

WILDLIFE RESEARCH

Increasing the accuracy and efficiency of wildlife census with unmanned aerial vehicles: a simulation study

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ABSTRACT

Context. Manned aerial surveys are an expensive endeavour, which is one of the core reasons for insufficient data coverage on wildlife monitoring in many regions. Unmanned aerial vehicles (UAVs) can be a valid, cost-efficient alternative, but the application of UAVs also comes with challenges. Aim. In this explorative simulation study, our aim was to develop an efficient layout of UAV surveys that could potentially overcome challenges related to double counts of individuals and even area coverage, and that would minimise off-effort travel costs. Methods. Based on different simulated survey layouts we developed hypothetically for the Katavi National Park in Tanzania, we quantified the advantages that UAVs might offer. We then compared these findings with manned aerial surveys. Key results. The proposed new survey design and layout indicated an increase in survey efficiency of up to 21% when compared with conventional survey designs using parallel transect lines. Despite the complex flight pattern, the accuracy of the flight paths of the UAV outcompeted those of manned aerial surveys. The adapted survey layout enabled a team of two operators with a small battery-powered UAV to cover an area of up to 1000 km² per day, without specific infrastructural requirements. Conclusion. Our calculations may serve as a vital spark for innovation for future UAV survey designs that may have to deal with large areas and complex topographies while reducing operational effort. Implications. UAV applications, if well designed, provide useful complementation, if not replacement, for manned aerial surveys and other remotely sensed data collections. Our suggested survey design is transferable to other study regions, and may be useful for applying UAVs efficiently.

Keywords: accuracy, conservation, drones, protected area, simulation, survey design, wildlife census, zigzag survey.

Introduction

Wildlife conservation requires the collection and interpretation of high-quality data adhering to appropriate sampling frequency and accuracy (Friess and Webb 2011; Blanco *et al.* 2012). To this end, remote-sensing systems have a high potential to deliver cost-efficient (Wang *et al.* 2019) and reliable, unbiased data (Hodgson *et al.* 2018) through non-invasive collection techniques (Hu *et al.* 2020), even in inaccessible and remote areas (Hyun *et al.* 2020; Duporge *et al.* 2021). Because of these advantages, remotely sensed images have made considerable advancements in wildlife monitoring (Franchomme 2020; Harrity *et al.* 2020).

Although less affected by some core limitations of conventional ground surveys or satellite-based studies, aerial-based monitoring of wildlife experiences challenges such as habitat-dependent detectability (Boulinier *et al.* 1998; Field *et al.* 2005; Pollock *et al.* 2006). Nevertheless, aerial surveys allow complex survey designs and even coverage of study areas, including those with difficult or inaccessible terrain. Moreover, if designed adequately, they may diminish the likelihood of double counting moving animals (Vermeulen *et al.* 2013; Hodgson *et al.* 2018), because the risk of double counts is higher when using long, parallel transects in aerial surveys (Bouché *et al.* 2012; Brack *et al.* 2018).

Manned aerial surveys that cover a representative percentage of the total area currently still constitute the main approach to wildlife population surveys over large spatial scales, though unmanned aerial vehicles (UAVs) may efficiently and reliably fill prevalent shortcomings (Fust and Loos 2020). Despite current legal restrictions (Cleguer et al. 2021), the merits of UAV-based surveys include its programmability, which allows surveying predefined complex survey patterns (Cabreira et al. 2019), which might be necessary to ensure an even and constant area coverage probability, for example in highly heterogeneous landscapes. An even and constant area coverage probability can be achieved through adjustments of the layout of the flight transects (Strindberg and Buckland 2004). Moreover, the programmability of UAVs may also be beneficial in rugged topographies. Here, survey data from UAVs may accurately account for variability in survey transect width and therefore survey effort, as a result of varying flight height, by combining information on image footprint (i.e. the width of the surveyed strip) with the flight log data. Besides, steady altitudes can be achieved through autonomous contour following of the terrain, which is a difficult endeavour for manned aerial surveys, allowing to further minimise bias in count methods (Bouché et al. 2012). Moreover, UAVs expose a lower risk for staff compared with manned aerial surveys in such complex survey settings. Additionally, their programmability makes UAV surveys fully repeatable while minimising double counts through appropriately designed survey layouts, accounting for the potential movement of animals between transect lines.

