

Title

Drones count wildlife more accurately and precisely than humans

Authors

Jarrold C. Hodgson^{1*}, 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.

Affiliations

¹School of Biological Sciences, University of Adelaide, Adelaide, SA 5005, Australia.

²School of Biological Sciences, Monash University, Clayton, VIC 3800, Australia.

³School of Computer Science, University of Adelaide, Adelaide, SA 5005, Australia.

⁴Institute of Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7001, Australia.

⁵Antarctic Conservation and Management, Australian Antarctic Division, Department of the Environment and Energy, Kingston, TAS 7050, Australia.

Corresponding author

Jarrold C. Hodgson

School of Biological Sciences, University of Adelaide, SA 5005, Australia.

Email: jarrod.hodgson@adelaide.edu.au

1 **Abstract**

2 Ecologists are increasingly using technology to improve the quality of data collected on wildlife,
3 particularly for assessing the environmental impacts of human activities. Remotely Piloted
4 Aircraft Systems (RPAS; commonly known as ‘drones’) are widely touted as a cost-effective
5 way to collect high quality wildlife population data, however, the validity of these claims is
6 unclear. Using life-sized seabird colonies containing a known number of replica birds, we show
7 that RPAS-derived data are, on average, between 43% and 96% more accurate than data from
8 the traditional ground-based collection method. We also demonstrate that counts from this
9 remotely sensed imagery can be semi-automated with a high degree of accuracy. The
10 increased accuracy and precision of RPAS-derived wildlife monitoring data provides greater
11 statistical power to detect fine-scale population fluctuations allowing for more informed and
12 proactive ecological management.

13 **Keywords**

14 bird, drones, ecology, population monitoring, RPAS, UAV, UAS, wildlife

15 **Introduction**

16 Wildlife populations are undergoing dramatic declines in response to a wide range of
17 human-induced threats (Dirzo *et al.* 2014; Tilman *et al.* 2017). High quality ecological data
18 are vital to monitor such changes. Emerging technologies, such as camera traps (Rowcliffe &
19 Carbone 2008) and radio telemetry (Hussey *et al.* 2015; Kays *et al.* 2015), have increasingly
20 been used to address this challenge (Moll *et al.* 2007; Hebblewhite & Haydon 2010; Pimm *et*
21 *al.* 2015), especially when wildlife populations are rapidly fluctuating, highly mobile or
22 located in remote habitats.

23 Remotely Piloted Aircraft Systems have been heralded as a game changer in ecology (Jones,
24 Pearlstine & Percival 2006; Watts *et al.* 2010; Koh & Wich 2012; Anderson & Gaston 2013;
25 Marris 2013; Chabot & Bird 2015; Linchant *et al.* 2015; Christie *et al.* 2016). They are used
26 for data collection in an increasingly diverse suite of ecological applications, including
27 identification of floristic biodiversity of understorey vegetation (Getzin, Wiegand &
28 Schöning 2012), monitoring for poaching activities (Mulero-Pazmany *et al.* 2014), and bird
29 surveys (Sarda-Palomera *et al.* 2012; Chabot, Craik & Bird 2015). However, there has been
30 little consideration of the quality of data obtained using RPAS compared to more
31 conventional methods (see Hodgson *et al.* (2016a) for an exception).

32 We assessed the accuracy of RPAS-facilitated wildlife population monitoring in comparison
33 with the traditional ground-based counting method. The task for both approaches was to
34 derive an estimate of the size (i.e. number of individuals) of 10 replica seabird colonies. Each
35 replica colony had a different known number of life-sized individuals. We hypothesised that
36 RPAS-derived counts would be more accurate and more precise than those generated using
37 the traditional approach, confirming RPAS-technology as revolutionary for ecological
38 monitoring.

39 **Materials and methods**

40 *Study site and simulated colony set-up*

41 Fieldwork (#epicduckchallenge) was completed at a metropolitan beach in South Australia
42 (Port Willunga, 35°15'33 S, 138°27'41 E) in accordance with relevant permits (Department of
43 Environment, Water and Natural Resources scientific research permit: M26523-1; City of
44 Onkaparinga location permit: 4138). The experimental design, including the majority of
45 anticipated statistical analyses, was pre-registered (Hodgson *et al.* 2016b).

46 Ten simulated Greater Crested Tern *Thalasseus bergii* breeding colonies were constructed
47 using commercial, life-size, plastic duck decoys (~ 25.5 x 11.3 cm, 185 cm² footprint).
48 Decoys provided a realistic representation of the nesting seabird stimuli observers encounter
49 in the field. Colonies were situated separately on the beach, above the high water mark, in
50 sandy areas that represented analagous nesting habitat. These were typically devoid of
51 vegetation but often contained natural beach debris.

52 As inter-individual interactions are thought to influence colony layout, a model of nesting
53 pressure was applied to an underlying hexagonal grid to generate unique, unbiased colony
54 layouts (Hodgson *et al.* 2016b). The hexagonal grid was re-created in the field using a wire
55 mesh, upon which grid cell centres were marked (mean density: 11.39 m⁻²). Pre-counted
56 wooden skewers were placed one per cell at a random location within all cells identified as
57 occupied in the colony layout map. The mesh was removed and each skewer was replaced
58 with a decoy facing approximately into the wind. The number of skewers retrieved was taken
59 to be the true number of individuals in the colony. Colony sizes were between 463 and 1017
60 individuals. One individual was placed in each occupied cell.

61 *Ground counting approach*

62 Ground counts were made by experienced seabird counters using a standard field technique
63 (Hodgson *et al.* 2016a). Counters used tripod-mounted spotting scopes or binoculars as
64 required. Hand-held tally counters were used to assist counting. Observation viewpoints at
65 similar altitude to the colony and which provided the optimum vantage were selected (Fig. 1).
66 Viewpoints were positioned 37.5 m from the nearest bird in the colony – this is the flight
67 initiation distance for Caspian Tern *Hydroprogne caspia* (Moller *et al.* 2014) and so is a
68 biologically-plausible minimum approach distance for a similar species in the field. Counts
69 ($n = 61$) were 7 ± 2.65 min (s.d.) in duration. Four to seven counters each made a single blind
70 count of the number of individuals in each colony. The numbers of counters were selected

71 based on a preliminary power analysis (Hodgson *et al.* 2016b) which investigated the sample
72 sizes necessary to detect small (~ 10%) differences in mean counts and count variances
73 between ground and RPAS-derived counts to high (80%, 90%, and 95%) power. Counters
74 had no knowledge of the true number of individuals in colonies or the colony set-up
75 technique. Counts were made between 0930 and 1645 on one day, resulting in variation in
76 illumination and shadows.

