



Drones count wildlife more accurately and precisely than humans

Jarrold C. Hodgson¹  | Rowan Mott²  | Shane M. Baylis² | Trung T. Pham³ | Simon Wotherspoon^{4,5} | Adam D. Kilpatrick¹ | Ramesh Raja Segaran¹ | Ian Reid³ | Aleks Terauds⁵ | Lian Pin Koh¹

¹School of Biological Sciences, University of Adelaide, Adelaide, SA, Australia

²School of Biological Sciences, Monash University, Clayton, Vic., Australia

³School of Computer Science, University of Adelaide, Adelaide, SA, Australia

⁴Institute of Marine and Antarctic Studies, University of Tasmania, Hobart, Tas., Australia

⁵Australian Antarctic Division, Department of the Environment and Energy, Antarctic Conservation and Management, Kingston, Tas., Australia

Correspondence

Jarrold C. Hodgson
Email: jarrod.hodgson@adelaide.edu.au

Funding information

Australian Government Research Training Program Scholarship; Australian Research Council and Conservation International

Handling Editor: Nigel Yoccoz

Abstract

1. Knowing how many individuals are in a wildlife population allows informed management decisions to be made. Ecologists are increasingly using technologies, such as remotely piloted aircraft (RPA; commonly known as “drones,” unmanned aerial systems or unmanned aerial vehicles), for wildlife monitoring applications. Although RPA are widely touted as a cost-effective way to collect high-quality wildlife population data, the validity of these claims is unclear.
2. Using life-sized, replica seabird colonies containing a known number of fake birds, we assessed the accuracy of RPA-facilitated wildlife population monitoring compared to the traditional ground-based counting method. The task for both approaches was to count the number of fake birds in each of 10 replica seabird colonies.
3. We show that RPA-derived data are, on average, between 43% and 96% more accurate than the traditional ground-based data collection method. We also demonstrate that counts from this remotely sensed imagery can be semi-automated with a high degree of accuracy.
4. The increased accuracy and increased precision of RPA-derived wildlife monitoring data provides greater statistical power to detect fine-scale population fluctuations allowing for more informed and proactive ecological management.

KEYWORDS

bird, drones, ecology, population monitoring, remotely piloted aircraft, surveys, unmanned aerial vehicle, wildlife,

1 | INTRODUCTION

Human activities are creating environmental conditions that pose threats and present opportunities for wildlife. In turn, this creates challenges for conservation managers. Some species have benefited from anthropogenic actions. For example, many invasive species profit from human-assisted dispersal (Banks, Paini, Bayliss, & Hodda, 2015; Hulme, 2009), and mesopredators may thrive following human-driven

loss of top predators (Ritchie & Johnson, 2009). However, in many cases, wildlife populations are undergoing alarming declines, and extinction rates are now as high as 100-fold greater than the background extinction rate (Ceballos et al., 2015). Ecological monitoring is essential for understanding these population dynamics, and rigorous monitoring facilitates informed management. The effectiveness of management decision-making is often dependent on the accuracy and timeliness of the relevant ecological data upon which decisions are

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2018 The Authors. *Methods in Ecology and Evolution* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

based, meaning that improvements to data collection methods may herald improved ecological outcomes from management actions.

Emerging technologies are increasingly being adopted by ecologists to improve data collection and capture novel data (Hebblewhite & Haydon, 2010; Moll, Millsbaugh, Beringer, Sartwell, & He, 2007; Pimm et al., 2015). Advances in genetic techniques have resulted in the cost-effective application of environmental DNA sampling to the detection of endangered species and invasive species (Sigsgaard, Carl, Moller, & Thomsen, 2015; Smart, Tingley, Weeks, van Rooyen, & McCarthy, 2015; Smart et al., 2016). Camera traps and acoustic recorders have become established tools for determining whether a species is present at a site, and estimating population density (Marques et al., 2013; Rowcliffe & Carbone, 2008). Furthermore, animal-borne telemetry devices have revolutionised our understanding of animal movements, including their interactions with the environment, and species distributions (Hussey et al., 2015; Kays, Crofoot, Jetz, & Wikelski, 2015). Such technologies have been vital in advancing our understanding of wildlife and answering fundamental questions, such as how many individuals are in a population and whether that population trajectory is increasing or decreasing.

Remotely piloted aircraft (RPA; commonly known as "drones," unmanned aerial systems or unmanned aerial vehicles) have seen a rapid uptake by ecologists for data collection. This surge in popularity has arisen largely due to their ability to carry remote sensing instruments that collect data at scales highly suited to monitoring ecological phenomena (Anderson & Gaston, 2013). Compared to remote sensing instruments mounted to spacecraft and conventional aircraft, RPA are more suited to collecting extremely fine spatial and temporal resolution data at the discretion of the user. These benefits have led many practitioners to label RPA as a powerful tool for wildlife ecology (Chabot & Bird, 2015; Christie, Gilbert, Brown, Hatfield, & Hanson, 2016; Jones, Pearlstine, & Percival, 2006; Linchant, Lisein, Semeki, Lejeune, & Vermeulen, 2015; Watts et al., 2010). Consequently, RPA are being used for data collection in an increasingly diverse suite of ecological applications, including transect counts of African elephants *Loxodonta africana* (Vermeulen, Lejeune, Lisein, Sawadogo, & Bouche, 2013), monitoring for poaching activities (Mulero-Pazmany, Stolper, van Essen, Negro, & Sassen, 2014), detecting reptile and arboreal mammal nests (Evans, Jones, Pang, Saimin, & Goossens, 2016; Wich, Dellatore, Houghton, Ardi, & Koh, 2016), and estimating the body condition of cetaceans and pinnipeds (Christiansen, Dujon, Sprogis, Arnould, & Bejder, 2016; Krause, Hinke, Perryman, Goebel, & LeRoi, 2017).

