Accounting for detectability and abundance in survey design for a declining species

Phoebe A. Burns¹,² | Claire McCall³ | Kevin C. Rowe² | Marissa L. Parrott⁴ | Ben L. Phillips¹

¹School of BioSciences, University of Melbourne, Parkville, Victoria, Australia
²Sciences Department, Museums Victoria, Melbourne, Victoria, Australia
³Wildlife Unlimited Pty. Ltd, Bairnsdale, Victoria, Australia
⁴Wildlife Conservation and Science, Zoos Victoria, Parkville, Victoria, Australia

Correspondence
Phoebe A. Burns, School of BioSciences, University of Melbourne, Melbourne, Vic. 3010, Australia.
Email: phoebe.burns@live.com

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Abstract

Aim: As populations decline they become harder to detect simply because there are fewer animals to observe. In such cases, survey effort that was once reliable may become inadequate and the species incorrectly labelled locally extinct, causing management efforts to cease. For declining populations, then, we need to determine the survey effort necessary to detect the species, assuming only a single individual is present at a site. Detectability, however, often varies widely with seasonal, behavioural and environmental variables. Thus, we need statistical analyses and survey design which can deal with highly variable detection rates and allow us to detect even very small populations. This is especially true in Australia, where many mammal species are experiencing serious decline. Here, we examine a threatened Australian rodent, the New Holland Mouse (Pseudomys novaehollandiae): we determine minimum survey requirements for reliable detection and show that historical survey effort is inadequate to assert local extinction.

Location: Victoria, Australia.

Methods: Using a 48-year live-trapping dataset, we estimated P. novaehollandiae abundance and detectability using N-mixture modelling in a Bayesian framework, testing the effects of seasonal fluctuations and environmental variables to determine ideal conditions for occupancy surveys. We used these findings to assess the adequacy of historical resurvey efforts in confirming local extinctions.

Results: We found that detectability followed seasonal fluctuations distinct from changes in abundance, was strongly reduced by brighter moon phases, and slightly increased over the course of a survey and when raining. When abundance was low, standard historical survey efforts were inadequate to assert the species’ absence with appropriate statistical confidence, indicating that further surveys would be required to test purported local extinctions.

Main conclusions: Our results highlight the potential for considerable intra-species heterogeneity in detectability caused by shifting local abundances and survey...
1 | INTRODUCTION

Misinterpretation of “absence” data can have catastrophic consequences for threatened species and their conservation (Boakes, Rout, & Collen, 2015; Chadès et al., 2008; Kéry, 2002). Whether through insufficient effort, poor survey conditions or other factors, non-detections may be recorded as absences when a species is in fact present (MacKenzie et al., 2002; Rout, Heinze, & McCarthy, 2010; Wintle, Kavanagh, McCarthy, & Burgman, 2005). Inaccurate assessments of species’ occurrence and abundance also bias species distribution models and misinform habitat associations (GuillerArroita, 2016; GuillerArroita, Lahoz-Monfort, MacKenzie, Wintle, & McCarthy, 2014; Lahoz-Monfort, GuillerArroita, & Wintle, 2014). In situations where threat mitigation and preservation of an occupied area depends on timely proof of a species’ occurrence and abundance (e.g., exclusion zones in logging coupes for critically endangered Leadbeater’s Possum; Nelson et al., 2017), or where intervention is critical for a species’ persistence (e.g., managing remnant frog populations following decimation by Chytrid fungus; Scheele et al., 2014), false absence data can actually contribute to local extinctions (Boakes et al., 2015; Rout et al., 2010). To minimize the risk of this occurring, there is an acute need for informed, rationalized survey effort and critical interpretation of survey data (Boakes, Fuller, McGowan, & Mace, 2016; Reed, 1996).