Current constraints in flight time and speed of UAVs require efficient use of the available power resources, especially when power is supplied by rechargeable batteries, which represent a major weight proportion of UAVs. Current manned aerial transect surveys generally follow a design composed of a series of parallel lines, which limits their efficiency by losses through 'off-effort' (i.e. transit between transects) travels between transect lines (Strindberg and Buckland 2004). To address this disadvantage, a zigzagshaped survey design that enables almost continuous sampling has been widely adopted for ship-based monitoring of marine organisms (Pollard and Buckland 1997). Yet, its application in aerial surveying has so far been limited to offshore observations (e.g. bats (Hatch et al. 2013) or whales (Shelden et al. 2015)), in part as a result of the complexity in the required flight pattern. The application of zigzag survey design comes with disadvantages, depending on the chosen approach to determine the angles between subsequent zigzagging 'branches'. Generally, subsequent transect lines are not fully independent in their statistical sense, which might bias the results. Furthermore, the simpler equal-angle or equally spaced zigzag design can lead to uneven coverage probability, particularly on irregular shapes of the survey regions (Strindberg and Buckland 2004). Nevertheless, simple sampling algorithms have frequently been chosen

for easier implementation despite their statistical weaknesses. To counteract some of these analytical limitations, a zigzag survey design implementing the continuous adjustment of the transect line angle, in accordance with the current shape of the survey region, has been suggested and successfully applied (Dick and Hines 2011; Hammond *et al.* 2013; Bortolotto *et al.* 2016; Harbitz 2019).

The overarching aim of this article is to suggest ways to increase the reliability and accuracy of aerial wildlife sample counts through the efficient use of UAVs. Due to their ability to autonomously follow complex flight paths, we investigate through flight simulations the use of UAVs to monitor terrestrial animals by adapting zigzag-shaped survey designs. Specifically, we propose more efficient survey layouts with the target to minimise double counts of moving animals. We then explore the limitations of the survey layouts to estimate the feasibility for its application, especially in relation to area coverage. Our calculations of the benefits of the application of UAVs using a case study simulation in the Katavi National Park in Tanzania may serve as a guideline for survey designs that complement current limitations in the practical applications. Our approach consists of a series of four consecutive experiments: (1) exploration of the effects of various survey design and animal-related parameters on the maximal achievable coverage; (2) analysis of the impact of different survey block shapes and layouts on the relevant required flight distances and the resulting benefit of the zigzag transect flight plan over a comparable parallel transect flight plan; (3) assessing the potential of an optimised survey layout, which aims to increase survey efficiency by reducing in-field logistics; and (4) assessment of flight path accuracy and its effect on coverage consistency within areas of complex topography, by using contour-following transects.

Materials and methods

Several studies applying a zigzag survey design have adjusted the outline of the survey regions to fulfil the requirements for even coverage probability, but our approach is to apply this method within complex survey block layouts by adjusting the transect directions and continuously leading to a zigzagging arrangement of individually curved transect lines (Fig. 1), following the suggestions of Strindberg and Buckland (2004).

To minimise the risk of double counting animals in consecutive transects within one flight, we furthermore limited the adjusted angle of transect direction, in accordance with the potential speed of animal movements between subsequent transect strips, and the flight speed of the UAV. The angle should be small enough that any animal observed on one transect moving towards the subsequent transect line should not be able to reach the area of the next surveyed strip before the UAV has passed over that area. Assuming averaged animal speeds of movement, we calculated the



Fig. 1. Comparison between (a) parallel and (b) zigzag transect lines. (c) To further improve the zigzag sampling design, we limited the angle α between consecutive transects to minimise the risk of double counting. The dotted line in (c) is identical to the transects in (b) and serves as a comparison.

potentially maximum travelled distance from one point of observation, which then defined the minimal distance of the subsequent transect to that point, resulting in the definition of a critical minimum angle $\alpha_{\rm crit}$ needed between consecutive transect lines accordingly (Fig. 1*c*).

Experiment 1: We initially assessed zigzag transects on simple rectangular survey polygons. To analyse the effect of transect length on maximum achievable coverage, we calculated survey transects of areas of 200 km² size with varying widths between 1 km and 10 km. Additionally, we varied the potential speed of moving animals between 5 and 90 km/h.

