Estimating site occupancy and detectability of the threatened partridge pigeon (Geophaps smithii) using camera traps

Davies, Hugh F.; Rioli, Willie; Puruntatameri, José; Roberts, Willie; Kerinaiua, Colin; Kerinaiua, Vivian; Womatakimi, Kim Brooks; Gillespie, Graeme R.; Murphy, Brett P.

Published in:
Austral Ecology

DOI:
10.1111/aec.12755

Published: 01/08/2019

Document Version
Peer reviewed version

Estimating site-occupancy and detectability of the threatened partridge pigeon (*Geophaps smithii*) using camera traps

Hugh F. Davies[1*], Willie Rioli[2], José Puruntatameri[2], Willie Roberts[2], Colin Kerinaiua[2], Vivian Kerinauia[2], Kim Brooks Womatakimi[2], Graeme R. Gillespie[3,4], and Brett P. Murphy[1]

[1] NESP Threatened Species Recovery Hub, Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, Northern Territory, 0909, Australia.

[2] Tiwi Land Council, Winnellie, Northern Territory, 0821, Australia.

[3] Flora and Fauna Division, Department of Environment and Natural Resources, Northern Territory Government, Berrimah, Northern Territory, 0828, Australia.

[4] School of BioSciences, The University of Melbourne, Victoria, 3010, Australia.

* Corresponding author contact: E: hugh.davies@cdu.edu.au M: 0417 828 202

Abstract:

Since European settlement, many granivorous birds of northern Australia's savanna landscapes have declined. One such example, the partridge pigeon (*Geophaps smithii*), has suffered a significant range contraction, disappearing from at least half of its pre-European range. Multiple factors have been implicated in this decline, including the loss of traditional Aboriginal burning practices, grazing by large exotic herbivores, and predation by feral cats (*Felis catus*). While populations of partridge pigeon on the Tiwi Islands may be particularly important for the long-term persistence of this species, they too may be at risk of decline. However, as a reliable method to detect this species has not yet been developed and tested, we lack the ability to identify, at an early stage, the species' decline in a given location or region.

This severely limits our capacity to make informed management decisions. Here, we demonstrate that the standard camera trapping approach for native mammal monitoring in northern Australia attained an overall probability of detecting partridge pigeon greater than 0.98. We thus provide a robust estimate of partridge pigeon site-occupancy (0.30) on Melville Island, the larger of the two main Tiwi Islands. The information presented here for the partridge pigeon represents a critical first step towards the development of optimal monitoring programmes with which to gauge population trajectories, as well as the response to remedial management actions. In the face of ongoing biodiversity loss, such baseline information is vital for management agencies to make informed decisions and should therefore be sought for as many species as possible.

Keywords:

Decline, feral cats, fire, monitoring, partridge pigeon

Introduction:

The current global rate of species extinction and population decline is jeopardising the functionality of the ecosystems on which all life on Earth depends (Barnosky et al., 2011, Dirzo et al., 2014). Since European settlement in 1788, the biota of the Australian continent has proven exceptionally susceptible to decline and extinction. While Australia's native mammals have been hardest hit, Australia's birds have also suffered greatly (Recher and Lim, 1990, Garnett et al., 2011). Of the 1266 bird species known to be present when Europeans arrived, 2.2% are now extinct, and 12% are currently considered threatened (Garnett et al., 2011). A recent estimate suggests that around 10 species or subspecies are likely to become extinct in the next 20 years without intervention (Geyle et al., 2018b).

Despite being superficially intact, with little large-scale land clearing, the tropical savanna landscapes of northern Australia have suffered substantial faunal declines (Franklin, 1999, Woinarski et al., 2015). While the most notable of these declines has been the widespread collapse of small- to medium-sized mammal communities (Ziembicki et al., 2014, Woinarski et al., 2015), granivorous birds have also declined (Franklin, 1999). Of the 49 native granivorous birds that occur across the tropical savannas of northern Australia, 12 (24%) have declined, and one species, the paradise parrot (*Psephotus pulcherrimus)*, is now extinct (Franklin, 1999). The partridge pigeon (*Geophaps smithii*) is one such species that has suffered significant range contraction across northern Australian savannas, disappearing from at least half of its pre-European distribution (Franklin, 1999, Fraser et al., 2003). Multiple factors, most related to the availability of critical seed resources, have been implicated in the decline of this species, including the loss of traditional Aboriginal burning practices (particularly the loss of fine-scale, patchy fire mosaics), grazing by large exotic herbivores and predation by feral cats (*Felis catus*) (Fraser et al., 2003, Woinarski, 2004, Woinarski et al., 2017). Garnett et al. (2011) outlined two key knowledge gaps that needed to be addressed for the effective conservation of this species: 1) population trends at the species' population strongholds; and 2) the relative impacts of grazing and cat predation on populations.

Due to their unusually high abundance, populations of the partridge pigeon on the Tiwi Islands (situated 25 km off the northern Australian coast), have been suggested to be particularly important for the long-term persistence of this species (Woinarski, 2004). However, as several of the potential drivers of this species' decline operate on the Tiwi Islands (including frequent fire, large exotic herbivores and feral cats), these populations may also be at risk. As the historic concurrent decline of native rodents and granivorous birds on mainland northern Australia was thought to reflect the depletion of a common food resource (Woinarski et al., 2001), the recent decline of Tiwi Island native mammal species may also suggest that this species may be at risk

(Davies et al., 2018). However, despite the very real threat of population decline, an effective monitoring approach for this species has not been identified, and as a result, a robust estimate of partridge pigeon distribution on the Tiwi Islands, with which to evaluate future declines, has not yet been derived.