Many bird species are highly suited to RPA-facilitated population monitoring. RPA have been used to assess the breeding status of the canopy-breeding hooded crow *Corvus cornix* (Weissensteiner, Poelstra, & Wolf, 2015) and to take a census of multispecies assemblages of songbirds (Wilson, Barr, & Zagorski, 2017). They have also been a useful tool in collecting valuable datasets of species which congregate and/or those that frequent known sites to breed. For example, RPA have been used to estimate the size of staging flocks of geese (Chabot & Bird, 2012), take population censuses of colony nesting species of gull, tern and penguin (Chabot, Craik, & Bird, 2015; Ratcliffe et al., 2015; Sarda-Palomera, Bota, Padilla, Brotons, & Sarda, 2017; Sarda-Palomera et al., 2012), and also make a rapid population estimate of

the Tristan albatross *Diomedea dabbenena* at a remote island where nests are at low density (McClelland, Bond, Sardana, & Glass, 2016). While some studies have investigated the variability of RPA surveys compared to traditional methods (Chabot et al., 2015; Hodgson, Baylis, Mott, Herrod, & Clarke, 2016), to date, rigorous quantification of the accuracy of RPA-derived data has been limited.

We assessed the accuracy of RPA-facilitated wildlife population monitoring compared to the traditional ground-based counting method. The task for both approaches was to count the number of fake birds in each of 10 replica seabird colonies. Each replica colony had a different known number of life-sized individuals. Although the replica colonies lacked the flying or moving individuals of real colonies, the stationary decoys provided a realistic representation of the nesting seabird stimuli that observers encounter in the field. We hypothesised that counts from RPA-derived imagery would be more accurate and more precise than those generated using the traditional approach, confirming that RPA technology is a significant advance for ecological monitoring.

2 | MATERIALS AND METHODS

2.1 | Study site and simulated colony set-up

Fieldwork (#epicduckchallenge) was completed at a metropolitan beach in South Australia (Port Willunga, 35°15'33S, 138°27'41E). The beach comprised pale cream to golden-coloured sand, natural debris and was largely devoid of rocks. The terrain was representative of a low-lying sand cay, gently sloping from the high water mark up to a small (0–1.5 m), natural, vegetated embankment. The experimental design, including the majority of anticipated statistical analyses, was pre-registered (Hodgson, Baylis, Mott, & Koh, 2016).

Ten simulated greater crested tern *Thalasseus bergii* breeding colonies were constructed using commercial, life-sized, plastic duck decoys (c. 25.5 × 11.3 cm, 185/cm² footprint). Colonies were situated separately on the beach, above the high water mark, in sandy areas that were analogous to nesting habitat. These areas had minimal topographic variation, and were typically devoid of vegetation but often contained natural beach debris.

As the interactions of individuals are thought to influence colony layout, a model of nesting pressure was applied to an underlying hexagonal grid to generate unique, unbiased colony layouts (Hodgson, Baylis, Mott, & Koh, 2016). The hexagonal grid was recreated in the field using a wire mesh, upon which grid cell centres were marked (mean density: 11.39/m²). Pre-counted wooden skewers were placed one per cell at a random location within all cells identified as occupied in the colony layout map. The mesh was removed and each skewer was replaced with a decoy facing approximately into the wind. One individual was placed in each occupied cell. The number of skewers retrieved was taken to be the true number of individuals in the colony. Colony sizes were between 463 and 1,017 individuals.

2.2 | Ground counting approach

Ground-based counts (ground counts) were made using a standard field technique (Hodgson, Baylis, Mott, Herrod, et al., 2016). All observers

were ecologists with experience observing and counting birds, primarily in a professional or academic capacity. Counters used tripod-mounted spotting scopes or binoculars as required. Hand-held tally counters were used to assist counting. For each colony, the observation viewpoint (Figure 1e) was selected because it provided the optimum vantage, was at a similar altitude to the colony and was 37.5 m from the nearest bird. This distance is a biologically plausible minimum approach distance as it is the flight initiation distance of the Caspian tern *Hydroprogne caspia* (Moller, Samia, Weston, Guay, & Blumstein, 2014), a similar species to that being replicated. Counts ($n = 61$) were 7 ± 2.65 min (*SD*) in duration. Each of the four to seven counters made a single blind count of the number of individuals in each colony. The numbers of counters were selected based on a preliminary power analysis (Hodgson, Baylis, Mott, & Koh, 2016), which investigated the sample sizes necessary to detect small (c. 10%) differences in mean counts and count variances between ground counts and counts from RPA-derived imagery to high (80%, 90% and 95%) power. Counters had no knowledge of the true number of individuals in the colonies or the colony set-up technique. Counts were made between 09.30 and 16.45 hr on 1 day in late autumn, resulting in variation in illumination and shadows. During this period, wind speed was low to moderate (c. 5–20 kt), cloud cover varied (15%–75%) and visibility was high (>500 m).

2.3 | RPA description, flight characteristics and data collected by RPA

A small, off-the-shelf quadcopter (Iris+, 3D Robotics) was used as a platform to image each colony. After positioning the RPA in the centre of the colony at 15 m above-ground level, it was piloted in “altitude hold” mode to make a vertical ascent without movement in other

axes. The RPA was loitered for short periods (c. 10 s) at 30, 60, 90 and 120 m above-ground level (sample heights) to enable the capture of several photographs at each height. Sampling was restricted to a height of 120 m as this is a common maximum limit for standard RPA flight. Ground control station connection (Mission Planner, planner.ardupilot.com) was utilised and total flight time for missions was 5–7 min. All missions were in accordance with local regulations and flown by the same licensed pilot. Samples were collected within 40 min of the completion of ground counts.