Experiment 2: To quantify the increase in efficiency of zigzag transect design over the conventional parallel survey approach, we compared flight times of surveys covering differently shaped and sized areas. An initial test survey was conducted on an area of 110 km^2 , with an approximately square shape, with realised coverage of approximately 10%. The assumed animal speed was set at 10 km/h.

Because UAV operations might involve some extensive in-field logistics, we furthermore examined the possibility of conducting several consecutive surveys starting at a central takeoff and landing point. We thereby aimed at flight times per survey of maximum 60 min and area coverage of 15%. Three different layouts were tested: (*a*) an arrangement of four rectangular areas of 7.5 km \times 10 km, locating the common takeoff point at the central point in the middle between the four rectangles, resulting in a total area of 300 km²; (*b*) an arrangement of four diamond-shaped areas of 10 km \times 15 km, with the takeoff point at the central point in the middle between the four diamonds, resulting in a total area of 300 km²; and (*c*) an arrangement of seven hexagonal areas of 9.2 \times 9.2 km, where the takeoff point was located in the centre of the central hexagon, covering a total area of 511 km² (Fig. 2). All survey flights were simulated both for parallel transect lines and modified adjusted zigzag transects for further efficiency comparison.

Experiment 3: To optimise flight efficiency, we assessed the feasibility of additionally minimising the time of transit flights between the takeoff location and survey blocks, while securing even and constant area coverage. In accordance to findings of a previous study (Linchant et al. 2015), we studied a hexagonal rosette petal-shaped layout of flight patterns, which - due to its central takeoff and landing point - allowed us to maximise on-transect flight time. This layout is defined by a radial sequence of twelve petal-shaped survey blocks, which are surveyed by zigzagging over two adjacent petals within one flight, covering one petal from the centre point to the perimeter, and inverse on the subsequent petal. We here applied the same approach as in the prior experiments by adjusting the zigzagging angle in accordance to the petal outline to avoid double counting within each survey block.

Experiment 4: To illustrate the potential ability of UAVs to safely conduct surveys in areas with difficult topography, we assessed the flight path accuracy of contour-following transects. Contour transects can provide a solution for block counts in mountainous terrain by flying along elevation



Fig. 2. Three different survey block layouts compared for efficiency in this study: (*a*) rectangular shape; (*b*) diamond shape; and (*c*) hexagonal shape. The star indicates the location of the takeoff and landing point of the UAV.

contours (Quang and Becker 1999), which requires high accuracy in flight altitude and flight path, and thereby high agility of the aircraft. At low flight altitudes, flying an aircraft in close proximity to mountains comes with an increased risk of crash and potential fatalities. To assess the accuracy of contour transects conducted by a UAV, we investigated the deviation of its flight path from the contour lines in terms of lateral and vertical distance from the programmed transect. We compared the realised, logged flight altitude above ground against the planned contour height, as well as the minimum distance of the logged flight path from the measured contour line vertices.

Study area

To illustrate the different aspects mentioned above and to provide estimates of 'real-world' survey scenarios, we selected the Katavi National Park (hereafter Katavi NP, 6.62° –7.34°S, 30.74° –31.84°E) in southwestern Tanzania as a study area. This protected area provides good ground for testing the different facets of UAV-based surveying, because it consists of vast flat areas as well as hilly sections with steep escarpments close to the eastern park boundary. The park's remote location off the beaten tourist tracks (0.3% of total tourists visiting Tanzanian protected areas in 2014; World Bank 2018) results in relatively low income and funds for park management, which in turn asks for increased efficiency in monitoring programs, as potentially provided by UAV technology (Fust and Loos 2020).

Katavi NP covers a total area of 4471 km², and elevation is between 800 and 1640 m ASL. As a result of the partly dense wooded vegetation and flooded plains, accessibility of certain areas is difficult, in particular throughout and shortly after the rainy season. The escarpment area selected for contour transects covers 156 km² (6.79° – $7.06^{\circ}S$, 31.52° – $31.70^{\circ}E$) at the eastern border of the park, and includes mountain slopes ranging from 1000 to 1600 m ASL. The contour lines of 1100 m, 1200 m, 1300 m, 1400 m and 1500 m were processed. Their sinuosities ranged between 0.54 and 0.62, were 51.7–59.8 km long and consisted of between 108 and 233 turns (radius: min. 20 m, max. 2100 m), according to the ROCA (ROad Curvature Analyst) approach (Andrasik and Bil 2016).

