Learning to fly: integrating spatial ecology with unmanned aerial vehicle surveys

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Abstract. Despite the increasing importance of new survey tools such as unmanned aerial vehicles (UAVs), the implications of how their spatial deployment may interact with species detection errors have not yet been assessed. Acknowledging and incorporating these errors are crucial for accurate population estimation and improved management. To address this important gap in our knowledge, and to discover how flight plans should be selected to reduce overall error, we simulated contrasting UAV flight surveys over a range of population densities and dispersion patterns using different detection errors. We found that if a survey is carried out using an individual transect that low and slow flights consistently provide the best estimates of abundance and occupancy. However, the greater sampling area afforded by higher or faster flights resulted in more complex guidelines for estimates of abundance or occupancy over larger study areas. For highly clustered populations, especially those at low densities, a high and fast survey is preferable, as its greater area coverage best enables detection of local occupancy. The performance rankings of flight plans were sensitive to the underlying species detectability and, to a lesser extent, population density and aggregation. This suggests that UAV survey plans need to account for the spatial and movement ecology of target species, and that flight plans should adapt as an invasive species spreads, or a threatened species contracts. We encapsulate our results in a decision tree to guide flight planning for given survey objectives, detectability, and ecological context. Importantly, these findings provide guidance to other fields with transect-based surveys such as manned aviation and road or ground transects that trade-off sampling area and precision of estimates. Promising new technologies such as UAVs will be best utilized by ecologists if detection errors, and their interaction with the spatial ecology of the species, are carefully assessed.

Key words: abundance estimation; detectability; drones; occupancy; population monitoring; remotely piloted aircraft systems; simulation; spatial analysis; surveys; unmanned aerial system.

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INTRODUCTION

Sound ecological understanding and effective management decisions require reliable species occurrence and abundance data (Conroy and Noon 1996, Guillera-Arroita et al. 2014). For example, predicting species range expansion in the context of climate change (Fordham et al. 2013) or invasion requires models to be updated with reliable observations from the edge of species’ ranges (Huntley et al. 2010). Precise occurrence data are similarly required for effective conservation planning, particularly for rare (Hermoso and Kennard 2012) or mobile species...
Understanding patterns of spread is important for optimal management of invasive pathogens or pests (Baxter and Possingham 2011, Rasmussen and Hamilton 2012, Parnell et al. 2014), and early detection of incursions can be crucial for their eventual containment and eradication (Mehta et al. 2007). Poor-quality or inconsistent data can lead to scientific uncertainty and impair management and policy decisions (Hayward et al. 2015). Detection errors in particular have the potential to greatly reduce the reliability of inferences, and therefore recommendations, made using occurrence data (Guiller a-Arroita et al. 2014, Guillera-Arroita 2017). Obtaining reliable data on species occurrence and abundance can be expensive and logistically challenging however, potentially rendering monitoring an inefficient option for ecological managers with limited budgets (McDonald-Madden et al. 2010). Promising new methods for monitoring continue to develop, but despite the enthusiasm surrounding the introduction of new sensors and different approaches to collecting data, the need to understand the abundance and spatial distribution of populations remains fundamental to the management of ecological processes (Rew and Cousens 2001).

Unmanned aerial vehicles (UAVs, also known as remotely piloted aircraft systems or RPAS) offer enormous potential to improve ecological monitoring and surveillance in the environment and agriculture (Kalaris et al. 2014), enhancing the range, accessibility and repeatability of remote detection (Linchant et al. 2015), and reducing interference and disturbance compared to direct surveys by humans (Jones et al. 2006, Sárdá-Palomera et al. 2012). While gathering aerial imagery has often been prohibitively cumbersome and expensive (Hardin and Jackson 2005), UAVs have emerged within the last decade as a cheaper and more efficient option and now look likely to revolutionize the collection and application of ecological and environmental data (Anderson and Gaston 2013, Jurdak et al. 2015, Bhardwaj et al. 2016). With ongoing reductions in payload size and weight, compared to older remote-sensing instrumentation requiring larger aircraft (Anderson and Gaston 2013, Bhardwaj et al. 2016), the resultant maneuverability and resolution of UAVs expand the ecologists’ toolkit and can broaden the capacity for hierarchical sampling (Jones et al. 2006). As purchase and operation costs continue to decrease (Chabot and Bird 2012), the main constraints on UAV operation are legal and insurance restrictions on range and altitude (Hardin and Jackson 2005, Chabot and Bird 2012, Linchant et al. 2015) and poor weather affecting flight success and image quality (Sárdá-Palomera et al. 2012, Campbell et al. 2015).

