1 **Using camera traps to determine occupancy and breeding in burrowing**

2 **seabirds**

3

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13 **ABSTRACT**

14 Burrowing seabirds are important in commercial, ecological and conservation terms. Many

15 populations are in flux owing to both negative and positive anthropogenic impacts, but their ecology

16 makes measuring changes difficult. Reliably recording key metrics, the proportion of burrows with

17 breeding pairs, and the success of breeding attempts, requires burrow-level information on

18 occupancy. We investigated the use of camera traps positioned at burrow entrances for determining

19 the number of breeding pairs in a sample to inform population estimates, and for recording breeding

20 success. Linear Discriminant Analyses of time series activity patterns from camera traps successfully

21 partitioned breeding and non-breeding burrows at different stages of the breeding season and had

22 reasonable predictive ability to determine breeding status on a small test dataset. Compared with

23   traditional techniques for determining burrow occupancy (e.g. manual burrow inspection and

24   playback of conspecific calls at burrow entrances), camera traps can reduce uncertainty in estimated

25   breeding success and potentially breeding status of burrows. Significant up-front investment is

26   required in terms of equipment and human resources but for long-term studies camera traps can

27   deliver advantages, particularly when unanticipated novel observations and the potential for

28   calibrating traditional methods with cameras are factored in.

29

30   **INTRODUCTION**

31   Seabirds are a major component of marine food webs consuming prey volumes commensurate with

32   commercial fisheries (Barrett et al., 2006; Danckwerts et al., 2014). In the Southern Oceans one

33   taxonomic group, the Procellariiform petrels, is second only to penguins in terms of avian biomass

34   (Catry et al., 2003) and volume of prey consumed (Croxall et al., 1984). By transferring nutrients

35   from pelagic to marine and coastal ecosystems, petrels make significant contributions to global

36   geochemical cycles (Otero et al., 2018). These inputs, together with soil modification from their

37   burrow-nesting habit result in positive influences on island biodiversity (Graham et al., 2018;

38   Sekercioglu, 2006). However, petrels are also highly susceptible to invasive predators which have

39   precipitated catastrophic declines in many populations resulting in 45 of 97 species (46%) being

40   threatened with extinction (BirdLife International, 2018; Croxall et al., 2012; Dias et al., 2019).

41   Collectively there are strong commercial, ecological and conservation incentives for understanding

42   petrel population trends, but they are difficult to monitor (Rodríguez et al., 2019). Seasonal

43   occurrence, nocturnal activity at colonies and challenges in finding, counting and ascertaining the

44   contents of burrows all contribute to high levels of uncertainty when populations are assessed (Bird

45   et al., submitted; Rodríguez et al., 2019). The most important metrics for tracking conservation

46   status and population-level responses to impacts are the number of breeding burrows and their

47   success rate, both of which rely upon one-off, or repeat measures of burrow occupancy.

48   In recent years, audio playback for small species and manual burrow inspections for larger species

49   have emerged as the most widely used occupancy detection methods in burrowing seabird studies

50   (Bird et al., submitted). Playback requires calibration to account for non-responsive birds (Soanes et

51   al., 2012). This is an invasive and time-consuming process. Because response rates vary seasonally

52   and between life history stages (Berrow, 2000; Ratcliffe et al., 1998; Ryan et al., 2006) repeated

53   calibration would be required to collect population-level information on breeding success. This is

54   unethical and logistically impractical. Furthermore, detailed ecological study at the burrow level

55   using playback is not possible because response rates of individual birds vary temporally. As such,

56   playback is only suitable for determining the proportion of occupied burrows at a population-level

57   (Parker and Rexer-Huber, 2016). Studies typically assume that occupied burrows represent breeding

58   pairs, and the occupancy rate is then used to adjust burrow counts when estimating breeding

59   population size. Yet not all occupied burrows are occupied by breeding birds, resulting in

60   unquantified error in final estimates (Parker and Rexer-Huber, 2016). In contrast, burrow inspection

61   can provide more detailed information about individual burrow contents, but it is disruptive to

62   petrels. Investigator disturbance can result in high rates of nest abandonment, reduced hatching

63   success, high divorce rates between disturbed pairs, and emigration of immature birds from natal

64   colonies (Carey, 2009). To meet ethical guidelines and ensure data is representative of natural

65   parameters, manual burrow inspection has evolved away from early methods which involved partial

66   burrow excavation. In recent times, the use of purpose-built burrow inspection scopes has become

67   prevalent, but accuracy is highly variable according to the quality of equipment available (Carlile et

68   al., 2019; Lavers et al., 2019). Manual burrow inspection is also labour intensive, and repeat visits to

69   measure breeding success still have uncertainty around outcomes when burrows change from

70   occupied to empty between visits.

71   Use of camera traps in ecological studies has become common because they can provide time series

72   data on the activity of individuals (Wearn and Glover-Kapfer, 2019). They have been used to

73   measure seabird breeding phenology and provide indices of abundance for above-ground nesting

74   species, but their use in studies of burrowing seabirds has mainly been limited to understanding

75   predation pressures by invasive alien species (Edney and Wood, 2020). Fischer et al. (2017) assessed

76   the suitability of camera traps for studying diving-petrels *Pelecanoides* spp. by pairing them with

77   Radio Frequency Identification tags deployed on five birds, with tag readers at the burrow entrance.

78   They found detection rates were low, perhaps owing to the size and behaviour of the birds—diving-

79   petrels are small, arrive and depart rapidly from their burrows, and are very well insulated reducing

80   the chance of infra-red triggers—and concluded camera traps appear unsuitable for studying

81   breeding biology in diving-petrels.

82   There has been no test of whether continuous observations using camera traps can overcome

83   shortcomings of playback and manual burrow inspection. Unlike playback no calibration is required,

84   and long-term deployments could reveal outcomes of breeding events in individual burrows with

85   higher resolution than intermittent manual inspections. If so, camera traps have the potential to

86   considerably improve burrowing seabird conservation assessments providing reliable information

87   with low uncertainty on occupancy, the proportion of burrows occupied by breeding pairs, and

88   breeding success.