Flight planning and data processing

All UAV flight data of this study have been produced by SITL (Software In The Loop) simulation within the Mission Planner software (Osborne 2020). The UAV airframe used for this study had an electric (hybrid) quadplane configuration, i.e. it had a fixed-wing setup plus additional propulsion units that enabled vertical takeoff and landing (VTOL) capabilities. We assumed the UAV to achieve airspeeds of over 100 km/h, which may allow flight durations of over 1 h and result in flight distances of more than 100 km with one battery charge. These assumptions were based on the flight performance of currently available commercial UAVs with takeoff weights of less than 10 kg, such as Wingcopter 178 (Wingcopter, Weiterstadt, Germany), Nimbus VTOL (Foxtech, Tianjin, China) or DeltaQuad (Vertical Technologies, Badhoevedorp, The Netherlands). Electric propulsion was deliberately chosen because of its low noise level and consequent low disturbance effect on wildlife, even though a combustion engine-based solution would boost flight time to 4-6 h.

Flight path waypoints of the different survey designs have been calculated directly within Mission Planner software, in R (R Core Team 2020, R packages: rgdal, sampSurf, Orcs, spdep and rgeos) and GIS (QGIS (QGIS Development Team 2021) and ArcMap (ESRI 2011)) for parallel transects, modified adjusted-angle zigzag transects and contourfollowing transects respectively. Survey blocks were defined as polygons of varying sizes and shapes in GIS. The different survey designs have been processed in the following different ways:

- 1. In the case of parallel transects, we imported these polygons directly into the mission planning software, where a grid survey has been defined according to the required parameters (e.g. distance between transect lines and direction).
- 2. We calculated the zigzag transect patterns and the corresponding waypoints within R. According to the

survey goal, the setting of the required parameters (direction of transect baseline, coverage ratio, critical minimum angle α_{crit} , waypoint distance), as well as flight variables such as transect strip width, loiter radius of the UAV (Supplementary fig. S1), the survey polygon was downloaded and the start point of the transect on the polygon boundary defined. Following the description of Strindberg and Buckland (2004), the transect angle was calculated in a step-wise manner based on the varying height of the survey block at each point along the transect baseline. If the calculated angle exceeded the critical minimum angle α_{crit} of double-count avoidance, the angle was set according to the critical value. Reaching the boundary of the survey block, the survey was interrupted and continued by the subsequent transect in the opposite direction further along the boundary line at a distance resulting from the defined transect strip width and turning radius of the UAV (detail A in Supplementary fig. S1). This process was continuously repeated to cover the entire survey block. The resulting effective coverage ratio was calculated and the waypoints stored for subsequent integration in the mission planning software.

3. For the contour transects, contour lines have been created based on interpolated, high-resolution Mapzen DEM data (https://registry.opendata.aws/terrain-tiles/), and simplified in ArcMap to reduce the number of waypoints. Simplification tolerance has been set to 50 m. The vertices of the resulting, simplified contour lines have been used as waypoints for the flight path programming in Mission Planner.

Unless otherwise specified, all tests mentioned above were conducted assuming the average speed of continuously moving animals to be 10 km/h. UAV flight speed was set at 100 km/h for parallel and zigzag surveys, and reduced to 65 km/h for contour-following surveys to allow for higher accuracy in the flight path. All flights were at altitudes of 100 m above ground, and flight times include the usual duration of 2 min for vertical takeoff and landing of a VTOL UAV. Survey strip width of all transects in experiments 1 and 2 was set at 200 m, based on the chosen flight altitude and the resulting ground footprint of a vertical (nadir), dual side-by-side camera setup of standard cameras with horizontal fields of view (hFOV) of 45° each. By the simple integration of a third camera, flight analysis of the survey layout in experiment 3 was based on a survey strip width of 300 m, paralleling common strip parameters applied in manned aerial survey.

During all simulations, we assumed favourable meteorological conditions. We limited the movement of the UAV airframe in terms of maximum angles around the roll and pitch axis at 35° (roll) and $-25/+20^{\circ}$ (pitch) to ensure realistic flight patterns.

