

WILDLIFE RESEARCH

A comparison of methods for monitoring a sparse population of the red fox (Vulpes vulpes) subject to lethal control using GPS telemetry, camera traps and sand plots

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ABSTRACT

Context. The introduced red fox has driven the decline or extinction of numerous wildlife species in Australia, yet little information exists on the population densities of foxes in most ecosystems. Fox monitoring programs will differ widely depending on the goals of management, which, in turn, will determine whether the appropriate metric is a density estimate, or some proxy thereof, and the time and resources required. Aims. This study aims to assist wildlife managers to design fit-forpurpose monitoring programs for foxes by providing a better understanding of the utility and precision of various monitoring methods. Methods. We surveyed foxes monthly over four consecutive years in a semi-arid region of Australia by using sand plots, camera traps and GPS telemetry. The resultant data were used to produce population estimates from one count-based method, two spatially explicit methods, and two activity indices. Key results. The incorporation of GPS-collar data into the spatial capture-recapture approaches greatly reduced uncertainty in estimates of abundance. Activity indices from sand plots were generally higher and more variable than were indices derived from camera traps, whereas estimates from N-mixture models appeared to be biased high. Conclusions. Our study indicated that the Allen-Engeman index derived from camera-trap data provided an accurate reflection of change in the underlying fox density, even as density declined towards zero following introduction of lethal control. This method provides an efficient means to detect large shifts in abundance, whether up or down, which may trigger a change to more laborious, but precise, population monitoring methods. If accuracy is paramount (e.g. for reintroduction programs) spatially explicit methods augmented with GPS data provide robust estimates, albeit at a greater cost in resources and expertise than does an index. Implications. Our study demonstrated that the shorter the survey period is, the greater is the likelihood that foxes are present but not detected. As such, if limited resources are available, longer monitoring periods conducted less frequently will provide a more accurate reflection of the underlying fox population than do shorter monitoring periods conducted more often.

Keywords: canid pest ejector, fox baiting, mark–resight, N-mixture model, population index, predator control, sodium fluoroacetate, spatially explicit.

Introduction

Since its introduction to Australia in the 1800s (Rolls 1984), the red fox ('fox', *Vulpes vulpes*) has become one of the country's most destructive mammalian predators. The fox has driven the decline or extinction of numerous species of endemic terrestrial mammals (Woinarski *et al.* 2015; Doherty *et al.* 2016) and is also regarded as a major predator of livestock (Saunders *et al.* 1995; Saunders and McLeod 2007). The most recent economic figures have estimated that foxes cost the Australian economy approximately US\$500 million annually (Bradshaw *et al.* 2021) through direct loss and damage, as well as for management interventions. Nevertheless, despite the impact of foxes in Australia, in most ecosystems, little information exists on their population densities.

The specific objectives of a fox monitoring program will differ widely depending on the goals of management, which, in turn, will influence the time and resources that monitoring efforts demand. For instance, a predator eradication program conducted inside a fenced reserve prior to the reintroduction of endangered wildlife species (e.g. Legge *et al.* 2018; Ruykys and Carter 2019) will demand greater resources than do short-term fox control programs (cf. Greentree *et al.* 2000; Gentle 2005). For the former, accuracy is imperative as density approaches zero, and elimination of predators from the control area, whereas for the latter, a trend model may suffice as evidence of the expected decline. Irrespective of the objectives, an underlying assumption of all population monitoring programs is that the methods used are a true reflection of the underlying population parameter of interest.

