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Research Article

Monitoring the Abundance of Wild and Reintroduced Bilby Populations

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ABSTRACT Monitoring techniques that are non-invasive and use evidence of target species presence are particularly useful, especially for rare or highly dispersed species. We developed and tested a technique using DNA extracted from scats in conjunction with spatially explicit capture-recapture (SECR) analyses to monitor the abundance of greater bilbies (*Macrotis lagotis*) within wild and reintroduced populations in Western Australia, and verified its application against a recently reintroduced founding population. The greater bilby is an iconic threatened species and the focus of conservation management, but no efficient and reliable method to monitor their abundance has been implemented. Estimated abundance using our method (21 ± 5 [SE]), was close to the founding population at Mount Gibson (16). Wild populations monitored from 2013–2018 were relatively small, isolated, and particularly vulnerable to threats; 2 populations were extirpated during this study. A reintroduced population at Matuwa increased sevenfold over 9 years. We demonstrate that when threats are managed appropriately across a large area, and bilbies are reintroduced, they can rapidly increase in number without the need for predator exclusion fencing. © 2020 The Wildlife Society.

KEY WORDS burrowing, density, exclosure, fence, feral cats, genetics, Lorna Glen, marsupial, microsatellite, survey.

Non-invasive monitoring techniques that use evidence of the presence of target species, such as tracks, burrows, dens, pellets, and scats, have become increasingly preferred methods, particularly for species that are highly dispersed or elusive (Piggott and Taylor 2003, Proulx and Do Linh San 2016, Alibhai et al. 2017, Fragoso et al. 2019, Brown et al. 2020). Genetic material collected non-invasively (e.g., scats, shed hairs), in particular, has successfully been used to monitor a range of species globally (Banks et al. 2003, Wilson et al. 2003, Sheehy et al. 2014) and is particularly useful in the case of threatened or rare species that may be vulnerable to disturbance (Puechmaille and Petit 2007, Baldwin et al. 2010).

The greater bilby (*Macrotis lagotis*; bilby) is a threatened, elusive, burrowing marsupial with dispersed populations in remote areas of arid northern Australia (Bradley et al. 2015, Cramer et al. 2017). Despite a number of studies focusing on occupancy (Southgate et al. 2019) and mapping areas where bilbies are present (Southgate 1990, Bradley et al. 2015, Dziminski et al. 2020), no efficient and reliable method to monitor their abundance has been implemented. Refining survey and monitoring techniques is a research priority for the conservation of this species (Woinarski et al. 2014, Bradley et al. 2015, Cramer et al. 2017) and unbiased data are required to correctly determine its conservation status (International Union for Conservation of Nature [IUCN] 2012) or to assess the response of a population to management actions (Lyons et al. 2008).

The bilby was once widespread across most of mainland Australia (Marlow 1958; Seeback et al. 1990; Abbott 2001, 2008; Bradley et al. 2015). The bilby is now listed as vulnerable under the Commonwealth Environment Protection and Biodiversity Conservation Act 1999 (EPBC 1999), the Western Australian Biodiversity Conservation Act 2016 (Government of Western Australia 2016), and internationally on the IUCN Red List of Threatened Species (IUCN 2020). This species is beneficial taxonomically, as an ecosystem engineer (i.e., by modifying and creating habitat for other species; James and Eldridge 2007, Newell 2008, Chapman 2013, Fleming et al. 2014, Hofstede and Dziminski 2017), is important culturally to traditional owners (Paltridge 2016, Walsh and Custodians of the Bilby 2016), and is of national iconic significance (Bradley et al. 2015).

Since the late 1800s, bilbies have disappeared from at least 80% of their former range (Southgate 1990), and the lesser bilby (*Macrotis leucura*), a closely related species, has become extinct (Burbidge et al. 2008). The decline in bilbies has been attributed to a number of threats working directly or in combination with each other. These threats include predation by introduced feral cats and red foxes (*Vulpes vulpes*; Paltridge 2002, Bradley et al. 2015), changed and

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inappropriate fire regimes (Southgate and Carthew 2006, 2007; Southgate et al. 2007; Bradley et al. 2015), and the degradation of bilby habitat through pastoralism, introduced herbivores, and clearing (Southgate 1990, Pavey 2006, Bradley et al. 2015, Department of Environment 2016). The current distribution of the bilby is now restricted to the Tanami Desert, Northern Territory (Johnson and Southgate 1990), the Great Sandy, Little Sandy, and Gibson deserts, parts of the Pilbara and Kimberley in Western Australia (Friend 1990; Fig. 1), and an outlying population between Boulia and Birdsville in southwest Queensland (Gordon et al. 1990).

Traditional capture-mark-recapture or spotlighting studies are not suitable or efficient to estimate bilby abundance. Bilbies are trap-shy and not attracted to any form of bait, and reliably trapping an individual involves significant effort to find an occupied burrow and fence it in with traps or dig traps into the burrow (Southgate et al. 1995, Lavery and Kirkpatrick 1997, Moseby and O'Donnell 2003, McGregor and Moseby 2014). This technique is extremely labor-intensive and is a partially destructive method of sampling. Direct observation is difficult because bilbies are cryptic and very hard to observe in the wild. Bilbies are low to the ground, and vegetation often obscures spotlighting attempts; further, a significant proportion of animals may be underground.

Tracks are an unreliable indicator of bilby abundance, especially when densities are high (Paltridge and Southgate 2001, Southgate et al. 2005). Some researchers have attempted to use burrow counts (Burrows et al. 2012, Moseby et al. 2012); however, the correlation between the number of burrows and bilby abundance is poor and unreliable (Southgate et al. 1995, Lavery and Kirkpatrick 1997). A single bilby may use up to 18 burrows, sometimes up to 1 km apart, and may use up to 3 different burrows in a night (Lavery and Kirkpatrick 1997, Moseby and O'Donnell 2003). New burrows are readily dug, burrows can be abandoned, and old burrows can be reworked and reoccupied at any time (Southgate and Possingham 1995, Lavery and Kirkpatrick 1997, Moseby and O'Donnell 2003).

Bilby scats are relatively easy to find and distinctive for trained observers (Moseby et al. 2009, Southgate et al. 2019). Simply counting scats is not reliable as an index method because there is no way of excluding recounts of individuals, and the use of distance sampling of scats requires the scat deposition and decay rates to be accurately known to estimate the number of bilbies, but these rates may vary with location and season (Buckland et al. 2001, Lollback et al. 2015). Sampling bilby scats, and coupling this with genotyping individuals from the DNA in their scats, may allow an accurate calculation of bilby abundance within a population. Bilby scats are easy to collect and store, and viable DNA can readily be extracted from them (Smith et al. 2009, Carpenter and Dziminski 2017).

The objective of this study was to develop an accurate technique of estimating the number of individual bilbies within a population. Additional objectives were to test the validity of the technique at a population where a known founding population was recently reintroduced, to test the technique across large and small wild populations, and use the technique to determine the abundance of bilbies at Matuwa, where bilbies were reintroduced without predator exclusion fencing and have expanded throughout a 250,000-ha managed area.