Results

Experiment I

In the rectangular survey blocks of experiment 1, there was a quasilinear relationship between α and the animal:UAV speed ratio resulting from their geometric relationship and the UAV's short transit time between transects. For animal:UAV speed ratios (v_a/v_{UAV}) between 0.05 and 0.9, the critical minimum angle α_{crit} varied between 85.7° and 45° respectively (Table 1), independent of transect length.

The analysis of maximum coverage possible using the modified, adjusted zigzag approach indicated a strong dependency on transect length. Assuming a rectangular shape of the survey block, the decrease in possible coverage followed a logarithmic-like increase in width of the area (Table 1, Fig. 3); for example, ranging from 42.7% for

Table 1. Effects of variation in the animal:UAV speed ratios for different animal speeds on the critical minimum angle α_{crit} and their resulting maximum coverage according to adapted survey block widths.

UAV speed (VUAV)			100	km/h		
Animal speed (v _a)	5 km/h	10 km/h	15 km/h	20 km/h	30 km/h	90 km/h
Animal:UAV speed ratio (v_a/v_{UAV})	0.05	0.1	0.15	0.2	0.3	0.9
Critical minimum angle $\alpha_{\rm crit}$	85.7 °	82.7 °	80.0 °	77.0 °	70.0 °	45.0 °
Survey block width [m]			Maximum	coverage		
1000	53.5%	47.1%	42.7%	38.7%	32.1%	21.8%
2000	44.5%	36.3%	31.1%	27.0%	20.7%	12.3%
3000	38.2%	29.5%	24.5%	20.7%	15.3%	8.6%
4000	33.5%	24.9%	20.3%	16.8%	12.2%	6.6%
5000	29.7%	21.5%	17.3%	14.2%	10.1%	5.4%
7500	23.3%	15.9%	12.6%	10.1%	7.1%	3.6%
10 000	19.1%	12.8%	10.0%	7.9%	5.4%	2.8%



Fig. 3. Maximum coverage of the rectangular-shaped layout adjusted to the speed of different species, here shown for the elephant (black dashed line), the giraffe (grey dotted line) and the cheetah (black solid line).

rectangles of 1 km width to 10% for areas of 10 km width, assuming an animal:UAV speed ratio v_a/v_{UAV} of 0.15.

Experiment 2

Completing an aerial survey on a square area of 110 km^2 by parallel transect lines took between 76.9 and 87.7 km of total flight distance, resulting in flight times of 48–55 min respectively, depending on the direction of the transect baseline. By applying a modified adjusted zigzag design, covered flight distances were reduced to 69.6–72.5 km, leading to an increase in efficiency in terms of flight distance of between 10.5 and 21% (Table 2).

In view of conducting multiple surveys starting at a central point by using different survey block layouts, results indicated a benefit of 12–16% for zigzag pattern surveys over the conventional parallel transect surveys (Table 3). A diamond-shaped survey block layout showed an increased efficiency

as compared with rectangular and hexagonal layouts, zigzag surveying on average an area of 1.9 km^2 per minute flight time at 15% coverage. Due to the additional flight time required to reach the different survey blocks, the hexagonal layout resulted in a mean area of 1.6 km^2 covered per minute flight time at similar coverage. The resulting total flight times for the entire surfaces varied accordingly, between 160 min for 300 km² and 327 min for 513 km². Detailed data of the various survey flights are presented in the supplementary material (Supplementary Tables S1–S3).

Experiment 3

With the application of a rosette-shaped survey layout, a total area of 175 km² could be surveyed at 15% coverage within 50 min, resulting in an area of 2.9 km² per min. The chosen hexagonal layout of 12 rosette petals resulted in a total area of over 1000 km² surveyed from a single central location

Table 2. Comparison of modified zigzag and parallel survey approaches in relation to the survey direction in a square area.