77 *RPAS description, flight characteristics and data collected by RPAS*

78 A small, off-the-shelf quadcopter (Iris+, 3D Robotics) was used as a platform to image each
79 colony. After positioning the RPAS in the centre of the colony at 15 m above ground level, it
80 was piloted in altitude hold mode to make a vertical ascent without movement in other axes.
81 The RPAS was loitered for short periods (~ 10 seconds) to enable the capture of several
82 photographs at 30 m, 60 m, 90 m and 120 m above ground level (sample heights). Sampling
83 was restricted to a height of 120 m as this is a common maximum limit for standard RPAS
84 flight. Ground control station connection (Mission Planner, planner.ardupilot.com) was
85 utilised and total flight time for missions was 5-7 min. All missions were in accordance with
86 local regulations and flown by the same licenced pilot. Samples were collected within 40 min
87 of the completion of ground counts.

88 Imagery was captured using a compact digital camera (Cyber-shot RX100 III, Sony –
89 resolution: 5,472 x 3,648 px; sensor: CMOS; sensor size: 13.2 x 8.8 mm; lens: ZEISS
90 Vario-Sonnar T). Exposure time was set at 1/2000 seconds using shutter priority mode.
91 Photographs were captured successively (~ 1 sec intervalometer) using the Sony
92 PlayMemories Time-lapse application in jpeg format and at minimum focal length (8.8 mm).
93 The camera was mounted facing downward using a custom vibration dampening plate. The
94 footprint of a single image at each height encompassed the colony for all replicates. For
95 analysis, only the image captured closest to the middle of the loiter time period for each
96 sample height was used. These images (scenes; $n = 40$) were cropped (colony area < 50% of
97 footprint) so that the image footprint was identical for each sample height for a given colony.
98 High quality imagery was obtained for six of the ten colonies. Imagery for the remaining four
99 colonies was affected by vibration-blur caused by a failure of the sensor attachment, likely
100 due to wind speeds near the limit of the capability of the RPAS platform. Scenes are archived
101 online (Pham & Hodgson 2017).

102 The ground sample distance (GSD), being the distance between adjacent pixel centres on the
103 ground, for sample heights were 0.82 cm, 1.64 cm, 2.47 cm and 3.29 cm (Fig. 1). When
104 photographed at nadir, this approximated to 275, 69, 30 and 17 pixels per individual
105 respectively. The variance in GSDs was intended to represent the resolutions commonly
106 achieved in wildlife monitoring applications, which result from sensor and sampling height
107 variations.

108 *Manual RPAS image counting approach*

109 Manual counts of perceived individuals in digital imagery were completed following a
110 technique previously implemented for RPAS-derived monitoring of living seabirds (Hodgson
111 *et al.* 2016a). Systematic counts were made using the multi-count tool within an open source,
112 java-based scientific image processing program (ImageJ, <http://imagej.net/>). A grid plugin
113 was used to overlay a square matrix (cell sizes: 70,000, 15,000, 8,000 and 4,000 pixels for
114 each sample height) and counters were instructed to view the colony sequentially (gridcell-
115 by-gridcell: left to right, top to bottom). Counters were encouraged to zoom in to each cell as
116 they progressed and, upon completion, review their count at different levels of zoom until
117 they were satisfied they had counted all individuals. For each sample height, seven to nine
118 individuals counted each colony. Counters had no knowledge of the experimental setup and
119 only one had experience ground counting colonial birds.

120 *Semi-automated aerial image counting approach*

121 In each scene, digital bounding boxes were used to manually delimit a percentage of
122 individual birds (Supplementary Fig. 1a). Areas of background were also delimited. These
123 data were used to train a linear support-vector machine (a discriminative classifier; Cortes &
124 Vapnik 1995), which predicted the likelihood of each pixel being a bird or background when
125 applied to the corresponding scene (Supplementary Fig. 1b). Instead of relying on colour
126 intensities, we computed rotation-invariant Fourier histogram of oriented gradient (Liu *et al.*
127 2013) features for each pixel used in the training processes. This resulted in the classifiers
128 being trained to determine which features distinguished birds from the background. The
129 predicted likelihood (score) maps indicated the approximate locations of birds in the scenes,
130 and detections were generated by applying a threshold to the likelihood maps. This process
131 unavoidably resulted in redundant bird proposals (Supplementary Fig. 1c) and so the final
132 detection results were obtained by suppressing redundant proposals via minimising an energy
133 function (Pham *et al.* 2016; Supplementary Fig. 1d). This function encoded the spatial

134 distribution of objects and is informed by our knowledge of how the birds nest (e.g. two birds
135 cannot occupy the same location). The source code and dataset are archived online (Pham &
136 Hodgson 2017).

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

140 *Statistical methods*

141 All analyses were carried out in *R* version 3.2.2 (R Core Team 2016). Pre-registered analyses
142 were designed to investigate how within-colony absolute count error, within-colony
143 variability of counts, and within-colony bias of counts differed between count techniques
144 (Hodgson *et al.* 2016b).

145 For each test, a generalised linear mixed model was fit between the response (e.g. absolute
146 count error) and the technology used to make the count (e.g. ground-count, manually counted
147 RPAS at 30 m height, semi-automatically counted RPAS at 30 m height), with colony
148 included in the model as a random effect (Supplementary Information 1). To investigate
149 effects of counting technique on absolute count error, we defined the response as the absolute
150 difference between the true number of birds in a colony and the counted number of birds. To
151 investigate effects of counting technique on count-variability, we defined the response as the
152 absolute difference between each count and the mean of counts of the same colony taken
153 using the same method. Count variability was not estimated for semi-automated counts as
154 there was only a single semi-automated count per colony. To investigate the effect of
155 counting technique on relative count bias, we defined the response as the difference between
156 the true number of birds in the colony and the counted number of birds. For the absolute
157 count error model, we used a Quasipoisson distribution, and for the variability and bias
158 models, we used a Gaussian distribution. For each model, post-hoc Tukey tests were used to
159 test for differences in the response between all pairs of treatment levels.