STUDY AREA

The study was undertaken between 2013 and 2018 and the area included a vast portion of arid northern Western Australia (Fig. 1). Bilbies are a generalist species once being found across a large portion of Australia and a wide variety of bioregions (Marlow 1958; Seeback et al. 1990; Abbott 2001, 2008; Bradley et al. 2015). Bilby populations monitored were at Mount Gibson, Matuwa, and across the northwest of Australia in the Pilbara and Dampierland bioregions (Thackway and Cresswell 1995, Australian Government 2019).

Mount Gibson (29.7°S 117.4°E) is a wildlife sanctuary on the interface of the Avon Wheatbelt and Yalgoo bioregions (Thackway and Cresswell 1995, Australian Government 2019) in Western Australia (Fig. 1). It is managed by the Australian Wildlife Conservancy (AWC) and has a 7,838-ha feral predator-free fenced exclosure into which bilbies have been reintroduced (AWC 2019).

Matuwa (26.2°S 121.6°E) is a 250,000-ha former pastoral station (Lorna Glen) that is co-managed by the Department of Biodiversity, Conservation and Attractions (Western Australia) and the Martu Traditional Owners for conservation purposes. It lies on the interface of the Murchison and Gascoyne bioregions (Thackway and Cresswell 1995, Australian Government 2019). Stock and feral herbivores (mainly feral camels) have been excluded since 2000 (Morris et al. 2007*a*), annual aerial baiting with Eradicat® (Government of Western Australia, Western Australia) and supplementary foot-hold trapping of feral cats has been undertaken since 2004 (Algar et al. 2013), and fire has been managed to create a vegetation age mosaic and for protection from wildfires (Burrows and Butler 2013). Between 2007 and 2010, 144 bilbies were reintroduced into an unfenced area (Morris et al. 2007*a*, *b*; Miller et al. 2010; Pertuisel 2010), and are now found contiguously across the reserve. There is a fenced exclosure (Fig. 2); however, bilbies were never reintroduced into it.

Because of the large scale of the study area, climate (Bureau of Meteorology 2020), geology (Cockbain 2014), and vegetation (Beard et al. 2013) vary widely. Rainfall across this area varies from extremely limited and unpredictable in the inland deserts to tropical annual monsoonal wet seasons in the northern areas, and temperatures can vary from below 0°C to over 50°C. Vegetation where bilbies are found in this area usually consists of spinifex (*Triodia* spp.) hummock grasslands, shrublands (mostly wattle [*Acacia* spp.] dominated), and open woodlands, with substrates suitable for burrowing. Dominant fauna across the area where bilbies are found includes various macropods, varanid lizards, emus (*Dromaius novaehollandiae*), Australian bustards (*Ardeotis australis*),

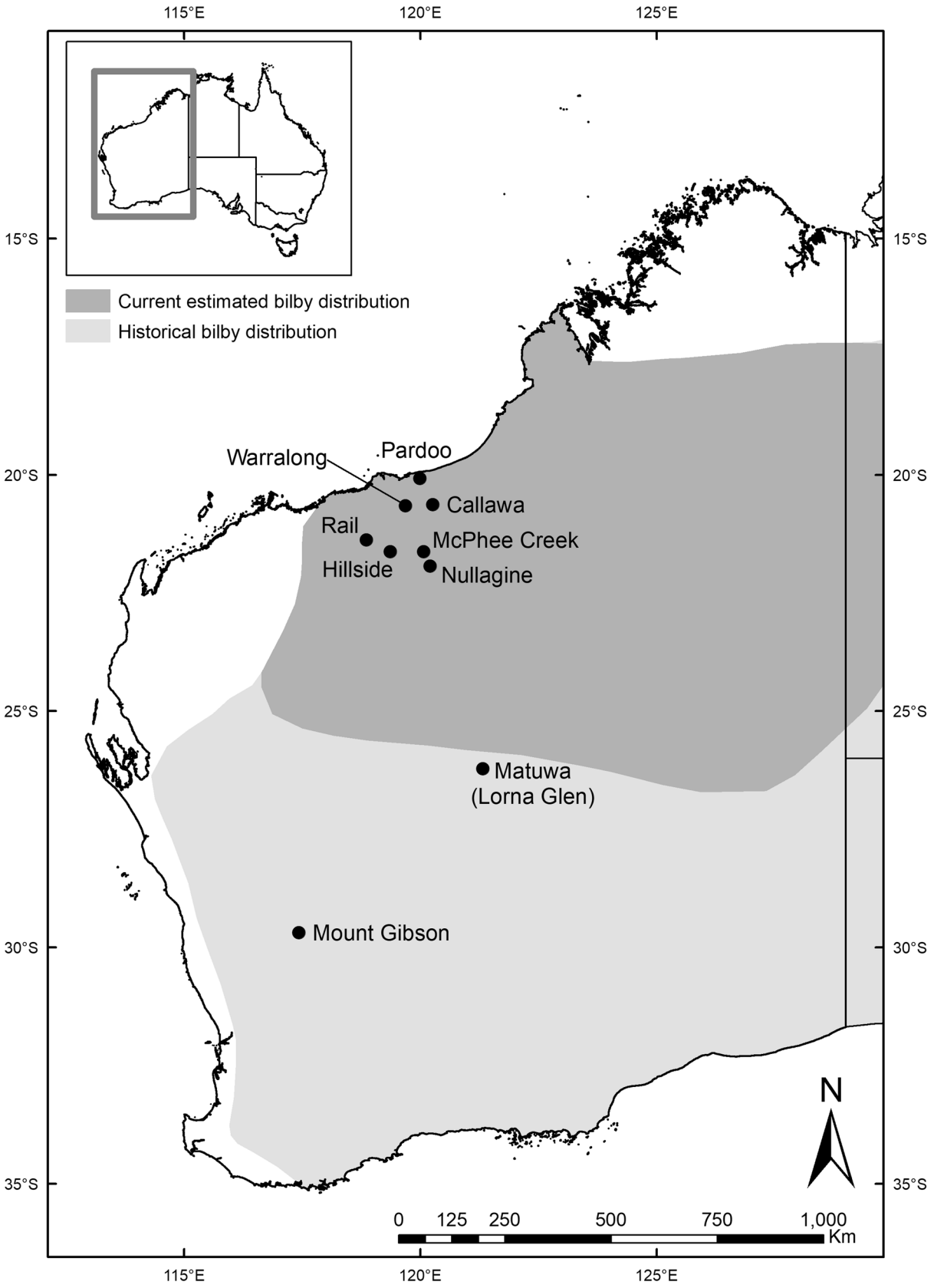

Figure 1. Locations of monitored bilby populations in Western Australia, 2013–2018.