Past surveys of the partridge pigeon have relied on point-count surveys. While providing important information on species occurrence, such methods have been criticised as having inherently biased detection probabilities (Pendleton, 1995). For example, the necessity of observers to be present in an area during bird point-counts may change the behaviour of birds (Fuller and Langslow, 1984), biasing the detectability of certain species. Such bias can have significant ramifications when quantifying population trajectories and potential threatening processes, resulting in sub-optimal decision making. The increased utilisation of camera traps for threatened species monitoring reflects the advantages they offer over other monitoring approaches (O'Connell et al., 2011). Camera trap studies have primarily focussed on mammal species, however, they are increasingly being used as an effective approach for the monitoring of birds (O'Brien and Kinnaird, 2008). While a standardised methodology for vertebrate monitoring using camera traps in northern Australia already exists, it was developed to optimise the detection of a range of cryptic and elusive mammal species (Gillespie et al., 2015). However, this method could be used to monitor bird species.

Here, we use ancillary data obtained during a study of Tiwi Island native mammals to quantify the efficacy of the standardised camera trap methodology for vertebrate biodiversity surveys in northern Australia to reliably detect the partridge pigeon (Gillespie et al., 2015). The criteria against which this was judged was a minimum overall detection probability of 0.85 suggested by Guillera-Arroita et al. (2014). We also aimed to provide a baseline estimate of partridge pigeon distribution on Melville Island with which to gauge future population change. To further elucidate the drivers of partridge pigeon decline in northern Australian savannas, we also investigate the biophysical correlates of partridge pigeon site-occupancy and detectability on Melville Island.

Method:

Study site:

Melville Island (5788km^2) is the larger of the two main Tiwi Islands and Australia's second-largest island, located ~20km off the coast of Australia's Northern Territory (Figure 1). The islands are relatively flat (≤103 m above sea level), and lack the large rocky escarpments that characterise areas of mainland northern Australia. The Tiwi Islands experience a tropical monsoonal climate with distinct wet (November–April) and dry seasons (May–October). There is a substantial rainfall gradient on Melville Island, from 1400 mm in the east, to 2000 mm in the northwest. The major vegetation types are savanna woodlands and open forests dominated by eucalypts (namely *Eucalyptus miniata*, *E. tetrodonta* and *Corymbia nesophila*), with a predominantly grassy understorey. Shrub density is highly variable, and studies on the mainland have shown that it is negatively affected by frequent, high-intensity fires (Russell-Smith et al., 2003, Woinarski et al., 2004). Fire mapping of the Tiwi Islands, has shown that an average of 54% of the savannas were burnt each year from 2000 to 2013, with 65% of this area burning in the late dry season (Richards et al., 2015).

While there is currently no evidence to suggest any recent change in fire intensity or frequency, feral animal densities or exotic plants on the Tiwi Islands, Davies et al. (2018) reported significant declines in the native mammal fauna of Melville Island, albeit less severe than has occurred on the adjacent mainland in recent decades (Woinarski et al. 2010).

The bird fauna of the Tiwi Islands has previously been surveyed as part of broad-scale monitoring programmes conducted from 1990–1992 (98 sites) and 2000–2002 (351 sites). These surveys involved point-counts of birds at each site. Across the 449 sites monitored during these surveys, the partridge pigeon was recorded at only 22 sites, a 'naïve' occupancy rate of 4.9%, or 7.9% of eucalypt-dominated woodland or open forest sites (thought to be the preferred habitat of the partridge pigeon). Unfortunately, these data could not be used to quantify the site-level detection probability of each bird species using this method, thereby precluding a robust estimate of site-occupancy.

Study species:

The partridge pigeon (*Geophaps smithii*) is a small-medium sized (~200 g) ground-dwelling, granivorous pigeon (Woinarski, 2004). It is a mostly grey-brown bird with a distinctive bright red or yellow patch of bare skin around the eye. The eastern subspecies (*G. s. smithii*), present on the Tiwi Islands, has a red eye patch and the western subspecies (*G. s. blaauwi*) has a yellow eye patch. The partridge pigeon is largely sedentary, but capable of moving greater distance (5–10 km) (Fraser, 2001). The species is listed as Vulnerable under Australia's Environment Protection and Biodiversity Conservation Act 1999, and on the IUCN Red List (BirdLife International, 2012).

Data collection:

During the dry season of 2015, 88 sites were surveyed across Melville Island. All sites were located in eucalypt-dominated savanna woodland and open forest. The original focus of this survey was to investigate the correlates of native mammal distribution. As such, sites were chosen to capture the large variation in both annual rainfall and fire history on Melville Island. Each site was separated by at least 1 km and surveyed using motion-triggered camera traps following the approach outlined in Gillespie et al. (2015). Specially, camera-trapping involved five horizontally facing motion-sensor cameras left continuously recording (24-h per day) for a minimum of 35 consecutive days. All five cameras were deployed at a height of 70 cm in a diamond formation, with each camera separated by 50 m (encompassing an area of 0.5 Ha). Camera traps were baited with a mixture of peanut butter, oats and honey. To maximise the likelihood of being triggered by animals lured to the bait, each camera was carefully positioned to ensure that the bait was in the centre of the field of view (Gillespie et al., 2015). Vegetation within each camera's field of view was cleared to reduce the chance of false triggers and to reduce the risk posed by fire. Of the five cameras deployed at each site, two were Reconyx HC550 Hyperfire white flash cameras (Reconyx Inc., Holmen, USA), while the remaining three were Reconyx PC800 Hyperfire Professional infra-red flash cameras. All cameras were set to take three image bursts per trigger, with a 1-s delay between images. The sensitivity of each camera was set to high, with cameras re-arming instantly after being triggered.