To gain maximum benefit from UAV surveys, there is a need to choose appropriate spatial strategies for their deployment (Jurdak et al. 2015). With the relatively recent recognition of UAVs’ considerable potential to assist in ecological and environmental monitoring (Koh and Wich 2012, Anderson and Gaston 2013, Linchant et al. 2015), as yet scant attention has been paid to how the nature of UAV errors in detecting individuals should influence flight protocols for abundance estimation and monitoring (see Dan dois et al. 2015 for factors affecting forest structure measurement by UAV). New detection methods such as UAV surveys inevitably require fine-tuning, and exploring such errors and how they might be minimized by choosing specific flight options is essential. For example, lower end unmanned systems may lack spatial accuracy (Watts et al. 2010) and may even have lower detection success than human observers, but can perform well if there is sufficiently high contrast between target and background (Chabot and Bird 2012).

Unmanned aerial vehicle surveys of ecological populations involve a pathway of steps, from planning decisions on flight paths and height, to image acquisition, merging, and processing, and image analysis for species identification. Despite rapid improvement in image analysis methods, each of these steps can contribute to high levels of radiometric (contrast and tonal) or geometric (spatial) errors (Morgan et al. 2010). Consequently, trade-offs and decisions made by ecologists throughout the implementation of UAV surveys—from camera positioning or aircraft speed, to the choice of image-processing algorithm—will affect the resultant overall level of detection error. Although some individual studies have reported on species detection success for particular surveys (Sárdá-Palomera et al. 2012, Hodgson et al. 2017), most have concentrated on the potential for species detection per se.
(Linchant et al. 2015), and there has been little
guidance to assist with spatial planning of UAV-
based population monitoring. Species patterns of
occurrence may themselves influence the survey
design necessary to collect appropriate data
(MacKenzie and Royle 2005). There is conse-
sequently an unmet need for general rules of mini-
mizing the effect of detection errors, given both
the UAV flight-plan options and the properties
of the target population. With the widespread and
growing adoption of UAV technology, develop-
such guidelines for UAV-based monitoring is
of pressing importance.

Here, we employ a grid-based simulation
model of UAV surveys of populations with con-
trasting densities and spatial dispersion, to inves-
tigate the errors in predicting population
abundance and occurrence that arise under alter-
native flight plans and their associated detection
errors. We further investigate the performance of
the flight plans by applying them to virtual UAV
surveys of three simulated species differing in
their population growth and spatial dynamics.
While our approach could be applied to other
image sources, such as satellites, ecologists using
UAVs for data acquisition have more direct
control over flight paths and coverage. The rapid
uptake and application of UAV surveys,
with increasingly availability of off-the-shelf
equipment (Chabot and Bird 2012), imply that
for practitioners with some drone capability but
limited access to sophisticated UAV operations
teams or technological expertise, general rules
are needed.

**MATERIALS AND METHODS**

**Spatial populations**

We chose a simulation approach as it allowed
extensive testing of a range of flight strategies,
detection error levels, and species attributes. We
provide a diagrammatic overview of our model
steps in Fig. 1. We generated synthetic popula-
tions of organisms occupying a 50 × 50 cell grid,
with dispersion spectra ranging from strictly reg-
ular, through purely random, to highly clumped
distributions. We seeded the grid with popula-
tions of N individuals, that is, population densi-
ties of $\rho = N/2500$ individuals per cell. For the
strictly regular distribution, we allocated individ-
uals to cells that were evenly spaced across an
$m \times m$ lattice within the 50 × 50 grid, where
$m = N^{1/2}$; if $N^{1/2}$ was non-integer (e.g.,
for $N = 250$, $N^{1/2} = 15.8$), we used the next greatest
even integer (e.g., $m = 16$) to seed the grid and
then removed excess individuals at random to
reduce the overall population back to N. Using
even values for $m$ allowed us to better align with

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**Fig. 1.** Model flowchart. Darker rows along the sampled transects indicate higher probabilities of detecting an individual.
our simulated flight plans, which repeated over blocks of eight rows. We generated the random distributions by choosing cell locations at random for each individual (selecting x-y coordinates independently from a uniform [1,50] distribution), and the highly clumped distributions by placing all individuals in a single cell, chosen at random. We then generated spatial patterns progressing from regular to random to clumped by replacing proportions of individuals from the regular or clumped distributions with individuals from the random distribution (e.g., Appendix S1: Fig. S1). We represent the progression of spatial pattern using a “contagion coefficient” $c = -1.0, -0.9, \ldots 1.0$, where $c = -1, 0$, and 1 correspond to complete regularity, randomness or clumping, respectively. We confirmed that this procedure generated an acceptable gradation in spatial structure for the resulting distributions using the Clark-Evans index, a common dispersion statistic that takes values of 0, 1, and 2.15 for perfectly clumped, random and regularly distributed populations, respectively (Krebs 1999; Appendix S1: Fig. S2).

