occur in highly clumped aggregations around territorial breeding grounds (or 'leks)' (Balmford 1992; Deutsch 1994) that persist for years. Consequently, aerial sample counts where transects are not aligned in similar orientation give wildly varying estimates for this species (Modha and Eltringham 1976). This species was heavily impacted by poaching in the 1980s, with RSO-based population estimates of approximately 5300 in 1995 (Lamprey and Michelmore 1995; Sommerlatte and Williamson 1995) and 7458 in 1999 (Lamprey 2000). Since that time, with improved management of MFPA, this population has increased exponentially, with 9315 estimated in 2005 (Rwetsiba and Wanyama 2005), 36 234 in 2012 (Rwetsiba et al. 2012), and 58 313 in 2014 (Wanyama et al. 2014). With kob numbers evidently increasing so rapidly, the ability of RSOs to effectively count them is called into question.

This research, funded by the oil company Total E&P Uganda (TEPU) originated from the need to conduct accurate baseline surveys of large mammal populations in MFPA ahead of TEPU's licenced oil development in the area (Patey 2015; MacKenzie et al. 2017). Company health and safety regulations prohibited the use of single-engine aircraft carrying 'passenger' RSOs, and this was therefore a camera-only operation.

In this paper, we recognize that a variety of remote-sensing imaging techniques may be used for counting wildlife, for example, the use of aerial sensors on aircraft and UAVs, satellite sensors, oblique or vertical imaging, continuous strip sampling, point sampling, and total coverage imaging. We use the generic term 'camera-counts' to distinguish these broad remote-sensing methods from observer counts. The OCC method is just one of many camera-count systems, but our experiments in Uganda appear to be the first to use this specific oblique-imaging technique.

Methods

Survey area

The survey area of 5037 km^2 encompasses the Murchison Falls Protected area, which includes Murchison Falls National Park and the contiguous Bugungu and Karuma Wildlife Reserves. MFPA is spanned by the River Nile, and is comprised in the north-west of sub-humid open grasslands, and in the south and east of thickets and dense woodland. The park is still recovering from massive poaching in the 1970s and 80s, when the elephant population was reduced from 12 000 to several hundred, and other species were equally impacted (Douglas-Hamilton et al. 1980; Eltringham and Malpas 1980; Lamprey and Michelmore 1995; Rwetsiba and Nuwamanya 2010).

The survey area was divided into four strata, Block 1, North, South, and Bugungu (BWR), see Figure 1. In a standard SRF pattern repeated in all four surveys, transects of 5 km spacing were orientated north-south across the Nile. Additional transects were interleaved to 2.5 km spacing in Block 1 to provide more precise estimates, since this area, destined for major oil development, has the highest wildlife density in MFPA. Figure 1 also shows the tree cover derived from the Global Forest Watch database (Hansen et al. 2013; Global Forest Watch, 2018) and the distribution of the most numerous species, Uganda kob (*Kobus kob* ssp. *thomasi*) in the first survey.

We conducted four surveys of MFPA; MU1, June 2015, at the end of the 'first rains'; MU2, September 2015, the mid-dry season; MU3, December 2015, at the end of the 'second rains'; MU4, April 2016, the middle of the 2016 'first rains'. With the virtual failure of the second rains of 2015, the surveys were conducted during an uncharacteristically dry period in MFPA.

Camera and aircraft specifications

With reference to aircraft operations, we use the standard aviation units of feet for altitude and knots for airspeed since the measurement instruments in the aircraft are calibrated in these units; survey guidelines use them (Craig 2012; PAEAS, 2014) and survey practitioners understand them. Nevertheless, where these are applied, we also convert them to SI units for further clarity.

In MFPA, animals spend much of the time in the shade under tree canopies. Aerial cameras must be inclined obliquely to capture these groups. We used a Cessna 210 aircraft (registration 5X-MLW) with large opening 'clear-vision-panels' in the second-row windows, through which oblique cameras were mounted, see Figure 2. Initial field testing indicated that 45^{o} inclination gave the best balance of strip, overlap and side-view beneath tree canopies, with less influence of aircraft tilt due to turbulence.

MFPA harbours Uganda's largest population of oribi (*Ourebia ourebi* ssp. *cottoni*), a small antelope of body length approximately 60 cm, and cameras must have the 'pixel density' and associated ground-sampling-distance (GSD) (Neumann 2008; O'Connor et al. 2017) of < 6 cm at 500 ft (152 m) height above ground level (HAGL) to resolve this species. Video systems have not yet achieved this definition and therefore for each survey, we used standard digital-single-lens-reflex (DSLR) cameras. Initially, for MU1, these were 2 x Nikon D80 12-megapixel cameras; for MU2-MU4, 2 x Nikon D3200 cameras of 24-megapixel density (6016 x 4000 pixels); and for MU4, 2 x Nikon D810 36-megapixel supplementary cameras for testing in Block 1 infill transects (see Fig. 2). The digital imagery was acquired in standard medium compression JPG format; raw formats were not used due to file storage issues.

Using Nikon lens field-of-view specifications (Edin 2014) and trigonometry, we calculated strip width as a function of camera angle, lens focal length and HAGL. We set and taped the zoom lens at 35 mm to capture a strip of 144 m to conform to the standard SRF strip-width of 130–150 m (Norton-Griffiths 1978; PAEAS, 2014). The theoretical GSD for the D3200 system was 2.1 cm at the inner edge of the frame footprint and 3.3 cm at the outer edge, but the Bayer array in the sensor degrades this to approximately 4.2 and 6.6 cm, respectively (Aerial-Survey-Base, 2014; Bull 2014), with forward velocity of the aircraft further degrading the GSD to ~ 8 cm at the inner edge (O'Connor et al. 2017). Auto-ISO settings were adjusted to a minimum ISO of 800, to acquire images at shutter speeds of 1/1000th s or faster.