89   Here we investigate the use of camera traps for monitoring the breeding biology of several species

90   of burrowing petrel on sub-Antarctic Macquarie Island. We assess the performance of cameras for: i)

91   recording nest-level activity; ii) recording breeding success rate; and iii) inferring the ratio of

92   breeding to non-breeding burrows. Finally, we compare the results from camera traps with

93   traditional playback and burrow-inspection methods.

94

95   **METHODS**

96   *Study site and species*

97　　Macquarie Island (54°30'S, 158°57'E) has many of the characteristics that make surveying and

98　　monitoring burrowing petrels challenging. Lying approximately 1,500 km south-east of Tasmania,

99　　almost midway between Australia and Antarctica, it is remote and therefore costly to visit. The

100　island's status as a UNESCO World Heritage Site and Tasmanian Nature Reserve means invasive

101　research activities and visitation are restricted. It is 12,785 ha in area, 34 km long and up to 5 km

102　wide, rugged with sections of coastal cliffs and a steep escarpment rising to an upland plateau

103　reaching 400 m above sea level. The sub-Antarctic climate and potential for extreme weather

104　conditions (Adams, 2009; Pendlebury and Barnes-Keoghan, 2007), the terrain, and the limited access

105　to medical facilities mean strict health and safety protocols are in place to protect personnel, and

106　these also place constraints on fieldwork capacity. Furthermore, the island's size, terrain, steep

107　slopes and fact that vegetation communities are recovering following decades of impacts by

108　European Rabbits *Oryctolagus cuniculus* (Springer, 2016) all make finding and studying seabird

109　burrows difficult. The friable peat soils in many seabird colonies are fragile. Safe, low impact access

110　is challenging.

111　Our study addressed two large-bodied species: Grey Petrel *Procellaria cinerea* (950-1,220 g) and

112　White-headed Petrel *Pterodroma lessonii* (750-780 g); and two medium-bodied species: Blue Petrel

113　*Halobaena caerulea* (171-253 g) and Antarctic Prion *Pachyptila desolata* (116-160 g; Jouventin,

114　1985). All four species nest in burrows dug predominately in peat substrate.

115　Constraints on the location and timing of fieldwork meant we were unable to compare all burrow

116　assessment methods across all species, but we compare the utility of each method at least between

117　a large-bodied and a medium-bodied species.

118

119　*Camera-traps*

120   Six Reconyx HC600 trail cameras were deployed at the entrance to Grey Petrel burrows from 10th

121   June 2017 to 22nd November 2017. In 2018, six Reconyx HC600 and four Spypoint Force 10 trail

122   cameras were deployed outside Grey Petrel burrows from 1st April to 2nd November (Figure 1).

123   Twenty Spypoint Force 10 cameras were deployed outside Blue Petrel burrows from 15th August

124   2018 to 4th February 2019 (see Figure S1-5 for burrow identification). Cameras were all set to 'high'

125   sensitivity, to take three images per trigger with 1 second interval between, and no delay between

126   triggers. They were checked at intervals to replace batteries and memory cards.

127   We tagged all images manually in ExifPro 2.1.0 (http://www.exifpro.com/index.html), discarding any

128   images associated with camera set-up. We tagged images that featured a bird with the species, the

129   number of individuals (rarely >1), and whether there was a chick. We also tagged behaviours:

130   burrow entries, exits and tidying of the burrow entrance which appeared to be associated with

131   breeding.

132   To assess camera performance, we recorded periods of camera inactivity, we compared the total

133   numbers and ratios of false triggers to target triggers, the mean numbers of events per day between

134   cameras, and the ratio of entries to exits. For behavioural analysis, we grouped images into

135   'events'—series of consecutive images separated by no more than 5 minutes. We plotted the

136   number of events per day against date for both adults and chicks. We relabelled entries and exits as

137   'transits' and plotted the total per day against date, together with the number of tidying events

138   recorded.

139   We manually inspected all Grey Petrel burrows with camera traps at the entrance four times during

140   the period over which cameras were deployed (5 months in 2017 and 7 months in 2018) to

141   determine breeding status and breeding success at the burrow. To understand whether adult

142   activity patterns derived from the cameras could be used to reliably infer breeding status of burrows

143   we derived test variables: mean number of events, duration of absences in days, the proportion of

144   days where high activity was recorded (> 5 events), and the proportion of days where low activity

145   was recorded (1-5 events). We derived these variables for each stage of the breeding season:

146   incubation, early chick-rearing and late chick-rearing (fledging was dropped owing to low adult

147   activity). We tested for correlation between the variables by dropping one of a pair of variables if

148   their r^2 was > 0.6, and then used principal component analysis (PCA) to look for patterns in our data.

149   Then we classified breeding and non-breeding burrows using linear discriminant analysis (LDA). PCAs

150   and LDAs were performed for each breeding stage. Because our burrow sample was small, we used

151   all full-season time series to build the LDA models. We derived a test dataset from cameras that

152   malfunctioned during the season for which only partial time-series were available and used these to

153   test the models. Breeding success was derived from chick activity recorded at the burrow entrance.

154   Analyses were conducted in R using the 'tidyverse', 'MASS', 'FactoMineR' and 'caret' packages

155   (Kuhn, 2008; Lê et al., 2008; R Core Team, 2020; Venables and Ripley, 2002; Wickham et al., 2019,

156   see Supplementary Code).