The probability of finding a species at a site if it is present—the species’ detectability—is central to appropriate survey design (GuillerArroita, Ridout, & Morgan, 2010; MacKenzie et al., 2002; Reed, 1996; Wintle, Walshe, Parris, & McCarthy, 2012). Detectability varies widely among species, even for closely related taxa (Wintle et al., 2005). Within species, detectability can vary with a multitude of factors, such as seasonal changes in behaviour (Kéry, 2002; Willson, Winne, & Todd, 2011), habitat quality (Wintle et al., 2005), temperature (Smith, Bull, & Driscoll, 2012), elevation (Kéry, 2008), rainfall (Otto & Roloff, 2011; Wintle et al., 2005), wind speed (Wintle et al., 2005) and moon phase (Gilmore, 2016; Lillywhite & Brischoux, 2012). Survey technique, effort and duration can also affect detection probabilities (Molyneux, Pavey, James, & Carthew, 2018; O’Connell et al., 2006). In capture-based surveys, animals may acclimate to the presence of a trap, becoming more trappable or less trappable over the duration of a survey as they overcome trap neophobia, become “trap happy”, or develop avoidance behaviour (Gibson, 2011; Tasker & Dickman, 2001; Willson et al., 2011). Failure to investigate and understand these factors when planning surveys and interpreting survey results can lead to misinterpretation of species’ abundance and population trends, or even premature assumption of the species’ local extinction (Kéry, 2002; Kéry et al., 2009).

Detectability also varies systematically with abundance (Kéry, 2002; McCarthy et al., 2013; Scheele & Gillespie, 2018). Simply, if all other survey and site conditions remain constant, the more individuals present, the greater the chance of detecting the species. This can be captured in a relationship between individual- and species-level detection probability: \( P_s = 1 - (1 - P_i)^N \). Here, \( P_i \) is the mean probability of detecting an individual at a site, \( N \) is the number of animals present at that site, and \( P_s \) is the resultant species-level detectability (Royle & Nichols, 2003). Where abundance changes over time, species-level detection will vary in concert. The effect of abundance on species-level detection is a particular issue for surveys of declining species. Here, detectability worsens with the decline of the species: survey effort that was once adequate to detect the species becomes inadequate (Kéry, 2002).

Adequate survey design for declining species must consider potential declines in abundance jointly with environmental, seasonal and methodological influences on detectability and survey efficacy. Happily, statistical models developed over the last decade now enable us to incorporate detection probability and abundance as linked processes that influence the number of individuals we observe in a given survey (Royle & Dorazio, 2009). By fitting these models to historical survey data, we can often make inference on both detection and abundance. Such an enterprise not only allows us to estimate population sizes, but also detection probabilities for given survey effort (Royle & Dorazio, 2009). By specifying an abundance of one (that is, a single animal), we can estimate survey effort required to reliably detect even the smallest population. Such knowledge is critical if we are to manage declining species and not inadvertently contribute to their extinction through ignorance of where populations remain (Kéry, 2002; Kéry et al., 2009).

These considerations are particularly acute in Australia, which is in the midst of the most rapid mammalian extinction crisis in recorded history (Woinarski, Burbidge, & Harrison, 2015). Here, understanding of threatened species’ current and past distributions is typically poor (Bilney, Cooke, & White, 2010). Initial historical detections of Australian species often happened by chance, or as part of broad-scale surveys with minimal per-site survey effort (e.g., Victorian Fisheries and Wildlife Department surveys of the 1970s; Emison, Porter, Norris, & Apps, 1978; Gilmore, 1977). Haphazard survey effort means that many species can go undetected in an area for decades, not because they are absent necessarily, but because no effort is made to survey for them (Boakes et al., 2016; Burns,
When resurvey efforts are later conducted and the species is not detected, we struggle to know when or why the species disappeared, and even whether they are truly extirpated or we have just not tried hard enough to find them (Boakes et al., 2016; Burns et al., 2016; Reed, 1996; Woinarski, Burbidge, & Harrison, 2018). This has repeatedly been demonstrated in rediscoveries of “Lazarus” species in Australia—species that have gone undetected for so long that they were falsely presumed extinct, such as the Leadbeater’s Possum (Gymnobelideus leadbeateri, found again in 1961 after 50 years, or the Mountain Pygmy Possum (Burramys parvus), known only from fossil records until 1966 (Short & Smith, 1994). While historical knowledge gaps are often irreparable, and we can only hypothesize about prior distributions and the timing and causes of decline for many species, we can still make use of these haphazard detection histories to improve future monitoring efforts, and to identify local extinctions with statistical confidence.