The cameras operated automatically for 4 h, with external power and data storage cards sufficient for 8000 images. Images were acquired at 2 s intervals, using external intervalometers, to provide overlapping coverage (46% overlap) at a ground speed of 105 knots (194 km.hr^{-1}). We geo-referenced all images to 100 m in UTM coordinates using software software linking the GPS tracklog to the exact time of each image (GPS-Photo Link and RoboGeo). Each survey generated 24 000 geo-referenced high-resolution images, giving a total of 96 000 images for interpretation.

Height control

The width of the transect, and hence sample size, is dependent on the aircraft height above ground level (HAGL). In compliance with aircraft low-level flight regulations in Uganda, the prescribed HAGL was 500 ft (152 m). We measured HAGL as the difference in height above mean sea level (HAMSL) between the aircraft navigation GPS and the terrain below at that precise location. Terrain elevation is determined from the Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) Version 4.1 (Jarvis et al. 2008). This method is made possible by recent developments in GPS technology, the GPS Standard Position Service (SPS) (Kaplan and Hegarty 2006) and the SRTM model with associated EGM96/08 geoid datums (Lemoine et al. 1998; Rodríguez et al. 2006; Pavlis et al. 2012; Mukul et al. 2015). Positioning data from global SPS monitoring stations indicate the highest GPS accuracy, with low 'height dilution of precision', over the Congo basin and extending into Uganda (NTSB, 2018).

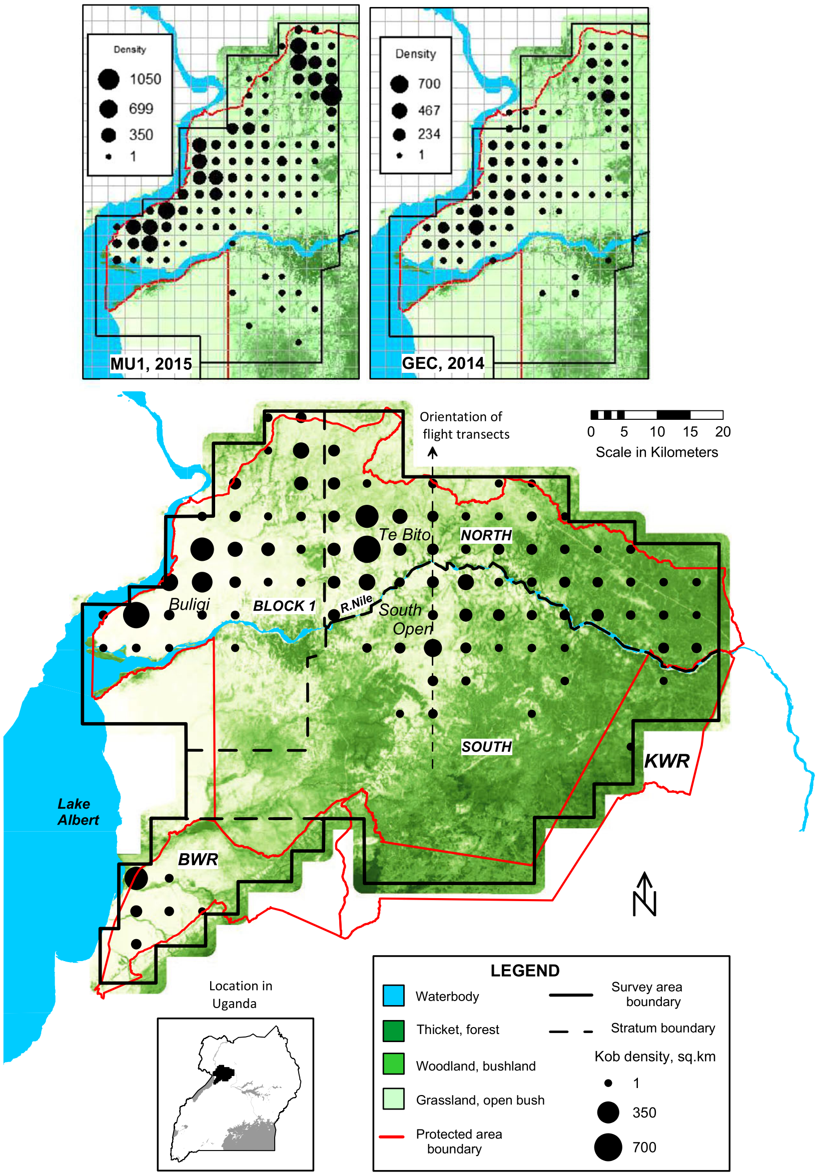

Figure 1. Map of the Murchison Falls survey area. The lower map shows the 5 km sample grid over the entire survey area with distribution and density of Uganda kob. KWR is Karuma Wildlife Reserve.The two upper maps show the kob distribution for Block 1, plotted on the 2.5 km sample grid, for the OCC-based MU1 survey of June 2015, and the RSO-based GEC survey of May 2014.