Data analysis:

We used single-season occupancy models to investigate the correlation between each predictor variable (Table 1) and the distribution of the partridge pigeon. Site-specific detection histories were created by dividing each camera survey into separate one-day sampling occasions. At each site, partridge pigeon detections were pooled across the five cameras (i.e. 1 = one or more partridge pigeons detected on any of the five cameras at the site on that day, 0 = no partridge pigeons detected on any camera on that day). Given the large number of variables and the large number of potential models, occupancy modelling was conducted in a two-step process. First, we ran all combinations of the 10 variables hypothesised to influence the detectability of the partridge pigeon with the eight predictors of site-occupancy fixed as a saturated model (1024 models). Model selection based on Akaike's Information Criterion (AIC) was then used to identify the most parsimonious model in the candidate set. Second, we ran all combinations of the eight variables postulated as potential drivers of partridge pigeon site-occupancy (256 models). This was done with detectability constrained to the most important variables identified in step one. Model selection based on AIC was then used for a second time to identify the most parsimonious model in the candidate set. As occupancy models specifically account from imperfect detection, we used the best fit model to quantify the probability of detecting the partridge pigeon at each site. This was calculated as:

$$1 - ((1 - p)^n)$$

Where p is the estimate of detecting the partridge pigeon in each sampling occasion (each day) and n is the average number of sampling occasions conducted at each site (i.e. 43 days).

We assessed the fit of the most saturated model with three goodness-of-fit tests based on parametric bootstrapping: Pearson's chi-square statistic, the sum of squared errors and the Freeman-Tukey chi-square statistic. These methods repeatedly simulate datasets based on the fitted model, and then evaluate the probability that the observed history of simulations has a reasonable chance of occurring (MacKenzie and Bailey, 2004). All analyses were conducted using the unmarked package (Fiske and Chandler, 2011) in the statistical program R (R Development Core Team, 2013).

Results:

The partridge pigeon was detected at 24 of the 88 sites, a naïve occupancy rate of 27%. The most parsimonious model suggested that the probability of detecting the partridge pigeon at each 5-camera survey site during one sampling occasion (i.e. on a single day) was 0.15. Given the length of time that each site was surveyed (≥35 days), the overall probability of detecting the partridge pigeon at each site was > 0.98 (Table 2). Using this survey method, the minimum optimal level of overall detection probability for accurate estimation of occupancy (i.e. 0.85: Guillera-Arroita et al., 2014) would be reached after 12 days (Figure 2). Due to the very high overall probability of detecting the partridge pigeon, if present, the estimated rate of occupancy by the best model (0.30) was similar to both the naïve (0.27) and null model estimates (0.28) (Table 2).

Modelling revealed no significant association between any of our predictor variables and site-occupancy by the partridge pigeon on Melville Island (Figure 3). The detectability of the partridge pigeon was significantly negatively associated with fire extent, the time of year the site was surveyed. and annual rainfall (Figure 3). The detectability of the partridge pigeon was significantly positively associated with the patchiness of fires (i.e. more detectable in areas with patchy fires), the probability of feral cat detection and dingo activity (Figure 3).

Discussion:

Since European settlement, the partridge pigeon (*Geophaps smithii*) has suffered significant range contraction across northern Australia (Fraser et al., 2003, Woinarski, 2004). While the Tiwi Islands remain a stronghold for this species, the presence of multiple hypothesised drivers of this species' decline (i.e. frequent fire, large exotic herbivores and feral cats), suggests that these populations may be at risk of decline. To help establish a benchmark against which to measure future decline of the partridge pigeon, we have demonstrated that this species can be reliably detected using an array of camera traps, and provided an estimate of site-occupancy across a key stronghold for this species (Melville Island). To achieve accurate estimation of site-occupancy, a recommended minimum level of overall detection probability is 0.85 (Guillera-Arroita et al., 2014). We demonstrated that our approach would achieve this after just 12 days, thus highlighting the potential utility of camera traps for the ongoing monitoring of the partridge pigeon.

Modelling the environmental correlates of partridge pigeon site-occupancy and detectability provided valuable insight. The lack of any significant association between site-occupancy and the hypothesised drivers of partridge pigeon decline (i.e. frequent, homogeneous fires, feral cats or large herbivores) may indicate that these factors have not yet driven a significant range contraction of partridge pigeon on Melville Island. However, given no temporal replication in our study, our inability to identify any significant environmental correlates of partridge pigeon site-occupancy on Melville Island should not be taken as evidence that these populations are safe from decline, or that they are not currently declining. For example, partridge pigeon may have previously been more widespread on Melville and subsequently contracted to the distribution observed in this study. Furthermore, the data used here were collected as part of a survey that was not specifically designed to elucidate the environmental correlates of partridge pigeon occupancy. Consequently, a more adequately designed survey may have been required to properly evaluate the hypothesised threats to partridge pigeon populations on Melville Island.