160 Semi-automated count data were added to the experimental design subsequent to our
161 pre-registration of the analysis which necessitated minor analysis modification. The addition
162 of semi-automated count data, with a single replicate per colony, required fitting colony ID as
163 a random effect instead of as a fixed effect in each model.

164 Statements comparing the accuracy of RPAS-derived counts to ground-based counts are
165 based on the mean within-colony Root Mean Squared Error (RMSE) of that counting
166 approach, standardised as a proportion of the true count within each colony (Supplementary
167 Information 2). For instance, a statement that RPAS-derived counts are '95% more accurate
168 than ground-counts' means that, within-colony, the RMSE for RPAS-derived counts is 5%
169 the RMSE for ground-based counts, representing a 95% reduction in RMSE.

170 To investigate the probability of counting each individual correctly, we developed models
171 with a variety of possible counting outcomes for each object (Supplementary Information 3).
172 We assumed that there are $N = n_0 + n_1 + n_2$ objects that are counted by an observer, of which
173 n_1 are counted correctly, n_0 are missed and n_2 are double counted. We assumed that $n = (n_0,$
174 $n_1, n_2)$ is multinomially distributed with probability $p = (p_0, p_1, p_2)$. In this structure, $n_0, n_1,$
175 n_2 are latent and the observer can only report the total count $M = n_1 + 2n_2$. Allowing each
176 object to be at most double counted constrains n considerably, and the probability mass
177 function can then be formulated. We adopted a Dirichlet prior for p ($p \sim \text{Dirichlet}(a)$) making
178 the conditional distribution of p : $p|n(k) \sim \text{Dirichlet}(a+n(k))$.

179 We then ran a Gibbs sampling routine for p by alternately sampling $n(k)$ and p from these
180 two distributions. Since there was considerably more variation between ground counts
181 compared to manual RPAS counts, we ran the analyses for each ground counter separately,
182 and pooled data across counters for manual RPAS counts. The RPAS analyses were run
183 separately for each sample height, and two sets of analyses were undertaken, one with data
184 from all colonies, and the other with data from the subset of colonies with high quality
185 imagery. This statistical approach does not account for objects being mistakenly identified as
186 birds (i.e. false positives). Furthermore, as this model assumes each individual is counted
187 independently, which may not always be true (particularly for ground counters who tend to
188 count in clusters), care needs to be taken in the interpretation of the estimated probability
189 values (and their variance).

190 To compare the semi-automated counts to that of the people counting the images, we first
191 took the semi-automated count after 10% of training data had been used for each scene. Ten
192 percent of training data was consistently identified as a threshold over which little
193 improvement in counts occurred for all scenes. We compared this count to each of the manual
194 counts of the same image using ANOVA for all scenes, and also for those scenes of high

195 quality. We also used Poisson generalized linear models to make more quantitative
196 comparisons of the two approaches.

197 *Code availability*

198 R scripts used for analyses are available in the Supplementary Information.

199 *Data availability*

200 The pre-registered experimental design is available via the Open Science Framework (**URL*
201 *to be made public on publication**). The count data, scenes and code for the image-analysis
202 algorithm are archived online (**URL to be made public on publication**).

203 **Results**

204 *Manual RPAS-derived image counting versus ground counts*

205 On average across all colonies, RPAS-derived counts were between 43% and 96% more
206 accurate than ground counts, depending on the sample height (between 92% and 98% for the
207 colonies with high quality imagery; Supplementary Table 1). The mean absolute error was
208 significantly smaller for RPAS-derived counts at all heights compared to ground counts (all
209 $P < 0.001$; Fig. 2a).

210 No significant increase in count accuracy was achieved by obtaining imagery from heights
211 lower than or equal to 90 m. Using data only from colonies with high quality imagery, there
212 was no significant change in count accuracy across the range of heights. The lower accuracy
213 of ground counts was due to significant underestimations of the true number of individuals in
214 colonies (Fig. 2b). RPAS-derived counts from imagery obtained at 30 m and 60 m did not
215 significantly under- or overestimate the true number of individuals in a colony, and there was
216 no evident bias in RPAS-derived counts at any height for colonies with high quality imagery
217 (Fig. 2b).

218 Using data from all colonies, RPAS-derived counts from 30 m and 60 m had a much higher
219 probability (90% and 50%, respectively) of correctly counting an individual than counts from
220 ground observers ($< 10\%$) (Fig. 3). However, 90 m and 120 m probabilities were largely
221 indistinguishable from the ground count probabilities, with a slightly higher likelihood of
222 missing individuals compared to counting them twice (Supplementary Fig. 3, 4). Colony
223 counts made from high quality imagery had a much higher probability of individuals being
224 counted correctly, with $> 85\%$ probability of correctly counting an individual at all heights
225 (Fig. 3). By contrast, ground counts had a low probability of counting an individual correctly,
226 with the probability of double counting and missing an individual varying considerably
227 between observers (Fig. 3 and Supplementary Fig. 3, 4).

228 RPAS-derived counts were more precise (i.e. had lower inter-observer variability) than
229 ground counts, regardless of the height at which imagery was obtained ($t_{4,560} -10.21$ to -13.37 ,
230 all $P < 0.001$; Supplementary Fig. 5). RPAS-derived counts were more precise for imagery
231 obtained at 30 m compared to those obtained from 120 m ($P = 0.01$), however, there were no
232 significant differences in precision among RPAS-derived counts at different heights for
233 colonies with high quality imagery (all $P > 0.98$).

234 *Semi-automated RPAS approach*

235 By increasing the percentage (1 – 30%) of individuals used as training data for the image-
236 analysis algorithm, 10% training data was consistently identified as a threshold above which
237 little improvement in count accuracy was achieved in this semi-automated approach
238 (Supplementary Fig. 2). There was no significant difference between counts that were made
239 with 10% training data and those made by manual counting of RPAS-imagery across all
240 scenes. The semi-automated results were 94% similar to manual counts across all scenes
241 (98% for the colonies with high quality imagery; see also Supplementary Table 1).