Survey design	Maximum coverage (%)	Survey direction (°)	Flight time [min]	Flight distance [km]	Benefit in flight distance of zigzag (%)	
Mod. zigzag	10.1	40	46	72.5	21.0	
Parallel	10.1	40	55	87.7	21.0	
Mod. zigzag	10.0	3	44	69.6	10.5	
Parallel	10.0	3	48	76.9	10.5	

Area shape	Survey design	Total area surveyed [km ²]	Total flight time [min]	Total flight distance [km]	Area surveyed [km ² min ⁻¹]	Benefit in flight distance of zigzag (%)
Rectangular	Parallel	300	200	326.0	1.5	12.9
	Mod. zigzag		180	288.8	1.7	
Diamond	Parallel	300	184	300.2	1.6	16.0
	Mod. zigzag		160	258.8	1.9	
Hexagonal	Parallel	513	365	591.7	1.4	12.2
	Mod. zigzag		327	527.2	1.6	

Table 3. Comparison of multiple survey block layouts.



Fig. 4. A rosette-shaped survey layout applied to the Katavi National Park, Tanzania. The different colours indicate individual flights of the UAV, which can be conducted from a single central takeoff and landing location. Basemap: ESRI Shaded relief layer (obtained through QuickMapServices QGIS plugin), Map data ©2019 ESRI.

within 6 h of flight time, which can be achieved within one survey day (Fig. 4). An assessment of the entire study area of Katavi NP is thereby feasible within a time period of 4–5 days, minimising in-field logistics significantly.

Experiment 4

Survey flights following the contour lines of the eastern escarpment of Katavi National Park (Fig. 5) exhibited good accuracy despite their complex geometry. The distance of the flight paths from the according contour lines was between 10.8 and 15.7 m on average (Fig. 6a, Supplementary Table S4). The resulting flight height above ground was slightly above the programmed flight level of 100 m, ranging from 100.4 to 109.9 m on average (Fig. 6a, Supplementary Table S4).

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Discussion

So far, UAVs haven't been established as a common approach applied for wildlife monitoring over large areas because of a range of logistical, technical and legal aspects (Fust and Loos 2020). One of the shortcomings in applying UAVs for monitoring is the lack of mature application standards and guidelines to design and conduct wildlife counts in accordance with the specific capabilities of these aerial systems. With this simulation study, we present different approaches for surveying to gain a better understanding of how to conduct survey operations on wildlife more accurately and efficiently with the help of UAVs. In the following, we provide evidence for the validity of our suggested survey design and highlight the merits and limitations of UAV application in wildlife monitoring. The suggested survey



Fig. 5. Contour line transects of survey area of the eastern escarpment of Katavi National Park, Tanzania, and segmentation of the whole park area into hexagonal survey blocks for comparison. Dark solid lines illustrate the various flown transects. Basemap: ESRI Shaded relief layer (obtained through QuickMapServices QGIS plugin), Map data ©2019 ESRI.

layouts have been developed for general wildlife surveys, but they may be useful for surveying single species as well.

In comparison with manned aerial surveys, our simulations demonstrate that similar area coverage by effort is possible through UAV-based surveys. The daily area covered through manned aerial surveys is constrained by fuel amount, availability of airfield infrastructure and fatigue of the observers (and pilots) after approximately 3 h of continuous survey time. Based on a survey effort of 15%, the resulting area covered corresponds to 740 km² per manned flight (Jachmann 2002; Frederick et al. 2010; Georgiadis et al. 2011; Grossmann et al. 2014; DNPW 2016; Schlossberg et al. 2016), compared with 75-175 km² per UAV operation (depending on chosen strip width and survey design). However, this potential area coverage is hampered by off-transect flight durations in manned surveys (e.g. through return flights to the airstrip and to refuelling stations). These off-transect flights add additional costs to the operation. On average, off-transect flights in manned aerial surveys account for 1.15 h per flight (Frederick et al. 2010; Grossmann et al. 2014; TAWIRI 2016, 2019), reducing the effective flight time on-transect to roughly 2 h.