Our analysis demonstrated significant predictors of partridge pigeon detectability. These results can provide insight on the potential threats to these populations, and can also be utilised to optimise future monitoring of populations of the partridge pigeon. The partridge pigeon was significantly less detectable in areas that experience large, frequent fires, as well as sites with minimal fire patchiness. While potentially influenced by other factors, the detectability of a species generally increases with abundance (McCarthy et al., 2013). Given this assumption, our results suggest that this species may be negatively affected by large, frequent fires, and require a fine-scale, patchy mosaic of burnt and unburnt areas. As such, our results support the work of Fraser et al. (2003), who suggested that the partridge pigeon requires open, recently burnt areas in which to forage, as well as unburnt areas for nesting and shelter.

Despite the hypothesised susceptibility of partridge pigeon to predation (Woinarski, 2004), the detectability of the partridge pigeon was positively associated with feral cats and dingoes. If the detectability of partridge pigeon reflects its abundance, this may indicate that on Melville Island, predation by feral cats and dingoes has not had a significant negative impact on populations of the partridge pigeon. There are a few plausible explanations why this may be the case. First, Melville Island supports relatively intact populations of native mammals compared to other areas of northern Australia. As native mammals are selectively preyed upon by feral cats (Kutt, 2012), the predation pressure imposed on other non-mammal species, such as the partridge pigeon, may be lower than in other areas. Second, recent evidence suggests that feral cat densities are lower on the Tiwi Islands (H. Davies, unpublished data) than the adjacent mainland. As such, our results may be specific to Melville Island, and do not discount predation as a potential major factor in the contraction of populations of the partridge pigeon across northern Australian savannas. Future research should aim to quantify the contribution that predation by feral cats and dingoes have made to the contraction of ground-dwelling bird species.

The time of year that sites were surveyed was significantly negatively associated with partridge pigeon detectability i.e. the partridge pigeon became less detectable throughout the dry-season of 2015. Information such as this has important implications for designing optimal monitoring programmes. For example, Geyle et al. (2018a) utilised existing data on the detectability and occupancy of a threatened rodent to demonstrate that conducting surveys when detectability is highest resulted in not only an increased capacity to detect population decline, but decreased survey effort and associated costs. Therefore, conducting surveys of the partridge pigeon on Melville Island early in the year (i.e. when detectability is highest) could offer similar benefits, and future work should aim to develop such optimised monitoring.

While we have demonstrated that camera traps can effectively detect the partridge pigeon on Melville Island, the applicability of such methods for the ongoing monitoring of other birds will strongly depend on the target species. It is likely that the ground-dwelling sedentary nature of the partridge pigeon make it particularly suitable for monitoring using camera traps, but this will not be the case for most bird species (O'Brien and Kinnaird, 2008), for which point count surveys and bioacoustic recording will likely remain as more effective survey methods. When such methods are used, we emphasize the importance of quantifying the probability of detection, as it has important implications for both the confidence in the predicted species occurrence, and the statistical power to detect future population change (Einoder et al., 2018).

In conclusion, we have demonstrated the efficacy of a standardised camera trap methodology to reliably detect the threatened partridge pigeon in northern Australia. In doing so, we have provided a baseline estimate of partridge pigeon site-occupancy on Melville Island, and investigated the environmental factors influencing partridge pigeon site-occupancy and detectability. Information such as this sets the foundation for the development of optimal monitoring programmes with which to gauge population trajectories, as well as the response to remedial management actions. In the face of ongoing biodiversity loss, such baseline information is vital for management agencies to make informed decisions and should therefore be sought for as many species as possible.

Acknowledgements:

We thank the Tiwi Land Council and Tiwi traditional owners for their ongoing support of scientific research on their land. We also thank the field assistance provided by Tiwi College staff and students, Jaime Heiniger, Casey Visintin, Chris Davies, John van Osta, Fin Roberts, Hayley Geyle, Phoebe Burns and Amélie Corriveau. This work was supported by the Australian Research Council (DE130100434), the Paddy Pallin Foundation, the Holsworth Wildlife Research Endowment, CSIRO and the Northern Territory Government. BPM was supported by a fellowship from the Australian Research Council (FT170100004).

References:

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B. & Ferrer, E. A. 2011. Has the Earth's sixth mass extinction already arrived? *Nature,* 471**,** 51.

BirdLife International 2012. *Geophaps smithii. The IUCN Red List of Threatened Species 2012: e.T22690689A38954667.*

Crowley, G. 2008. Cockatoo grass *Alloteropsis semialata* as a keystone species in northern Australia. *Northern Territory Naturalist***,** 58.

Davies, H. F., McCarthy, M. A., Firth, R. S. C., Woinarski, J., Gillespie, G. R., Andersen, A. N., Geyle, H., Nicholson, E. & Murphy, B. P. 2017. Top-down control of species distributions: feral cats driving the regional extinction of a threatened rodent in northern Australia. *Diversity and Distributions,* 23**,** 272-283.

Davies, H. F., McCarthy, M. A., Firth, R. S. C., Woinarski, J. C. Z., Gillespie, G. R., Andersen, A. N., Rioli, W., Puruntatameri, J., Roberts, W., Kerinaiua, C., Kerinauia, V., Womatakimi, K. & Murphy, B. P. 2018. Declining populations in one of the last refuges for threatened mammal species in northern Australia. *Austral Ecology,* 43**,** 602-612.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B. & Collen, B. 2014. Defaunation in the Anthropocene. *Science,* 345**,** 401-406.