242 **Discussion**

243 RPAS-derived data were more accurate and more precise than the traditional data collection
244 method validating claims that RPAS will be a revolutionary tool for ecologists. Never has the
245 importance of accurate wildlife population monitoring data been greater than at present given
246 the alarming population declines observed in animal species across the globe (Dirzo *et al.*
247 2014). By facilitating accurate census, RPAS will provide ecologists with confidence in
248 population estimates from which management decisions are made. Furthermore, the superior
249 precision of RPAS-derived counts increases statistical power to detect population trends,
250 owing to the lower type II error rate in statistical analysis that comes with comparing
251 measures with smaller variance (Gerrodette 1987). The improved precision of wildlife
252 population census using RPAS has been demonstrated for free-living seabird colonies
253 (Hodgson *et al.* 2016a) suggesting our results are generalizable to natural settings.
254 Differences in accuracy and precision between RPAS-facilitated and traditional survey
255 methods can be attributed to the sources, and magnitude, of variance introduced into the two
256 approaches which are strongly affected by the different vantages of the two methods
257 (Hodgson *et al.* 2016a).

258 We have conducted two independent analyses of how count error differs across count
259 approaches: a Frequentist analysis which estimates mean absolute count error, and a Bayesian
260 analysis which estimates the probability of double-counting or missing individual animals.
261 The two analyses are in agreement on the broad patterns: RPAS-derived counts are estimated
262 to have lower error than ground counts in both analyses, and the error-rate is fairly insensitive
263 to sample height for RPAS-derived counts. The Bayesian analysis makes restrictive
264 assumptions about the process by which counting errors occur, and these assumptions may
265 not fully reflect real-world counting processes. Nevertheless, the Bayesian analyses provide a
266 first estimate of the extent to which overall count accuracy is dependent on the
267 double-counting of some individuals cancelling out the effect of missing others. As an
268 extreme example, our analysis suggests that < 10% of animals are correctly classified as a
269 single animal in typical ground counts.

270 Manual counting of RPAS-derived imagery returned high quality data, but also involved
271 substantial labour investments. Recent advances in digital sensors and image-analysis
272 techniques have been increasingly employed to streamline the detection process (Chabot &
273 Francis 2016). By applying a semi-automated image-based object detection algorithm to each

274 scene, we vastly improved efficiency compared to the manual RPAS-derived census.
275 Importantly, the reduction in person-hours provided by this semi-automated approach did not
276 diminish data quality. This will be of particular interest in today's research environment
277 where funding for conservation is limited (Waldron *et al.* 2013) and researchers are under
278 ever more pressing time commitments (Fischer, Ritchie & Hanspach 2012).

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

286 The ability to collect data with higher accuracy, higher precision, and less bias than the
287 existing approach confirms that RPAS are a scientifically rigorous data collection tool for
288 wildlife population monitoring. This approach also produces a permanent record, providing
289 the unique opportunity to error-check, and even recount with new detection methods, unlike
290 ground count data. As RPAS platforms, sensors and computer vision techniques continue to
291 develop, it is likely that the accuracy and cost effectiveness of RPAS-based approaches will
292 also continue to improve.

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300 **Author contributions**

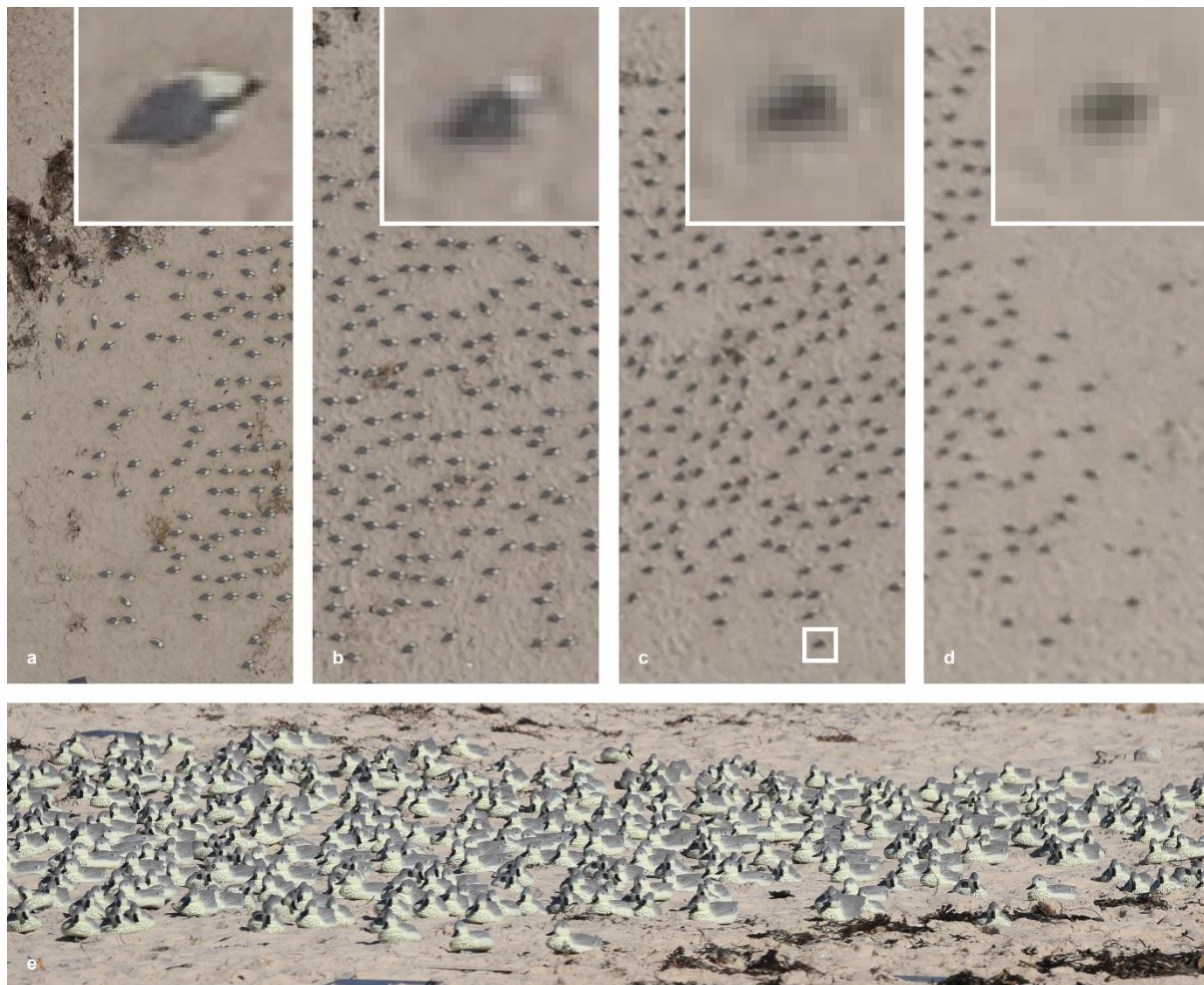
301 J.C.H., R.M., S.M.B., A.T. and L.P.K. designed the study, analysed the data and wrote the
302 manuscript. A.D.K. assisted with designing the study. J.C.H., R.M., S.M.B., A.D.K., R.R.S.
303 and L.P.K. collected the data. T.T.P., J.C.H., L.P.K. and I.R. developed the semi-automated
304 detection technique.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