Imagery was captured using a compact digital camera (Cyber-shot RX100 III, Sony—resolution: $5,472 \times 3,648$ px; sensor: CMOS; sensor size: 13.2×8.8 mm; lens: ZEISS Vario-Sonnar T). Exposure time was set at $1/2,000$ s using “shutter priority” mode. Photographs were captured successively (c. 1 s intervalometer) using the Sony PlayMemories time-lapse application in jpeg format and at a focal length of 8.8 mm for all sample heights. The camera was mounted facing downwards using a custom vibration dampening plate. The footprint of a single image at each height encompassed the colony for all replicates. For analysis, only the image captured closest to the middle of the loiter time period for each sample height was used. These images (scenes; $n = 40$) were cropped (colony area <50% of footprint) so that the image footprint was identical for each sample height for a given colony. High-quality imagery was obtained for six of the 10 colonies. Imagery for the remaining four colonies was affected by vibration-blur caused by a failure of the sensor attachment, likely due to wind speeds near the limit of the capability of the RPA platform. Scenes are archived online (<https://doi.org/10.5061/dryad.rd736>).

The ground sample distance (GSD), being the distance between adjacent pixel centres on the ground, for sample heights were 0.82, 1.64, 2.47 and 3.29 cm (Figure 1). When photographed at nadir, this

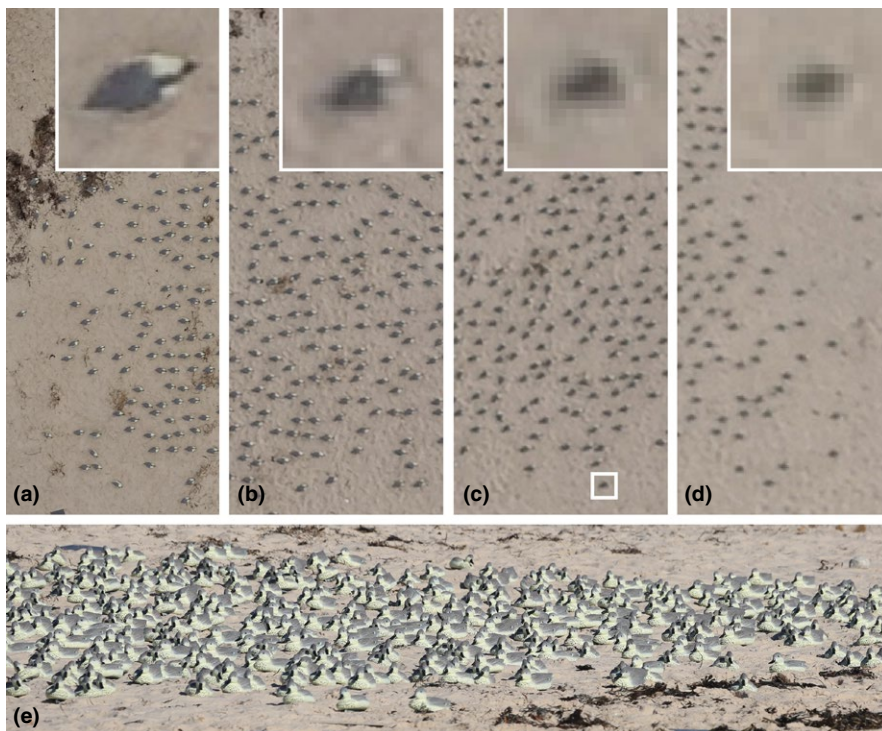


FIGURE 1 Aerial vantage of a replica seabird colony compared with the ground counter's viewpoint. One colony represented by a mosaic of images (a–d) photographed from a remotely piloted aircraft-mounted camera at varying heights (30, 60, 90 and 120 m) and resulting ground sample distances (GSD; 0.82, 1.64, 2.47 and 3.29 cm). Insets are of the same individual (square; c) at each height, displaying the decrease in resolution relative to an increase in GSD. (e) View of the colony from a ground counter's standing position

approximated to 275, 69, 30 and 17 pixels per individual respectively. The variance in GSDs was intended to represent the resolutions commonly achieved in wildlife monitoring applications, which result from sensor and sampling height variations.

2.4 | Manual counting approach for RPA-derived imagery

Manual counts of perceived individuals in digital imagery were completed following a technique previously implemented for RPA-facilitated monitoring of living seabirds (Hodgson, Baylis, Mott, Herrod, et al., 2016). Systematic counts were made using the multicount tool within an easy-to-use, open source, java-based scientific image processing program (ImageJ, <http://imagej.net/>). This tool is used by manually placing a mark on each object to be counted and then computing a tally of the number of marks placed. A grid plugin was used to overlay a square matrix (cell sizes: 70,000, 15,000, 8,000 and 4,000 pixels for each sample height) and counters were instructed to view the colony sequentially (gridcell by gridcell: left to right, top to bottom). Counters were encouraged to zoom in to each cell as they progressed and, upon completion, review their count at different levels of zoom until they were satisfied they had counted all individuals. For each sample height, seven to nine individuals counted each colony. Counters had no knowledge of the experimental set-up and only one had experience in ground counting colonial birds.