Direct estimates of population abundance and/or density are generally most desirable (Porteus et al. 2019), although they typically require more costly and labour-intensive field methods (Sadlier et al. 2004; Jones 2011) and high levels of precision may not be needed for the management objectives. As an alternative to direct population estimates, ecologists often make inferences about populations across space and time by using indices as proxies for population abundance and/or density (Schwarz and Seber 1999; Sollmann et al. 2013a; Stephens et al. 2015; Falcy et al. 2016). Indices can be any measure of animals, or their signs, that are expected to vary directly with population size (Caughley 1977). However, their use is contentious because the assumption of a direct and constant relationship between the index and true abundance/density is rarely verified (Pollock et al. 2002; Stephens et al. 2015). Consequently, there is long-standing discussion in the ecological literature about the use, and misuse, of indices (e.g. Edwards 1998; Anderson 2001; Johnson 2008; Gopalaswamy et al. 2015; Falcy et al. 2016). Yet, despite this considerable uncertainty, indices remain the most commonly implemented method for monitoring fox populations (e.g. Thompson and Fleming 1994; Thomson et al. 2000; Sharp et al. 2001; Gentle et al. 2004; Olsson et al. 2005; Moseby and Hill 2011; Bengsen 2014; Robley et al. 2014; Benshemesh et al. 2020). Noting that developments in scat genotyping is bridging the gap between the simplicity of using sign and the marking of individuals to estimate density (Piggott et al. 2008).

In this study, we compare two commonly applied activity indices and one count-based method with two spatially explicit methods for monitoring the abundance of red fox. This research was conducted in a semi-arid region of Australia over four consecutive years. Our primary objectives were to (1) determine whether activity indices show direct and/or constant correlations with fox population abundance estimates over time, and (2) evaluate the precision of the various methods for detecting change in fox abundance. Midway through the study, we introduced lethal control to reduce the abundance of foxes and we expected to observe a concomitant decline in the subsequent indices and population estimates. Our findings will assist wildlife managers to design fit-for-purpose fox monitoring programs to guide local decision-making and species-based management (*sensu* Jennelle *et al.* 2002), while also having broad application for monitoring other wildlife species with non-distinct pelage and/or similar behaviour.

Materials and methods

Study area

Our study was conducted at Scotia Wildlife Sanctuary, a 64659 ha private conservation reserve in south-western New South Wales, Australia (-33.15°S, 141.06°E; Fig. 1), owned and managed by Australian Wildlife Conservancy. Approximately 8000 ha of the sanctuary is surrounded by an electrified conservation fence, to establish two adjacent 4000 ha exclosures, from which foxes (and feral cats) have been excluded since 2004 (Stage 1) and 2007 (Stage 2), and to which five threatened mammal species have been reintroduced successfully (Roshier et al. 2020). The climate is semi-arid with low and highly variable rainfall (spatially and temporally) that averages 230 mm per year with high evapotranspiration (1500 mm per year) and low relative humidity (average: 20%) (Australian Wildlife Conservancy, unpubl. data). Cool winters (average maximum temperature: 17°C) and hot summers (average maximum temperature: 30°C) characterise the site, with annual temperature extremes ranging from -6° C to 48° C. The landscape features stable east-west sand dunes of red sand and sandy solonised brown soil over clay (Westbrooke et al. 1998). Vegetation is predominantly multi-stemmed Eucalyptus spp. ('mallee') open-shrubland with a Triodia scariosa ('spinifex') understorey or mixed-shrub understorey (predominantly Senna, Dodonaea and Eremophila spp.), and Casuarina pauper woodland on the swales and open flats (Westbrooke et al. 1998). Red foxes are the largest predator present and their population in the study area was not subject to any form of population control during the 6 years prior to this study commencing.

Data collection

Camera traps

During the 4-year study, we monitored fox populations by using camera traps with passive-infrared sensors (HC600, Reconyx, Holmen, WI, USA) placed at 98 sites across 14 000 ha (Fig. 1). Sixty-three of these sites were located along roads and were monitored for the entirety of the study, except when 28 sites were removed during April and May 2016 to facilitate camera re-conditioning. An additional 35 sites were located away from roads and were operational for 7 months (July 2017–January 2018). All sites contained a single camera, except for nine road sites that had paired cameras (i.e. one camera either side of the road) to provide



Fig. I. Location of (a) Scotia Wildlife Sanctuary and (b) camera traps and sand plots across the study area.

information for a related study. Detections from each camera pair were pooled together, so that data were comparable with

single cameras (i.e. no detections were counted twice). Camera sites were spaced between 750 m and 2000 m

apart. Further details on camera placement are provided in Carter *et al.* (2019). We conducted 48 camera-trapping sessions at monthly intervals, encompassing the period from 1 October 2015 until 25 September 2019. Each session consisted of 24 consecutive trapping occasions (i.e. 24-h periods from 09:00 hours to 08:59 hours), unless problems were noted with camera operability, whereby trap usage was accounted for in the analysis.