157

158   *Playback and burrow inspection*

159   Both playback and manual burrow inspection have been used to determine occupancy of Grey

160   Petrel, Antarctic Prion and Blue Petrel burrows (Barbraud et al., 2009; Brothers and Bone, 2008;

161   Dilley et al., 2017). However, *Pterodroma* petrels vocalise during aerial displays at night, but rarely

162   respond from the nest chamber to stimuli during the day, so manual inspection is required for

163   White-headed Petrels (Brothers, 1984; Sinclair, 1981). We preferentially chose to manually inspect

164   burrows because we were concerned that variable response rates to playback would affect nest-

165   level data (Schulz et al., 2006), but we compared with playback for medium-bodied species where

166   we had low confidence in manual inspections.

167   We first visited burrows during incubation or early chick-rearing in the 2017-2018 breeding seasons

168   of our four study species. We inspected 237 White-headed Petrel burrows with a homemade

169   burrowscope (Figure S6). A second observer independently checked the same burrows with a

170   handheld Canon Powershot camera held at arm's length down the burrow to calibrate the two

171   methods and allow correction of data from previous years when cameras were used. We checked

172   242 Grey Petrel burrows by handheld camera or burrowscope, and 247 Blue Petrel and 76 Antarctic

173   Prion burrows with the burrowscope. A burrow was recorded as 'empty' when the observer believed

174   they could see the end of the burrow and any side chambers were visible in images, or 'uncertain' if

175   the end was not visible. In occupied burrows we noted the number and identity of adult birds, eggs,

176   and chicks.

177   We revisited burrows to check breeding status and the outcome of breeding attempts through the

178   season. All burrows in which eggs, recent eggshell or chicks were found in the burrow or at the

179   entrance were recorded as breeding burrows. If adults were present during the first visit but not

180   subsequently the breeding status was 'uncertain'. Burrows with adults present later in the season

181   were recorded as non-breeding. The repeat visits were used to calibrate earlier visits—the status of

182   burrows labelled originally as 'uncertain' often became clear on second or third visits, and we

183   estimated our type 1 error rate by identifying breeding burrows originally labelled as 'empty'.

184   For comparison with occupancy and uncertainty estimates from our initial burrow inspections we

185   used playback for both medium-sized species. Playback provides information on the proportion of

186   burrows occupied, relying on birds responding when a recording of a conspecific vocalising is played

187   near their burrow entrance. It is common in studies of small-bodied species whose burrow entrances

188   are small, precluding manual inspection (Perkins et al., 2018). Response rates are known to vary so

189   following Soanes et al. (2012) we repeated playback 4 times to a sample of 61 Antarctic Prion

190   burrows and 9 times to 66 Blue Petrel burrows and used the 'du Feu' single-session mark/recapture

191   method of population estimation to estimate the overall proportion of occupied burrows in our

192   sample with confidence limits (du Feu et al., 1983).

193

194   **Results**

195   *Recording nest-level activity and breeding success from cameras*

196   Overall camera traps proved to be very effective. The expected target species was recorded on all

197   cameras placed at burrow entrances. One camera placed at a burrow entrance for a night equates to

198   one 'trap night'. We recorded 47,179 images of Blue Petrels during 3,554 trap nights, and 42,705

199   images of Grey Petrels during 2,677 trap nights. However, performance varied greatly between the

200   two types of cameras we deployed. The ratio of target triggers to false triggers was much higher for

201   Reconyx cameras compared with the SpyPoint cameras, and the proportion of trap nights where >0

202   images were captured, i.e. the camera was known to be recording, was also higher (Table 1). In

203   reality, short periods of several days where no images were captured are likely to reflect genuine

204   absences of activity, whereas long periods (e.g. >10 days) with no target or false triggers likely reflect

205   camera malfunction, especially in SpyPoint cameras given their high false trigger rate. Although we

206   primarily deployed Spypoint cameras at Blue Petrel burrows and Reconyx at Grey Petrel burrows,

207   the relative differences in performance are still apparent in the one Reconyx camera at a Blue Petrel

208   burrow and the four SpyPoint cameras at Grey Petrel burrows (Table 1). Overall SpyPoint cameras

209   were far more likely to be triggered when no animal was present, and there were many more days,

210   irrespective of species, when the cameras did not record any images.

211   Despite the stark difference in camera performance, we recorded specific behaviours at all burrows

212   such as entries and exits, digging, tidying at burrow entrances, chicks emerging and exercising,

213   predators (Brown Skua *Catharacta antarctica*) and competitors entering burrows (e.g. Antarctic

214   Prions in Blue Petrel burrows and Sooty Shearwaters in Grey Petrel burrows; Figures S7-8). While we

215   were interested in burrow-level variation in behaviours recorded, the variance in certain behaviours,

216   for example the ratio of entries to exits, suggests that positioning of cameras has an important

217   bearing on what is recorded. Some cameras recorded five times more entries than exits, while

218   others recorded five times more exits than entries (Table 1).

219   While camera make and positioning influenced the type and level of activity recorded at each

220   burrow, averaging activity by classifying events and specific behaviours, both makes of camera

221   provided season-long activity signatures for many burrows (Figures 2 and 3). The mean number of

222   events recorded per day that burrows were visited was 4.10 for Blue Petrels and 2.58 for Grey

223   Petrels. For both species the between-burrow variance in the mean number of events per day (SD

224   1.73 for Blue Petrels and SD 1.12 for Grey Petrels) was lower than the within-burrow variance (SD

225   3.95 for Blue Petrels and SD 1.76 for Grey Petrels), suggesting that the activity captured was

226   relatively uniform across burrows.

227   Peak activity at Blue Petrel burrows is apparent early in the breeding season, tailing off later in the

228   season (Figure 2). There are cyclic patterns in activity spikes with periods of absence or reduced

229   activity between them. Generally, we also observed bouts of tidying around the burrow entrance

230   early in the breeding season at burrows with high activity peaks. Burrows 05 and 20 lack early-

231   season activity peaks, and burrow activity ceases earlier in the season than at e.g. burrows 02, 09

232   and 18. Unfortunately it is also evident from the rug plots in Figure 2 how poorly the Spypoint

233   cameras performed (burrows 02-21) with few cameras recording right through to the end of the

234   season.