Height-to-fly (HTF) waypoint codes derived from SRTM were loaded to the aircraft navigation GPS indicating to the pilot at 1 km intervals (20 s flying time) the HAMSL required to maintain a separation of 500 ft (152 m) with the terrain below. On completion of the survey, we superimposed the geo-location points for each image onto the SRTM DEM; the difference between the GPS-recorded image HAMSL and the SRTM elevation at that point is the height above ground. This is known as the GPS-DEM HAGL (or 'GD-HAGL') as used throughout this study.

Image strip-width calibration

We conducted the strip-width-calibration according to standard methods of the Pan-African Elephant Aerial

Figure 2. Camera installation in the Cessna 210 aircraft, right side cameras, survey MU4 (April 2016), with cameras angled at 45°through the open 'clear-vision-panels'. The main right-side camera is the further camera (Nikon D3200, 24 MP), but in MU4 an additional camera pair was added for testing (Nikon D810, 34 MP), here the nearer camera (tests not reported here). The system was duplicated on the left side of the aircraft.

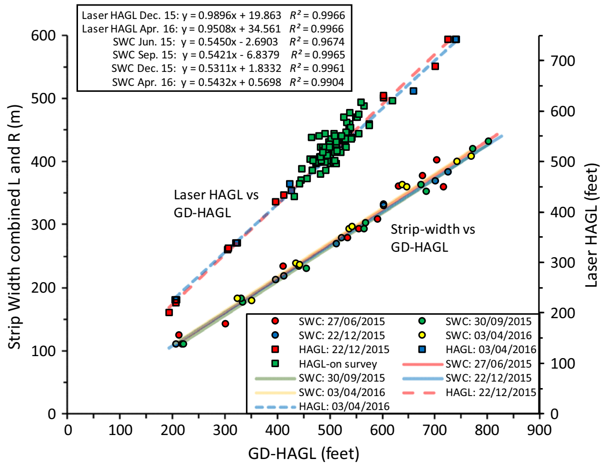

Figure 3. Correlation of GD-HAGL with strip-width (left axis) and laser altitude (right axis) at strip-width-calibrations (SWC) for MU1-4 on the specified dates. Also shown are GD-HAGL measures against the on-survey laser altitude measures taken at height reference waypoints in the MU4 survey.

Census (PAEAS, 2014), with flight overpasses at increasing HAGL from 200 to 700 ft (61–213 m) across 30 m ground-marks on the Gulu base runway. HAGL was recorded from the 'zeroed' pressure altimeter, vertical laser rangefinder and by GD-HAGL. We measured strip-width and frame footprint area using a 45° perspective grid superimposed on each overpass image to divide the 30 m marker intervals and 45 m runway width into smaller (3–15 m) sub-intervals. For all four calibrations, GD-HAGL and laser-HAGL correlations exceeded R^2 of 0.99, while the correlations between GD-HAGL and strip width exceeded R^2 of 0.96 in all cases, see Figure 3. As a further test, GD-HAGL was tested against laser HAGL during the survey itself, at waypoints along transects in MU4 (Fig. 3). On strip-width calibration it was found that slight internal miscalibrations in camera/ zoom lens electronic coupling resulted in a 37 mm focal length for a 35 mm focal length indication, giving at 500 ft an actual strip width of 134 m, a frame footprint of 1.99 ha and frame overlap of 46%, see Figure 4.

To derive an independent estimate of the strip-width during the survey, we measured 80 randomly selected images in Block 1 in MU1 and MU3 by superimposing these onto recent (post-2010) high-definition GoogleEarth (GE). The image corners were carefully aligned to ground features on GE such as road markings, bushes and anthills, see Figure 5. The calibrations proved accurate; for MU1, the measured mean strip width is 139.4 m ± 14.31 (SD, $n = 80$) in comparison with the width for all Block 1 photopoints derived from the GD-HAGL calibration of 143.0 m ± 15.26 (SD, $n = 12\,680$). For MU3, the strip width is 135.3 m ± 18.73 (SD, $n = 80$) in comparison with the HAGL estimate of 136.8 m ± 13.64 (SD, $n = 10\,477$).

Airphoto interpretation

The images were interpreted by a team of four Ugandan interpreters, who had prior experience in aerial point sampling (APS) imagery for landuse (Lamprey 2005; Marshall et al. 2017) and with species and habitats of MFPA. The primary species for interpretation were elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), Rothschild's giraffe (*Giraffa camelopardalis* ssp. *rothschildi*), Lelwel hartebeest (*Alcelaphus buselaphus* ssp. *lelwel*), Uganda kob (*Kobus kob* ssp. *thomasi*), waterbuck (*Kobus ellipsiprymnus* ssp. *defassa*), oribi, warthog (*Phacochoerus africanus* ssp. *massaicus*) and hippopotamus (*Hippopotamus amphibius*). Bohor reedbuck (*Redunca redunca*), mid-sized between oribi and kob, and similar in form to both, are found in MFPA. Their numbers are low, generally 'less than 0.3.km^{-2} where they are common' in Africa (IUCN Red List, 2016); they are not counted in RSO surveys in Murchison and were excluded from interpretation.