Cameras were attached to a galvanised steel post driven into the ground, with the sensor positioned 0.5 m above ground, aimed approximately 4.5 m away. Cameras recorded five consecutive images when triggered, with no time delay, and highest trigger sensitivity and image quality. Images were stamped with date, time and camera location. Cameras recorded monochromatic images at night and colour images during the day under ambient light. No lures or baits were used to attract predators to cameras.

Sand plots

A sand-plot monitoring program for foxes (and other species) had been in place at Scotia for 9 years prior to our study commencing (Australian Wildlife Conservancy, unpubl. data). Within our study area, this historical program included 60 sand plots (covering four roads) spaced approximately 500 m apart. For consistency, we maintained the historical survey methods in the current study; however, we considered the 500-m spacing to be too close, so we selected a subset of 17 antecedent sand plots spaced approximately 2000 m apart. This spacing was selected to (a) maximise the spatial coverage of the sand plots throughout the study area, and (b) increase the independence of each sand plot. Sand plots were positioned on the existing road network and monitored daily for a 4-day period each month, coinciding with cameratrapping sessions. Sand plots consisted of an area of sand (approximately 1.2 m wide) raked smooth across the entire width of the road (i.e. gutter to gutter). On the following morning, sand plots were inspected for the presence of fox footprints by the same experienced operator (J. S.) for the entirety of the study. Each plot was then smoothed clean in preparation for the following day. In the event that rain and/or wind obscured footprints on some plots, all data from that day were abandoned and all plots were re-surveyed the following day until 4 days of undisturbed data were collected. All sand plots were assumed to be independent and every set of fox tracks that entered and exited an individual plot were treated as independent detections. No lures were used and the same sand-plot locations were surveyed for the duration of the 4-year study (Fig. 1).

Fox identification

Because of their uniform pelage, individual red foxes cannot be identified reliably from photographs unless marked artificially (Guthlin *et al.* 2014). To identify individuals on camera-trap images, we fitted 28 foxes with GPS collars (Q4000E, Telemetry Solutions, Concord, CA, USA) over a

3-year period; seven foxes were caught and collared between October 2015 and March 2016, 10 foxes during July-December 2016, and 11 foxes during June-September 2017. Collars operated for approximately 4 months (before being programmed to detach from foxes automatically) and recorded location fixes at 20-min intervals between 17:00 hours and 09:00 hours and at 96-min intervals between 09:00 hours and 17:00 hours (for further details, see Roshier and Carter 2021). Individual foxes were identified in cameratrap images by comparing the image time stamp with all available GPS data (additional details are provided in Carter et al. 2019). Photographs of known individuals recorded ≤60 min apart at the same camera were not included in the analysis. Likewise, photographs of unmarked foxes recorded ≤60 min apart at the same camera were considered to be the same individual, and were not included in the analysis, unless body markings enabled clear distinction between individuals within this time period, or there was a second individual in a photograph. All camera-trap images were viewed and classified manually by the same operator (A. C.), without the use of machine learning or artificial intelligence software (e.g. Norouzzadeh et al. 2018; Tabak et al. 2019).

Fox management

During the first half of the study (October 2015–September 2017; Sessions 1–24) the fox population was not subject to any form of population control. Lethal fox control, subsequently, commenced in October 2017 (Session 25), and this was maintained constantly until the study ended in September 2019 (Session 48). Two control methods were implemented, namely, canid pest ejectors (hereafter 'CPEs') and fresh-meat baits (hereafter 'baits'), both containing 3.0 mg of the toxicant sodium fluoroacetate (hereafter '1080'). Because of the nature of fox management, the exact number of foxes removed during the study remained unknown.