Because UAVs are able to operate without the need for sophisticated airfield infrastructure, survey missions can

make full use of the flight durations, minimising off-transect losses. Because of its off-transect flight durations, wildlife surveys using manned aerial operations can, at a maximum, produce two to four flights of 2 h of effective survey time per day, whereas six to seven missions of 1-h survey-time each can be achieved in the same period with UAVs. In terms of daily coverage, manned aerial surveys outcompete UAV surveys as a direct result of the difference in flight speed: manned aerial surveys can capture 1480-2400 km², whereas UAVs may capture 525-1000 km² when the aim is to survey 15% of the target area. Thus, although it may take twice as long to survey a similar area with UAVs, only half of the staff is needed for UAV operations: manned aerial surveys often require one pilot, a flight coordinator and up to four observers, but UAV operations require only one pilot and one assistant or driver. In terms of cost-effectiveness, these conditions provide comparable inputs and outputs from both survey approaches. However, UAVs outcompete manned aerial surveys in terms of their flight path accuracy, which is required to be a minimum of 50 m in manned aerial surveys (Craig 2012). Our simulations suggest a maximum of 15.7-27 m accuracy for highly complex flight patterns, which results from the high manoeuvrability of UAVs. Comparative studies with



Fig. 6. Violin plot of horizontal distance (*a*) of the resulting flight paths from the contour lines and (*b*) of resulting flight height above ground at different contour line elevations.

simple flight designs over flat terrain have furthermore described the increased altitude accuracy of UAVs of maximum 4–5.8 m, compared with 30.5 m achieved with manned aircraft (Hodgson *et al.* 2010). This increase in accuracy is a huge advantage, especially in regions with difficult terrain, in which the survey designs seek to undertake contour following.

In comparison with flight parameters of already conducted UAV surveys, our proposed approach stands out with its hitherto unachieved performance in wildlife data collection. Prior applications of unmanned aerial vehicles for wildlife monitoring showed limitations due to the chosen survey designs, flight endurance and speed of the applied aircraft and total size of the surveyed area. For large survey areas covering several 100 or 1000 square kilometres, where total wildlife counts would demand immense capacities and a sampling approach is better suited, we suggest that survey designs need to be carefully adapted and evaluated in terms of efficiency and resulting data accuracy. Our results indicate that, as long as the topography allows a constant flight altitude above ground level, a zigzagging transect layout provides an increase in survey efficiency compared with the commonly applied parallel transect layouts. Considering our approach to reduce the risk of double counts among transects, parameters such as the surveyed animal species, the outline of the survey area, as well as the requested coverage define the most appropriate survey design. High coverage percentages require shorter transects, and the animal movement speed furthermore puts limits on the maximum possible coverage, thus requiring narrower survey blocks. Although rectangular, hexagonal and diamond-shaped survey blocks might be better adapted for moderately sized survey areas, we recommend a petal-shaped, hexagonal survey design for large areas, because it provides the highest survey efficiency – at least for in-field logistics requirements.

Assessing reports of aerial survey of animal populations by UAVs (2009-2021), the majority focused on the total count approach, covering the area at 100% (Hodgson et al. 2010; Koh and Wich 2012; Bonnin et al. 2018; Bushaw et al. 2019), including overlapping data collection. Although this obviously impacts the time needed for surveying a given area, we suspect the requirement of photogrammetric approaches commonly applied on drone data as a reason for the chosen designs. Regulatory restrictions on flying beyond-line-of-sight might further have pushed researchers to embark on such a strategy, focusing on small areas around the takeoff location (Cleguer et al. 2021). Early adopters of UAV technology included experimental approaches, such as feature (e.g. rivers) following single strip sampling (Barasona et al. 2014), but later strip sampling surveys mostly applied a parallel transect lines design (Chrétien et al. 2016; Sykora-Bodie et al. 2017; Preston et al. 2021). By doing so, sampling efforts varied hugely between 2% and 55%. The majority, however, sampled less than 10% of the area (Vermeulen et al. 2013; Guo et al. 2018), potentially resulting in increasingly biased data (Jachmann 2002). One exceptional study aiming at increased survey efficiency introduced a petal-shaped transect layout (Linchant et al. 2015), unfortunately leading to a low fraction of surveyed area of 6.1%. Although total counts by electrically powered UAVs covered only very small areas between 0.001 and 4 km², strip sampling surveys by UAV generally covered total areas smaller than 600 km² (Barasona et al. 2014) as a function of the respectively applied sampling intensity. Only one study assessed animal numbers over a larger extent (more than 16000 km²), applying a low sampling intensity of only 2% (Guo et al. 2018).