**Flight plans and errors**

We assumed that UAVs would sample linear transects along (east–west) rows of the grid. This is a reasonable assumption, especially in agricultural settings with linear crop-rows, and is consistent with typical ecological monitoring using UAVs (Linchant et al. 2015). We generated four contrasting flight options, as factorial combinations of flying at high or low altitude, at fast or slow speed. We assumed that slower flights would sample less of the region (half the number of transects per survey) than fast flights. We further assumed that flying low would afford a narrower transect width, sampling one grid-row per transect, whereas high-altitude flights could also include the two adjacent grid-rows, surveying 3-row transects.

The four contrasting flight plans have implications for the nature and magnitude of detection errors. We assumed that flights that attempt to cover more ground will incur greater detection errors, due to less image overlap from flying faster (Hardin and Jackson 2005) or poorer image resolution from flying higher (Watts et al. 2010, Lisein et al. 2015). We assigned probabilities of independently detecting each individual of the population in a sampled grid cell, given the flight survey method (Table 1), scaled to a theoretical underlying detection error rate $q$, which we interpret here as including detection failures only (i.e., ignoring false positives). We focused on the broad categories of altitude, flight velocity, and underlying error. While each of these encapsulates many subsidiary components that may require additional exploration, it is the overall error that will influence detectability. Our aim here was to provide general guidance for ecologists seeking to understand trade-offs inherent in the use of UAVs for ecological surveys, rather than to prescribe specific technical settings for any one UAV-based monitoring operation.

### Simulation and analysis

We first simulated aerial surveys using the four flight-plan options for populations of 625 individuals ($p = 0.25$), spanning 21 levels of contagion ($-1 \leq c \leq 1$), with underlying detection errors of $q = 0.05$ and $q = 0.20$. This range of underlying error allows scenarios from high detection success rates to much lower detection success when errors are magnified by higher or faster flights seeking to cover more ground area.

**Table 1. Probability of independently detecting each individual in a grid-row, as a function of four flight options.**

| Row no. | Low, fast | Low, slow | High, fast | High, slow |
|---------|-----------|-----------|------------|------------|
| $t_1 - 2$ | $-$ | $-$ | $-$ | $-$ |
| $t_1 - 1$ | $-$ | $-$ | $1 - 3q$ | $1 - 4q$ |
| $t_1$ | $1 - q$ | $1 - 2q$ | $1 - 2q$ | $1 - 3q$ |
| $t_1 + 1$ | $-$ | $-$ | $1 - 3q$ | $1 - 4q$ |
| $t_1 + 2$ | $-$ | $-$ | $-$ | $-$ |
| $t_1 + 3$ | $-$ | $-$ | $-$ | $1 - 4q$ |
| $t_1 + 4$ | $-$ | $1 - 2q$ | $-$ | $1 - 3q$ |
| $t_1 + 5$ | $-$ | $-$ | $-$ | $1 - 4q$ |
| $t_1 + 6 = t_2 - 2$ | $-$ | $-$ | $-$ | $-$ |

etc.

Notes: Surveys are conducted in transects, sampling the $50 \times 50$ cell grid in repeating eight-row blocks starting with a randomly selected focal row $t_1$. Detection probabilities are given in terms of the underlying detection error, $q$. High surveys can sample grid-rows adjacent to the focal row, with increased error, and fast surveys can double the number of rows sampled, again at the cost of increased error. Non-sample rows for each flight plan are indicated by dashes.
We repeated the simulation experiment for 1000 iterations of each flight plan over 100 realizations of each level of contagion. We calculated the estimated abundance and occupancy within each sampled row and for the population as a whole (calculated pro-rata to the number of grid-rows sampled; for example, Vermeulen et al. 2013). We analyzed survey performance in terms of the abundance and occupancy estimation errors for each flight plan, density, and dispersion combination by calculating the % deviation:

\[
\% \text{ deviation} = \frac{100(\text{actual} - \text{estimated})}{\text{actual}}
\]

We conducted sensitivity analyses of flight performance to combined changes in spatial pattern (contagion, c) with (1) underlying detection error \(q\) and (2) population density \(\rho\). We varied the spatial pattern from 50% regular to 50% clustered in steps of 10% randomization (\(c = -0.5, -0.4, \ldots, 0.5\)), choosing to focus on the mid-range of contagion as most realistic ecological patterns will include appreciable levels of spatial randomness.