CPEs are an Australian derivative of the 'M-44' or 'humane coyote getter', as they are known elsewhere (Allen 2019). CPEs are mechanical devices that are buried partly in the ground, with a baited lure head, containing a sealed toxicant capsule, remaining exposed above ground level. When a fox attempts to remove the lure by pulling upward, the toxicant in the capsule is propelled into its mouth via a springloaded piston. An upward pull force of 1.6-2.7 kg is required to activate CPEs (Marks and Wilson 2005), which prevents many non-target species from accessing the toxicant. On 1 October 2017, we distributed 145 CPEs throughout the study area, placed at approximately 1-km intervals along the existing road network (Fig. 2). A variety of lures was used to create bespoke bait heads that contained a combination of dried liver, dried chicken, dried red meat, manufactured dog cubes, fish meal, and/or dried liver soaked in fish oil. These bait types were swapped every 2-3 months. For the first 4 months, CPE were inspected at



Fig. 2. Location of baits and canid pest ejectors (CPEs) at Scotia Wildlife Sanctuary.

2–4-day intervals in an effort to identify triggers made by foxes fitted with GPS collars. Thereafter, inspections and servicing (lubricating and refreshing bait heads) occurred at approximately 1-month intervals. If CPEs had been triggered since the previous visit, the toxicant capsule was replaced and the lure head refreshed as necessary.

The use of meat-based baits (chicken wings, red meat) impregnated with 1080 is currently the most widespread and effective method of fox control in Australia (West and Saunders 2007; Mahon 2009). Hence, on 24 October 2017, we began supplementing CPEs with fresh chicken wings injected with 1080, distributed across 196 bait sites (Fig. 2). Nominally, baits were placed at 1-km intervals along the existing road network, although preference was given to placing baits (rather than CPEs) at road intersections; so, in some instances, bait spacing was at approximately 500 m. All sites were checked after 3 and 6 days and any baits taken were replaced. The final check was made after 8 days, when all remaining baits were removed. An additional nine baiting programs were implemented (using a combination of chicken wings, fresh beef meat, and chicken eggs) throughout the remainder of the study, with baits checked at 3-day intervals and remaining in place for a maximum of 10 days before being removed. When all control sites were combined, most roads across the study area contained alternating CPEs and baits at 500-m intervals.

Data analysis

Activity indices

Sand-plot and camera-trap data were analysed to produce two separate indices:

1. the Allen–Engeman (AI) index: the average number of tracks per sand plot, per day (or photographs per camera, per day). Variance of the AI was estimated following

Engeman (2005). First, a linear mixed model was fitted to the data of the form:

$$x_{ij} = \mu + S_i + D_j + e_{ij}$$

where x_{ij} is the number of tracks (or independent sets of photographs) from the *i*th sand plot/camera site on the *j*th day, μ is the mean number per sand plot/camera site per day, S_i is the random effect owing to *i*th sand-plot/camera site, D_j is the random effect owing to the day on which the observation was made, and e_{ij} is the random error term that is assumed to be independent and identically distributed, with a mean 0 and variance σ_e^2 . Variance estimation of the AI index, when all sample sizes were equal, was calculated as follows:

$$\sigma_{\rm AI}^2 = \frac{\sigma_s^2}{S} + \frac{\sigma_d^2}{D} + \frac{\sigma_e^2}{\rm SD}$$

where *S* and *D* are the sample sizes of the sand plots/camera sites and days respectively, and σ_s^2 , σ_d^2 and σ_e^2 are, respectively, plot-to-plot/site-to-site variability, daily variability and random observational variability associated with each plot/trap each day (Engeman 2005).

2. the Catling index: the percentage of sand-plot nights with fox tracks (or camera-trap nights with independent sets of fox photos; following Catling and Burt 1994).