The New Holland Mouse (Pseudomys novaehollandiae), a threatened rodent species native to south-east Australia, has a classically haphazard detection history. The small (12–28 g), nocturnal species was first described in 1843, but went entirely undetected for almost a century between 1886 and 1967 (Mahoney & Marlow, 1968). It was first captured in the states of Victoria, Tasmania and Queensland in 1970, 1976 and 1996, respectively (Van Dyck & Lawrie, 1997; Hocking, 1980; Seebeck & Beste, 1970). Like many native Australian rodents, P. novaehollandiae is readily lured by standard mammal bait (rolled oats, peanut butter and golden syrup) and easily trapped when at high local abundance (McCall, Reside, & Collyer, 2015), thus its poor early detection history is likely due to lack of effort, rather than it being an innately cryptic species. Resurvey efforts since these initial discoveries indicate that many populations have declined, potentially to local extinction (Lazenby, Bell, Driesen, Pemberton, & Dickman, 2018; Wilson, 1996; Wilson, Lock, & Garkaklis, 2017). Historically, the standard survey effort for P. novaehollandiae was three consecutive nights of live trapping using 30 Elliott traps, with abundance indices drawn from trap success or capture–mark–recapture data (Atkin & Quin, 1999; Lock & Wilson, 1999; Quin, 1996; Wilson, White, Hanley, & Tidey, 2005). As the species declines in abundance, this effort may no longer be sufficient for detection, and low-abundance populations may be mistakenly considered extinct. Further, abundance estimates may be clouded by seasonal fluctuations in detectability, due both to true shifts in abundance and to behavioural changes across the year; dispersal of young occurs in March–May following the November–March breeding season (Fox, 1982; Kemper, 1980; Wilson, 1991; Wilson et al., 2005). With purported local extinctions at seven of 12 historically occupied regions in Victoria (Quin, 1996; Wilson et al., 2017), there is an acute need to delineate the species’ current distribution to guide management efforts and test causes of decline.

Here, we assess the effects of seasonal and environmental variables on the abundance and detectability of P. novaehollandiae. We define minimum-abundance survey requirements for reasonable confidence in the species’ absence and identify key factors to consider in survey planning and the interpretation of historical data.

## METHODS

### Survey data

We collated Victorian *P. novaehollandiae* Elliott trapping survey data spanning 48 years from the species’ initial detection in the state in 1970 to April 2018, sourced from historical field notes, recent reports and our own survey work (see Table S1 for list of surveys and Appendix 1 for published data sources). Briefly, animals were trapped in Elliott small live mammal traps (Elliott Scientific Co.; size 90 mm × 100 mm × 330 mm) baited with a mixture of peanut butter, golden syrup and rolled oats. Each trap contained non-absorbent nesting material for insulation and was wrapped in a plastic tube for protection during poor weather conditions. We recorded nightly trap results as counts of individuals, nightly trap effort, survey dates and precise locality. Following quality control measures, we included data from 330 surveys of 111 sites (>100 m apart; *P. novaehollandiae* movements recorded during surveys are usually <100 m; Quin, 1996; Lock & Wilson, 1999) in south-east Melbourne and Gippsland, collected over 347 unique nights, totalling 36,274 trap nights. Average survey effort was 31 Elliott traps (range: 8–100 traps) set for 3.5 nights (range: 1–6 nights). We were unable to extract site dimensions from the dataset and instead use survey effort (number of Elliott traps) as a proxy for site area, as traps were commonly spaced 10–20 m apart and increasing the number of traps in a grid or transect increased the area of a site.

### Abundance-detectability modelling

We used the N-mixture model approach of Royle and Nichols (2003) to jointly estimate site-level abundance (where a site represents the surveyed area and not the local population size) and individual-level detectability. This approach uses repeated count data to estimate individual-level detectability (*P* in the above formula) and site-level abundance (*N*), which together affect the site-level detectability of a species (*P*). The likelihood of the data (the number of individuals captured each night) is described by a binomial distribution parameterized with the true number of individuals at the site and individual-level detection probability. The “true” number of individuals at a site is treated as a latent variable, drawn from a Poisson distribution, where the expected value of the Poisson is specified with a linear model (and in this case, a log link). Individual detectability is also specified as a linear model (and a logit link) in which covariates affect detection.