For image analysis, the interpretation team was divided into two sub-teams, A and B. Transect start and end times were determined from the GPS tracklogs, and teams worked through strings of images with reference to these recorded times in image EXIF files. From MU2 onwards, to ensure a systematic interpretation, images were assigned to sub-teams on the basis of left/ right cameras

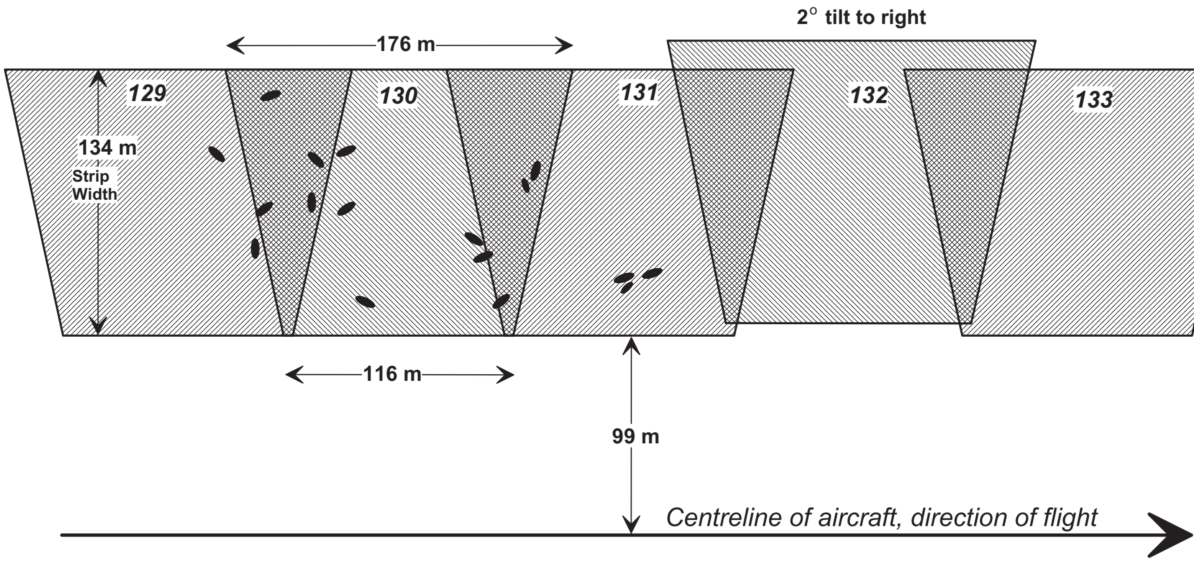

Figure 4. Dimensions of image strip and frame footprints at 500 ft HAGL, with displacement of image 132 due to 2° aircraft tilt to the right. The dots are simulated animals, which might be imaged once, or in overlaps. Tests were conducted comparing total counts of even-framed images (eg image 130) to all-frame counts to evaluate any double-counting (see text).

and alternating transects, see Table 1. The two sub-team interpreters worked on even- and odd-number images, respectively, and kept in step to agree on species identification and partitioning of wildlife herds in image overlaps. Interpretation was conducted using standard software for viewing and annotating JPG images and their associated EXIF files. Each interpreter transcribed his/ her image meta-data and counting results to hardcopy datasheets for entry in the survey spreadsheet database. For each of the four MFPA surveys described in this paper, the 24,000 images were interpreted in 6 weeks by 4 interpreters.

Bias in animal counting

Biased counting results in a shift of estimation in one direction (Caughley 1974; Norton-Griffiths 1978). For bias we determined if there were differences between interpreter teams in the number of encounters of a species, using the traditional Chi-square (χ^2) test (PAEAS, 2014). To estimate double-counting in image overlaps, in survey MU3, we reinterpreted 2500 alternate (even numbered) images for odd number transects 1, 3, 5….15 in Block 1, with all animals counted in each image. Each even-number image is treated as a point-sample without overlap, with area determined using the image footprint calibration. With 104 matched subunit estimates of density, we use the Bayes paired-sample t-test (Kruschke 2013), computed in JASP as an interface with R (Marsman and Wagenmakers 2017), to determine Bayes Factor weights in favour of the null hypothesis of no difference in estimates (H_o) between the full- and alternate-frame datasets.

As a final check for both errors and biases ahead of the Jolly II analyses, all meta-database records of the key species of elephant, buffalo and giraffe were visually verified against their images by an experienced specialist for correct identification, enumeration and avoidance of double counting.

Data analysis, comparing RSO and OCC population estimates

All four OCC surveys were analysed according to the standard Jolly II ratio-method where the strip transects are the sample units (Jolly 1969; Caughley 1977; Norton-Griffiths 1978; Gasaway et al. 1986). For each survey, Jolly II was applied to each of the four strata and these results were then combined to give the overall population estimates and standard errors for the MFPA survey area. Between the four OCCs, we then test the null hypothesis that estimates are not significantly different at $\alpha = 0.05$, calculating t as the difference of the estimates divided by the square root of their pooled variances (Cochran 1954; Norton-Griffiths 1978; Gasaway et al. 1986).