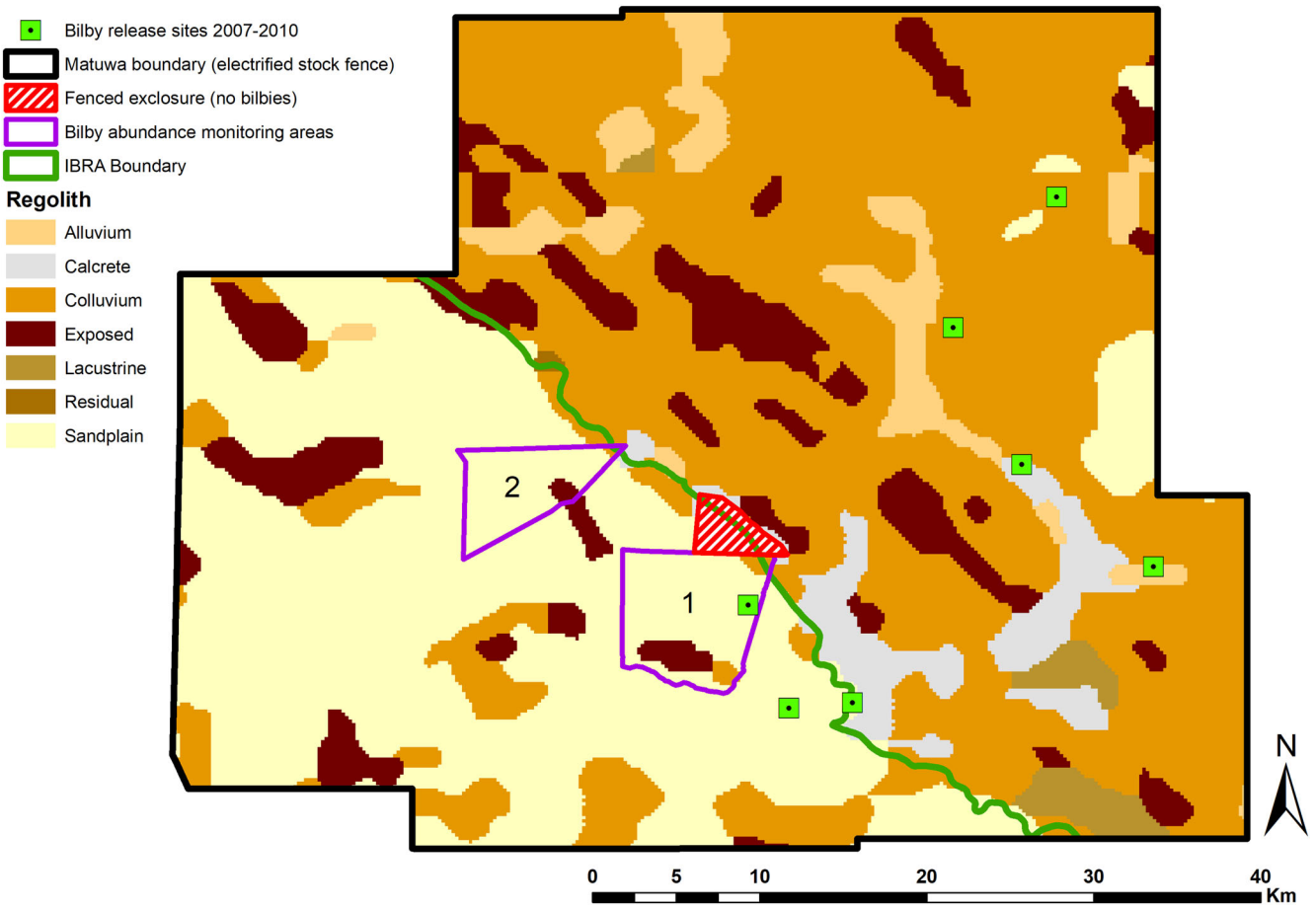

Figure 2. Areas at Matuwa (formerly Lorna Glen Station), Western Australia, where we monitored bilby abundance in 2015–2016: Possum Lake (area 1; 2015, 2016) and New Market Bore (area 2; 2016). Southwest of the Interim Biogeographic Regionalisation for Australia (IBRA) boundary is the Murchison bioregion and northeast of the IBRA boundary is the Gascoyne bioregion. Regolith represented in the legend: alluvium in drainage channels, floodplains, and deltas; calcrete, including massive, nodular, and sheet-like accumulations of carbonate, usually alluvial-colluvial but locally residual minor opaline silica and chalcedony; colluvium, which were slope deposits, including colluvium and sheetwash; exposed rock, saprolite, and saprock; lacustrine deposits, including lakes, playas, and fringing dunes; residual or relict material, including ferruginous, siliceous, and calcareous duricrust; and sandplain, mainly eolian, including some residual deposits.

feral camels (*Camelus dromedarius*), domestic cattle, feral cats, and dingos (*Canis lupus dingo*).

METHODS

Populations Monitored

We monitored the abundance of bilbies within 9 populations across Western Australia (Fig. 1) using a technique combining genotyping individuals from DNA extracted from scats with spatially explicit capture-recapture (SECR) analyses. We tested the validity of our monitoring technique at Mount Gibson, where a known founding population was recently reintroduced. We used the technique to monitor bilbies at Matuwa and at natural wild populations across the Pilbara region of Western Australia (Fig. 1), which are smaller, more discrete, and isolated. The differences between a large contiguously occupied area and small, discrete, isolated wild populations required variations in the sampling and analyses, which are described below. We undertook all research according to the standards of the Animal Ethics Committee of the Department of Biodiversity, Conservation and Attractions, Western Australia (approval number 2019-27C).

Validation population.—We sampled a single recently reintroduced population in 2017. The AWC released 16 bilbies into the Mount Gibson fenced exclosure in December 2016. Of these, 10 were female, and some of these were confirmed to be carrying young. We undertook abundance sampling during 25–28 April 2017. The pouch period for bilbies is around 80 days, the gestation period is 14 days, and litter size is 1–2 (McCracken 1990, Southgate et al. 2000, Ballantyne et al. 2009, Johnston et al. 2010, Menkhorst and Knight 2011). The period between translocation and sampling provided sufficient time for some recruitment, and possibly some mortality; therefore, there was potential for new individuals to be detected.

We defined a sampling area of 2,368 ha at the northern end of the exclosure for the validation study. We selected this area because animals were released in this area, and nearly all subsequent detections of individuals occurred here

(Volck and Thomaz 2018). On 27 km of transects traversed on foot, we collected 85 scat samples. The AWC provided tissue samples from the 16 founding individuals.

Contiguous population occupying a large area.—We sampled a reintroduced population at Matuwa in 2015 and 2016. Within the 250,000-ha contiguously occupied population we subsampled 2 areas (Possum Lake and New Market Bore) to determine densities within these areas (Fig. 2). We stratified substrate type to estimate the abundance of bilbies across Matuwa. Major substrate types across Matuwa are represented by the regolith (Department of Mines, Industry Regulation and Safety, Western Australia 2019) and partially by soil landscape mapping (Department of Primary Industries and Regional Development, Western Australia 2019). As such, we used the regolith categories (Fig. 2) in the calculation of bilby numbers derived from SECR density. We excluded exposed regolith (exposed rock, saprolite, and saprock) because they are not used by bilbies. For 2015, we used the SECR density for the Possum Lake subsampled area, and for 2016, the mean SECR density of the 2 subsampled areas, to calculate bilby numbers across Matuwa (excluding exposed regolith and the fenced exclosure). We calculated a more conservative estimate using only the sandplain regolith (sandplain, mainly eolian, including some residual deposits) for both years because the 2 subsampled areas were sandplain regolith, and this was the substrate with the most observed bilby activity (M. A. Dziminski, Department of Biodiversity, Conservation and Attractions, Western Australia, personal observation).