235   The Grey Petrel dataset was more complete, with the exception of the Spypoint cameras at burrows

236   10, 11 and 13 (Figure 3). Again, there are clear cyclic patterns of burrow attendance. Recording

237   began during incubation by which point adult attendance at most burrows was relatively uniform.

238   During nest inspections no eggs, chicks or signs of breeding such as nest material were recorded in

239   burrows 04, 08, 12, 13 or 16, and each of these burrows was only occupied during the first visit.

240   These burrows were empty during all subsequent visits and were all considered to be non-breeding

241   burrows after multiple visits. Nevertheless, the cameras show that all of them remained in use for

242   much of the season. Burrows 08 and 12 have higher activity peaks than the breeding burrows at

243   comparable stages of the breeding season, and the gaps between peaks appear to be longer.

244   Chicks were recorded in all other burrows during manual inspections, but the fate of the breeding

245   attempts was sometimes uncertain. For example, burrow 03 was empty when visited on 26th

246   October but the camera showed the chick had first emerged when downy some weeks earlier, and

247   had attained full adult plumage when last recorded on the camera on 23rd October. From the

248   cameras we inferred that all chicks in these study burrows fledged successfully, as well as the

249   fledging date from each burrow (Figure 3).

250

251   *Inferring breeding and non-breeding burrows*

252   We were particularly interested in whether the activity signatures from each burrow can be used to

253   infer breeding status of the burrows. From the PCA there is weak evidence that absences tend to be

254   longer during incubation and there are more low-activity days at breeding Grey Petrel burrows than

255   non-breeding burrows (Figure 4). Later in the season during early and late chick-rearing absences are

256   longer at non-breeding than breeding burrows, but when birds are present there is more activity at

257   the burrow entrance of non-breeding burrows while breeding burrows are characterised by low

258   activity (Figure 4).

259   These apparent differences are also evident in the group means of the predictor variables we used in

260   LDAs (Table 2). The three LDAs were broadly able to discriminate between breeding and non-

261   breeding burrows in our training data (Figure 5). However, the analyses of absences and activity data

262   during incubation and late chick-rearing misclassified the non-breeding burrow 13 based upon the

263   partial time series available (Table 3).

264

265   *Comparisons with traditional methods*

266   First, we compared approaches for measuring burrow occupancy. Figure 6 shows that using a

267   burrowscope resulted in higher sensitivity (true positives) and specificity (true negatives), lower

268   uncertainty and lower type 1 error (false negatives) when predicting burrow occupancy compared

269   with using playback. For example, comparing panel a) using a burrowscope to inspect Antarctic Prion

270   burrows with panel d) using playback, of 76 burrows inspected with a burrowscope we correctly

271   assigned 20 burrows as empty and 15 as occupied on the first visit—sensitivity + specificity = 46%.

272   However, we incorrectly identified 11 burrows as empty on first visit which were in fact occupied—

273   type 1 error = 24%. And we were uncertain about the occupancy of 30 burrows (39%) on first visit,

274   14 of which were subsequently identified as occupied while 16 remained uncertain. Using playback,

275   owing to our inability to distinguish between non-responsive birds in burrows and empty burrows,

276   we could not definitively assign any burrows as empty (Figure 6d). We correctly identified 72

277   burrows as occupied on first visit—sensitivity 26%—but were uncertain about the status of the

278   remaining 197 burrows (74%).

279   There is an important distinction between determining occupancy in individual burrows and

280   estimating overall population-level occupancy. The former is used to measure burrow-specific

281   variables such as breeding status and success. The latter to adjust burrow counts when estimating

282   the number of occupied burrows, either in a sample or in the whole population. We were able to

283   refine population-level estimates of occupancy derived from playback by calibrating the response

284   rate through repeat visits. We estimated overall occupancy in Blue Petrel burrows as 0.56 (95% CI:

285   0.42-0.70) after nine visits to calibrate our sample (Table S1). However, after achieving only 4

286   repeats for Antarctic Prions there was little flattening of the accumulation curve and the "du Feu"

287   method, possibly erroneously in this case, estimates that all burrows are occupied (Table 4). Through

288   repeated playback population-level occupancy can be estimated. However, while using a

289   burrowscope is challenging for medium-bodied species owing to the small size of their burrow

290   entrances, it still yielded tighter confidence intervals around the estimated occupancy statistic than

291   repeat-measures playback (Table 4).

292 Uncertainty was lowest when using the burrowscope at larger White-headed Petrel burrows. We

293 were able to correctly diagnose 218 of 233 (92%) burrows on the first visit, but 15 occupied burrows

294 (6%) were incorrectly diagnosed as empty. Uncertainty was greater with a handheld camera than a

295 burrowscope (25% compared with 2%, Figure 6) but type 1 error was not (Table 4).

296 Comparing methods for determining breeding status and breeding success, it is clear that playback is

297 incompatible with collecting the burrow-level information needed. Even with manual burrow

298 inspection, we were often unsure of breeding status on first visits alone because birds were not

299 manoeuvred to check whether they were incubating eggs in order to avoid undue disturbance.

300 However, by repeating visits through the season, we were able to determine the breeding status of

301 96 of 136 (70%) occupied White-headed Petrel burrows and 82 of 101 (82%) occupied Grey Petrel

302 burrows (Table 5). We estimated breeding success as 0.83 (0.75-0.90) and 0.77 (0.68-0.75) for

303 White-headed and Grey Petrels respectively after all visits. The two visits that were made to Blue

304 Petrel burrows were insufficient to estimate breeding success.

305 Occupancy is an inferior metric to breeding status of burrows but is used in one-off survey visits.

306 Through deployments (long and short) of camera traps at burrow entrances we believe it is possible

307 to reliably determine burrow breeding status given a sufficient sample size of known-status burrows

308 from which to model status as a function of nest-level activity. Furthermore, camera traps can

309 substantially reduce uncertainty in estimated breeding success.