We considered the extreme case of detection of a single propagule (complete clustering of a single individual in the grid: \(N = 1, c = 1\)) separately. We examined the effect of changing contagion in combination with either the underlying detection error (varied over \(q = 0.02, 0.04, \ldots, 0.24\)) or the population density (varied over \(\rho = 0.01, 0.04, \ldots, 0.25\)), at both low and high settings for the fixed parameter (\(\rho = [0.01, 0.25]\), and \(q = [0.05, 0.20]\), respectively). As above, we analyzed the performance (% deviation) of estimates arising from each flight plan for these parameter combinations and identified the best-performing flight choices and consequent estimation errors. We conducted a further sensitivity analysis on our assumption of how detection probabilities change with speed and altitude. Our default model assumed that increasing the number of rows sampled by flying higher or faster would both decrease the probability of detection in unit steps of \(q\) (Table 1), and so we analyzed the effect of smaller \((0.5 \, q)\) or larger \((1.5 \, q)\) “penalties” for high or fast flights (Appendix S1: Table S1), on flight performance.

**Simulated species detection**

Following the findings from these idealized dispersions, we tested the performance of the four flights on dynamically changing virtual populations. We simulated three contrasting species: a mammal with negligible population growth and limited movement; a plant pathogen with moderate spread of infection to adjacent plants (e.g., a rust or wilt); and a weedy plant with faster spread and population growth. For each species (referred to as mammal, pathogen and weed), we seeded the grid with 25 individuals \((\rho = 0.01)\), to reflect either a typically sparse population or the nascent phase of an incursion. We assigned random grid positions to the initial populations, placing the mammals across the entire grid, and the two invasive species within the bottom three rows to reflect an invasion front. Rates of population growth and diffusive and directional movement are given in Table 2. Actual destination cells for moving individuals were selected by randomizing the coordinates of target cells using triangular distributions. Directional invasive spread was assumed to occur northwards. We used a three-cell external boundary wherein individuals did not undergo further directional spread or population growth, but

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**Table 2. Rates of population change and movement for three contrasting simulated species:** Movement denotes spatial change of visible individuals and can be interpreted by species as representing mammal (localized but mobile fauna), weed (emergence of new plants along an environmental gradient or invasion front), and pathogen (infection of nearby plants and spore dispersal along environmental gradient).

| Species trait                             | Description                                      | Mammal | Weed | Pathogen |
|-------------------------------------------|--------------------------------------------------|--------|------|----------|
| Population growth rate, \(r\)             | Propagules per individual per time-step           | 0      | 0.2  | 0.05     |
| Directional spread of existing individuals, \(\beta_E\) | Northward dispersal (no. cells per time-step)     | 0      | 0    | 2        |
| Directional spread of propagules, \(\beta_P\) | Northward dispersal (no. cells per time-step)     | 0      | 4    | 2        |
| Random movement from existing location, \(\delta_E\) | Max no. cells per time-step, in all directions    | 10     | 0    | ±2       |
| Random component to propagule dispersal, \(\delta_P\) | Max no. cells per time-step, in all directions (not appl.) | ±2     | ±2   | ±2       |

*Note:* Random cell movement components of \(±\delta\) indicate destination cells chosen by random draws from a triangular distribution over \([-\delta, +\delta]\), in both N-S and E-W directions, that is, \(\delta = ±2\) implies 25 possible destination cells.
was semi-absorbing insofar as individuals could return to the 50 × 50 cell interior by random diffusion. We simulated the spatial dynamics (Appendix S1: Fig. S7) and UAV monitoring of the three species over 25 time-steps, recording the flight plans’ performances over 1000 iterations. We used Matlab software version 2016a (MathWorks 2016), and the code is provided as supporting information (Data S1).

**RESULTS**

Magnitude of estimation errors

For an underlying detection error of $q = 0.05$, the largest errors in estimating abundance or occupancy within grid-rows were typically up to 20% deviation (Fig. 2; Appendix S1: Fig. S6a, c), growing to as high as 80% when $q = 0.20$ (Fig. 2; Appendix S1: Fig. S6b, d).

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![Fig. 2](https://example.com/fig2.png)

**Fig. 2.** Deviations in estimating abundance in grid-rows (a, b), and regional abundance (c, d) and occupancy (e, f), for populations of 625 individuals populating a 50 × 50 grid at levels of contagion $-1 \leq c \leq 1$, for four contrasting flight plans subject to low (a, c, e) and high (b, d, f) levels of underlying detection error ($q$). Mean ± SE of 1000 runs.
These errors translated into larger deviations for their equivalent regional (whole-grid) abundance estimates, even exceeding 100% deviation depending on flight plan, but with best-performing flights typically achieving deviations of <50% (Figs. 3c, 4a, c). Occupancy estimates (Appendix S1: Figs. S3c–f, S4c–f) were marginally more precise than abundance estimates. All deviations (i.e., arising from estimating either abundance or occupancy of either grid-rows or populations) tended to be slightly larger for higher population densities (Figs. 3, 4; Appendix S1: Figs. S3–S6).