Wild populations - determining the extent of the population.—We sampled 8 wild populations (Callawa, Hillside, McPhee Creek, Nullagine, Pardoo, Rail, Warralong [Coongan], and Warralong [River]) between 2013 and 2018 (Table 1). Because wild populations are isolated and distinct, we were initially able to map the extent of each population boundary, and focused sampling on occupied rather than unoccupied surrounding habitat. We mapped the extent of populations using vehicles, all-terrain vehicles (ATVs, quad bikes), and on foot, depending on vegetation and terrain. We plotted global positioning system coordinates of the extent of bilby activity on electronic devices, and where no more sign of activity (tracks, scats, diggings, burrows) existed, we delineated the population boundary. We completed this process typically in 1–2 days, then overlaid transects to be traversed to ensure the population was evenly sampled. We used the population extent as the habitat mask in SECR analyses (see below).

Sample Collection

We positioned transects to sample population extents, ensuring access to start or end points from roads or tracks where available. We ensured transects crossed the majority of the population extent, within the constraints of access depending on terrain. Larger activity areas required longer transects to ensure coverage of activity areas. We traversed transects by vehicle, ATVs, and foot to collect bilby scats. Vehicle speed was at walking pace. We sampled each transect once. Individual bilbies deposit single or a small number of fecal pellets (usually 2–5) in a discrete group usually on top of, or within, the sand-spoil of food diggings. Bilby scats are difficult to age just by visual inspection.

We did not collect clearly decomposed or broken up scats. We found nearly all scats on top of, or within, the sand-spoil of a digging. Thus, we were able to assess the age of these scats by examining the state of decomposition of the associated digging. If the digging was very eroded and weathered, indicating it was created probably >2 weeks prior, then we did not collect the associated scats because the scats were less likely to yield DNA (Carpenter and Dziminski 2017). Initially, we collected some samples in paper envelopes and vials with silica gel beads, but we stored the majority of collected scats in labeled 30-ml plastic tubes, with approximately 33% filled with silica gel beads and a cotton wool ball, until DNA extraction. The silica gel ensured pellets remained dry because moisture degrades DNA. The cotton ball reduced rubbing of beads against pellets, which may remove bilby epithelial cells from the surface of the pellet, reducing available cells for DNA extraction.

We considered pellets in a group in contact with or very close to each other to be from 1 individual and stored these in 1 vial. We scooped pellets from the ground into the vial using the lid or a small stick, which we used only for the 1 sample to avoid cross-contamination. We transported vials with samples in a cooler bag, kept them out of the sun, and stored vials at room temperature until we performed DNA extractions. We did not remove scats from the field location that we did not collect in vials.

To determine where scats are likely to be deposited, and any visual cues associated with detecting scats in the field, we recorded the location of scats, whether at a burrow, at a digging, or in the open (not at a burrow or digging), at a subset of 7 populations. If we located scats at a digging, we recorded observations of whether the scats were buried or exposed at a subset of 4 populations.

DNA Extraction, PCR Amplification, and Genotyping

We used the QIAGEN QIAamp DNA Stool Minikit (QIAGEN, Hilden, Germany) as per the manufacturer's protocol, which included the scraping of 100 mg of material from the outside of each pellet, for extractions completed from 2013 to the beginning of 2014. Further testing of different extraction methods in 2014 resulted in amending the protocol to the one described by Carpenter and Dziminski (2017). After 2014 we employed a single elution using 100 µL of buffer ATE and stored DNA samples at −20°C until we amplified samples using polymerase chain reaction (PCR). We extracted DNA from tissue samples using a standard salting out extraction protocol (Sunnucks and Hales 1996).

We undertook PCR amplification using up to 8 bilby-specific polymorphic microsatellite markers (Moritz et al. 1997, Smith et al. 2009) amplified across 2 multiplexes with fluorescent-labeled markers from the G5 filter set: multiplex 1 (B02 [6FAM], B17 [VIC], B56 [PET], and B66 [NED]) and multiplex 2 (B55 [6FAM], B22 [VIC], B41 [PET], and B63 [NED]; Moritz et al. 1997, Smith et al. 2009). We ran PCRs as described in Carpenter and Dziminski (2017)

Table 1. Sampling parameters and maximum likelihood spatially explicit capture-recapture densities of bilbies at monitored populations in Western Australia, 2013–2018.

Population	Area (ha)[a]	Number of scats collected	Genotyping success	Number of individuals detected on transects	Total transect effort (km)	Density (individuals/ha)	SE
Callawa							
2015	483	48	0.31	8	8.11	0.0291	0.0130
Hillside							
2014	64	49	0.33	3	7.92	0.0475	0.0299
2017	64	17	0.29	3	7.92	0.0475	0.0299
McPhee Creek							
2013	64			≥2[b]			
2015	64	13	1.00	1	4.47		
2016		0		0	Search out to 25 km in all directions[c]		
2017		0		0	Search out to 25 km in all directions[c]		
Nullagine							
2014	192	36	0.22	1	15.70		
2015	182	46	0.61	2	9.91	0.0110	0.0089
2016	165	84	0.43	2	7.89	0.0121	0.0097
2017	128	66	0.35	3	5.51	0.0234	0.0147
Pardoo							
2013	590	40	0.23	6	12.07	0.0316	0.0203
2014		1		1	Search out to 30 km in all directions[c]		
2015		0		0	Search out to 30 km in all directions[c]		
2016		0		0	Search out to 30 km in all directions[c]		
Rail							
2014	49	50	0.38	2	7.75	0.0415	0.0335
2015	49	19	0.32	1	7.75		
2016	49	37	0.14	2	7.75	0.0684	0.0616
2017	49	20	0.30	1	7.75		
2018	42	23	0.39	2	5.98	0.0609	0.0502
Warralong Coongan							
2016	143	143	0.11	6	11.94	0.0484	0.0211
2018	26	31	0.81	3	5.02	0.1145	0.0720
Warralong River							
2018	259	77	0.29	7	10.34	0.0360	0.0148
Matuwa (Possum Lake)							
2015	7,062	227	0.52	26	45.29	0.0080	0.0017
2016	7,354	133	0.41	29	50.80	0.0132	0.0031
Matuwa (New Market Bore)							
2016	7,253	105	0.51	21	20.69	0.0109	0.0033
Mount Gibson							
2017	2,368	85	0.89	17	27.09	0.0088	0.0023

[a] Subsampled areas of a larger contiguously occupied area for Matuwa population, population extent within the exclosure for Mount Gibson, and natural population extent for all other populations.
[b] One roadkill and ≥1 individual(s) observed on remote cameras after roadkill.
[c] Area searched extensively on all-terrain vehicle and on foot for 1 week.

with 2–4 μL of DNA used in a 12.5-μL reaction for each replicate. We initially performed a minimum of 2 PCRs for each scat sample. We compared results, and where these samples provided a consensus result, we did not complete further PCRs. For samples where alleles were not clear or were inconsistent, we ran a third PCR to confirm the genotype of the individual. Where we could not achieve genotyping across all loci from the initial PCRs, we undertook no further PCRs for that sample, and eliminated the sample from the dataset.

We stored plates containing PCR products at −20°C until fragment analysis. We analyzed PCR products on an ABI3730XL Sequencer and sized fragments using Genescan LIZ 500 size standard (Applied Biosystems, Waltham, MA, USA). We scored alleles using GeneMapper version 5 (Applied Biosystems). We reviewed results manually to ensure consistent scoring of alleles and to confirm any genotyping errors such as the presence of false alleles (Bonin et al. 2004, Broquet and Petit 2004, Waits and Paetkau 2005) and allelic dropouts (Broquet and Petit 2004). We considered an allele to be a true allele when it was replicated at least twice across 3 PCRs.