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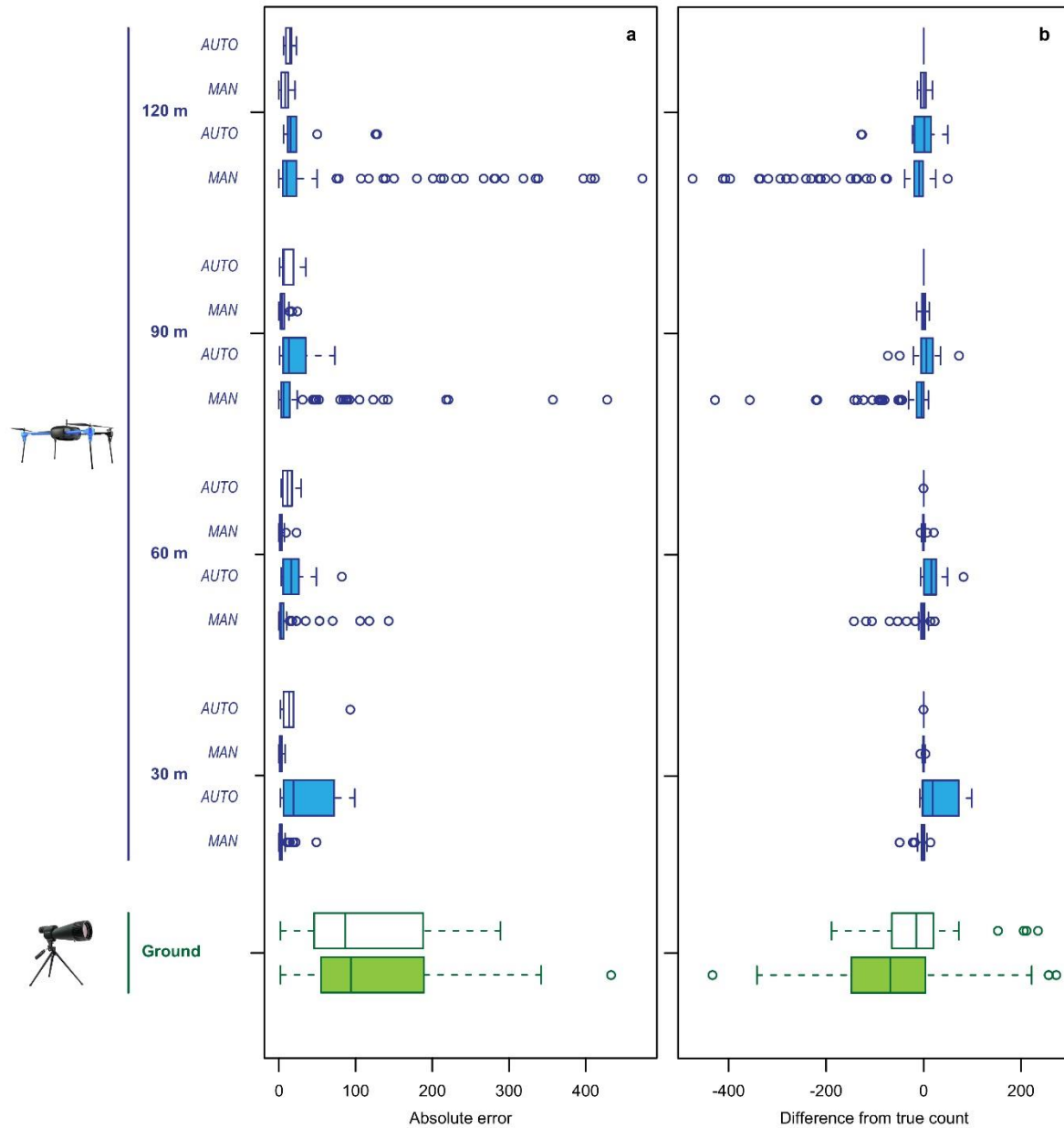
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Figure 1: Aerial vantage of a replica seabird colony compared with the ground counter's viewpoint. One colony represented by a mosaic of images (a-d) photographed from a RPAS-mounted camera at varying heights (30 m, 60 m, 90 m and 120 m) and resulting ground sample distances (GSD; 0.82 cm, 1.64 cm, 2.47 cm 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.