**Grid-row estimates**

In individual rows, lower and slower flights always yielded the most precise estimates (lower % deviation) of abundance and occupancy (Fig. 2a, b; Appendix S1: Figs. S4, S6), regardless of dispersion, underlying error, or overall population density. The percentage deviation in grid-row estimates was consistent in terms of flight rankings: Both of the lower flights resulted in smaller percentage deviations than both higher flights and, for a given altitude, slower flights gave more precise estimates than faster flights. Our sensitivity analyses of the combined effect of underlying detection error $q$, contagion coefficient $c$, and population density $\rho$ confirmed the superiority of low and slow flights for estimating abundance and occupancy in individual grid-row, and that changes in the detection error $q$ caused the main effect on deviation in estimates (Appendix S1: Fig. S4). Sparse populations also produced lower grid-row errors (Appendix S1: Fig. S6).

![Fig. 3](image-url)

**Fig. 3.** Minimum levels of deviation (a, c) in regional abundance estimates of low and high density ($\rho = 0.01, 0.25$) populations, and the best flights (b, d) that produced them. Minimum deviations are from the mean deviations of 1000 simulated flights over each of 100 simulated populations at each level of contagion $c = -0.5, -0.4, \ldots -0.5$, and underlying detection error $q = 0.02, 0.04, \ldots 0.24$. 
Population estimates and sensitivity
Estimating regional population abundance or occupancy produced more nuanced results than estimating abundance or occupancy for individual rows, and any given altitude-speed combination could be the best choice depending on the level of population clustering (contagion, \( c \)) and the underlying detection error \( q \). For example, as the underlying detection error increases, the best abundance (and occupancy) estimates for spatially random populations \( (c = 0) \) are progressively given by high-fast, high-slow, low-fast, and low-slow flights (Fig. 3b, d). In general, population abundance was best predicted by higher altitude flights if the underlying detection error was small \( (q < 0.1) \) or if the population was spatially clustered \( (c > 0; \) Figs. 3b, d, 4b). Slower high-altitude flights gave lower percent deviation as error sizes increased \( (q = 0.20) \), especially if the population was spatially clustered. For large detection errors coupled with regularly or randomly distributed populations, lower flights were the more reliable (Figs. 3d, 4d), with low-slow flights preferable at larger densities.

The ranking of flight plans was similar for estimating overall occupancy as for abundance (Appendix S1: Figs. S3, S5). The effect of spatial distribution, however, played a lesser role in rankings. Lower flights were generally preferable for estimating occupancy, apart from estimating low-density occupancy at low levels of underlying error.

Sensitivity of deviations in abundance estimates to combined parameter changes for population density \( (\rho) \) and contagion \( (c) \) showed that either density or contagion could play significant roles in flight performance. Deviation of abundance estimates increased markedly at low...
densities, and as populations become more clustered, and this effect was consistent for underlying detection errors of $q = 0.05$ and $q = 0.20$ (Fig. 4). High and fast flights produced the best abundance estimates of clustered populations, if the underlying detection error was low; for higher errors, high-slow or low-fast flights were preferable. Slower flights produced the lowest deviations for under-dispersed populations (Fig. 4b, d), although high-fast flights could still be the best option for very sparse populations and low detection errors ($p = 0.01, q = 0.05$). The effect of contagion was less important than density for estimating overall abundance were affected (Fig. 3b, d). In contrast, the best row estimates, irrespective of underlying $q$-values, resulted in low and fast flights being out-performed by high and slow flights. Lower grid-rows. Lower and slow flights prefered under given circumstances. For example, decreasing the probability of detection in faster flights, while increasing it for higher flights, resulted in low and fast flights being recommended less often than under default assumptions (Fig. 5d, h; compare Fig. 3b, d), due to being out-performed by high and slow flights.