310

311 **Discussion**

312 Conservation assessments focus on the portion of populations that are breeding, i.e. those which

313 carry the reproductive potential of the species (IUCN, 2019). The challenge of determining the size

314 and trends of burrowing-seabird breeding populations when only burrow entrances are visible at the

315 surface is now decades old, yet there has been little research into the activity of seabirds at burrow

316   entrances or the relationship between this activity and breeding status and success of individual

317   burrows. We found that camera traps positioned at burrow entrances were able to collect time

318   series activity patterns from which we could infer breeding status and breeding success of individual

319   burrows. Provided the cameras used are fit-for-purpose, camera traps provided higher resolution

320   data on the number of successful breeding attempts from a sample of burrows than is possible

321   through burrow inspection.

322   Despite our relatively low sample size, we were able to discriminate effectively between breeding

323   and non-breeding burrows using partial time-series data, suggesting that a thorough investigation of

324   type 1 and 2 error rates around inferred breeding status is warranted. LDAs had higher sensitivity

325   when identifying breeding burrows than non-breeding burrows from our small test dataset. Activity

326   patterns associated with breeding are likely to be relatively uniform given that incubation shift

327   duration and provisioning rates are all energetically determined (Chaurand and Weimerskirch, 1994;

328   Jouventin, 1985). In contrast, non-breeding birds are not bound to a chick and can take longer

329   absences. Non-breeding shearwaters are known to spend up to four times longer at the surface than

330   breeding birds (Bonnaud et al., 2009), consistent with our observation of the highest activity peaks

331   outside non-breeding burrows and the group means from LDAs.

332   Importantly the ratio of breeding to non-breeding burrows varies in dynamic populations.

333   Populations undergoing expansion, for example following invasive species eradication, can have high

334   proportions of immigrant and immature birds which may prospect without attempting to breed. In

335   declining populations experiencing high predation rates prospecting birds can be disproportionately

336   impacted resulting in a higher proportion of occupied burrows supporting breeding birds (Bonnaud

337   et al., 2009). Differentiating between breeding and non-breeding burrows is, therefore, important,

338   but it is difficult with traditional methods which we show are prone to high uncertainty. For future

339   studies we would focus on increasing our sample size to assess whether linear discriminant models

340   can be improved to increase their predictive ability. It would also be valuable to see how variable

341 burrow entrance activities are between breeding sites. Calibration might only be necessary at a

342 handful of sites to train LDAs that can be applied elsewhere to new camera trap datasets.

343 Regardless of the eventual reliability of camera trap LDAs for inferring breeding status of burrows,

344 using camera traps in consort with other methods provides valuable information. For example, in

345 the non-breeding burrows we followed, the camera traps revealed high rates of burrow activity but

346 paired with manual inspection we found these burrows were rarely occupied in the daytime.

347 Playback studies suffer from the untested assumption that occupied burrows support breeding birds

348 (Schulz et al., 2006). Camera trap deployments could potentially be used to test this assumption and

349 calibrate playback for use as a rapid assessment method. Additionally, the activity data from camera

350 traps could be used to inform survey design by providing information on peak seasonal activity.

351 Interestingly the early chick rearing LDA from mid-season was best at predicting breeding status of

352 our test burrows. Most surveys focus on the start of the breeding season when birds are most vocal

353 and responsive to playback and burrow inspection causes low disturbance or the end of the

354 breeding season when breeding success can be inferred.

355 Camera traps have a number of potential advantages over traditional survey methods. Playback is

356 only applicable to occupancy estimation, not to studying breeding numbers and success. We have

357 found burrow inspection to be observer biased, its reliability varies according to the quality of the

358 burrow-scope available (Lavers et al., 2019), and it can cause disturbance. The accuracy of estimates

359 of breeding success are also dependent upon the frequency of burrow checks, whereas camera traps

360 can yield precise timings of key events such as fledging or predation. Camera trap studies are less

361 susceptible to personnel bias, and once established can potentially be repeated with relative ease

362 and minimal disturbance. It is unclear how representative an occupancy estimate is when it is based

363 upon data from a single season as is often the case. Occupancy varies between years because some

364 species do not breed annually (Chastel, 2008), and stochastic events make some years more

365 conducive to breeding than others. Adopting methods that can span several breeding seasons with

366   little inter-annual bias in data collection will help to uncover some of these important patterns in

367   seabird breeding dynamics.

368   We recorded several unexpected species and behaviours at cameras with serendipitous benefits.

369   There is no reliable data on historic seabird populations on Macquarie Island before the impacts of

370   invasive species (Brothers, 1984). Small petrels were reportedly abundant on coastal slopes but their

371   identity is uncertain (Jones, 1980). Within living memory Antarctic Prions have been confined to the

372   upland plateau so our camera trap images of them frequenting a lowland Blue Petrel colony and

373   entering Blue Petrel burrows are the first records of the species utilising lowland areas since pest

374   eradication. Similarly, White-headed Petrels have a restricted range and were reportedly absent

375   from the north of the island, however, one individual at a Grey Petrel burrow on North Head, the

376   extreme northern end of Macquarie Island and outside their current breeding range was recorded

377   on our cameras. While these observations highlight the potential of cameras for gathering ecological

378   data, Fischer et al.'s (2017) conclusion that camera traps are unsuitable for studying breeding

379   biology at individual diving-petrel nests also applies in part to our study species. Not all entries and

380   exits are captured by camera traps, and the precise position of the deployed camera can strongly

381   affect what is recorded. Camera traps would, therefore, not be reliable for high resolution

382   behavioural and phenological research such as studying incubation shift duration, and the frequency

383   of chick provisioning.