N-mixture modelling

N-mixture models are a commonly used method to estimate abundance by using spatially replicated count data, without requiring individual animals to be uniquely identifiable. Counts of animals at Site *i* and Time *j* (Y_{ij}) are assumed to be conditionally independent binomial random variables, based on the number of individuals actually present at Site *i* and Time *j* (N_{ij}) during the survey, detected with probability p_{ij} . That is, $Y_{ij}|p_{ij} \sim B(N_{ij}, p_{ij})$.

N-mixture models were run using the *pcountOpen* function in the *unmarked* package (v. 0.13.1, Fiske and Chandler 2011) in R (v. 3.6.1, R Core Team 2018). Given the 4-year duration of this study, populations were assumed to be closed within the primary survey periods (i.e. monthly sessions), and open between the primary periods. The Akaike information criterion (AIC, Akaike 1974; Buckland *et al.* 1997) was used to select the mixture distribution (Poisson, zero-inflated Poisson or negative binomial), and conduct model selection. In addition, we explored the influence of one site-level covariate on detectability (whether the trap was set on a road), while all other parameters were kept constant. Values of *K*, a parameter required to bound the integration, were explored to ensure that they were set large enough, such that model estimates were not affected.

Spatial mark-resight modelling (SMR-MLE)

Spatial capture–recapture (SCR) and spatial mark– resight (SMR) methods provide density estimates of marked (or partially marked) populations, using the spatial pattern of recapture events of marked animals (Borchers and Efford 2008; Royle et al. 2014). Even though SCR models can be fitted to populations without any marked individuals, marking a subset of the population is recommended where possible (Chandler and Royle 2013). SCR and SMR utilise heterogeneity in capture probability caused by the proximity of animals' home-range centres to traps. SMR values of fox density at Scotia have been estimated previously within a maximum-likelihood framework (i.e. package 'secr', Efford 2019) in Carter et al. (2019). For brevity, we do not repeat the analysis here, but do convert these estimated fox densities to abundance in each of the primary survey periods, on the basis of all camera-trap data and an effective survey area of approximately 57 000 ha. This area was created using a 4000-m buffer around the trap locations in each survey, with inaccessible habitat removed (i.e. an 8000-ha fenced region that excludes foxes; Fig. 1). The choice of a 4000-m buffer was based on GPS location data (cf. Roshier and Carter 2021) that indicated that foxes rarely moved beyond this distance.

Spatial mark-resight modelling augmented with GPS-collar information (SMR-Bayes + GPS)

Spatial mark-resight analyses augmented with GPS-collar data were conducted within a Bayesian framework, following the approach of Sollmann et al. (2013b) and Whittington et al. (2018). In the context of spatial mark-resight analyses, telemetry and GPS-collar data provide additional information on individual location and movement. Sollmann et al. (2013b) extended spatial mark-resight models to utilise the spatial information from GPS-collared racoons to inform model parameters on spatial location. We adapted their approach, using the GPS-collar data from 28 collared foxes. Because GPS collars were not deployed on foxes in every session, estimates were available for only a portion of the sessions surveyed. We ran two Markov-chain Monte Carlo chains of the algorithm, with 100 000 iterations each, discarding the first 10000 iterations as burn-in. To check for chain convergence, we calculated the Gelman-Rubin statistic R-hat (Gelman and Rubin 1992) by using the R package coda (v. 0.19-3, Plummer et al. 2006). Values >1 indicate lack of convergence.

Ethics statement

All work relating to this study was conducted as approved by and in accordance with the Animal Care and Ethics Committee of the Secretary of NSW Trade and Investment (Approval Numbers 13/1344), Animal Care and Ethics Committee of the Secretary of NSW Industry, Skills and Regional Development (Approval Numbers 13/1344#5, 16/1354, 16/1354#1) and the Office of Environment and Heritage, NSW National Parks and Wildlife Service (Scientific License number SL100473).