**Simulated species detection**

The ranking of flights was constant for estimates of the simulated species abundance in grid-rows. Lower flights gave more precise grid-row estimates than high flights, and within a given altitude, slower flights were preferable, and thus, low and slow flights always yielded the best row estimates, irrespective of underlying detection error, $q$ (Appendix S1: Figs. S8a–f, S9a–f). In contrast, flight performances and rankings for estimating overall abundance were affected by the error size, $q$, and by dynamic changes in species dispersion. Fast flights were preferable for the randomly moving mammal population (Fig. 6a, b), with higher errors requiring lower altitude flight (Fig. 6b). For invasive species, low and slow flights performed the worst for the initial, spatially clumped populations, but improved once the populations began to spread (Fig. 6c–f), and low flights of both velocities were generally preferable. With high precision detection ($q = 0.05$, Fig. 6a, c, e), however, relative flight rankings could change or even reverse, with high and fast flights giving the best estimates of regional abundance when populations were more clustered or at low density. Flight performances for estimating regional occupancy (Appendix S1: Figs. S8g–i, S9g–i) were very similar to those for estimating abundance. For the special case of early detection of an incursion, the ground coverage provided by high and fast flights was best at detecting a single individual in the grid ($N = 1, c = 1$), over most levels of underlying detection error (Fig. 7).

**Discussion**

The ecological research community has a long history of striving to get the best possible population estimates (Petersen 1896, Lincoln 1930) and incorporating species detectability in those estimates can be essential (MacKenzie et al. 2002, Guillera-Arroita et al. 2014). We have incorporated detectability and other factors within a detailed simulation analysis to explore the impact of flight choices on the accuracy of ecological surveys using UAVs. By examining the interactions between detection error and the aggregation and density of ecological populations, we have found that a one-size-fits-all approach is unlikely to be optimal, and may often be misleading. We encapsulate our results in a decision-tree format (Fig. 8), which can serve as an indication of how technological capability and ecological context should guide the choice of UAV flight. The multiple branching of the decision tree emphasizes that flight strategies should change to reflect the spatiotemporal dynamics of target populations and the detectability of the target species with the equipment available. Our findings have significant repercussions for detecting rare or sparsely distributed species, measuring range expansion under climate change, delimiting areas of incursion of invasive
Fig. 5. Analysis of model sensitivity to structure of detection errors, showing flight choices that minimize the deviation in estimating regional abundances of low (a–d; $\rho = 0.01$) and high density (e–h; $\rho = 0.25$) populations (compare Fig. 2b, d). Error structure was altered from Table 2 by increasing or decreasing the penalties applied for speed or altitude by 0.5 $q$. Mean deviations were calculated from 1000 simulated flights over each of 100 simulated populations at each level of contagion $c = -0.5, -0.4, \ldots 0.5$, and underlying detection error $q = 0.02, 0.04, \ldots 0.24$. 
alien species, and planning long-term monitoring programs for species reintroductions and for population estimation in general.

One advantage of UAV surveys is the greater spatial resolution afforded by their lower and slower flight paths compared to manned aircraft (Watts et al. 2010, Anderson and Gaston 2013). Here, we found that UAV flights that were themselves lowest and slowest were consistently the most accurate in estimating abundance and occupancy for individual grid-rows. Relative flight performances changed however when row estimates were translated into overall population estimates, due to the differences in sample size resulting from each flight plan. Flights at higher altitude, and thus with a

Fig. 6. Deviations in estimating regional abundance of three simulated species under low (a, c, e) and high (b, d, f) levels of underlying detection error ($\eta = 0.05, 0.20$). Mean ± SE of 1000 runs.
wider field of view or track width (Dandois et al. 2015, Hodgson et al. 2017), can sample more area and could therefore lead to improved population-level estimates if the underlying detection errors were low. Faster high flights (covering the most ground area) tended to perform well at low-density and aggregated populations; however, the increased detection error imparted by the speed-altitude combination meant that their performance could be easily compromised by high levels of underlying error (e.g., q = 0.2). As errors levels increase, the trade-offs between area sampled and detection precision decrease the relative performance of both high-altitude flights: Low and slow flights are more preferable for estimating abundance of random or regularly distributed populations. For highly aggregated populations, high-but-slow flights can provide the best compromise between area covered and sampling precision when detection errors are large (Fig. 8).

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**Fig. 7.** Proportion of 10,000 simulations in which a single incursion (one individual placed randomly in a 50 × 50 cell grid) was detected by each of four flight plans, assuming underlying detection errors of $q = 0.01, 0.02, \ldots, 0.024$.