Einoder, L. D., Southwell, D. M., Gillespie, G. R., Fisher, A., Lahoz-Monfort, J. J. & Wintle, B. A. 2018. Optimising broad-scale monitoring for trend detection: review and re-design of a long-term program in northern Australia. *In:* Legge, S., Robinson, N., Lindenmayer, D., Scheele, B., Southwell, D. & Wintle, B. (eds.) *Monitoring Threatened Species and Ecological Communities.* Clayton, Victoria: CSIRO PUBLISHING.

Fiske, I. & Chandler, R. 2011. unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software,* 43**,** 1-23.

Franklin, D. C. 1999. Evidence of disarray amongst granivorous bird assemblages in the savannas of northern Australia, a region of sparse human settlement. *Biological Conservation,* 90**,** 53-68.

Fraser, B. F., Lawson, V., Morrison, S., Christophersen, P., McGreggor, S. & Rawlinson, M. 2003. Fire management experiment for the declining partridge pigeon, Kakadu National Park. *Ecological Management & Restoration,* 4**,** 94-102.

Fraser, F. J. 2001. *The impacts of fire and grazing on the Partridge Pigeon: the ecological requirements of a declining tropical granivore.* Australian National University.

Fuller, R. & Langslow, D. 1984. Estimating numbers of birds by point counts: how long should counts last? *Bird study,* 31**,** 195-202.

Garnett, S., Szabo, J. & Dutson, G. 2011. *The action plan for Australian birds 2010,* Collingwood, Victoria, CSIRO publishing.

Geyle, H. M., Guillera-Arroita, G., Davies, H. F., Firth, R. S. C., Woinarski, J. C. Z., Murphy, B. P., Nimmo, D. G., Ritchie, E. G. & Nicholson, E. 2018a. Towards meaningful monitoring: a case study of a threatened rodent. *Austral Ecology*.

Geyle, H. M., Woinarski, J. C., Baker, G. B., Dickman, C. R., Dutson, G., Fisher, D. O., Ford, H., Holdsworth, M., Jones, M. E. & Kutt, A. 2018b. Quantifying extinction risk and forecasting the number of impending Australian bird and mammal extinctions. *Pacific Conservation Biology*.

Gillespie, G. R., Brennan, K., Gentles, T., Hill, B., Low Choy, J., Mahney, T., Stevens, A. & Stokeld, D. 2015. A guide for the use of remote cameras for wildlife survey in northern Australia. *National Environmental Research Program, Northern Australia Hub, Charles Darwin University*.

Guillera-Arroita, G., Lahoz-Monfort, J. J., MacKenzie, D. I., Wintle, B. A. & McCarthy, M. A. 2014. Ignoring imperfect detection in biological surveys is dangerous: a response to 'fitting and interpreting occupancy models'. *PLoS ONE,* 9**,** e99571.

Johnson, C. 2006. *Australia's Mammal Extinctions: a 50,000-year History,* Melbourne, Cambridge University Press.

Kennedy, M., Phillips, B. L., Legge, S., Murphy, S. A. & Faulkner, R. A. 2012. Do dingoes suppress the activity of feral cats in northern Australia? *Austral Ecology,* 37**,** 134-139.

Kutt, A. S. 2012. Feral cat (*Felis catus*) prey size and selectivity in north-eastern Australia: implications for mammal conservation. *Journal of Zoology,* 287**,** 292-300.

Lawes, M. J., Murphy, B. P., Fisher, A., Woinarski, J. C., Edwards, A. & Russell-Smith, J. 2015. Small mammals decline with increasing fire extent in northern Australia: evidence from long-term monitoring in Kakadu National Park. *International Journal of Wildland Fire,* 24**,** 712.

Legge, S., Kennedy, M. S., Lloyd, R. A. Y., Murphy, S. A. & Fisher, A. 2011. Rapid recovery of mammal fauna in the central Kimberley, northern Australia, following the removal of introduced herbivores. *Austral Ecology,* 36**,** 791-799.

Legge, S., Murphy, B., McGregor, H., Woinarski, J. C. Z., Augusteyn, J., Ballard, G., Baseler, M., Buckmaster, T., Dickman, C. R. & Doherty, T. 2017. Enumerating a continental-scale threat: How many feral cats are in Australia? *Biological Conservation*.

MacKenzie, D. I. & Bailey, L. L. 2004. Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics,* 9**,** 300-318.

McCarthy, M. A., Moore, J. L., Morris, W. K., Parris, K. M., Garrard, G. E., Vesk, P. A., Rumpff, L., Giljohann, K. M., Camac, J. S., Bau, S. S., Friend, T., Harrison, B. & Yue, B. 2013. The influence of abundance on detectability. *Oikos,* 122**,** 717-726.

McGregor, H., Legge, S., Jones, M. E. & Johnson, C. N. 2015. Feral cats are better killers in open habitats, revealed by animal-borne video. *PLoS ONE,* 10**,** e0133915.

Murphy, B. P., Paron, P., Prior, L. D., Boggs, G. S., Franklin, D. C. & Bowman, D. M. 2010. Using generalized autoregressive error models to understand fire–vegetation–soil feedbacks in a mulga–spinifex landscape mosaic. *Journal of Biogeography,* 37**,** 2169-2182.