Results

Fox monitoring and management

More than 110 000 camera-trap nights were conducted in this study, across the 98 camera-trap sites and 48 primary (monthly) sampling sessions. The maximum number of trap nights available at a single site was 1152 (i.e. 48 primary sessions \times 24 secondary occasions), and there were, on average, 955 (±233 s.d.) trap nights at each site (35 offroad sites were trapped for seven primary sessions only). Across the duration of the 4-year study, foxes were detected by cameras in every survey session except one (Session 42, March 2019; Supplementary material Table S1), and 90 of 98 individual sites had at least one fox detection.

Sand-plot surveys occurred in 44 of the 48 primary sampling sessions, with foxes being detected in 41 of these sessions. In 14 sessions, wind and/or rain caused the abandonment of a day's surveys, which required the addition of one extra survey day to obtain data from 4 days.

The time spent conducting camera-trap surveys and processing the resultant data in preparation for analyses varied depending on accessibility (Table 1). When on-road and off-road cameras were combined, each camera site required approximately 16 min work each month (1545 min/98 camera-trap sites). For sand plots, a standard monthly 4-day survey required an average of 7 h, 35 min. (\pm 1 h, 10 min s.d.) of person hours in the field to prepare the sand and record tracks. That equates to approximately 27 min per sand plot per month (455 min/17 plots). However, >31% of monthly sand-plot surveys (14/44) required an extra day of field work (mean effort 1 h, 53 min, \pm 17 min s.d.) because a day's data were ruined by inclement weather.

During the first 24 sessions when there was no fox control (October 2015–September 2017), the mean number of independent fox detections on cameras per session was 116 (\pm 68 s.d.), with detections at 64% (\pm 16 s.d.) of sites, on average. During the final 24 sessions when fox control was implemented (October 2017–September 2019), the mean number of fox detections on cameras per session was 22 (\pm 18 s.d.), with detections at 22% (\pm 13 s.d.) of sites, on average. During the final session prior to commencement of lethal fox control (Session 24, September 2017), there were

90 fox detections on cameras. Two months later (Session 26, November 2017), fox detections on cameras had fallen by >50%, and by the following September (Session 36, September 2018), camera detections were down by almost 85% (Table S1). During the final year of our study (Sessions 37–48, October 2018–September 2019), total camera detections in several sessions were in single figures and down >90% from total detections in Session 24 (September 2017; Table S1).

Detections on sand plots also fell following the commencement of fox control. During the 2 years prior to control, there was an average of 10 (\pm 6 s.d.) fox detections per session, with detections occurring at 36% (\pm 18% s.d.) of the 17 sites, on average. During the 2 years of lethal control, there was an average of 2 (\pm 2 s.d.) fox detections per session, with detections at 12% (\pm 9% s.d.) of the 17 sites, on average. During the final year of monitoring, in most sessions, fox prints were recorded at one or two sand plots only (Table S1).

Nine of the eleven foxes fitted with GPS collars in June-September 2017 were within the study area at the commencement of lethal fox control on 1 October 2017. For the first 3 weeks of lethal control, only CPEs were deployed; none of which was triggered, and no kills of collared or unmarked foxes were recorded. Fresh-meat baits were first deployed on 24 October, and across the 196 bait sites, 24 baits were removed after 3 days, 20 baits were removed during Days 4-6, whereas another 21 baits were taken from Days 7-8 (Fig. 3). Examining the GPS data from collared foxes indicated that three of nine collared foxes took baits and died on the third day of the baiting program, one fox took a bait and died on Day 7, and three other collared foxes died in the same period but their precise movements in the day prior to their death could not be deduced because the GPS units in their collars malfunctioned. Another collared fox is likely to have triggered a CPE and died on 31 October 2017, 30 days after CPEs were first activated. Only one of nine collared foxes remained alive at the end of October 2017, which equates to an 89% reduction in the collared population during the first month of baiting. The one collared fox that survived (5.4 kg d) had access to 10 CPEs and 13 fresh-bait stations within its home range (fox MF366 in Roshier and Carter 2021). This individual