394

395 **Figure 2: Accuracy and bias of RPAS and traditional wildlife monitoring approaches.**

396 The absolute error (a) and difference from the true count (b) of each method. Data from all

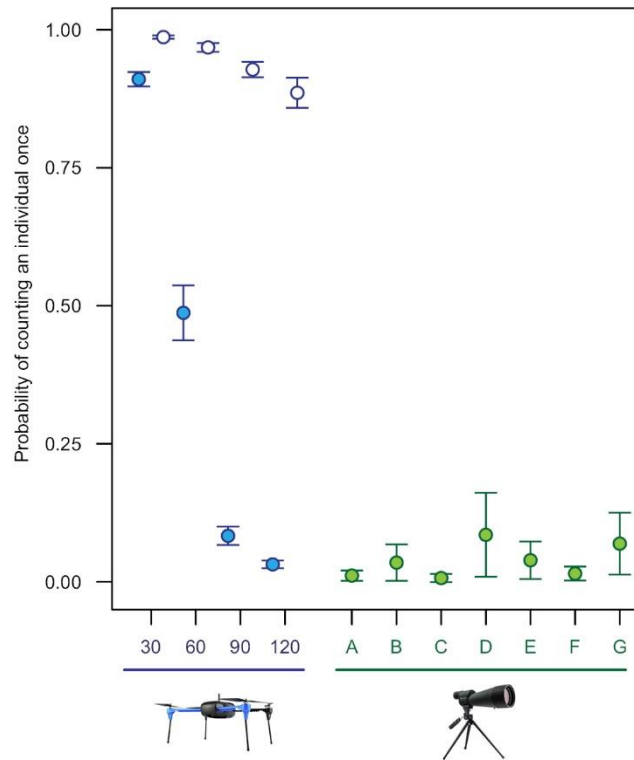
397 colonies ($n = 10$; shaded) and also for the subset of colonies with high quality imagery

398 ($n = 6$; unshaded) are presented for both RPAS-derived (blue) and ground (green) counts.

399 RPAS-derived manual-human (Man) and semi-automated (Auto) counts are displayed and

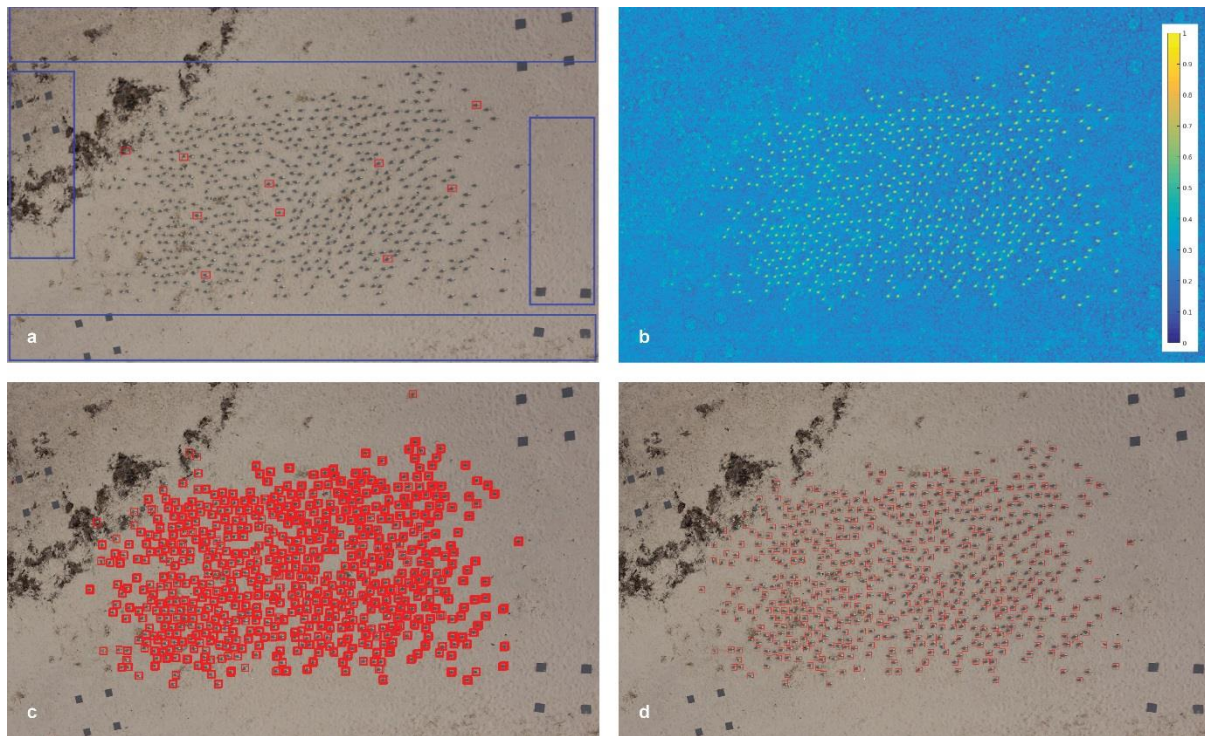
400 data are grouped by height which reflects ground sample distance (GSD; 30 m height = 0.82

401 cm GSD, 60 m = 1.64 cm, 90 m = 2.47 cm, 120 m = 3.29 cm).