O'Brien, T. G. & Kinnaird, M. F. 2008. A picture is worth a thousand words: the application of camera trapping to the study of birds. *Bird Conservation International,* 18 (S1)**,** 144-162.

O'Connell, A. F., Nichols, J. D. & Karanth, K. U. 2011. *Camera Traps in Animal Ecology: Methods and Analyses,* New York, Springer.

Pendleton, G. W. 1995. Effects of sampling strategy, detection probability, and independence of counts on the use of point counts. *In: Ralph, C. John; Sauer, John R.; Droege, Sam, technical editors. 1995. Monitoring bird populations by point counts. Gen. Tech. Rep. PSW-GTR-149. Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station,* 149**,** p. 131-134.

R Development Core Team 2013. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Recher, H. & Lim, L. 1990. A review of current ideas of the extinction, conservation and management of Australia's terrestrial vertebrate fauna. *In:* Saunders, D. A., Hopkins, A. J. M. & How, R. A. (eds.) *Australian ecosystems : 200 years of utilization, degradation and reconstruction : proceedings of a symposium held in Geraldton, Western Australia.* Chipping Norton, NSW: Surrey Beatty & Sons for the Ecological Society of Australia.

Richards, A. E., Liedloff, A. & Schatz, J. 2015. Tiwi Islands CFI capability project report. Australia: CSIRO.

Russell-Smith, J., Whitehead, P. J., Cook, G. D. & Hoare, J. L. 2003. Response of *Eucalyptus*-dominated savanna to frequent fires: Lessons from Munmarlary, 1973–1996. *Ecological Monographs,* 73**,** 349-375.

Stokeld, D., Fisher, A., Gentles, T., Hill, B., Triggs, B., Woinarski, J. & Gillespie, G. R. 2018. What do predator diets tell us about mammal declines in Kakadu National Park? . *Wildlife Research***,** 92-101.

Woinarski, J. 2004. *National Multi-species Recovery plan for the Partridge Pigeon [eastern subspecies] Geophaps smithii smithii, Crested Shrike-tit [northern (sub)species] Falcunculus (frontatus) whitei, Masked Owl [north Australian mainland subspecies] Tyto novaehollandiae kimberli; and Masked Owl [Tiwi Islands subspecies] Tyto novaehollandiae melvillensis, 2004 - 2009,* Darwin, Department of Infrastructure Planning and Environment.

Woinarski, J., Murphy, B., Legge, S., Garnett, S., Lawes, M., Comer, S., Dickman, C., Doherty, T., Edwards, G. & Nankivell, A. 2017. How many birds are killed by cats in Australia? *Biological Conservation,* 214**,** 76-87.

Woinarski, J. C. Z., Burbidge, A. A. & Harrison, P. L. 2015. Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences,* 112**,** 4531-4540.

Woinarski, J. C. Z., Milne, D. J. & Wanganeen, G. 2001. Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Northern Territory, Australia. *Austral Ecology,* 26**,** 360-370.

Woinarski, J. C. Z., Risler, J. & Kean, L. 2004. Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical Eucalyptus open forest, Northern Territory, Australia. *Austral Ecology,* 29**,** 156-176.

Ziembicki, M. R., Woinarski, J. C., Webb, J. K., Vanderduys, E., Tuft, K., Smith, J., Ritchie, E. G., Reardon, T. B., Radford, I. J., Preece, N., Perry, J., Murphy, B. P., McGregor, H., Legge, S., Leahy, L., Lawes, M. J., Kanowski, J., Johnson, C., James, A., Griffiths , A., Gillespie, G. R., Frank, A., Fisher, A. & Burbidge, A. A. 2014. Stemming the tide: progress towards resolving the causes of decline and implementing management responses for the disappearing mammal fauna of northern Australia. *Therya,* 6**,** 169-225.

Tables:

Table 1: Description and justification of the variables used in analyses to assess the correlates of partridge pigeon distribution on Melville Island.

Explanatory variable	Description and justification for inclusion	Variable used in analyses to predict:
Fire extent	Following Lawes et al. (2015), a remote-sensed fire variable derived from fine-scale (30 x 30 m) LANDSAT satellite imagery, representing the proportion of the area surrounding each site that was burnt in each year, averaged over the five years preceding partridge pigeon sampling. Calculations were made using an area with a radius of 3.2 km (Lawes et al., 2015).	• Occupancy and detectability
Rainfall	Mean annual rainfall (Australian Bureau of Meteorology, 2015). This variable was included as the partridge pigeon has suffered the greatest decline through the lower rainfall areas of its distribution (Franklin, 1999). Furthermore, feral cat densities tend to be lower in areas of high rainfall (Legge et al., 2017).	• Occupancy and detectability
Dingo activity	The proportion of nights that dingoes were recorded on camera at each site. This was taken as an approximation of dingo activity at each site. Included in analyses to investigate the potential beneficial impacts of dingoes on the partridge pigeon via a negative influence of dingoes on feral cats (Johnson, 2006, Kennedy et al., 2012). The partridge pigeon may also by susceptible to direct dingo predation (Woinarski, 2004, Stokeld et al., 2018).	• Occupancy and detectability
Fire patchiness	Following Lawes et al. (2015), this metric of the spatial heterogeneity of fires was calculated by measuring the distance to the nearest burnt–unburnt boundary at the end of each calendar year, within a circular area (radius of 3.2 km) surrounding each site. We then calculated the mean of all distance values to get an annual measure of patchiness for the area surrounding each site. We derived this measure for every site in each of the five years preceding mammal sampling and calculated the mean of these five values. Low values indicate areas of low patchiness i.e. areas dominated by large homogeneous patches of either burnt or unburnt vegetation. Fine-scale patches of burnt and unburnt	• Occupancy and detectability