UAV-based aerial surveys have so far heavily relied on (affordable) battery-powered multirotor vehicles (Bushaw *et al.* 2019; Ott 2020) and light-weight fix-wing aircraft (e.g. Rey *et al.* 2017; Barnas *et al.* 2018), which generally come with low flight endurance and/or restricted flight envelopes. This reduces the risk of economic losses in case of failures or crashes, but also has significant effects on the potential application of small UAVs in large-scale assessments. Most aircraft used in previous surveys with weights below 5 kg featured cruise speeds of less than

50 km/h (compared with heavier and more expensive vehicles that achieved 100 km/h and more), which obviously limited their operational range or resulted in an increased logistical effort as a result of the small area covered. Therefore, we strongly advise the use of aircrafts at speeds of minimum 100 km/h, because the risk of blurred images due to increased speed can be greatly reduced with the use of adapted, modern imaging technology.

Our novel survey design for UAV applications in the wildlife monitoring sector avoids uneven area coverage probability and decreases the risks of double counts, thereby enhancing the accuracy of survey results. Besides these merits, UAV-borne sampling offers a high degree of re-processibility and reproducibility through the use of photographic surveying. Photo and video imagery techniques deliver similar detection rates of wildlife compared with visual detection (Hambrecht et al. 2019), which is why these techniques are also increasingly applied in manned aerial surveys (Lamprey et al. 2020). Independent of the technique involved, the extraction of animal data should be conducted carefully with respect to potential multiple appearances of animals on subsequent images. The application of camera stabilisation systems to counteract the effects of variation in aircraft attitude on image footprint, as well as precise data on location and direction of the images taken, furthermore enhances accuracy in survey results based on distance sampling techniques. The efficiency of photographic surveying can be further enhanced by covering a larger survey area by adding supplementary camera(s) to increase the strip widths of the survey transects, at the risk of increased image distortion.

Nevertheless, the practical applications for UAVs in wildlife monitoring are facing several challenges and limitations. First and foremost, UAV applications require legal permits - and the jurisdictional conditions are partly unclear and subject to change in several countries. Moreover, these permits typically do not allow operators to fly the UAV out of visual sight, which, however, is necessary to cover large survey areas as suggested in our simulation. Additionally, technical limitations include constraints in battery capacity, which may reduce the duration of single flight missions and thereby potentially lower the daily coverage of the operation. Likewise, challenges of technological origin, such as restricted accuracy of flight altitude measurements solely based on GPS data or of the digital elevation model applied in-flight planning, might impair consistency in the ground footprint of airborne images. Although not yet very commonly applied, those challenges could be handled by active altitude over ground measurement through laser-based distance sensors. Despite the highly efficient collection of data by UAVs, data processing and extraction from aerial images require additional capacities to fully benefit from this method, through automatised object detection processes for example, either after downloading the images to computers or during

flight by the use of smart cameras with embedded image processing hardware that allows real-time, in situ image analysis. Although our findings show how to facilitate some in-field logistics through well-developed survey designs, splitting surveys across several days may still host the risk of double counts. Similar to most other sampling-based wildlife survey approaches, wildlife number estimations from UAV-borne survey data succumb to the influence of speciesspecific traits on their accuracy: unequal wildlife distribution due to habitat preference, dispersal, habitat-related detectability, and animal size and density have to be considered while planning wildlife surveys and determining parameters such as survey effort. In future research, flight simulation studies as applied in this study could be overlaid with dynamic animal movement models to specifically investigate the importance of such influences. Besides, our simulations assumed stable and favourable meteorological and wind conditions, which may, in real settings, influence the flight path accuracy and flight duration.

Conclusion

To the best of our knowledge, our simulation study is one of the first investigations comparing efficiency and accuracy of different transect flight plans for the purpose of wildlife monitoring. We show that UAV applications, if well designed, provide useful complementation, if not replacement, for manned aerial surveys and other remotely sensed data collections. Our simulations for the Katavi National Park exemplify these merits, especially in complex terrains over a vast area. Our suggested method is transferable to other study regions and may be useful for applying UAVs efficiently. Even though we show that it is technically feasible to use UAVs in a way that is advantageous over manned aerial surveys, further support through legislative and additional technical features might be necessary to broadcast UAVs for application in wildlife conservation.

Supplementary material

Supplementary material is available online.

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Data availability. Data will be made available through the research data repository of the Leuphana University Lüneburg (https://pubdata.leuphana.de) at the time of publication of the manuscript.

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