**Fig. 8.** Decision tree indicating the progression of key questions in determining preferred UAV survey flight strategies. Abbreviations are as follows: q, underlying detection error; $\rho$, regional population density; c, degree of population aggregation (contagion); and Y/N, for yes/no answers.
Differences in flight choice between abundance and occupancy estimation may become important depending on which approach is required by the management or research objective. Here, however, we found that flight plans tended to perform similarly in predicting occupancy or abundance for non-clustered and low-density populations, with the estimate deviations somewhat lower in magnitude. This is not surprising as any positive estimated density in an occupied cell will lead to occupancy being correctly predicted. Population aggregation ($c > 0$) did produce differences between abundance and occupancy prediction at moderate densities. Although the rankings of flight plans in almost all cases were similar to those for occupancy estimation, there was a greater tendency for higher flights to best predict abundance in more clustered populations (Fig. 4b, d). Indeed, for the extreme case of incursion of a single propagule ($N = 1, c = 1$), the best flight option is high and fast over most simulated error levels, although for very high values of $q$ (reflecting, e.g., more cryptic species or lower grade equipment), slower high-altitude flights may be preferable (Fig. 7). This has particularly important implications for using UAVs to detect sparsely distributed or isolated occurrences of a target organism, such as newly arrived and emergent propagules of invasive species (Moody and Mack 1988, Levick et al. 2015).

The importance of flight choice is emphasized in our simulated species surveys, where relative flight performance can change as populations spread or grow, depending on the survey objective (precise grid-row vs. regional abundance estimates) and the magnitude of the underlying detection error (Fig. 6; Appendix S1: Figs. S8, S9). As the invasive (pathogen and weed) populations spread, low and slow flights become preferable overall unless the underlying detection error is acceptably low for higher flights. It is important to note, however, that empirical calibration would be necessary to evaluate whether underlying detection errors as low as $q = 0.05$ are realistic in field conditions (see Model assumptions and caveats).

Model assumptions and caveats

Our model has necessarily made implicit and simplifying assumptions about the ecological setting, detection error structure, and costs. For example, in order to gain broad insights, we have left the resolution of our grid deliberately vague. The legal requirement to keep UAVs within view suggests a maximum grid extent of $2 \times 2$ km if the human operator is located in the center (Hardin and Jackson 2005), or grid cells of side 40 m, which is a realistic scale for ground-truthing field surveys. Our perception of spatial pattern and interpretation of occupancy patterns may depend on the spatial resolution of sampling units (Efford and Dawson 2012). To this end, nested hierarchical surveys (possibly iterative) could fine-tune the sampling process (Boileau and Legendre 1998) and potentially play a key role in optimized monitoring for new invasions (Vicente et al. 2016).

We based our error structure on an underlying detection error $q$, which had the strongest effect on the best flight choice. Field detectability from aerial sources can vary substantially, however, and our error levels are not unreasonable (Abd-Erahman et al. 2005, Conroy et al. 2008, Franke et al. 2012, Hodgson et al. 2017). Aerial detection errors are also likely to depend on environmental context and habitat (Linchant et al. 2015), even varying between 0% and 100% for multispectral ungulate surveys using microlite aircraft (Franke et al. 2012). In our study, there are reasonably clear contexts for preferring high-fast flights (smaller underlying errors with a low-density or aggregated population) or low-slow flights (under-dispersed population, larger errors). High-slow and low-fast flights, however, involve trading off some sampling precision for increased sampling area (vs. low and slow flights), and although they produced deviations of similar magnitudes (broadly, within $\pm10\%$ deviation, Appendix S1: Figs. S3b, S5b), the exact error structure may change their relative performance in a given situation.

Linking detection errors to flight altitude also entailed some assumptions. We implicitly assumed a fixed flying height would generate predictable errors, whereas terrain complexity as well as interfering objects or phenomena between the capture device and target species would affect detectability. In reality, the error may have a complex relationship with height: Low altitude surveys can sometimes give larger errors (Garcia-Quitiano et al. 2008), especially in
complex environments, and non-terrestrial species themselves can alter their altitude (particularly marine organisms; Jones et al. 2006, Hodgson et al. 2017). We have restricted the flight choice indicatively to between two heights and two speeds, but more detailed research into the relationships between errors, height, and speed of UAVs could allow more precise planning and optimization of the flight plan. Our simulated aerial sampling procedure also ignores the possibility of false positives, instead operating on the probability that each individual actually present is detected (and the assumption that each detected individual actually is present). In practice, false positives and false negatives are unlikely to offset each other in terms of management implications (Abd-Elrahman et al. 2005), and so an important focus of future research would be to structure our overall error structure and magnitude of detection errors may affect our recommendations, they also highlight essential areas for further research. There is a particular need to investigate the nature of detection errors for specific UAV platforms. To ecologists, the structure and magnitude of detection errors are likely not as intuitive as expected population dispersion or density, and our sensitivity results suggest that detection error has the strongest influence on estimate deviation. Sensitivity analysis of changes in the additional errors caused by flying higher or faster (Fig. 5) indicated reasonable concomitant changes to flight recommendations (e.g., decreases in both errors favoring high-fast flights). Nonetheless, the exact error level at which flight altitude or speed should be changed is unlikely to be known with great precision. Ideally, the flight plans chosen for surveys would be based on knowledge of detection errors that were calibrated in advance by field trials—indeed, pilot studies. While such calibration may allow development of reasonable flight plans, further decomposition of the underlying detection error $q$ with regard to its multifaceted component error sources and magnitudes, while not trivial, could assist in decisions to upgrade equipment by revealing which elements may contribute most to error reduction (e.g., improved lens), or indeed if improvement is impossible (e.g., if mainly limited by physical laws such as light attenuation).