Using the procedure above, we also compare the results of the OCC surveys with two previous RSO sample counts of MFPA conducted in June 2012 (Rwetsiba et al. 2012) and May 2014 (Wanyama et al. 2014), the latter as a component survey of the PAEAS (the 'Great Elephant

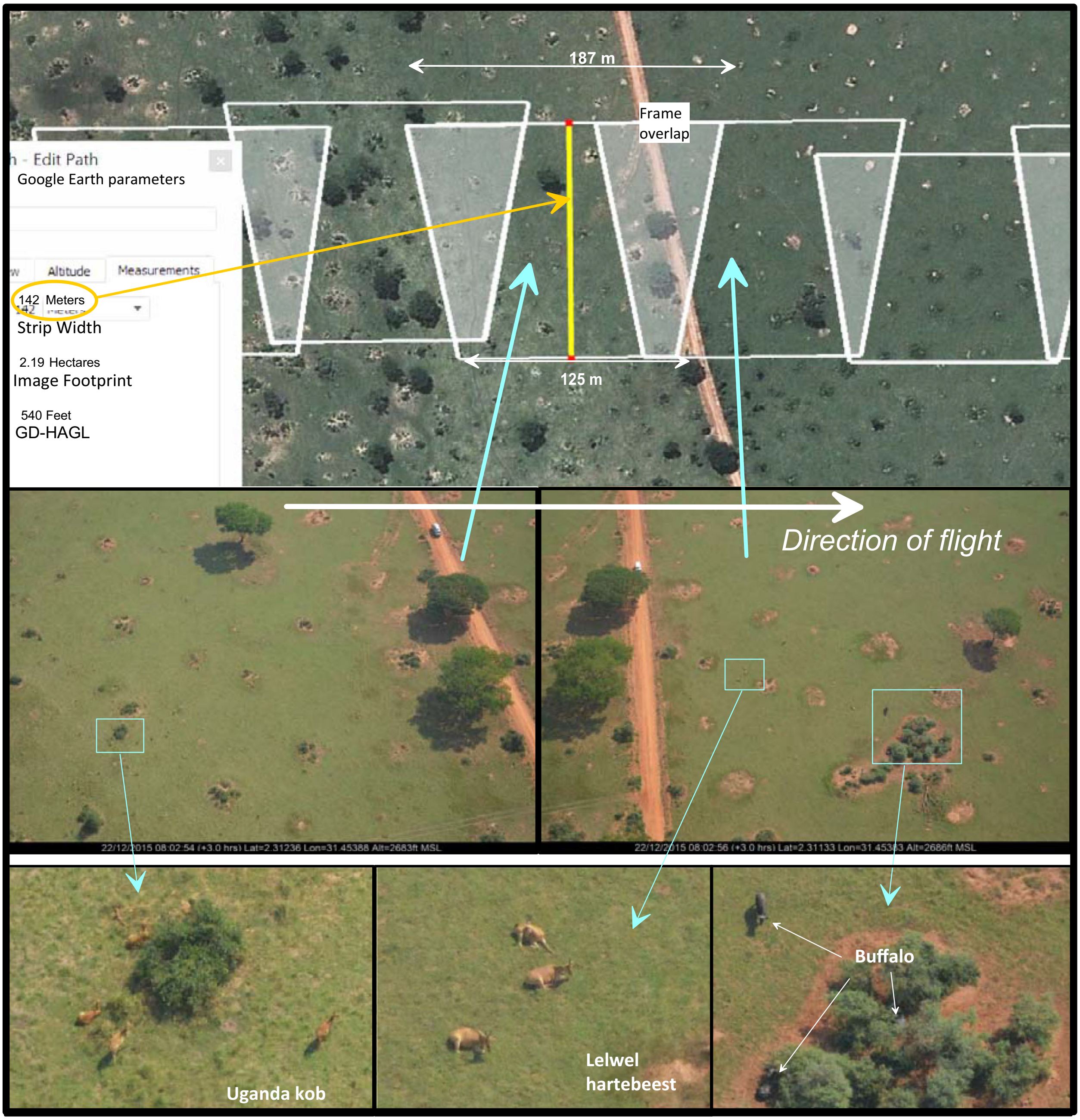

Figure 5. Example of measurement of image strip-width and footprint on Google Earth image (top), for Block 1, survey MU1, and identification of species in OCC imagery, below. In this example, at 540 ft (165 m) HAGL over this rise in terrain, the GE strip-width dimension is indicated as 142 meters and image footprint at 2.19 hectares. Slight aircraft 'tilt' due to turbulence results in small strip displacements, as shown at top, but the influence on strip width is not significant below a bank angle of 5°.

Census' or GEC). Both were conducted according to normal SRF practice, with the GEC survey conforming specifically to new survey guidelines (Craig 2012; PAEAS, 2014). RSO recording was by the 'sub-unit method', where animal observations were assigned by RSOs to 2.5 km subunits along the transect called out by the front-seat-observer. Using χ^2, we test the null hypothesis that both the RSO and OCC surveys encountered the species ('encounters') in the same number of subunits of the survey area.

Table 1. Alternating assignment of transects and camera sides to interpreter sub-teams A and B, example from the start of MU3

Date	Transect	Start Time	End Time	Team A Camera	Team B Camera
20/12/15	38	08:25:21	08:33:59	Left	Right
20/12/15	36	08:35:37	08:43:35	Right	Left
20/12/15	34	08:49:23	09:01:49	Left	Right
20/12/15	32	09:04:25	09:16:21	Right	Left

Results

OCC counting bias and probability of detection

Once the image allocation protocols had been finalized for MU2-4 (Table 1), testing for differences in encounter rates between Team A and B using χ^2 indicated no significant differences between teams. For example in MU2, Team A encountered Uganda kob 667 times, while Team B encountered kob 644 times ($\chi^2 = 0.403$, d.f. = 1, $P = 0.525$). In MU3, Team A encountered kob 675 times whilst Team B encountered kob 694 times ($\chi^2 = 0.264$, d.f. = 1, $P = 0.606$). In MU2, team encounters of elephant were 10 and 18 ($\chi^2 = 2.286$, d.f. = 1, $P = 0.131$), and in MU3 elephant encounters were 13 and 11 ($\chi^2 = 0.167$, d.f. = 1, $P = 0.683$). The exception is hartebeest in MU3, with 188 and 117 encounters, respectively ($\chi^2 = 16.53$, d.f. = 1, $P < 0.001$), resulting from underestimation by one interpreter. In general, both interpreter teams were well matched, with only small differences survey by survey.