We completed allele matching using the R package AlleleMatch (Galpern et al. 2012). We examined unclassified samples and samples that matched multiple unique genotypes manually and excluded them if they could

not be matched or classified as new unique genotypes. We flagged and examined any remaining mismatched alleles to determine if there were genotyping errors. Genotypes identified along transects only provide information on the number of individuals detected specifically on transects, which requires further analysis to calculate the number of individuals within the extent of the population.

Abundance Analyses

We used SECR (Efford 2004) to estimate densities and numbers of animals within the areas of activity. We undertook maximum likelihood SECR analyses using the R package secr. We completed spatial analyses using ArcGIS (Esri, Redlands, CA, USA) and QGIS software (QGIS Development Team).

We constructed habitat masks for each colony by generating the integration mesh using a buffer around the transects of $4 \times \sigma$ (σ = spatial scale parameter: Efford 2019*b*, *c*) and clipping with the population extent polygons for wild populations (area outside the population extent excluded), the outside of the exclosure at Mount Gibson (bilbies only inside of the exclosure and the area beyond the fence excluded), and the inside of the exclosure at Matuwa (no bilbies inside the exclosure and the area within the fence excluded). We grouped all samples at each monitoring event into a single sampling session and occasion.

We used data from a subset of monitoring events (~36% of dataset) of wild populations (Hillside in 2014 and 2017; Rail in 2014, 2016, and 2018; Warralong Coongan in 2016), the contiguous large population (Matuwa Possum Lake in 2015), and the validation population (Mount Gibson in 2017) to compare detectors, detection functions, and maximization methods. For each of these monitoring events, we calculated densities and numbers of animals. We used processing time (3.4 GHz Core i7-47704 core processor [Intel, Santa Clara, USA] with 16 GB RAM) together with Akaike's Information Criterion (AIC) to assess the efficiency and quality of each model. We then selected and used the best performing model based on AIC and processing time for all subsequent SECR analyses.

Detectors.—A detector in SECR is defined as a method of sampling, for example a trap, camera, or search point, a transect or area (Efford et al. 2004). We used polygon and transect detectors in model comparisons. We used polygon detectors to represent the sampling area along transects. To construct polygon detectors, we used the greatest distance of the collected samples from their corresponding transect at each monitoring event plus the addition of 1 m as a radius to generate search polygons around each transect. We then clipped these polygons using the population extent (for wild populations and the validation population), merged any overlapping polygons, and used these as polygon detectors in the SECR analyses. We used the actual positions of collected samples within the polygons for analyses. We used actual transects traversed within the population extents as transect detectors in SECR analyses. We collapsed the position of each sample onto the nearest point on the transect line for analyses.

Detection functions usually describe the decline in detection probability with distance from the home-range center for point detectors (e.g., animal traps; Efford 2004); however, for polygon and transect detectors in SECR, only hazard-based detection functions are allowed (Efford 2019*a*). These detection functions model the cumulative hazard of detection (Efford 2019*a*). We used 5 detection functions in model comparisons: hazard halfnormal (HHN), hazard hazard rate (HHR), hazard exponential (HEX), hazard cumulative gamma (HCG), and hazard variable power (HVP). Each offers alternative shapes for the detection function, with HHN and HEX having 2 parameters, and the remainder having 3 parameters (Efford 2020).

The SECR models using polygon and transect detectors may be prone to problems generating poor variance estimates and missing values for the standard errors of real parameters, which can be overcome by using the Broyden–Fletcher–Goldfarb–Shanno (BFGS) maximization method (Efford 2019*a*). Therefore, we used both the standard Nelder-Mead and the BFGS maximization algorithms in model comparisons.

RESULTS

Between 2013 and 2018, we collected 1,350 bilby scat samples along 288 km of transects across the 9 monitored populations. The number of samples collected increased with the size of the population extent (Table 1). We recorded the locations of 1,082 scats, whether at a burrow, at a digging, or in the open (not at a burrow or digging) during 13 monitoring events at the subset of 7 populations. Scats were nearly always found at a digging (95%), with only 3% found on open ground and 2% at a burrow. Within the further subset of 4 populations, we recorded 250 observations of whether scats were buried or exposed at diggings. We found most scats exposed on or beside a digging (71%); 29% were buried out of sight within the spoil.

Model Selection

The model using transect detectors, the HEX detection function, and the Nelder-Mead maximization algorithm consistently performed efficiently and reliably. This model had faster processing times and did not result in any failures or errors across all calculations. The preparation of transect detectors was much simpler and faster than preparing polygon detectors. The HCG and HVP detection functions consistently caused the model to fail or caused errors. Of the 3 remaining detection functions, HHR had longer processing times and usually lower AIC and resulted in a higher density and abundance value. The HHN detection function had higher AIC values and a lower density and abundance value. The HEX detection function produced similar AIC values to the HHR detection function, resulted in density and abundance values between HHR and HNN detection functions, and had a fast processing time similar to the HNN detection function (Appendix A).

Polygon and transect detectors (Fig. 3A, B) generated similar results for given detection functions; however, using transect detectors resulted in much faster processing