Our abundance model incorporated an intercept, *μ*₁, and two continuous fixed effects: (a) survey effort (*E*: number of Elliott traps per night, as a proxy for the area of each site; increasing the number of traps per site here increases the size of the site, rather than the density of trapping effort, and larger sites would be expected to overlap with the home ranges of more individuals); and (b) to capture annual cycles in abundance, a first-order Fourier series (where the first constant is absorbed into *μ*₂ of day of the year (*D*: in radians). We also specified random effects of year of survey (*γ*; 25 levels), site (*s*; 111 levels; immediate survey location defined by continuous...
trapping grid or transect) and region (r; nine levels; geographically and reproductively isolated habitat patches).

\[
\log(N_i) = \mu_N + \beta_E E + \beta_2 \cos(D) + \beta_3 \sin(D) + \gamma_1 + s_i + r_i
\]

Our individual-detectability model comprised an intercept, \( \mu_N \) and four continuous fixed effects: (a) moon brightness (M: 0–1; 0 = new moon, 1 = full moon); (b) consecutive night of survey (T: 1–n nights); (c) daily rainfall (R: 24-hr rainfall prior to and including each survey night 6 a.m.–6 a.m., as recorded at nearest Bureau of Meteorology weather station, 10–30 km from sites; Bureau of Meteorology, 2018); and (d) time of year (D). The effect of time of year was again specified as a first-order Fourier series (where the first constant is absorbed into \( \mu_N \)) of day of the year (in radians) to specify annual cycles in detection. To assist interpretation, we graphed seasonal detectability as \( P_x \) rather than \( P_T \) thus accounting for seasonal fluctuations in abundance.

\[
\text{logit}(P_T) = \mu_T + \beta_4 M + \beta_5 T + \beta_6 R + \beta_7 \cos(D) + \beta_8 \sin(D)
\]

To aid numeric model fitting, we scaled all continuous variables (except day of the year) to have a mean of zero and unit variance. We used a Bayesian framework and sampled priors using JAGS v 4.3.0 (Plummer, 2017) via the package "rjags" (Plummer, 2016) in the program R v 3.4.3 (R Core Team, 2017). We set minimally informative priors (see Table 1), excluded a burn-in of 300,000 iterations and ran three chains for an additional 80,000 iterations sampling every fifth iteration. We assessed convergence using visual inspection of trace plots and the Gelman–Rubin convergence diagnostic (Gelman & Rubin, 1992).

### 2.3 Survey design

To compare the minimum survey effort (nights) required to obtain 95% confidence in \( P. \text{novaehollandiae} \) absence under different conditions, we calculated probability of false absence (\( A_x \)) values and plotted these against night of survey. As \( P_T \) (and so \( P_x \)) varies across survey night, \( T \), the probability of a false absence is given by

\[
(1 - P_{S,T}) (1 - P_{S,0})... (1 - P_{S,24}), \text{ where } P_{S,T} \text{ is the species-level detection on night, } T. \text{ To achieve 95% confidence in the species’ absence, } A_x \text{ must fall below 0.05. For all calculations, we set the number of traps to 30 Elliott traps (standard historical survey effort) and no rain during survey (most common state). To examine seasonal variation, we calculated } A_x \text{ values at new moon and full moon for the 1st January (summer), 1st April (autumn) and 1st October (spring), at minimum } (N = 1) \text{ and modelled annual peak average per-site abundance (} N = 3.5).\n
### 3 RESULTS

#### 3.1 Abundance-detectability modelling

Visual inspection of trace plots showed chain convergence and the Gelman–Rubin point estimates ranged from 1.00 to 1.04, with upper confidence intervals from 1.00 to 1.06. Our analysis found seasonal fluctuations in abundance (Figure 1a; Table 1), corresponding with the influx of new recruits during the breeding season in January–February (Fox, 1982; Kemper, 1980; Wilson, 1991; Wilson et al., 2005). Increasing number of Elliott traps set...
dance was explained by differences among years, sites and regions during a survey (Figure 2d).

Species’ detectability is intimately related to abundance, and as individuals died (Wilson, 1991; Wilson et al., 2005). However, seasonal effects on behaviour complicate the direct link between abundance and detectability; individual-level detectability fell dramatically over November–February, so even accounting for the higher abundance, species-level detectability was lowest over December–February (Figure 2a). This decline in detectability from November through February is commonly observed in the species.

3.2 | Survey design

The survey effort required to reach 95% confidence in the absence of P. novaehollandiae varied considerably with abundance, season and moon phase. We derived \( \pi_a \) values from the abundance-detectability model for 30 Elliott traps with no rainfall during the survey. With per-site abundance of 3.5 individuals, one or two nights of survey around a new moon in April or October would have a >95% probability of detecting the species. However, at minimum abundance (one animal per site), the number of consecutive nights survey required for 95% confidence in absence was up to five nights at a new moon in April and greater in other moon phases (Table 2; Figure 3). Surveys in December–February and surveys around full moons consistently required impractically high numbers of consecutive nights trapping for confidence in the species’ absence (Table 2; Figure 3).