384   We did encounter a number of challenges that will need addressing if camera traps are to be

385   adopted more widely in burrowing seabird studies. Most important was the vast gulf in performance

386   between the two makes of camera we used. Technologies are improving all the time, with open

387   source platforms now allowing remote sensing to be taken to scale for major monitoring

388   programmes (Hill et al., 2019), but it is worth noting the importance of budgeting appropriately for

389   survey equipment when the costs associated with visiting seabird islands are so high. Second,

390   tagging images is difficult. Citizen science platforms and improvements in machine learning are

391   transforming the ability of monitoring programmes to tag large image datasets (Norouzzadeh et al.,

392   2018; Willi et al., 2019), but behaviours may still be problematic. We had difficulty differentiating

393   chicks from adults close to fledging. Only by manually coding images did we develop a familiarity

394   with individuals which could aid identification. For example, bills of procellariform petrels develop

395   slowly, and chicks often had noticeably slender bills even close to fledging, but judgements like this

396   are highly subjective and potentially beyond a classification algorithm or volunteer programme. In

397   one case it became apparent that two different chicks from adjacent burrows were triggering one

398   camera. They were at different stages of development and could be readily identified. Ultimately

399   this allowed us to confirm fledging success and timing from two burrows the status of which was

400   uncertain based upon manual burrow-inspection, but after the first bird fledged the second

401   switched burrows temporarily. If this behaviour is common it adds an additional challenge to

402   determining breeding success. Cameras also needed some maintenance during the season. As well

403   as battery and SD card replacement, some lenses developed condensation, and vegetation growth

404   affected false trigger rates and obscured images.

405   We have shown that camera traps are highly effective at recording nest-level activity and behaviours

406   of burrowing seabirds, and importantly that breeding status can be modelled as a function of these

407   activity patterns. Significant investment is needed in terms of financial and human resources to

408   purchase cameras, deploy and maintain them, calibrate camera data with burrow breeding status,

409   and to tag images. Many of these investments can be front-loaded and we argue are worthwhile for

410   long-term monitoring thanks to the benefits camera traps deliver—reduced uncertainty, widely

411   applicable methodologies that can be applied by non-technical field workers, and low impacts on

412   study species. For short surveys this effort is unlikely to be worthwhile and traditional surveys will be

413   necessary.

414

415   **Authors' contributions**

416   JB conceived the ideas and designed methodology; JB and PP collected the data; JB analysed the

417   data; JB led the writing of the manuscript. All authors contributed critically to data interpretation,

418   drafts and gave final approval for publication.

419

433

434   **Data Sharing**

435   Raw data and full code for the analysis are available from the Australian Antarctic Data Centre.

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438

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578

579   **Table 1:** Performance metrics for Reconyx and SpyPoint cameras positioned at seabird burrow

580   entrances.

make	species	n burrows	target:false triggers	proportion of trap nights >0 images	entries:exits		
					min	max	SD
Reconyx	All	13	18.86	0.64	0.20	1.56	0.41
Reconyx	Grey Petrel	12	19.89	0.63	0.20	1.56	0.41
Reconyx	Blue Petrel	1	6.39	0.85	0.96	0.96	0.00
SpyPoint	All	24	1.30	0.39	0.52	5.67	1.09
SpyPoint	Grey Petrel	4	3.08	0.33	0.60	1.07	0.17
SpyPoint	Blue Petrel	20	0.95	0.40	0.52	5.67	1.16

581   **Table 2:** Group means for variables derived from adult activity at Grey Petrel burrow entrances that

582   were used in Linear Discriminant Analysis, and their contributions to the first linear discriminant.

stage	variable	breeding	non-breeding	LD1
	absences	1.87	1.70	-0.09
incubation	high activity	0.05	0.10	13.63
	low activity	0.59	0.28	-12.30
	absences	1.89	2.55	0.71
early chick-rearing	high activity	0.03	0.18	9.32
	low activity	0.59	0.38	-2.65
	absences	3.32	6.75	1.05
late chick-rearing	high activity	0.02	0.04	-11.69
	low activity	0.34	0.20	5.53

583   **Table 3:** Predicted breeding status in two known-status test burrows from Linear Discriminant

584   Analyses.

		prediction	
	LDA model	breeding	non-breeding
GP-NH-10: **breeding**	incubation	-	-
	early chick-rearing	0.9995	0.0005
	late-chick-rearing	0.9986	0.0014
GP-NH-13: **non-breeding**	incubation	1.0000	<0.0001
	early chick-rearing	0.0911	0.9089
	late-chick-rearing	0.9998	0.0002

585   **Table 4:** Burrow occupancy in different species estimated using different survey methods.

586   Occupancy and confidence intervals are calculated from diagnosed burrows only. Type 1 error was

587   not calculated for playback because occupancy status of all non-responsive burrows was listed as

588   'uncertain' owing to the possibility of non-responsive birds.

Method	Parameter	Antarctic Prion	Blue Petrel	White-headed Petrel	Grey Petrel
Playback*	Occupancy (± 95% CI)	1.00 (0.55-1.00)	0.56 (0.42-0.70)	-	-
Burrowscope	Occupancy (± 95% CI)	0.32 (0.19-0.46)	0.32 (0.26-0.39)	0.50 (0.43-0.56)	-
	Type 1 error	0.24	0.06	0.06	-
Handheld	Occupancy (± 95% CI)	-	-	0.66 (0.59-0.73)	-
camera	Type 1 error	-	-	0.02	-
Combined	Occupancy (± 95% CI)	0.67 (0.55-0.79)	0.40 (0.33-0.47)	0.59 (0.53-0.66)	0.42 (0.36-0.49)

589 **Table 5:** Inferred breeding status of seabird burrows based upon initial, and follow-up visits.