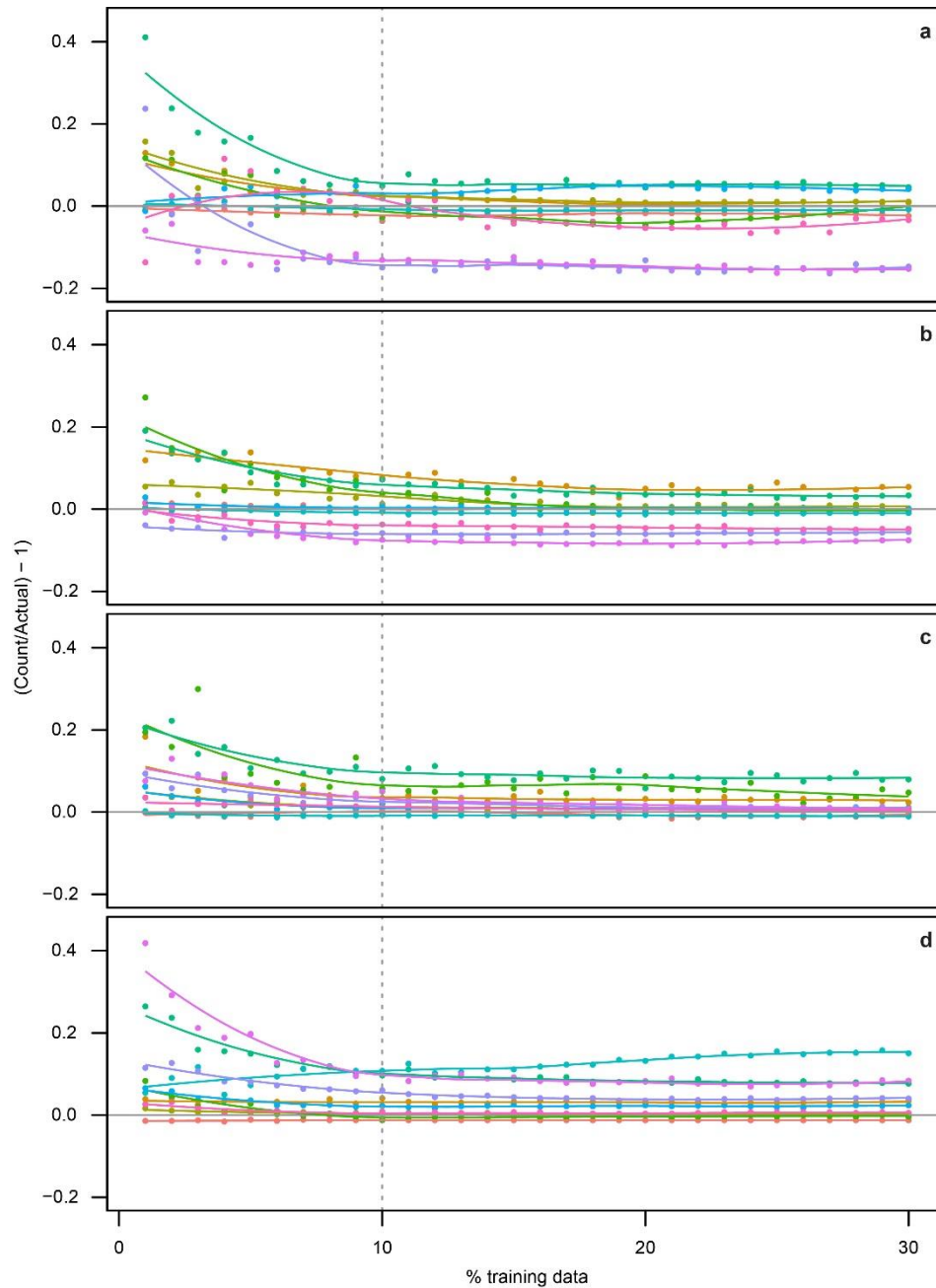
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403 **Figure 3: Probability of counting an individual in a colony once (correctly).** Data from all
404 colonies ($n = 10$; shaded) and also for the subset of colonies with high quality imagery
405 ($n = 6$; unshaded) are presented for RPAS-derived (blue) manual counts. These data are
406 grouped by height (m) which reflects ground sample distance (GSD; 30 m height = 0.82 cm
407 GSD, 60 m = 1.64 cm, 90 m = 2.47 cm, 120 m = 3.29 cm). Probabilities from ground count
408 data (green) for all colonies are estimated for each counter individually (A-G). Error bars
409 represent standard deviation.



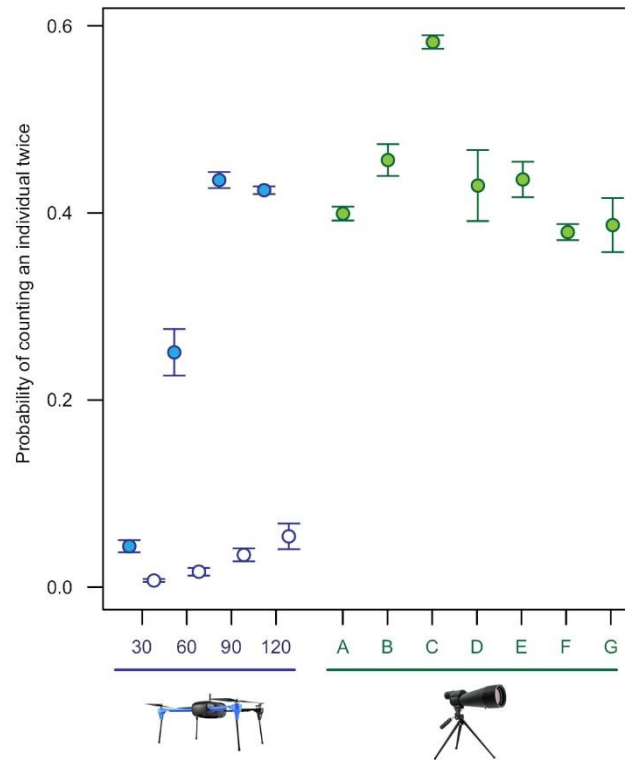
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411 **Supplementary Figure 1: Semi-automated detection and counting of wildlife using**
412 **computer vision techniques. (a)** User annotation of perceived target objects (red) and
413 background (blue). **(b)** score map generated by the trained classifier which has automatically
414 determined which image features distinguish objects from background, independent of scale
415 and orientation. Warmer colours indicate increasing likelihood of the pixel being a target
416 object. **(c)** target object proposals (red) computed by thresholding the score map. Object size
417 is estimated from the annotations. **(d)** final output (which includes a total count and detection
418 co-ordinates) where detected individuals are delineated (red) after redundant detections have
419 been automatically suppressed.