4 | DISCUSSION

Species’ detectability is intimately related to abundance, and as species decline, previously adequate survey effort can become inadequate (Kéry, 2002; McCarthy et al., 2013; Royle & Nichols, 2003). Here, we used a 48-year trapping dataset to examine how abundance and detectability vary independently and together with site and survey conditions. Our analysis demonstrates considerable variation in the abundance and detectability of the threatened and declining P. novaehollandiae and shows also how other factors (i.e., moon phase, seasonal behaviours) may at times have a stronger influence on detectability than abundance. Our modelling makes inference on individual-level detection, which allows us to calculate the survey effort required to detect the species when it is at minimum abundance (one individual at the site) and mean maximum abundance (approximately 3.5 individuals per site)—figures that vary considerably with changing survey timing and conditions. This minimum-abundance survey effort is the appropriate metric if we are to be confident that the species is not present, but has rarely been met when surveying for our species, and is substantially higher than the effort required to detect the species when it is at its historical peak mean per-site abundance. Failing to account for how detectability decreases as populations decline or as survey conditions change can massively underestimate the survey effort required to achieve confidence in a species’ absence or lead to poor estimation of species’ abundance (Stewart, Butler, Harris, Johnson, & Radke, 2017). This bias may cause us to falsely affirm the species’ absence at a site and so underestimate the species’ occupancy at a regional scale (Cubaynes et al, 2010; Mazerolle et al., 2007; Thompson, 2002).

While we can calculate species-level detectability at fixed abundance, abundance itself is a dynamic variable, changing in response to environmental conditions. Foremost for P. novaehollandiae is the effect of season on abundance. Abundance peaked in late January–early February (Figure 1a), coinciding with the late stages of the breeding season and recruitment of new individuals into the population and declined through May–September as individuals died (Wilson, 1991; Wilson et al., 2005). However, seasonal effects on behaviour complicate the direct link between abundance and detectability; individual-level detectability fell dramatically over November–February, so even accounting for the higher abundance, species-level detectability was lowest over December–February (Figure 2a).
In particular, adult males regularly disappear from the trapable population in November, then reappear as second-year males in March (Fox, 1982; Kemper, 1980; Wilson, 1991; Wilson et al., 2005). Poor detectability in November–February, despite high abundance, leaves April–October as the ideal survey period for *P. novaehollandiae*.

**FIGURE 2** Detectability estimates for *Pseudomys novaehollandiae* derived from N-mixture models (a) at a species-level (**Ps**; accounting for seasonal fluctuations in abundance) seasonally; and at an individual-level (**Pi**) (b) during different moon phases, (c) with increasing rainfall during a survey and (d) on different nights of a multi-night survey (per night, not cumulative). Shading indicates 95% prediction envelopes. All parameters in the model (Table 1) set to mean values for the calculation of each other parameter. Raw capture data (captures per night) shown as purple circles (*n* = 1,149; jittered for b–d).