Burrow type	Spp. detected	Number of visits	Occupied burrows			Empty	Uncertain
			Breeding	Non-breeding	Status uncertain		
Grey Petrel	Grey Petrel	1	11	-	90	135	4
	Grey Petrel	4	78	4	19	135	4
	Sooty Shearwater	1	-	-	2	-	-
	Sooty Shearwater	4	-	-	2	-	-
White-headed Petrel	White-headed Petrel	1	2	-	112	48	99
	White-headed Petrel	3	88	8	42	44	95
	Sooty Shearwater	1	2	-	6	-	-
	Sooty Shearwater	3	3	4	3	-	-
Blue Petrel	Blue Petrel	1	38	-	44	126	49
	Blue Petrel	2	39	-	44	126	48

590

Figure 1: Camera trap set-up and results: a) checking Spypoint cameras in a Blue Petrel colony, b) a Blue Petrel emerging from its burrow, c) a Recconyx camera outside a Grey Petrel burrow, and d) a Grey Petrel chick close to fledging exercising outside its burrow.
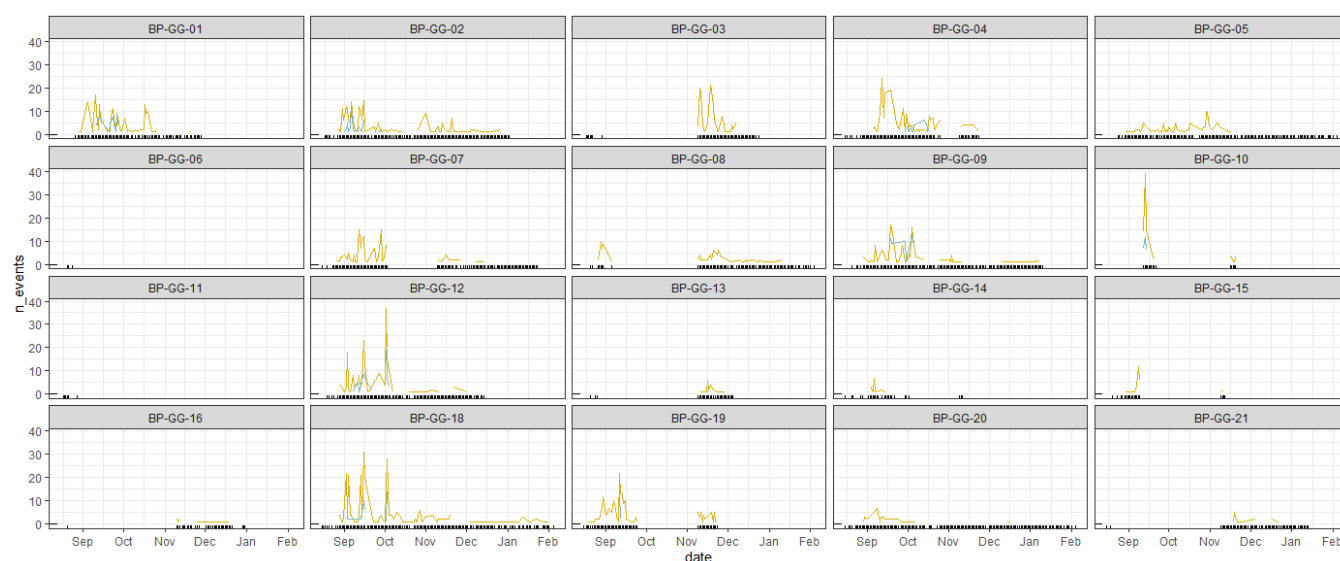
Figure 2: Combined entries and exits (yellow) and tidying events (blue) recorded at Blue Petrel burrow entrances during the breeding season. Rug plots show the days on which any images were captured, i.e. the camera was known to be functioning correctly.
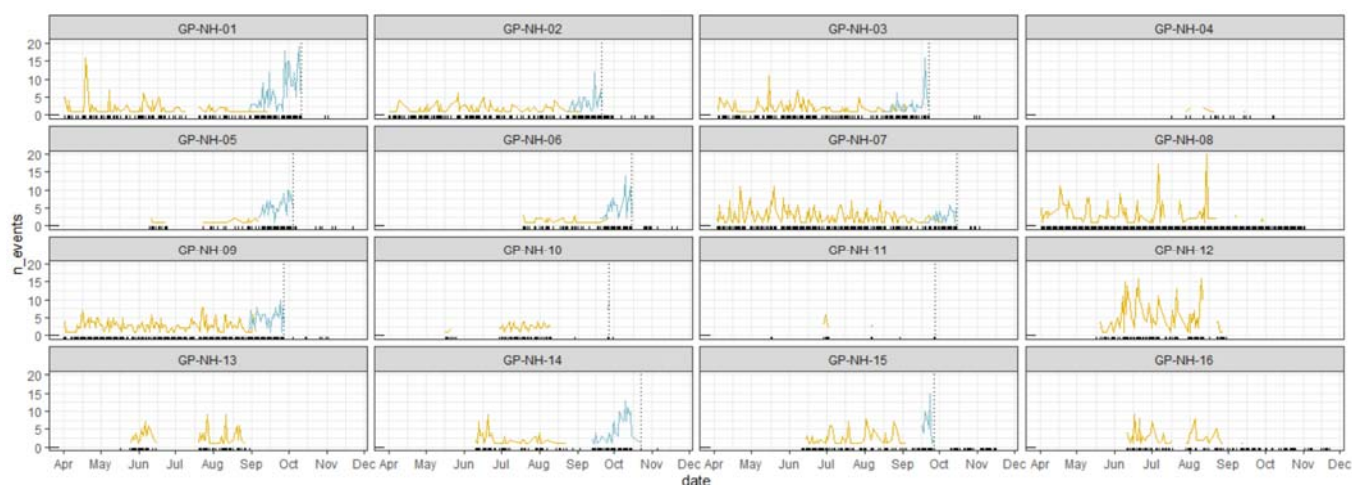
Figure 3: Total number of events featuring adults (yellow) and chicks (blue) at Grey Petrel burrow entrances during the breeding season. Rug plots show the days on which any images were captured, i.e. the camera was known to be functioning correctly. Vertical dotted lines represent inferred fledging dates.