Table I. Average monthly person hours (±s.d.) spent on camera-trap surveys.

ltem	Servicing ^A	Image download ^B	Image review ^C	Individual identification ^D	Total
On road (<i>n</i> = 72)	6:21 ± 0:39 ^E	0:43 ± 0:40	2:34 ± 1:21	0:42 ± 0:41	10:20
Off road $(n = 35)$	13:51 ± 0:18 ^F	0:17 ± 0:16	1:01 ± 0:13	0:16 ± 0:16	15:25

^AChange batteries and memory cards in the field.

^BFrom camera memory cards to cloud storage server.

^ERequired 131 km of driving.

^FRequired 30 km of walking and 101 km of driving.

^CExtract fox images.

^DUsing GPS tracking data and image time stamps.



Fig. 3. Monthly takes of canine pest ejectors (CPEs) and fresh-meat baits injected with 1080 from October 2017 to September 2019. Asterisk indicates that no fresh baits were laid.

remained active throughout the study area until 24 November 2017 when its collar drop-off mechanism activated. CPEs continued to be deployed until the end of the study in September 2019, and fresh-meat baits were deployed in each month (except in December 2017) until February 2018, and at 3-month intervals thereafter. It was not possible to determine whether non-target species removed baits or triggered CPEs. No carcasses of unmarked foxes (or non-target species) were found in the 2 years of lethal control.

Estimates of activity from sand plots and camera traps

The Allen–Engeman and Catling indices were near identical for each session ($R^2 = 0.97$) and the Catling index is not considered further in this analysis because it provides no means to generate confidence limits. In comparing activity indices from camera traps and sand plots, the metric from sand plots was generally higher and more variable than that derived from camera traps (Fig. 4). Although both indices recorded a decline in fox activity following introduction of lethal control, the confidence limits for the cameratrap data were much narrower in absolute terms than for the sand-plot data.

Estimates of abundance from camera-trap data

The number of marked foxes in a session ranged from 0 to 14, so SMR analyses were not possible in every session. Also,

during Session 7 (April 2016), no marked foxes were detected on any cameras, so abundance estimates during that session could not be obtained. Following the commencement of lethal control in Session 25 (October 2017), there were too few individually marked foxes remaining in the survey region to use SMR methods. In sessions with high congruence in the estimates between SMR-MLE and SMR-Bayes + GPS (i.e. October 2016, November 2016), the MLE approach is more uncertain and has wider confidence limits (Fig. 5). For the SMR-Bayes + GPS analysis, the Gelman-Rubin statistic R-hat for all sessions was ≤ 1 , indicating that the chains converged for the 10 sessions for which this method could be applied. Across these 10 sessions, the SMR-Bayes + GPS method produced abundance estimates of ~50 animals (range 35-78) in the study area (Fig. 5). This compared with an estimate of ~80 animals (range 27-230) for the same sessions using SMR-MLE. The confidence limits associated with both SMR methods in this analysis were improved (i.e. uncertainty was reduced) by including marked animals (pID) that were known to be on the grid in any particular session but were not detected.

Both the SMR–MLE and SMR–Bayes + GPS methods produced similar estimates when there were sufficient marked foxes on the grid to be detected (Fig. 5, also see Carter *et al.* 2019). As the number of marked foxes detected on cameras declined, SMR–Bayes + GPS models failed to converge, and the point estimates and confidence limits



Fig. 4. Fox activity $(\pm 95\% \text{ CI})$ as measured using the Allen–Engeman index. The dashed vertical line signifies commencement of lethal fox control. Note; camera-trap data presented here are for four occasions per session only, to align with sand-plot sampling periods. Supplementary material Fig. SI provides a comparison of indices derived from cameras, using 4 and 24 occasions per session. No sand-plot surveys occurred in October 2016, April 2017, May 2018, or August 2019, and no foxes were detected on cameras in March 2019.

inflated for SMR–MLE models, or failed if no marked foxes were detected, as in Session 7 (April 2016).