We tested for double counting in 8 transects in Block 1, for survey MU3 (December 2015). Jolly II estimation for all images gives 40 912 kob ± 15 951 (SE) for all-images, compared with 40 124 kob ± 14 432 (SE) for alternate images. For elephants, the estimate is 824 ± 611 (SE) for all-images, compared with 965 ± 616 (SE) for alternate images. We determine Bayes Factor weights in favour of the prior null hypothesis of no difference in estimates (H_o) between the paired subunit samples ($n = 103$). The evidence for H_o is 'strong' for elephants ($BF_{01} = 0.110$), and 'moderate' for buffalo ($BF_{01} = 0.142$), hartebeest ($BF_{01} = 0.301$), kob ($BF_{01} = 0.116$), waterbuck ($BF_{01} = 0.209$) and warthog ($BF_{01} = 0.331$). For giraffe, with just 7 subunit encounters, the evidence for H_o is 'anecdotal' ($BF_{01} = 0.339$). For oribi, the all-image estimate is 7939 ± 3915 (SE), the even-image estimate is 5368 ± 2274 (SE), and the Bayes Factor ($BF_{01} = 4.64$) infers that we should reject the null hypothesis. For oribi, we suggest that identification of oribi is improved in overlapped images. We conclude that in general, interpreters are partitioning herds effectively to avoid double counting.

Jolly II analysis and OCC–RSO comparison

Table 2 shows the Jolly II population estimates and standard errors of the four MU1-4 surveys of 2015–16, the GEC survey of 2014 and the UWA survey of 2012. Using t-tests, we test the null hypothesis that there is no difference in estimates between any of the surveys. We cannot reject the null hypothesis of no difference at $\alpha = 0.05$ ($t \leq 1.96$), with the exception of warthog between MU3 and MU4 ($t = 2.60$, $P < 0.02$). For most species therefore, there is no significant difference in population estimates, suggesting that the OCC method generates consistent results.

We then merge all estimates (Cochran 1954; Norton-Griffiths 1978) to give an overall estimate for MFPA, see Table 2. Merged OCC estimates for kob, waterbuck, oribi, and warthog are significantly higher than for both the GEC and UWA count. For kob, the OCC method gives a population estimate of 118 290 ± 13 473 (SE), which is 103% higher than the GEC RSO estimate of 58 313 ± 10 432 (SE). GEC estimates for kob, waterbuck and warthog are, respectively, 49%, 51%, and 43% of the OCC count. Oribi cannot easily be detected by RSOs, the GEC estimate being 5% of the OCC estimate.

Meanwhile, for larger species, we have a greater agreement of estimates. The GEC RSO estimate for hartebeest, an open grassland species, is 80% of the OCC estimate. For elephant, buffalo and giraffe, the RSO estimates are 90%, 85% and 94% of the OCC estimates, respectively, suggesting that observers trained under the PAEAS guidelines are detecting a high proportion of individuals. However, we note that all four OCC buffalo estimates were higher than the GEC estimate, the MU3 estimate by 60%, suggesting that further investigation is needed into accurate counting of this highly clumped species.

Table 2 also presents the number of subunits in which species are detected on a presence/absence basis for the UWA 2012, GEC 2014 and MU1 2015 counts. Using χ^2, we test this difference between the MU1 OCC and GEC 2014 counts. Hartebeest, kob, waterbuck and oribi were encountered in significantly more subunits in the 2015 OCC- count than in the 2014 RSO-count.

Our 2015/16 camera-count and comparative 2014 RSO count (Wanyama et al. 2014) are offset by one year; how much of the difference in the Uganda kob estimates is due to population growth over that one year, and how much to counting difference? Kob breed throughout the year and have high fecundity, females producing a calf every 280 days on average (Beuchner 1974). We use the data of Modha and Eltringham (1976) from Queen Elizabeth NP, where kob longevity is estimated at 8 years, and where 50% of calves survive their first year, to model a maximum growth rate for kob of approximately 12%

Table 2. Jolly II estimates $\hat{Y}$, and standard errors in brackets (SE) for surveys MU1, MU2, MU3 and MU4, for the merged MU1-4 results (bold), and for 2012 CITES-MIKE/UWA and 2014 GEC 2014 survey (bold).