2.5 | Semi-automated counting approach for RPA-derived imagery

In each scene, digital bounding boxes were used to manually delimit a percentage of individual birds (Figure 2a). Four larger areas of

background without birds were also delimited. These data were used to train a linear support-vector machine (a discriminative classifier; Cortes & Vapnik, 1995), which predicted the likelihood of each pixel being a bird or background when applied to the corresponding scene (Figure 2b). Instead of relying on colour intensities, for each pixel used in the training processes, we computed a rotation-invariant Fourier histogram of oriented gradient (Liu et al., 2013) features. This resulted in the classifiers being trained to determine which features distinguished birds from the background. The predicted likelihood (score) maps indicated the approximate locations of birds in the scenes, and detections were generated by applying a threshold to the score maps. This process unavoidably resulted in redundant bird proposals (Figure 2c) and so the final detection results were obtained by suppressing redundant proposals by minimising an energy function (Pham, Rezatofghi, Reid, & Chin, 2016; Figure 2d). This function encoded the spatial distribution of objects and was informed by our knowledge of how the birds nest (e.g. two birds cannot occupy the same location). The source code and dataset are archived online (<https://doi.org/10.4225/55/5a57f969d82e0>).

To determine the minimum amount of training data required for accurate detections relative to manual image counts, we varied the percentage of individual birds used as training data from 1% to 30% for each scene.

2.6 | Statistical methods

All analyses were carried out in R version 3.2.2 (R Core Team, 2016). Pre-registered analyses were designed to investigate how within-colony absolute count error, within-colony variability of counts and within-colony bias of counts differed between count techniques (Hodgson, Baylis, Mott, & Koh, 2016). For analyses of count error, we

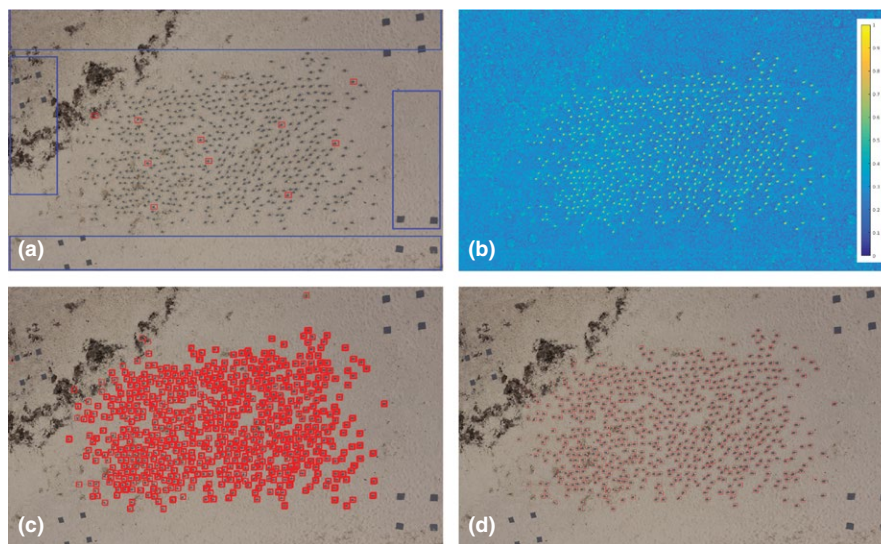


FIGURE 2 Semi-automated detection and counting of wildlife using computer vision techniques. (a) User annotation of perceived target objects (red) and background (blue). (b) Predicted likelihood (score) map generated by the trained classifier which has automatically determined which image features distinguish objects from background, independent of scale and orientation. Warmer colours indicate increasing likelihood of the pixel being a target object. (c) Target object proposals (red) computed by thresholding the score map. Object size is estimated from the annotations. (d) Final output (which includes a total count and detection co-ordinates) where detected individuals are delineated (red) after redundant detections have been automatically suppressed

consider our contrasts of experimental conditions to be conservative compared to typical field conditions. In the field, ground counters contend with the movement of live birds while counters of RPA-derived imagery use static images. Our use of decoys, therefore, removes a potential source of error for ground counters, whereas that source of error is minor or non-existent for counts made from RPA-derived images.

For each test, a generalised linear mixed model was fit between the response (e.g. absolute count error) and the technology used to make the count (e.g. ground count, manually counted RPA-derived image captured at 30 m height, semi-automatically counted RPA-derived image captured at 30 m height), with colony included in the model as a random effect. To investigate effects of counting technique on absolute count error, we defined the response as the absolute difference between the true number of birds in a colony and the counted number of birds. To investigate effects of counting technique on count variability, we defined the response as the absolute difference between each count and the mean of counts of the same colony taken using the same method. Count variability was not estimated for semi-automated counts as there was only a single semi-automated count per colony. To investigate the effect of counting technique on relative count bias, we defined the response as the difference between the true number of birds in the colony and the counted number of birds. For the absolute count error model, we used a Poisson distribution with quasi-likelihood estimation, and for the variability and bias models, we used a Gaussian distribution. For each model, post hoc Tukey tests were used to test for differences in the response between all pairs of treatment levels.

Semi-automated count data were added to the experimental design after our pre-registration of the analysis, and caused minor changes to the planned analysis. The addition of semi-automated count data, with a single replicate per colony, required fitting colony as a random effect instead of as a fixed effect in each model.

Statements comparing the accuracy of counts from RPA-derived imagery to ground counts are based on the mean within-colony root mean squared error (RMSE) of that counting approach, standardised as a proportion of the true count within each colony. For instance, a statement that counts from RPA-derived imagery are “95% more accurate than ground counts” means that, within-colony, the RMSE for counts from RPA-derived imagery is 5% of the RMSE for ground counts, representing a 95% reduction in RMSE.