We have implicitly assumed that the trade-offs in ground coverage correspond to equal airtime, and therefore equal costs, for all flight plans. The legal requirement for UAV operators to keep their airborne machines within close, often visual, range (Hardin and Jackson 2005, Watts et al. 2010) implies that travel and accommodation for an operations team may comprise the main cost of each survey. Therefore, our recommendations may change in cases where the main cost component is set-up, for example, transportation of equipment and personnel to the monitoring site, rendering per-hour UAV operations of relatively little impact and thus reducing the marginal cost of slower flights. Other factors in automated surveys not considered by our study raise further cost implications. For example, if repeat ongoing surveys are necessary, there may be recurring set-up costs. Increased image capture and analytic capability could reduce detection errors, but will inevitably require additional financial investment. If errors are overly high, it may be necessary to embrace the cost of including multiple signals or image sources (Conn et al. 2014) or switching to alternative data sources altogether (ground-truthing, piloted flight or satellite) to complement or replace UAV imagery. The expense of enhanced monitoring must be balanced against the resultant improvement in management (McDonald-Madden et al. 2010), even for species of considerable economic consequence such as some mammals (e.g., koalas; Field et al. 2004), plant pathogens (Carnegie and Cooper 2011), and weeds (Sinden et al. 2004).

These caveats lead to further trade-offs in determining the ideal flight plan for efficient UAV surveys. Given the overriding importance of detection error, the extra cost of using hierarchical (Bellehumeur and Legendre 1998) or repeated (MacKenzie et al. 2002) surveys may be necessary to reduce errors by providing complementary data. While our decision tree (Fig. 8) provides broad initial guidelines on the relative merits of contrasting flight plans, we suggest that
case-specific simulation may be warranted (Elphick 2008, Christie et al. 2015) to ascertain when and how often to sample, as well as how high and fast to fly, for a given set of management objectives and resources (Watts et al. 2010, Sarda-Palomera et al. 2012). The use of highly specialized equipment such as UAVs is rapidly becoming a field requiring specialized knowledge. Ecologists utilizing UAVs may need to conduct iterative field trials to understand and optimize the range of technical settings that contribute to the detection of specific target organisms. These setting include factors such as forward and side overlaps, sensor and spectral resolution, and shutter speed for optimal detection. While each of these may be worthy of improvement and exploration in more technical research settings, we rather provide here a broad conceptual envelope in which these elements might be improved.

Our approach could be used to iteratively refine regular surveys, by adaptively re-planning the flight mode based on the latest estimates of population aggregation and density. In effect, this would track the flight plans producing the lowest errors at each step in Fig. 6, entailing switches between flight plans that would be otherwise unexpected based on grid-row estimate precision alone (Appendix S1: Figs. S8, S9). Thus, our finding that individual row sampling precision does not necessarily extrapolate to reliable population estimates has significant implications for the efficiency and accuracy of automated aerial surveys.

CONCLUSIONS

The era of UAV detection remains in its infancy, with considerable advances and new applications likely (Koh and Wich 2012). As UAVs become increasingly adopted by the ecological community (Anderson and Gaston 2013), the excitement generated must be tempered by considered thought on how best to deploy these revolutionary tools. To our knowledge, no study has yet examined how UAV flight choices might interact with spatiotemporal features of ecological populations to generate error in population estimates. We have shown that, while population density and aggregation should inform flight decisions, the magnitude of underlying detection errors is fundamentally important to the appropriate choice of flight plan. Such exploratory modeling approaches could be further applied to other automated surveillance devices (Jurdak et al. 2015), and to freshwater or marine surveys. Indeed, our findings could have implications across all transect-based sampling methods that offer trade-offs between sampling coverage and detection error per unit area. We contend that automatic ad hoc implementation of UAV technology, without due attention to quantifying and minimizing the detection errors arising from their use, risks squandering valuable opportunities for improved collection, analysis, and understanding of ecological data.

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