**TABLE 2** Minimum survey effort (number of nights), using 30 Elliott traps with no rain, for 95% confidence in species-level detection of *Pseudomys novaehollandiae* if present (*A* < 0.05) at minimum abundance (*N* = 1) and modelled annual peak mean per-site abundance (*N* = 3.5).
Independent of abundance and season, individual-level (and so species-level) detection also varied across survey conditions. Detectability varied with moon phase and rainfall, and improved as surveys progressed. After seasonal shifts, moon phase had the strongest effect on the detectability of *P. novaehollandiae*. In some seasons, surveys conducted during the week of a full moon would require more than six times more survey nights to reach 95% confidence in *P. novaehollandiae* absence, compared with an otherwise identical survey around a new moon. This is consistent with findings that small mammal activity levels increase on moonless nights and is likely a response to the increased risk of predation on brightly illuminated nights (Gilmore, 2016; Prugh & Golden, 2014; Vickery & Bider, 1981). Our finding that *P. novaehollandiae* detectability improved with increasing rainfall during a survey may have a similar explanation in that cloud cover can reduce illumination. The inter-survey variation in detectability we observed, particularly with relation to moon phase, led to substantial variation in appropriate survey effort; variation that, if ignored, risks considerable wasted survey effort (and false absence results). By contrast, understanding patterns of variation in detectability allows us to design efficient monitoring and detection programs.
Given the considerations around naturally varying abundance and detectability, how should we allocate survey effort for *P. novaehollandiae*? There are two main survey types to consider: occupancy surveys, where only the species’ presence or absence is of interest; and demographic surveys, where more detailed questions are being asked about abundance, breeding, diet, genetics, etc. Clearly, both survey types should avoid the week around the full moon, because reduced activity here will give low detection rates. For occupancy surveys, trapping is best conducted during the peak species-level detection period in April–October and should be avoided November–February. Where a species’ abundance or detectability is highly variable (as our broad prediction envelopes indicate is the case here), the lowest values should be assumed before non-detection is interpreted as absence (Reed, 1996). Therefore, in defining minimum survey effort, we derive values from the lower end of model predictions. Provided occupancy surveys are conducted at the new moon (irrespective of rainfall), a minimum of five (April) or two (October) consecutive nights of survey are necessary to achieve statistical confidence in the species probable absence (a minimum-abundance survey effort). For demographic studies, timing is often determined by the research question; however, surveys should be wisely timed to work with seasonal fluctuations in detectability and abundance. Long-term, multi-year demographic studies require consistency in season(s) of survey to allow comparisons between years; and studies of short-term responses (i.e., to disturbance such as fire) must account for the effect of changing season underneath any perceived response. Furthermore, abundance estimates based on capture numbers should be interpreted in the context of detectability estimates, for example via N-mixture models as used here.

Except for times and places of highest detectability, historical resurvey efforts for *P. novaehollandiae* in Victoria fell below our newly defined minimum-abundance survey requirements. For instance, broad-scale surveys across historical and hypothesized *P. novaehollandiae* sites in Victoria in the 1990s typically used 30 Elliott traps per site for three nights in March–May (Quin, 1996; Quin & Williamson, 1996; Reside & Hooper, 1999). While this survey effort is sufficient if the species is at high abundance, we can now determine that it is an inadequate effort at low abundance and brighter moon phases. So, in those surveys and almost all others, survey effort has not been adequate to confidently assert absence or local extinction of *P. novaehollandiae*. This does not mean that the species has not declined or suffered local extinction. Habitat alteration and changes in land use make persistence in many locations implausible, and historically adequate effort that no longer detects a species is still a potential indication of decline. Rather, it means that the species may well persist (at low densities) in places where it is currently considered locally extinct. Further surveys are necessary before extinctions can be confirmed in several historical locations.

In many respects, *P. novaehollandiae* is a well-studied mammal species by Australian standards. That we could locate 40 years of survey data is testament to this. Given our findings, it seems very likely that other Australian mammal species (particularly rodents) will also have been inadequately surveyed in the past. This is both encouraging (many recorded “absences” may be false), but also daunting in that it lays bare the extent of effort required to adequately monitor a declining fauna. With this knowledge, the value of maximally effective survey design is abundantly clear. More generally, our work shows that failing to account for decreasing detectability as a species declines may contribute to premature assertion of local extinction and non-detection of novel populations. Given Australia’s current mammalian extinction crisis, delays in, or a lack of, threat mitigation and appropriate management of undetected and declining populations could rapidly exacerbate a species’ risk of extinction. This study highlights the enormous intraspecific heterogeneity in detectability, and how well-analysed historical data can provide new insights into a species’ current status as well as allowing us to design maximally efficient future surveys.

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**DATA ACCESSIBILITY**

Trapping data available online at Figshare: https://doi.org/10.26188/5d0b083523c27.

**ORCID**

Phoebe A. Burns https://orcid.org/0000-0003-1015-3775

Ben L. Phillips https://orcid.org/0000-0003-2580-2336

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APPENDIX 1: DATA SOURCES

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**BIOSKETCH**

**Phoebe A. Burns** recently completed her PhD at the University of Melbourne. Her research focuses on the conservation and management of threatened species. In particular, assessing species’ statuses, range shifts and declines through optimal survey techniques and designs, as well as identifying and addressing threatening processes. Phoebe works closely with land management and conservation agencies to effect on-ground change to support the persistence of threatened species.

Author contributions: P.A.B., B.L.P, C.M., K.C.R and M.L.P. conceived the ideas; P.A.B. and C.M. collected substantial parts of the dataset; P.A.B. and B.L.P. analysed the data and led the writing.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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