	MU1	MU2	MU3	MU4	Merged estimateMU1-4	CITES-MIKE/ UWA 2012	GEC 2014	Jolly II compare OCC:GEC t-statistic	% Diff. OCC: GEC	Number of subunits that species was encountered			χ2 test for difference OCC: GEC
	$\hat{Y}$ (SE)	$\hat{Y}$ (SE)	$\hat{Y}$ (SE)	$\hat{Y}$ (SE)	$\hat{Y}$ (SE)	$\hat{Y}$ (SE)	$\hat{Y}$ (SE)	t p		UWA 2012	**GEC 2014**	**MU1 2015**	χ2 p
Elephant	1651	1369	1345	2278	**1484**	1617	**1330**	0.29	12%	14	**10**	**12**	0.18
	(651)	(495)	(445)	(1007)	**(283)**	(599)	**(441)**	$P = 0.77$					$P = 0.670$
Buffalo	14 119	13 470	20 588	15 425	**15 159**	7506	**12 841**	0.60	18%	22	**22**	**19**	0.22
	(5152)	(2829)	(4884)	(3445)	**(1861)**	(1929)	**(3411)**	$P = 0.55$					$P = 0.639$
Giraffe	848	1258	1269	632	**919**	757	**860**	0.21	7%	4	**8**	**8**	0
	(298)	(290)	(445)	(240)	**(148)**	(350)	**(235)**	$P = 0.83$					$P = 1$
Hartebeest	10 132	11 993	8530	11 923	**10 136**	6263	**8108**	1.48	25%	46	**59**	**97**	9.26
	(1705)	(1658)	(1153)	(1829)	**(754)**	(1287)	**(1149)**	$P = 0.14$					$P = 0.002$
Uganda Kob	116 006	104 662	113 746	131 175	**118 290**	36 234	**58 313**	3.52	103%	97	**116**	**156**	5.88
	(27 541)	(29 366)	(29 348)	(23 126)	**(13 473)**	(6183)	**(10 432)**	$P < 0.001$					$P = 0.015$
Waterbuck	10 188	10 091	8989	13 273	**10 325**	6648	**5240**	4.28	97%	54	**54**	**84**	6.52
	(1928)	(1800)	(1491)	(2037)	**(888)**	(902)	**(790)**	$P < 0.001$					$P = 0.011$
Oribi	12 853	11 595	10 916	12 797	**11 928**	n/a	**543**	8.21	2097%	n/a	**7**	**70**	51.55
	(3087)	(2820)	(2423)	(2722)	**(1366)**		**(234)**	$P < 0.001$					$P < 0.001$
Warthog	11 068	11 668	9123	15 859	**11 586**	2508	**4986**	5.39	132%	27	**66**	**74**	0.46
	(1748)	(1756)	(1635)	(2004)	**(886)**	(544)	**(844)**	$P < 0.001$					$P = 0.499$
Hippo	n/a	2484	1374	2390	**1975**	790	**1683**	0.64	17%	n/a	**n/a**	**n/a**	n/a
	(n/a)	(565)	(480)	(641)	**(318)**	(271)	**(325)**	$P = 0.52$					

We test for significant differences in the Jolly II 2014 GEC and 2015-16 MU1-4 estimates (t-statistic), and using χ^2 for differences in encounters by subunit for the 2012, 2014 and 2015 MU1 surveys. The table also shows the proportional (%) difference in estimate between the MU1-4 merged estimate and the 2014 GEC estimates.

annum^{-1}. In MFPA, forage resources are not limited and predator numbers are low, with just 138 lions recorded north of the Nile in 2010–2012 (WCS, 2018). The modelled population growth rate is reflected in the RSO counts with an increase from 7548 kob in 1999 to 36 234 in 2012, and where the exponential rate of growth *r* is calculated at .121 (Sinclair et al. 2006). If the 2015 surveys had been conducted by RSOs, we would have expected the 2014 population, estimated at 58 000 (Wanyama et al. 2014), to have increased to approximately 65 000 in 2015. The OCC surveys estimated 118 000 kob for MFPA, indicating that the RSO count did not detect 45% of kob, and that a correction factor of 1.81 should be cautiously applied to previous RSO-based kob estimates. Similar conclusions (without assumptions of a 1-year increase) may be drawn for hartebeest with 20% not detected, giving a correction factor of 1.25; and waterbuck, with 49% not detected and correction factor of 2.03. For elephant and buffalo, although the estimates suggest that 10% and 15%, respectively, were not detected, this is not conclusive due to the high standard errors of the estimates.

Discussion

Our research shows that oblique camera-counts generate population estimates that are significantly higher and more consistent than those derived from RSO counts. The potential impact of camera-counts on nation-wide wildlife inventories is high. Our surveys increase the national population estimate for Uganda kob by 77%, from 77 759 (UWA, 2015) to 137 736. With improved protection, high rainfall and low levels of predation, kob in Block 1 have increased to a density of 78 kob.km^{-2}, well beyond the 'record' densities of 45 kob.km^{-2} in Toro Game Reserve in the 1960s (Beuchner 1974), and probably the highest ever recorded in Uganda (Modha and Eltringham 1976). The MFPA Uganda kob increase is probably unprecedented for any wild antelope population in recent times, with similarities to the exponential increase of wildebeest in the Serengeti in the 1970s and 80s (Sinclair 1979; Hopcraft et al. 2015) and the George River caribou herd in Canada from 1960–1990 (Messier et al. 1988) - the latter sadly in catastrophic decline to just 8000 of the estimated population of 800,000 in the 90s (Canada GNL 2018; Romea, 2018).

With regard to other species in MFPA, the Lelwel hartebeest, listed as Endangered by IUCN (IUCN Red List, 2017) and which was reduced in South Sudan from over 50 000 in the 1960s to just 1100 in 2007 (Fay et al. 2007), is shown in the camera-counts as having a relatively healthy and increasing population in MFPA; this is probably the most important population of this subspecies globally. Elsewhere, for species that aggregate in large numbers, camera-counts, might also positively alter national species inventories, for example, wildebeest in Maasai Mara in Kenya (Bhola et al. 2012), white-eared kob in South Sudan (Fay et al. 2007) and Saiga antelope in Kazakhstan (McConville et al. 2009). In the Serengeti, with over one million wildebeest (Hopcraft et al. 2015), periodic censuses of wildebeest and other migratory wildlife are now entirely conducted by vertical aerial-point-sampling (Norton-Griffiths 1973; TAWIRI-CIMU, n.d.).