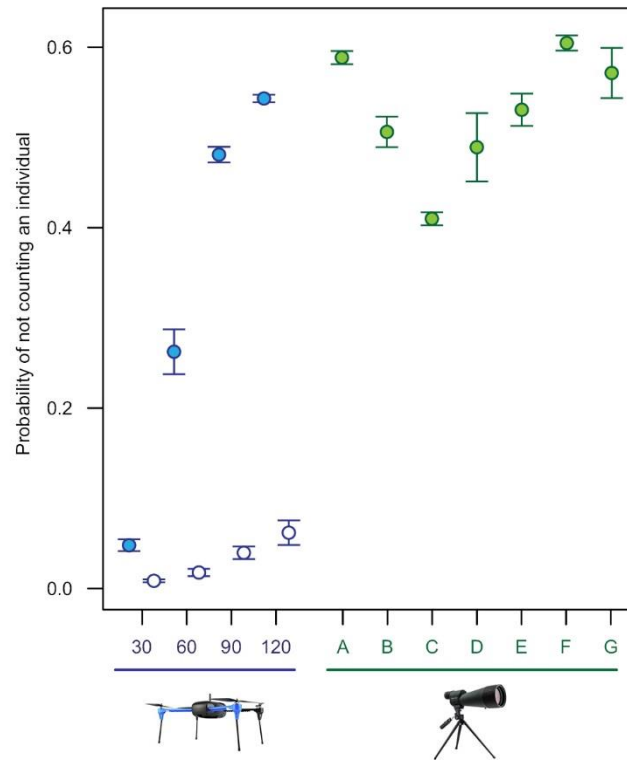
420

421 **Supplementary Figure 2: Improvement in accuracy of semi-automated detection counts**
422 **with increasing training data.** Colonies ($n = 10$) are represented by individual colours at
423 each height which reflects ground sample distance (GSD): 120 m height = 3.29 cm GSD (a);
424 90 m = 2.47 cm (b); 60 m = 1.64 cm (c); 30 m = 0.82 cm (d). Lowess smoothed trendlines
425 are displayed. Analyses were computed using count estimates generated from 10 % training
426 data (dashed line).



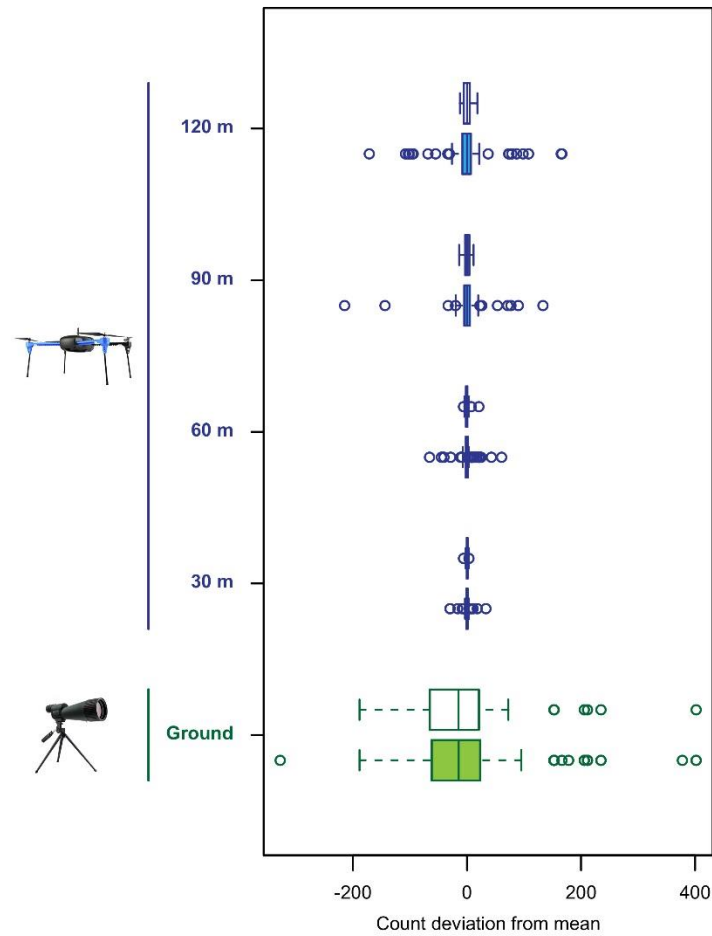
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428 **Supplementary Figure 3: Probability of counting an individual in a colony twice (double**
429 **counting).** Data from all colonies ($n = 10$; shaded) and also for the subset of colonies with
430 high quality imagery ($n = 6$; unshaded) are presented for RPAS-derived (blue) manual
431 counts. These data are grouped by height (m) which reflects ground sample distance (GSD);
432 30 m height = 0.82 cm GSD, 60 m = 1.64 cm, 90 m = 2.47 cm, 120 m = 3.29 cm).
433 Probabilities from ground count data (green) for all colonies are estimated for each counter
434 individually (A-G). Error bars represent standard deviation.



435

436 **Supplementary Figure 4: Probability of not counting (missing) an individual in a**
437 **colony.** Data from all colonies ($n = 10$; shaded) and also for the subset of colonies with high
438 quality imagery ($n = 6$; unshaded) are presented for RPAS-derived (blue) manual counts.
439 These data are grouped by height (m) which reflects ground sample distance (GSD; 30 m
440 height = 0.82 cm GSD, 60 m = 1.64 cm, 90 m = 2.47 cm, 120 m = 3.29 cm). Probabilities
441 from ground count data (green) for all colonies are estimated for each counter individually
442 (A-G). Error bars represent standard deviation.



443

444 **Supplementary Figure 5: Precision of RPAS and traditional wildlife monitoring**
445 **approaches.** Data from all colonies ($n = 10$; shaded, lower box in each course) and also for
446 the subset of colonies with high quality imagery ($n = 6$; unshaded, upper box in each course)
447 are presented for both RPAS-derived manual-human (blue) and ground (green) counts. Data
448 are grouped by height which reflects ground sample distance (GSD; 30 m height = 0.82 cm
449 GSD, 60 m = 1.64 cm, 90 m = 2.47 cm, 120 m = 3.29 cm).

450 **Supplementary Table 1: Mean percentage increase in accuracy of RPAS wildlife**
451 **monitoring approaches compared with the traditional ground count approach.**

452 Percentages are calculated for RPAS-derived human manual (Man) and semi-automated
453 (Auto) counts using data from all colonies ($n = 10$) as well as the subset of colonies with high
454 quality imagery ($n = 6$). Data are grouped by height which reflects ground sample distance
455 (GSD; 30 m height = 0.82 cm GSD, 60 m = 1.64 cm, 90 m = 2.47 cm, 120 m = 3.29 cm).

Height (m)	All colonies (%)		Colonies with high quality imagery (%)	
	Man	Auto	Man	Auto
30	96	77	98	88
60	90	84	97	88
90	74	80	94	89
120	43	77	92	85

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