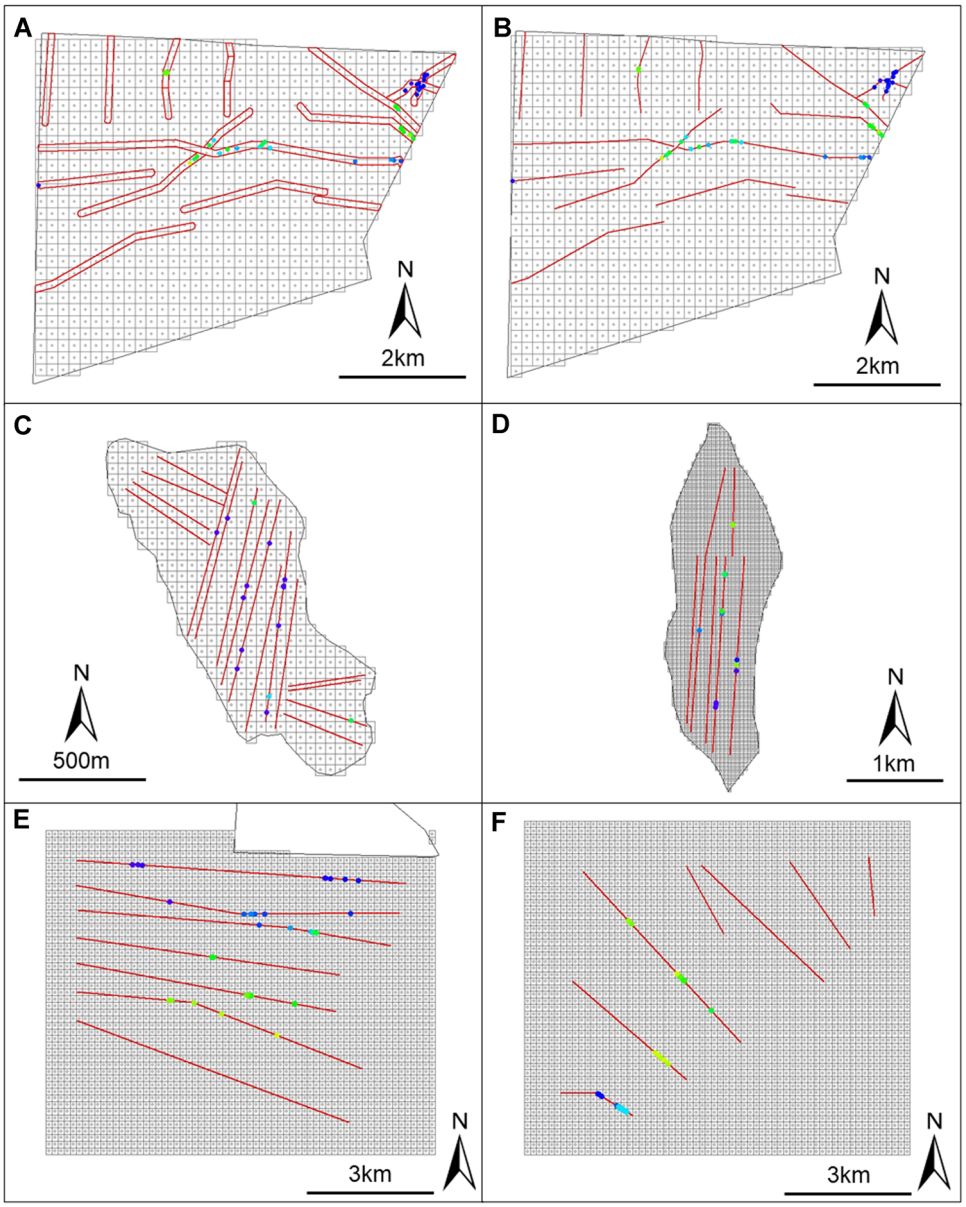

Figure 3. Examples of bilby population monitoring sites surveyed in Western Australia, 2013–2018: the validation population at Mount Gibson showing polygon detectors (A) and transect detectors (B); isolated wild populations at Hillside (C) and Warralong River (D); and contiguous populations occupying a large area in Matuwa at Possum Lake (E) and New Market Bore (F). Red lines represent polygon detectors in A and transect detectors in B to F. The spatially explicit capture-recapture integration mesh is represented in grey, and detections of individuals are colored points. The solid grey boundary represents the habitat mask: exclosure fence in A and B (bilbies only inside fence), population extent in C and D, and the excluded exclosure fence in E (no bilbies inside fence).

times. The maximization algorithm generally had no effect, apart from correcting any maximization errors that arose (e.g., using the HHR detection function with polygon detectors). Therefore, for subsequent SECR analyses, we used the model using transect detectors, the HEX detection function, and the Nelder-Mead maximization algorithm.

Population Sizes

Using maximum likelihood SECR analyses, we calculated a population size for the validation population (Mount Gibson) of 21 ± 5 (SE) individuals (Fig. 4) within the 2,368 ha of the exclosure that was occupied by bilbies and sampled (Fig. 3B). Of the 17 individuals identified on transects (Table 1), 9 were recaptures of the 16 founders.

At Matuwa, the extent of occurrence of bilbies has increased since reintroduction, and there are even records outside the 250,000-ha management area (M. A. Dziminski, personal observation). We subsampled Possum Lake, an approximately 7,000-ha area, in 2015 and resampled the area in 2016 together with a second similar sized area (New Market Bore; Table 1). We found a relatively higher number of bilbies present in the 2 subsampled areas at Matuwa (Possum Lake and New Market Bore) compared to wild populations (Fig. 4). Density at the Possum Lake area (Matuwa) increased between 2015 and

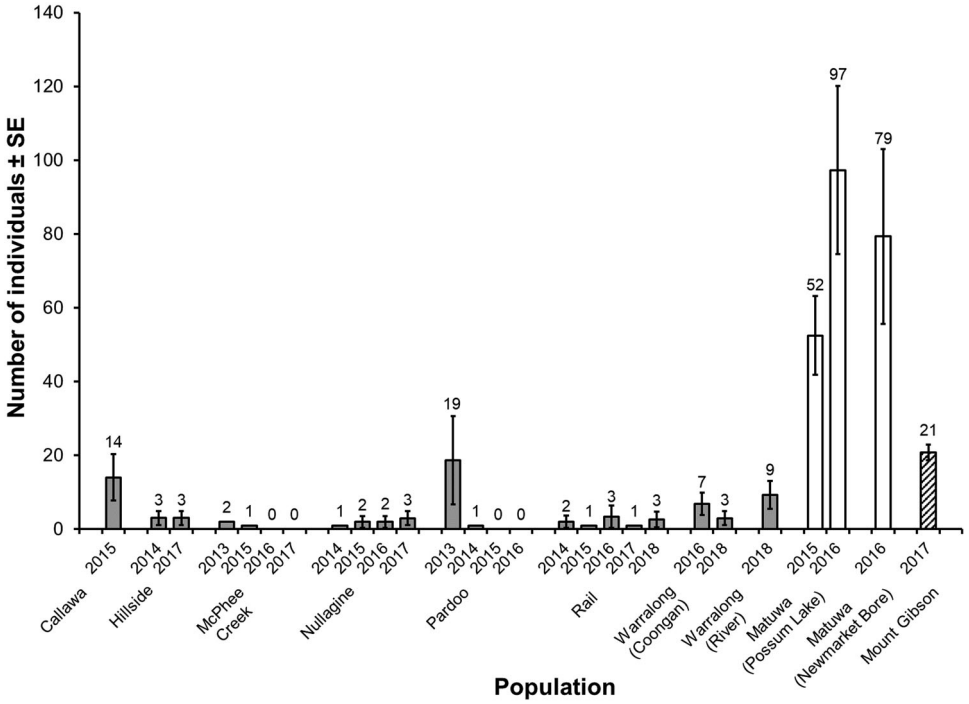

Figure 4. Abundance of bilbies from spatially explicit capture-recapture analyses for each monitoring event. Numbers above error bars indicate numbers of individuals. Shaded bars represent isolated distinct wild populations, open bars represent subsampled areas of a contiguous reintroduced wild population occupying a large area (Matuwa), and the hatched bar represents the validation population inside an exclosure fence (Mount Gibson), in Western Australia, 2013–2018.

2016, and densities were similar at both subsampled areas in 2016 (Fig. 3E, F; Table 1). Using densities from the subsampled areas across Matuwa and a total area of 221,470 ha (which excluded exposed regolith and the fenced exclosure), we calculated the estimated population size to be $1{,}772 \pm 376$ in 2015 and $2{,}669 \pm 709$ in 2016. The conservative population estimate for only sandplain regolith (80,551 ha) was 644 ± 137 in 2015 and 971 ± 258 in 2016.

Wild populations sampled in the Pilbara region ranged from 19 individuals (Pardoo), to a single individual in some cases (Fig. 4). Of the populations that we monitored across years, some remained stable (Hillside, Rail), 1 increased (Nullagine), and 2 decreased (McPhee Creek, Pardoo) and were lost (Fig. 4). We conducted searches around the sampled wild populations, usually out to 20 km and usually for 3–5 days; however, we did not find any nearby populations.