To compare the semi-automated counts to that of the people counting the images, we first took the semi-automated count after 10% of training data had been used for each scene. Ten percent of training data was consistently identified as a threshold over which little improvement in counts occurred for all scenes. We compared this count to each of the manual counts of the same image using ANOVA for all scenes, and also for those scenes of high quality. We also used loglinear models with a Poisson distribution to make more quantitative comparisons of the two approaches.

3 | RESULTS

3.1 | Manual counts from RPA-derived imagery vs. ground counts

On average across all colonies, counts from RPA-derived imagery were between 43% and 96% more accurate than ground counts, depending on the sample height (between 92% and 98% for the colonies with high-quality imagery; Table S1). The mean absolute error was significantly smaller for counts from RPA-derived imagery at all heights compared to ground counts (all $p < .001$; Figure 3a).

No significant increase in count accuracy was achieved by obtaining imagery from heights lower than or equal to 90 m. Using data only from colonies with high-quality imagery, there was no significant change in count accuracy across the range of heights. The lower accuracy of ground counts was due to significant underestimations of the true number of individuals in colonies (Figure 3b). Counts from RPA-derived imagery obtained at 30 and 60 m did not significantly under- or overestimate the true number of individuals in a colony, and there was no evident bias in counts from RPA-derived imagery at any height for colonies with high-quality imagery (Figure 3b).

Counts from RPA-derived imagery were more precise (i.e. had lower intercounter variability) than ground counts, regardless of the height at which imagery was obtained ($t_{4,560} = -10.21$ to -13.37 , all $p < .001$; Figure S1). Counts from RPA-derived imagery were more precise for imagery obtained at 30 m compared to those obtained from 120 m ($p = .01$); however, there were no significant differences in precision among counts from RPA-derived imagery at different heights for colonies with high-quality imagery (all $p > .98$).

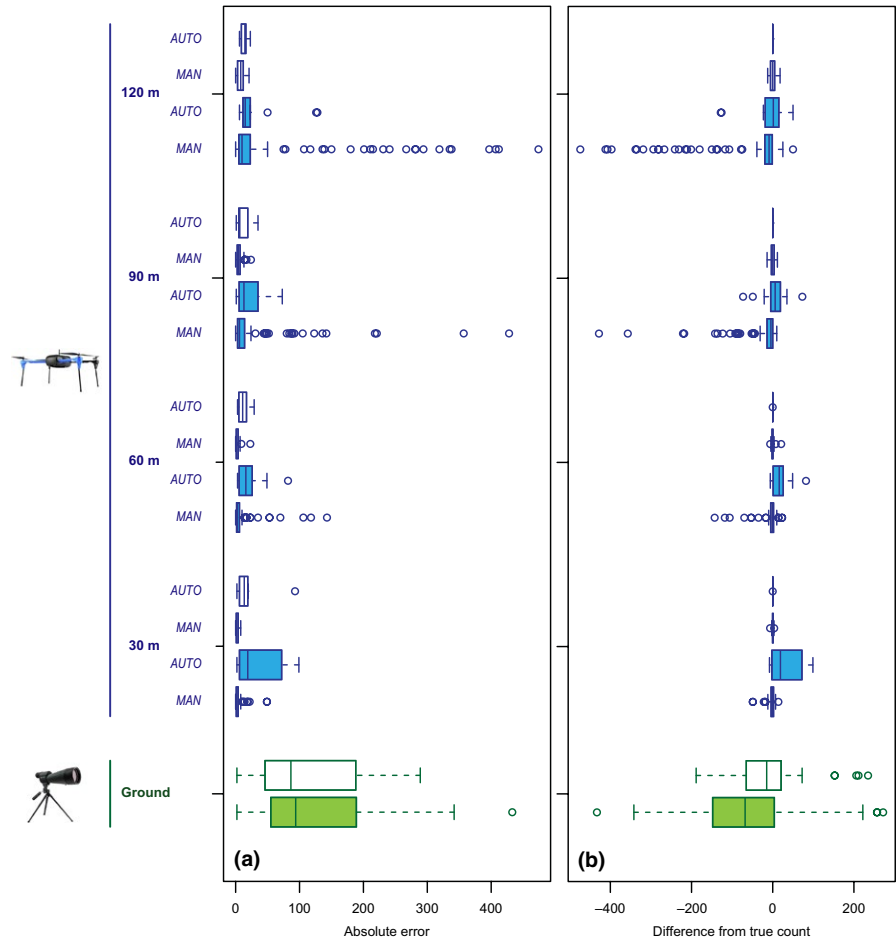
3.2 | Semi-automated counts from RPA-derived imagery

By increasing the percentage (from 1% to 30%) of individuals used as training data for the image-analysis algorithm, 10% training data was consistently identified as a threshold above which little improvement in count accuracy was achieved (Figure S2). There was no significant difference between counts that were made with 10% training data and those made by manual counting from RPA imagery across all scenes. The semi-automated results were 94% similar to manual counts across all scenes (98% for the colonies with high-quality imagery; see also Table S1).