	habitat are thought to be beneficial for the partridge pigeon (Fraser et al., 2003, Woinarski, 2004).	
Shrub density	A count of the number of shrubs in a 1 x 100 m quadrat at each site. Shrubs were defined as anything taller than 20 cm but shorter than 1.3 m, or taller than 1.3 m with a diameter at breast height of less than 5 cm. Shrubs with multiple stems were counted as a single individual. Vegetation structure has been demonstrated to reduce feral cat hunting success (McGregor et al., 2015), and therefore could have important flow-on effects on the occupancy and detectability of the partridge pigeon.	• Occupancy and detectability
Perennial grass abundance	A count of the number of 1 x 1 m segments in which perennial grass was recorded along a 1 x 100 m quadrat at each site. As a granivorous bird, the partridge pigeon may be dependent on the flush of seeds produced by perennial grasses as the start of the wet season when food resources are scant (Crowley, 2008).	• Occupancy and detectability
Probability of feral cat detection	Following Davies et al. (2017) and Davies et al. (2018), we used the predicted probability of detecting feral cats at each site as a correlate of partridge pigeon distribution. This was derived from spatially explicit generalised linear models as outlined in Murphy et al. (2010). The ground-dwelling nature of the partridge pigeon likely renders it particularly susceptible to feral cat predation (Woinarski, 2004).	• Occupancy and detectability
Feral herbivore presence	A binary variable indicating the presence or absence of large feral herbivores at each site. Feral herbivores on Melville Island include the introduced water buffalo (*Bubalus bubalis*) and horse (*Equus caballus*). Feral herbivores potentially influence partridge pigeon populations via impacts on the ground-layer vegetation that provide vital food and nesting resources (Woinarski, 2004, Legge et al., 2011).	• Occupancy and detectability
Julian day	The Julian day of the calendar year that sampling started at each site. This variable was included to account for potential seasonal bias of partridge pigeon detectability.	• Detectability only
Number of cameras operating	An observation level covariate to account for the variation in detectability arising from uneven numbers of cameras operating at different sites due to camera malfunction and destruction.	• Detectability only

Table 2: ΔAIC values for the null model (where occupancy and detectability parameters are assumed to be constant across all survey sites), and the most parsimonious model for partridge pigeon site-occupancy. Estimates of site-occupancy, probability of detection per sampling occasion, and the overall probability of detection also shown. The naïve occupancy estimate (i.e. the proportion of sites where the partridge pigeon were detected) is also shown. Values in brackets represent the 95% confidence interval.

Model	**ΔAIC**	**Occupancy (Ψ) (± CI)**	**Probability of detection per sampling occasion (p) (± CI)**	**Overall probability of detection**
Naïve	-	0.27	-	-
Null model	18.4	0.28 (0.1)	0.08 (0.02)	0.98
Best model	0.0	0.30 (0.2)	0.15 (0.1)	0.99

Figures:

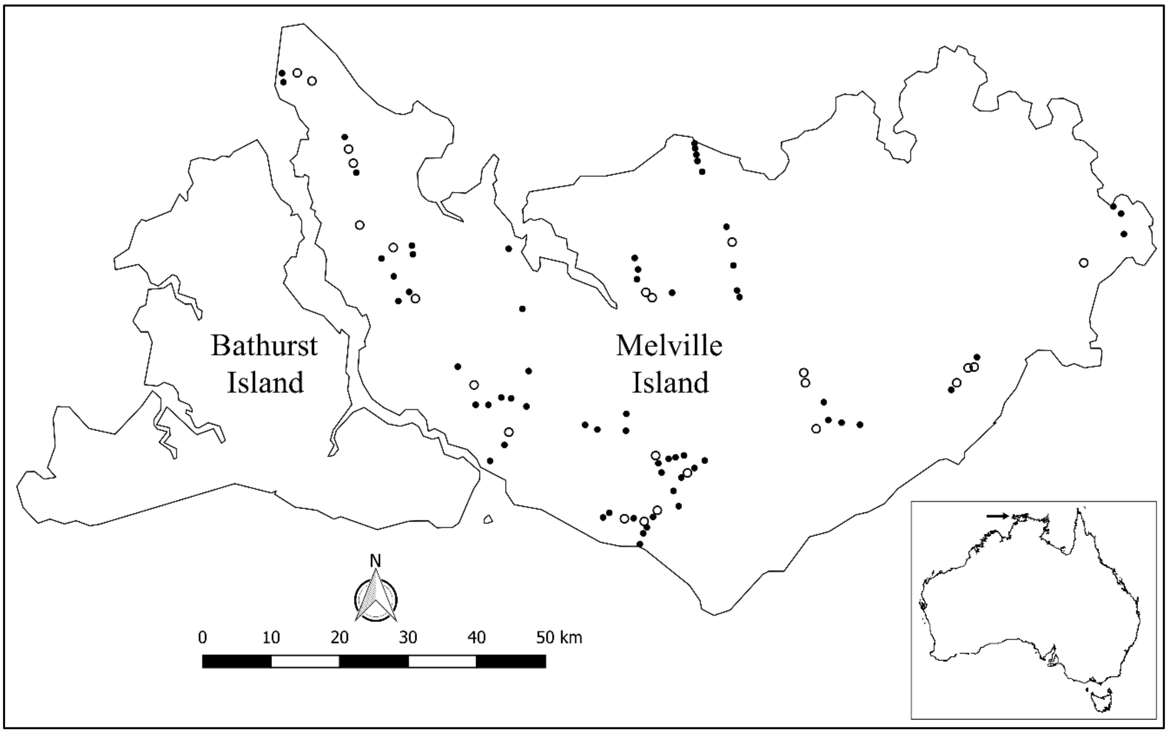

Fig. 1. The location of the 88 sites surveyed across Melville Island in 2015. Open circles indicate sites where the partridge pigeon was detected. The location of Melville Island relative to mainland Australia is shown in the inset.