In 2013 at the Pardoo population, we calculated 19 ± 12 individuals present in the area (Fig. 4). This population was confirmed as being in the same location since at least 2012 and there is anecdotal evidence from locals that bilbies were present here for up to 20 years. In 2014 we found the track of 1 individual and 1 scat, with no other fresh evidence of bilby presence. Almost the entire area had been burnt sequentially in 2012, 2013, and 2014 by large-scale hot wildfires (North Australia and Rangelands Fire Information [NAFI] 2019), and only several small patches of the once thick stands of curley-bark wattle (*Acacia monticola*) remained. We subsequently searched the area in a 6-km circumference on foot, and then 30 km by vehicle, and found no other fresh bilby evidence (Table 1). During these searches we consistently observed multiple feral cats exiting out of disused bilby burrows, indicating a possible increase in feral cat activity. Further extensive week-long searches in 2015 and 2016 (Table 1) confirmed bilbies were now absent from this area.

At McPhee Creek, during our surveys in 2014 and late 2015, we detected fresh bilby activity and identified 1 individual (Fig. 4). At the end of October 2015 an extensive large, hot wildfire burned the entire area and surrounding landscape (NAFI 2019). An additional 2 site visits in 2016 revealed no evidence of recent bilby activity (Table 1), although we observed several old burrows and relict diggings into the roots of Pilbara minni ritchi (*A. trachycarpa*) shrubs. We searched the surrounding area extensively for 1 week out to 25 km by foot, quad bike, and vehicle, with no evidence of bilbies detected. We visited the site again in May 2017 and detected no evidence of bilbies (Table 1). Only small patches of suitable vegetation remained unburnt.

DISCUSSION

Monitoring Approach

Our study developed and tested a novel approach to monitoring bilby abundance by combining DNA extracted from scats with SECR analyses to determine bilby abundance within populations at a number of locations. We tested the technique at a population where a known founding population was recently reintroduced, which provided a sensibility check of the technique and indicated the technique is

reliable. Until the development of this approach, no efficient and reliable method to monitor their abundance had been implemented to compare abundance of bilby populations. The technique is useful for monitoring abundance at small discrete populations and large populations occupying large areas. As such it will provide a useful tool for assessing the response of bilby populations to conservation management.

Few survey or monitoring techniques that measure abundance or density are validated against a population of known size (Allen and Engeman 2015). At the Mount Gibson bilby reintroduction site, we sampled the population 4 months after release to allow for some dispersal, formation of home ranges, and recruitment to occur, noting that some female founders were already carrying young. Some mortality may have also occurred within this period. Our estimate of 21 ± 5 individuals is certainly within the reproduction capability of the 16 initial founders released and we identified 8 new individuals, indicating recruitment did occur.

Bilby scats are well suited to this type of sampling; the high water-conserving capability of bilbies means their scats are relatively desiccated (Gibson and Hume 2000, Gibson et al. 2002), and the dry conditions in areas where bilbies are still present likely assists in the preservation of DNA on bilby scats (Carpenter and Dziminski 2017). Thus, DNA can be reliably extracted from bilby scats for up to 2 weeks after deposition (Carpenter and Dziminski 2017). Because rainfall may promote the decay of scat DNA (Piggott 2004, Brinkman et al. 2009), we recommend that sampling of bilby scats should be undertaken during the dry season and >2 weeks after rainfall.

No other species in arid and semi-arid Australia produces scats with the same characteristics as those of the bilby (Southgate et al. 2019). They are rarely found away from some form of bilby digging activity (Southgate et al. 2019). In our study, nearly all (95%) scats were at bilby diggings, and of those, most (71%) were exposed on or next to the digging; however, 29% were buried in the spoil of the digging, highlighting the need to search through diggings for scats. This makes finding bilby scats in the field relatively straight forward especially given that diggings provide an important visual cue that can be detected when walking, or slowly driving an ATV or 4-wheel drive vehicle, depending on the vegetation and terrain.

The HEX detection function we used in SECR analyses did not fail or produce errors in any case and had a fast processing time. Using transect detectors also resulted in much faster processing times and generated similar results to polygon detectors. Furthermore, because preparing polygon detectors requires lengthy manual processing in geographic information system software, this can be avoided by using transect detectors.

Monitoring Abundance—Wild Populations

Our estimates of abundance indicate that wild bilby populations in the Pilbara are isolated and consist of a small number of individuals. Thus, they are likely vulnerable to threats (Bradley et al. 2015), in particular large wildfires and predation. During the course of our study, 2 of the monitored populations were extirpated, both after extensive large-scale wildfires. Intense and large, landscape-scale wildfires destroy large areas that provide food resources and cover from predation (Johnson 2008, Woinarski et al. 2014). In northwestern Australia, intense fires create conditions that are favored by feral cats, probably because hunting success is improved, and feral cats strongly select areas recently burned by intense fires (McGregor et al. 2014, 2016).

We observed and documented the disappearance of the bilby population at Pardoo, after large, destructive wildfires. These wildfires destroyed large areas of mature curley-bark wattle shrubland, which provided adequate vegetation and food resources for the bilby population (Southgate et al. 2019). Although bilbies may be present in other areas near Pardoo, extensive searches in subsequent years confirmed bilbies were now absent in this area. Even though bilby populations in desert regions have been recorded moving up to 2.3 km/year, and 1 population was recorded moving 10.5 km in 3 years (Southgate and Possingham 1995), we believe our search was thorough enough to detect a population if it was present.

Similarly, we observed the disappearance of bilbies at McPhee Creek. Bilbies were known to exist here for a number of years (Outback Ecology 2014). Despite extensive surveys, we detected no bilbies from 2016 onwards after a large wildfire burned the site and surrounding landscape in 2015 (NAFI 2019).

Monitoring Abundance—Reintroduced Population

Our technique, with some modifications, can also be used to subsample larger contiguously occupied areas, to estimate population sizes. We demonstrated that a reintroduced bilby population has spread across a large area and has continued to increase in numbers. Our estimates of total population size at Matuwa are higher than estimates obtained by counting burrows (128–339 in 2012 and 312 ± 78 in 2015); however, Burrows et al. (2012, 2015) acknowledged the unreliability of using only burrow counts to estimate abundance. Our study showed that when threats are appropriately managed, bilby reintroductions outside a fenced enclosure can be successful. To increase the accuracy of the abundance estimate at Matuwa, we recommend future monitoring should include areas of colluvium regolith, which together with sandplain regolith, form the major bilby substrate at Matuwa (Fig. 2).

Reintroducing bilbies into fenced predator-free areas has become a popular strategy (Moseby and O'Donnell 2003, Helmstedt et al. 2014, Anson 2017), but it creates inherent problems in the future because these populations experience genetic bottlenecks (Miller et al. 2015, Lott et al. 2020). This strategy also requires additional management burdens of exchanging animals, harvesting from wild populations, managing overstocking with supplemental feeding, and removing stock or culling when fenced areas become overpopulated. Matuwa is an example of bilbies being reintroduced into a large area in which threats are appropriately managed without the use of a predator exclusion fence. We showed that in this situation, the bilby population has increased and

expanded, and warrants replication of similar large, managed reintroduction areas elsewhere.

MANAGEMENT IMPLICATIONS

We demonstrated the successful application of using DNA extracted from scats in conjunction with SECR analyses to reliably measure bilby abundance within defined populations, thereby addressing an identified knowledge gap. Future abundance monitoring using this technique will allow robust comparisons of population size between populations, and within populations over time. This approach is likely to be useful in measuring the effectiveness of management actions and can be used to conduct population genetic analyses to estimate the relationship and connectivity of populations and family groups.