4 | DISCUSSION

RPA-derived data were more accurate and more precise than the traditional data collection method, validating claims that RPA are a highly beneficial tool for ecologists. By facilitating accurate census data, RPA can provide ecologists with more confidence in population estimates from which management decisions can be made. Furthermore, the superior precision of counts from RPA images increases statistical power to detect population trends, owing to the lower type II

FIGURE 3 Accuracy and bias of remotely piloted aircraft (RPA) and traditional wildlife monitoring approaches. The absolute error (a) and difference from the true count (b) of each method. Data from all colonies ($n = 10$; shaded) and also for the subset of colonies with high-quality imagery ($n = 6$; unshaded) are presented for manual counts from RPA-derived imagery (blue) and ground counts (green). Manual (man) and semi-automated (auto) counts from RPA-derived imagery are displayed and data are grouped by height, which reflects ground sample distance (GSD; 30 m height = 0.82 cm GSD, 60 m = 1.64 cm, 90 m = 2.47 cm, 120 m = 3.29 cm)



error rate in statistical analysis that comes with comparing measures with smaller variance (Gerrodette, 1987). The improved precision of completing wildlife population censuses using RPA has been demonstrated for free-living seabird colonies (Hodgson, Baylis, Mott, Herrod, et al., 2016), suggesting our results are generalisable to natural settings. Differences in accuracy and precision between RPA-facilitated and traditional survey methods can be attributed to the sources and magnitudes of variance for each method, which are strongly affected by the different vantages (Hodgson, Baylis, Mott, Herrod, et al., 2016).

Manual counting from RPA-derived imagery returned high-quality data. We estimate that a reasonable detection rate for manual counting is at least 72 birds per min (unpublished data), demonstrating the suitability of this approach for colonies of less than a few thousand individuals. However, when the number of individuals is high, or repeat counts of colonies are required at different time points, the labour investment needed for manual counting can be substantial, so image-analysis techniques have been increasingly employed to streamline the detection process (Chabot & Francis, 2016). Our semi-automated image-based object detection algorithm required the manual delineation of a proportion of birds and four areas of background without birds to be used as training data. Delineations were comfortably made at a rate of 30 birds per min, and user intervention was not required once processing started. Accordingly, given 10% training data was sufficient for accurate counts, our semi-automated approach reduced

user time investment without diminishing data quality compared to the manual, RPA-derived census. While processing time will vary with computing power, we still consider employing the algorithm and inputting training data a more efficient use of user time. This will be of particular interest in today's research environment where funding for conservation is limited (Waldron et al., 2013) and researchers are under ever more pressing time constraints (Fischer, Ritchie, & Hanspach, 2012).

The capture quality and resolution of RPA-derived imagery heavily influenced the results of both human and semi-automated detection. Consequently, ecologists should determine the minimum required GSD for their context and optimise their sensor accordingly (e.g. resolution, focal length) relative to sample height. When determining an appropriate sample height, best practice protocols should be considered to minimise potential disturbance to wildlife (Hodgson & Koh, 2016), while complying with relevant local aviation legislation and achieving an acceptable sample area within the possible survey time period.

The ability to collect data with higher accuracy, higher precision and less bias than the existing approach confirms that RPA are a scientifically rigorous data collection tool for wildlife population monitoring. This approach produces a permanent record, providing the unique opportunity to error-check, and even recount with new detection methods, unlike ground count data. RPA-facilitated

monitoring also presents the opportunity to collect population data without entering breeding grounds or ecologically sensitive areas, thereby avoiding the disturbance associated with ground surveys. Furthermore, as RPA platforms, sensors and computer vision techniques continue to develop, it is likely that the accuracy and cost-effectiveness of RPA-based approaches will also continue to improve.

ACKNOWLEDGEMENTS

We particularly thank those who assisted with this study including Po-yun Wong, the ground support team and the numerous volunteers who made counts from the ground or RPA-derived imagery. We acknowledge the South Australian Department of Environment, Water and Natural Resources and the City of Onkaparinga for granting permits for this work (M26523-1 and 4138 respectively). J.C.H. is supported by an Australian Government Research Training Program Scholarship. L.P.K. is supported by the Australian Research Council and Conservation International.

AUTHORS' CONTRIBUTIONS

J.C.H., R.M., S.M.B., A.T. and L.P.K. designed the study, analysed the data and wrote the manuscript; A.D.K. assisted with designing the study; J.C.H., R.M., S.M.B., A.D.K., R.R.S. and L.P.K. collected the data; S.W. contributed to the analyses; T.T.P., J.C.H., L.P.K. and I.R. developed the semi-automated detection technique. All authors contributed to drafting the manuscript.

DATA ACCESSIBILITY

The pre-registered experimental design is available via the Open Science Framework: <https://doi.org/10.17605/osf.io/a6n3b> (Hodgson, Baylis, Mott, & Koh, 2016). The count data, scenes, semi-automated aerial image counting approach source code and dataset, and R script are available on the Dryad Digital Repository: <https://doi.org/10.5061/dryad.rd736> (Hodgson et al., 2018).