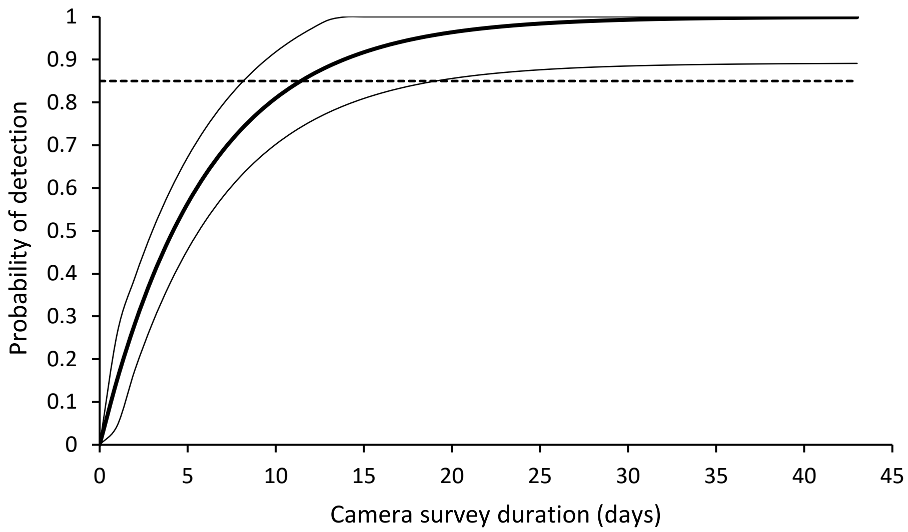

Fig. 2 The cumulative probability of detecting the partridge pigeon as a result of camera survey duration. Thin lines indicate the 95% confidence interval. The dashed line indicates 0.85, the minimum level of overall detection recommended for accurate occupancy estimation (Guillera-Arroita et al., 2014).

a) b)

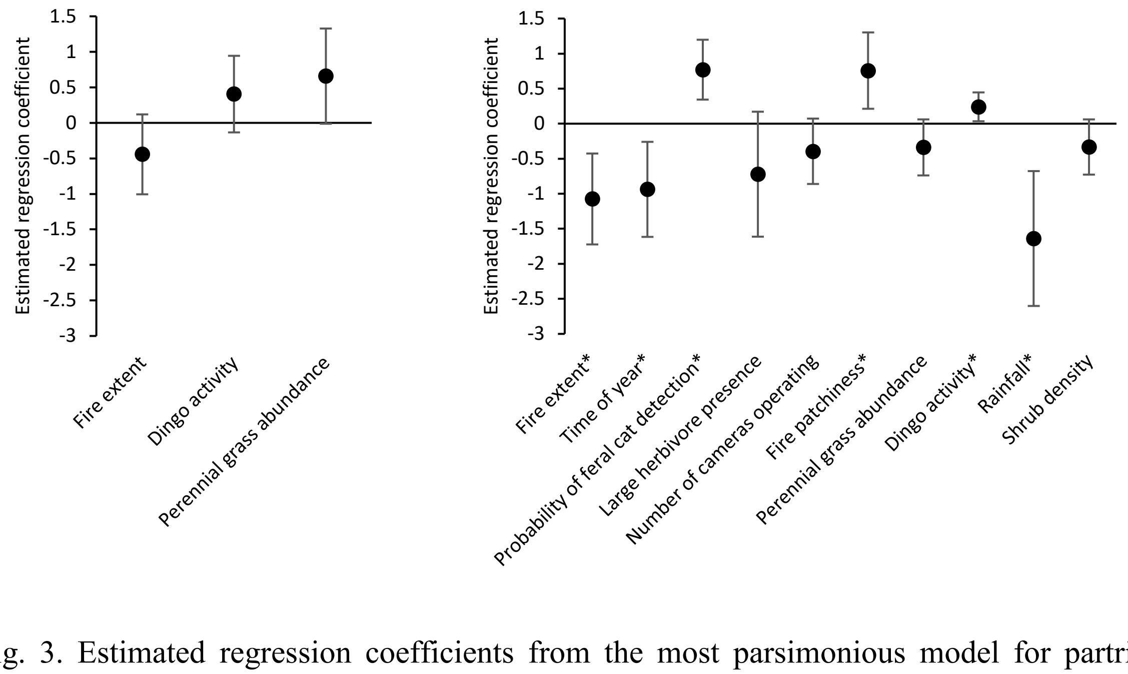

Fig. 3. Estimated regression coefficients from the most parsimonious model for partridge pigeon a) occupancy and b) detectability on Melville Island. Error bars indicate 95% confidence intervals. Asterisks indicate statistical significance.