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APPENDIX A. EFFECTS OF MODEL PARAMETERS ON SPATIALLY EXPLICIT CAPTURE-RECAPTURE ANALYSES

Table A1. Effects of model parameters on spatially explicit capture-recapture analyses from a subset of bilby populations in Western Australia, 2014–2017.

Detection function[a]	Maximization algorithm[b]	Density (individuals/ha)	SE	Number of individuals	SE	Akaike's Information Criterion (AIC)	Processing time (sec)	Model validation
Hillside 2014								
Polygon detector								
HHN	Nelder-Mead	0.0476	0.0300	3.04	1.91	406.89	776.45	
HHR	Nelder-Mead	0.0488	0.0303	3.11	1.93	404.32	8,301.89	Error
HEX	Nelder-Mead	0.0476	0.0299	3.03	1.91	403.76	745.78	
HCG	Nelder-Mead	0.0773	0.0000	4.93	0.00	93.09	4,981.39	Failed
HVP	Nelder-Mead	0.0484	0.0302	3.09	1.92	402.17	7,992.07	Error
HHN	BFGS	0.0476	0.0300	3.04	1.91	406.89	769.88	
HHR	BFGS	0.0476	0.0299	3.03	1.91	404.33	7,871.08	
HEX	BFGS	0.0476	0.0299	3.03	1.91	403.76	688.32	

(*Continued*)

Table A1. (*Continued*)

Detection function[a]	Maximization algorithm[b]	Density (individuals/ha)	SE	Number of individuals	SE	Akaike's Information Criterion (AIC)	Processing time (sec)	Model validation
HCG	BFGS	0.0000	0.0000	0.00	0.00		1,007.08	Failed
HVP	BFGS	0.0477	0.0300	3.04	1.91	402.03	10,798.68	
Transect detector								
HHN	Nelder-Mead	0.0475	0.0299	3.04	1.91	287.50	2.38	
HHR	Nelder-Mead	0.0474	0.0299	3.03	1.91	280.71	23.59	Error
HEX	Nelder-Mead	0.0475	0.0299	3.04	1.91	284.44	3.82	
HCG	Nelder-Mead	0.0412	0.0000	2.63	0.00	200.14	9.73	Failed
HVP	Nelder-Mead	0.0501	0.0306	3.20	1.95	281.72	23.76	Error
HHN	BFGS	0.0475	0.0299	3.03	1.91	287.50	2.03	
HHR	BFGS	0.0476	0.0299	3.04	1.91	280.71	17.67	
HEX	BFGS	0.0475	0.0299	3.03	1.91	284.44	2.30	
HCG	BFGS	0.0514	0.0000	3.28	0.00		15.69	Failed
HVP	BFGS	0.0506	0.0307	3.23	1.96	281.44	43.39	Error
Matuwa (Possum Lake) 2015								
Polygon detector								
HHN	Nelder-Mead	0.0059	0.0012	41.59	8.39	3,130.22	2,253.31	
HHR	Nelder-Mead	0.0090	0.0020	63.53	14.11	3,047.66	15,114.76	
HEX	Nelder-Mead	0.0080	0.0017	56.38	11.96	3,074.39	1,226.35	
HCG	Nelder-Mead	0.0023	0.0006	16.53	4.13	1,188.05	20,587.24	Error
HVP	Nelder-Mead	0.0083	0.0018	58.37	12.60	3,058.44	16,825.00	
HHN	BFGS	1251.1840	0.0000	8.84E + 06	0.00		57.27	Failed
HHR	BFGS	0.0090	0.0020	63.51	14.09	3,047.66	15,941.92	
HEX	BFGS	0.0080	0.0017	56.35	11.92	3,074.39	1,299.12	
HCG	BFGS	2.8561E + 10	0.0000	2.02E + 14	0.00		3,332.69	Failed
HVP	BFGS	0.0083	0.0018	58.45	12.67	3,058.44	11,666.95	
Transect detector								
HHN	Nelder-Mead	0.0064	0.0013	43.54	8.69	2,116.12	33.99	
HHR	Nelder-Mead	0.0085	0.0018	57.29	12.44	1,927.60	166.01	
HEX	Nelder-Mead	0.0078	0.0016	52.49	10.65	1,996.68	36.52	
HCG	Nelder-Mead	0.0610	0.0000	412.20	0.00	−3,396.45	127.08	Error
HVP	Nelder-Mead	0.0085	0.0018	57.55	12.27	1,924.81	231.68	Error
HHN	BFGS	0.0064	0.0013	43.55	8.69	2,116.12	33.42	
HHR	BFGS	0.0085	0.0018	57.29	12.26	1,927.60	200.57	
HEX	BFGS	0.0078	0.0016	52.52	10.65	1,996.68	34.68	
HCG	BFGS	8.1496E + 57	0.0000	5.51E + 61	0.00		8.80	Failed
HVP	BFGS	0.0085	0.0018	57.18	12.11	1,924.73	181.75	
Mount Gibson 2017								
Polygon detector								
HHN	Nelder-Mead	0.0080	0.0021	18.85	4.86	1,645.53	1919.73	
HHR	Nelder-Mead	0.0096	0.0026	22.78	6.06	1,538.04	23,443.98	Error
HEX	Nelder-Mead	0.0088	0.0023	20.83	5.39	1,601.61	1,661.94	
HCG	Nelder-Mead	0.0374	0.0040	88.53	9.44	−409.06	6,245.61	Error
HVP	Nelder-Mead	0.0090	0.0024	21.36	5.62	1,548.29	13,068.78	Error
HHN	BFGS	0.0080	0.0020	18.86	4.84	1,645.53	1,387.57	
HHR	BFGS	0.0092	0.0024	21.83	5.79	1,537.44	13,197.28	
HEX	BFGS	0.0088	0.0023	20.83	5.39	1,601.61	1,756.71	
HCG	BFGS	0.0000	0.0000	0.00	0.00		773.35	Failed
HVP	BFGS	0.0090	0.0024	21.38	5.64	1,548.29	11,676.02	
Transect detector								
HHN	Nelder-Mead	0.0080	0.0020	18.88	4.86	1,137.34	22.61	
HHR	Nelder-Mead	0.0092	0.0025	21.91	5.82	1,036.66	124.49	
HEX	Nelder-Mead	0.0088	0.0023	20.77	5.37	1,095.47	19.02	
HCG	Nelder-Mead	0.0000	0.0000	0.00	0.00	−178.42	36.62	Failed
HVP	Nelder-Mead	0.0092	0.0024	21.70	5.71	1,039.73	81.88	Error
HHN	BFGS	0.0080	0.0020	18.87	4.86	1,137.34	25.69	
HHR	BFGS	0.0092	0.0025	21.89	5.82	1,036.66	81.99	
HEX	BFGS	0.0088	0.0023	20.78	5.38	1,095.47	16.74	
HCG	BFGS	6.6534E + 28	0.0000	1.58E + 32	0.00		12.98	Failed
HVP	BFGS	0.0093	0.0023	21.95	5.45	1,039.76	142.19	Error

[a] HHN, Hazard halfnormal; HHR, Hazard hazard rate; HEX, Hazard exponential; HCG, Hazard cumulative gamma; HVP, Hazard variable power.
[b] BFGS, Broyden–Fletcher–Goldfarb–Shanno.