In addition to more precise counting, camera-counts have a number of key advantages over RSO-based surveys. Firstly, the imagery provides the full sample, frozen in time for verification and reanalysis of species numbers and strip-widths, and for further exploration of factors that determine visibility and distributions (Jacques et al. 2014; Schlossberg et al. 2016; Ndaimani et al. 2017). Secondly, while image interpreters need enthusiasm and patience, they do not need to be experienced to deliver consistent results. During the study, two interpreters departed and were replaced with new graduates who, after short training and mentoring, performed equally well. These findings are reflected in other image interpretation studies (Erwin 1982; Frederick et al. 2003) where untrained interpreters outperformed advanced remote sensing techniques (Terletzky and Ramsey 2016). Thirdly, there are safety dividends in excluding RSO passengers in low-level surveys and transiting to image-based methods; SRFs are operated at low-levels, where bird strikes, power lines and violent turbulence (especially in mountainous area) are hazards, and where engine failure is potentially catastrophic. Without RSOs who need to count at altitudes of 350 ft or lower (PAEAS, 2014), aircraft with camera-count systems can fly higher and still deliver high-resolution imagery for counting; currently, the optimum OCC height above ground level (HAGL) is set at 600 ft (Lamprey 2018).

The disadvantage of the OCC approach in its current stage is the high volume of imagery generated, and associated labour costs for interpretation. In assessing costs, a wildlife SRF budget is divided into three components; (1) the technical components of design, oversight, data management, data checking, analysis, mapping (GIS work) and reporting; (2) the cost of operating the aircraft; (3) the cost of the data acquisition, whether this is by RSOs (for flight allowances, salaries, accommodation in the field) or air-photo interpreters (for remuneration costs). OCC surveys do not increase components 1 or 2, although data checking might add a small increment. This might be offset by a cheaper aircraft, which could for example be a 2-seat aircraft or even microlight, since we no longer need to carry observers in a 4- or 6-seat aircraft. The larger cost of the OCC method is in component 3, where current calculations indicate that the OCC method costs approximately 25% more than RSO-based data acquisition. Given the offset with aircraft costs, the budget for a OCC survey, carried out at the same sampling intensity, is similar to that of an equivalent RSO survey. For the 12% sample for MFPA described in our study, the costs per sampled km^2 (total 605 km^2) are indicated as US \$64.km^{-2}, with 30% of this cost for image interpretation. The generation of estimates and distribution maps for each MFPA survey was achieved in three months, which was acceptable for the wildlife managers of the area.

Costs may also come down with the use of UAVs for imaging surveys. While great progress has been made in their use for wildlife surveys, endurance limitations restrict their use to small areas (Wang et al. 2019). In West Africa, for example, a UAV was successfully used for an elephant SRF of a small reserve of 940 km^2, but limitations on range and reliability meant that the exercise took many days to complete (Vermeulen et al. 2013). It was concluded that the exercise cost 10 times as much as with using a light aircraft. Today, a UAV may not complete more than one 60 km transect in MFPA, but in time, with improvements in reliability and endurance, UAVs will be routinely used for large area counts.

A major constraint to OCC efficiency is that, in emulating an RSO count, there are long stretches where no animals are encountered. Thus, for example, in the MU3 survey, 2165 out of 23 927 images (9.3%) captured target animals, and of these just 25, or 0.1% of the total, contained elephants. An important immediate avenue for investigation is to sub-sample the dataset to test if precision can be maintained at lower volumes of imagery (Norton-Griffiths et al. 2015), and to determine how to filter out true-negatives, the images with nothing in them. New techniques in machine learning now offer the possibility of species identification and enumeration, (Sirmacek et al. 2012; Rey et al. 2017; Eikelboom et al. 2019; Tabak et al. 2019), but it will take some time for experimental techniques to be operationalized for full-scale SRFs. Although research has focussed on specific species and sites, an immediate need is to derive AI systems which can simply filter out images with ‘something-of-interest’ from the > 80% of the true negatives. This leaves human interpreters with a greatly reduced workload.

Improvements in visible spectrum and thermal IR aerial sensors, both in manned aircraft and UAVs, now offer new opportunities for animal counts (Terletzky 2013; Lethbridge et al. 2019), with the highest successes in detecting objects with high contrast, for example, seals or penguins on ice-flows (Conn et al. 2014; McMahon et al. 2014; Borowicz et al. 2018). Researchers are also now turning to high-resolution satellite sensors such as Ikonos, GeoEye-1, and World-View-3 (Laliberte and Ripple 2003; Fretwell et al. 2017; Xue et al. 2017), especially for counts of waterfowl and seabirds. While there have been some advances in counting animals in the open savannas in Africa (Yang et al. 2014), it will take some years before these techniques can be applied in complex wooded savannah environments.

The development of remote-sensing methods for wildlife counts are moving forward rapidly, but at the same time the traditional RSO-based SRF count remains valuable and relevant to providing long-term wildlife trends to policy-makers (Ogutu et al. 2016). To determine the status of such key species as elephants, it is essential that efforts are continued to improve and standardize RSO-based counts (Jachmann 2002; Craig 2012; PAEAS, 2014). Where information is needed on the distribution and abundance of multiple species in a landscape, the OCC method described in this paper is a significant step in the evolution of more accurate and automated wildlife counting.

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Conflict of Interest

The authors declare no conflict of interest.

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