ORCID

Jarrod C. Hodgson  <http://orcid.org/0000-0003-0481-7360>

Rowan Mott  <http://orcid.org/0000-0002-3508-6479>

REFERENCES

- Anderson, K., & Gaston, K. J. (2013). Lightweight unmanned aerial vehicles will revolutionize spatial ecology. *Frontiers in Ecology and the Environment*, 11, 138–146. <https://doi.org/10.1890/120150>
- Banks, N. C., Paini, D. R., Bayliss, K. L., & Hodda, M. (2015). The role of global trade and transport network topology in the human-mediated dispersal of alien species. *Ecology Letters*, 18, 188–199. <https://doi.org/10.1111/ele.12397>
- Ceballos, G., Ehrlich, P. R., Barnosky, A. D., Garcia, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, 1, e1400253. <https://doi.org/10.1126/sciadv.1400253>
- Chabot, D., & Bird, D. M. (2012). Evaluation of an off-the-shelf unmanned aircraft system for surveying flocks of geese. *Waterbirds*, 35, 170–174. <https://doi.org/10.1675/063.035.0119>
- Chabot, D., & Bird, D. M. (2015). Wildlife research and management methods in the 21st century: Where do unmanned aircraft fit in? *Journal of Unmanned Vehicle Systems*, 3, 137–155. <https://doi.org/10.1139/juvs-2015-0021>
- Chabot, D., Craik, S. R., & Bird, D. M. (2015). Population census of a large common tern colony with a small unmanned aircraft. *PLoS ONE*, 10, e0122588. <https://doi.org/10.1371/journal.pone.0122588>
- Chabot, D., & Francis, C. M. (2016). Computer-automated bird detection and counts in high-resolution aerial images: A review. *Journal of Field Ornithology*, 87, 343–359. <https://doi.org/10.1111/jof.12171>
- Christiansen, F., Dujon, A. M., Sprogis, K. R., Arnould, J. P. Y., & Bejder, L. (2016). Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. *Ecosphere*, 7, e01468. <https://doi.org/10.1002/ecs2.1468>
- Christie, K. S., Gilbert, S. L., Brown, C. L., Hatfield, M., & Hanson, L. (2016). Unmanned aircraft systems in wildlife research: Current and future applications of a transformative technology. *Frontiers in Ecology and the Environment*, 14, 241–251. <https://doi.org/10.1002/fee.1281>
- Cortes, C., & Vapnik, V. (1995). Support-vector networks. *Machine Learning*, 20, 273–297.
- Evans, L. J., Jones, T. H., Pang, K., Saimin, S., & Goossens, B. (2016). Spatial ecology of estuarine crocodile (*Crocodylus porosus*) nesting in a fragmented landscape. *Sensors*, 16, <https://doi.org/10.3390/s16091527>
- Fischer, J., Ritchie, E. G., & Hanspach, J. (2012). Academia's obsession with quantity. *Trends in Ecology & Evolution*, 27, 473–474. <https://doi.org/10.1016/j.tree.2012.05.010>
- Gerrodette, T. (1987). A power analysis for detecting trends. *Ecology*, 68, 1364–1372. <https://doi.org/10.2307/1939220>
- Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 365, 2303–2312. <https://doi.org/10.1098/rstb.2010.0087>
- Hodgson, J. C., Baylis, S. M., Mott, R., Herrod, A., & Clarke, R. H. (2016). Precision wildlife monitoring using unmanned aerial vehicles. *Scientific Reports*, 6, 22574. <https://doi.org/10.1038/srep22574>
- Hodgson, J. C., Baylis, S. M., Mott, R., & Koh, L. P. (2016). A comparison of the accuracy of simulated animal counts using traditional and UAV-assisted methods. *Open Science Framework*. <https://doi.org/10.17605/osf.io/a6n3b>
- Hodgson, J. C., & Koh, L. P. (2016). Best practice for minimising unmanned aerial vehicle disturbance to wildlife in biological field research. *Current Biology*, 26, R404–R405. <https://doi.org/10.1016/j.cub.2016.04.001>
- Hodgson, J. C., Mott, R., Baylis, S. M., Pham, T. T., Wotherspoon, S., Kilpatrick, A. D., ... Koh, L. P. (2018). Data from: Drones count wildlife more accurately and precisely than humans. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.rd736>
- Hulme, P. E. (2009). Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, 46, 10–18. <https://doi.org/10.1111/j.1365-2664.2008.01600.x>
- Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., ... Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, 348, 1255642. <https://doi.org/10.1126/science.1255642>
- Jones, G. P., Pearlstine, L. G., & Percival, H. F. (2006). An assessment of small unmanned aerial vehicles for wildlife research. *Wildlife Society Bulletin*, 34, 750–758. [https://doi.org/10.2193/0091-7648\(2006\)34\[750:aaosua\]2.0.co;2](https://doi.org/10.2193/0091-7648(2006)34[750:aaosua]2.0.co;2)

- Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, 348, aaa2478. <https://doi.org/10.1126/science.aaa2478>
- Krause, D. J., Hinde, J. T., Perryman, W. L., Goebel, M. E., & LeRoi, D. J. (2017). An accurate and adaptable photogrammetric approach for estimating the mass and body condition of pinnipeds using an unmanned aerial system. *PLoS ONE*, 12, e0187465. <https://doi.org/10.1371/journal.pone.0187465>
- Linchant, J., Lisein, J., Semeki, J., Lejeune, P., & Vermeulen, C. (2015). Are unmanned aircraft systems (UASs) the future of wildlife monitoring? A review of accomplishments and challenges. *Mammal Review*, 45, 239–252. <https://doi.org/10.1111/mam.12046>
- Liu, K., Skibbe, H., Schmidt, T., Blein, T., Palme, K., Brox, T., & Ronneberger, O. (2013). Rotation-invariant HOG descriptors using Fourier analysis in polar and spherical coordinates. *International Journal of Computer Vision*, 106, 342–364. <https://doi.org/10.1007/s11263-013-0634-z>
- Marques, T. A., Thomas, L., Martin, S. W., Mellinger, D. K., Ward, J. A., Moretti, D. J., ... Tyack, P. L. (2013). Estimating animal population density using passive acoustics. *Biological Reviews of the Cambridge Philosophical Society*, 88, 287–309. <https://doi.org/10.1111/brv.12001>
- McClelland, G. T. W., Bond, A. L., Sardana, A., & Glass, T. (2016). Rapid population estimate of a surface-nesting seabird on a remote island using a low-cost unmanned aerial vehicle. *Marine Ornithology*, 44, 215–220.
- Moll, R. J., Millsbaugh, J. J., Beringer, J., Sartwell, J., & He, Z. (2007). A new “view” of ecology and conservation through animal-borne video systems. *Trends in Ecology & Evolution*, 22, 660–668. <https://doi.org/10.1016/j.tree.2007.09.007>
- Moller, A. P., Samia, D. S., Weston, M. A., Guay, P. J., & Blumstein, D. T. (2014). American exceptionalism: Population trends and flight initiation distances in birds from three continents. *PLoS ONE*, 9, e107883. <https://doi.org/10.1371/journal.pone.0107883>
- Mulero-Pazmany, M., Stolper, R., van Essen, L. D., Negro, J. J., & Sassen, T. (2014). Remotely piloted aircraft systems as a rhinoceros anti-poaching tool in Africa. *PLoS ONE*, 9, e83873. <https://doi.org/10.1371/journal.pone.0083873>
- Pham, T. T., Rezatofighi, S. H., Reid, I., & Chin, T.-J. (2016). Efficient point process inference for large-scale object detection. 2016 IEEE Conference on Computer Vision and Pattern Recognition (CVPR), pp. 2837–2845.
- Pimm, S. L., Alibhai, S., Bergl, R., Dehgan, A., Giri, C., Jewell, Z., ... Loarie, S. (2015). Emerging technologies to conserve biodiversity. *Trends in Ecology & Evolution*, 30, 685–696. <https://doi.org/10.1016/j.tree.2015.08.008>
- R Core Team. (2016). R: A language and environment for statistical computing. Vienna, Austria. Retrieved from <http://www.R-project.org>
- Ratcliffe, N., Guihen, D., Robst, J., Crofts, S., Stanworth, A., & Enderlein, P. (2015). A protocol for the aerial survey of penguin colonies using UAVs. *Journal of Unmanned Vehicle Systems*, 3, 95–101. <https://doi.org/10.1139/juvs-2015-0006>
- Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12, 982–998. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>
- Rowcliffe, J. M., & Carbone, C. (2008). Surveys using camera traps: Are we looking to a brighter future? *Animal Conservation*, 11, 185–186. <https://doi.org/10.1111/j.1469-1795.2008.00180.x>
- Sarda-Palomera, F., Bota, G., Padilla, N., Brotons, L., & Sarda, F. (2017). Unmanned aircraft systems to unravel spatial and temporal factors affecting dynamics of colony formation and nesting success in birds. *Journal of Avian Biology*, 48, 1273–1280. <https://doi.org/10.1111/jav.01535>
- Sarda-Palomera, F., Bota, G., Vinolo, C., Pallares, O., Sazatornil, V., Brotons, L., ... Sarda, F. (2012). Fine-scale bird monitoring from light unmanned aircraft systems. *Ibis*, 154, 177–183. <https://doi.org/10.1111/j.1474-919X.2011.01177.x>
- Sigsgaard, E. E., Carl, H., Moller, P. R., & Thomsen, P. F. (2015). Monitoring the near-extinct European weather loach in Denmark based on environmental DNA from water samples. *Biological Conservation*, 183, 46–52. <https://doi.org/10.1016/j.biocon.2014.11.023>
- Smart, A. S., Tingley, R., Weeks, A. R., van Rooyen, A. R., & McCarthy, M. A. (2015). Environmental DNA sampling is more sensitive than a traditional survey technique for detecting an aquatic invader. *Ecological Applications*, 25, 1944–1952. <https://doi.org/10.1890/14-1751.1>
- Smart, A. S., Weeks, A. R., van Rooyen, A. R., Moore, A., McCarthy, M. A., & Tingley, R. (2016). Assessing the cost-efficiency of environmental DNA sampling. *Methods in Ecology and Evolution*, 7, 1291–1298. <https://doi.org/10.1111/2041-210x.12598>
- Vermeulen, C., Lejeune, P., Lisein, J., Sawadogo, P., & Bouche, P. (2013). Unmanned aerial survey of elephants. *PLoS ONE*, 8, e54700. <https://doi.org/10.1371/journal.pone.0054700>
- Waldron, A., Mooers, A. O., Miller, D. C., Nibbelink, N., Redding, D., Kuhn, T. S., ... Gittleman, J. L. (2013). Targeting global conservation funding to limit immediate biodiversity declines. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 12144–12148. <https://doi.org/10.1073/pnas.1221370110>
- Watts, A. C., Perry, J. H., Smith, S. E., Burgess, M. A., Wilkinson, B. E., Szantoi, Z., ... Percival, H. F. (2010). Small unmanned aircraft systems for low-altitude aerial surveys. *Journal of Wildlife Management*, 74, 1614–1619. <https://doi.org/10.2193/2009-425>
- Weissensteiner, M. H., Poelstra, J. W., & Wolf, J. B. W. (2015). Low-budget ready-to-fly unmanned aerial vehicles: An effective tool for evaluating the nesting status of canopy-breeding bird species. *Journal of Avian Biology*, 46, 425–430. <https://doi.org/10.1111/jav.00619>
- Wich, S., Dellatore, D., Houghton, M., Ardi, R., & Koh, L. P. (2016). A preliminary assessment of using conservation drones for Sumatran orangutan (*Pongo abelii*) distribution and density. *Journal of Unmanned Vehicle Systems*, 4, 45–52. <https://doi.org/10.1139/juvs-2015-0015>
- Wilson, A. M., Barr, J., & Zagorski, M. (2017). The feasibility of counting songbirds using unmanned aerial vehicles. *Auk*, 134, 350–362. <https://doi.org/10.1642/Auk-16-216.1>

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Hodgson JC, Mott R, Baylis SM, et al. Drones count wildlife more accurately and precisely than humans. *Methods Ecol Evol*. 2018;9:1160–1167. <https://doi.org/10.1111/2041-210X.12974>