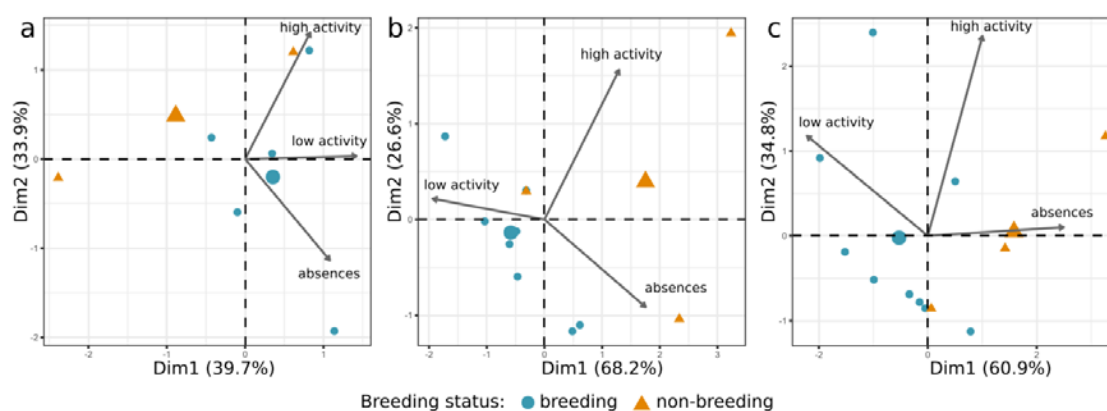
Figure 4: Principal Component Analyses of variables derived from adult activity data captured by cameras at Grey Petrel burrow entrances. Plot a) is activity data from during incubation, b) is from early chick-rearing and c) is from late chick-rearing. The larger symbols represent group means.
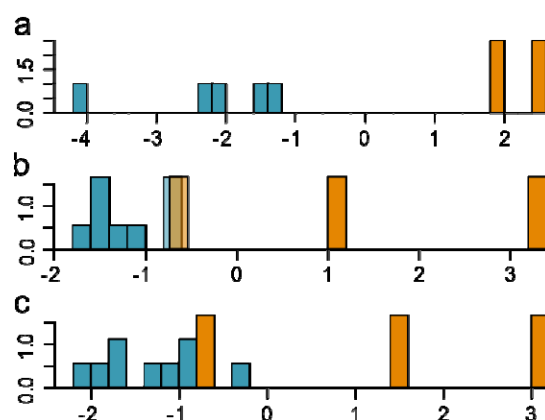
Figure 5: Linear Discriminant Analyses of breeding and non-breeding Grey Petrel burrows based upon variables derived from adult activity at burrow entrances. Model a) is activity data from during incubation, b) is from early chick-rearing and c) is from late chick-rearing. Breeding burrows are depicted in blue, non-breeding in orange.
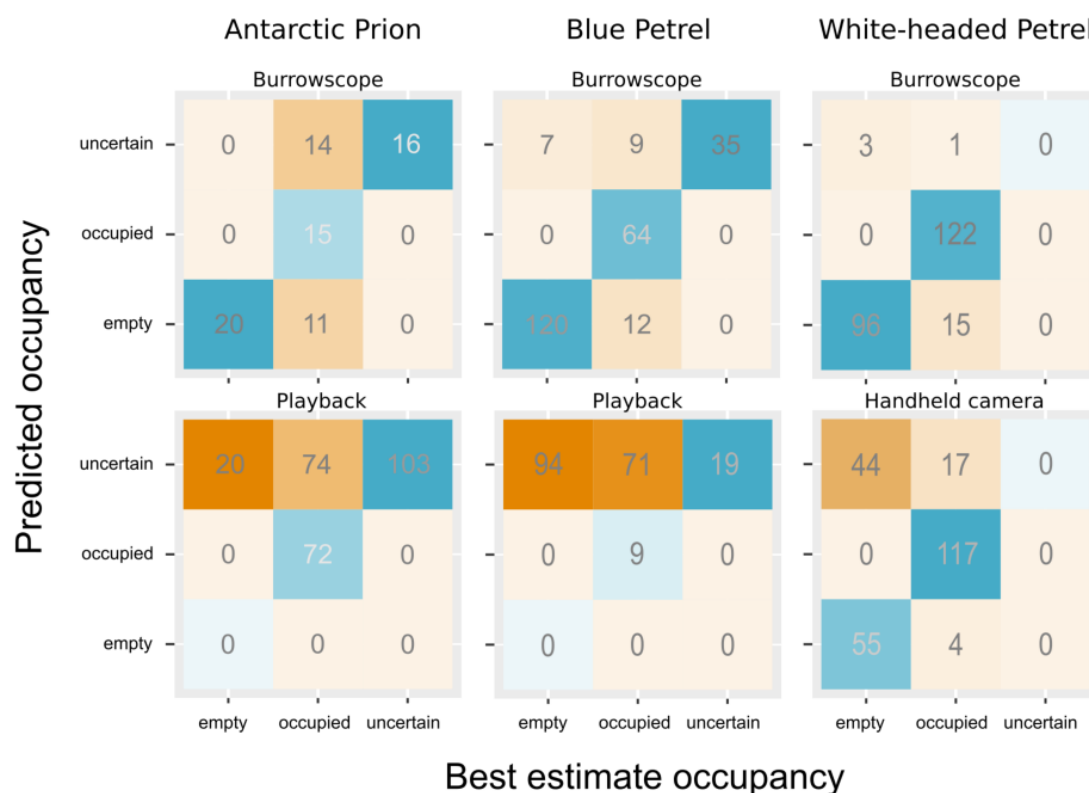
Figure 6: Confusion matrices of predicted versus observed occupancy from different methods. Predicted occupancy is based upon the first visit only, equivalent to one-off occupancy estimation feasible in most surveys. Observed occupancy is based upon all methods and all visits. Predicted = observed is shaded green, predicted ≠ observed is shaded yellow, with higher matching or mismatching ratios shaded darker.