The best-fitting N-mixture model (i.e. that with the lowest AIC) using the camera-trap data was a Poisson mixture, which had no covariates on the detection probability. As expected, since our camera-trap sites were not independent, estimates from N-mixture models appear biased high (i.e. higher than SMR-methods). In comparing the camera-trap N-mixture with the camera-trap Allen–Engeman index, which is the only other method we applied that does not require marked animals, the confidence intervals are much narrower for the Allen–Engeman index method (Fig. 6). We were unable to generate a plausible N-mixture model using the sand-plot data because the models failed to converge (see Discussion).

Discussion

The primary goal of our study was to assist wildlife managers design fit-for-purpose monitoring programs by providing a better understanding of the utility of various methods available for monitoring foxes. Because a subset of our fox population was fitted with GPS collars, we had a unique opportunity to compare a statistical method that is considered 'best-practice' for estimating population density (i.e. spatial

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capture–recapture using both MLE and Bayesian frameworks) with methods that are less arduous in terms of data collection, processing and analysis (i.e. simple counts of detection events expressed as the Allen–Engeman index and N-mixture models). Our comparison of these methods was made in terms of uncertainty and utility.

Abundance estimate methods

We found that the incorporation of GPS-collar data into the spatial capture-recapture approaches (i.e. SMR-Bayes + GPS vs SMR-MLE) greatly reduced uncertainty in estimates of abundance (Fig. 5). This was expected, given that the Bayesian approach can incorporate data from GPS collars to better estimate the distribution of individual activity centres (see Gerber and Parmenter 2015), whereas the maximum-likelihood approach cannot. In general, these two SMR approaches provided similar estimates of abundance, except in situations where marked detection events were sparse (e.g. Sessions 1-3, October-December 2015). Further, in sessions where there were few marked animals resighted, the SMR-Bayes + GPS models did not converge, and although SMR-MLE models could provide estimates in these instances, they were unrealistic and had wide confidence limits (e.g. Sessions 18-20, March-May 2017).



Fig. 5. Comparison of abundance estimates using spatial mark-resight methods, namely, spatial mark-resight modelling augmented with GPS-collar information (SMR-Bayes + GPS) and spatial mark-resight modelling using maximum-likelihood estimation (SMR-MLE). Density estimates are converted to abundance and presented with \pm 95% Cl. The dashed vertical line signifies commencement of lethal fox control.



Fig. 6. Comparison of abundance estimates (\pm 95% CI) derived from counts, namely N-mixture model (LHS) and the Allen–Engemen index (RHS), using camera-trap data (24 occasions each session).

We acknowledge that obtaining uniquely marked animals is not often feasible in studies of fox populations and that additional methods not implemented here have been used successfully to measure fox abundance elsewhere. For instance, several studies have used non-invasive genetic sampling to demonstrate changes in fox abundance following lethal control programs (e.g. Piggott et al. 2008; Berry et al. 2012, 2013), but inclusion of such methods was beyond the scope of our study. Instead, in addition to SMR analyses, we also analysed our data using count-based indices and N-mixture modelling. N-mixture models typically assume that the population is demographically closed (but extensions exist), individuals are not counted at more than one site, and all individuals have the same probability of being detected (Royle 2004). Our results showed that N-mixture estimates were comparable to those from SMR methods but the uncertainty was much greater (compare Figs 5 and 6). Here, camera traps were specifically placed to ensure that SMR methodology could be used (i.e. individually marked animals detected across multiple sites), violating an assumption of N-mixtures. Given that sites were not independent, although the total number of animals using each site remains unbiased, abundance estimates for the survey region are biased positively because animals moving between sites are double counted (Keever et al. 2017). In addition, in many situations, N-mixture models did not converge. Barker et al. (2018) found that when p is low or highly variable, N can be unidentifiable (Barker et al. 2018; Link et al. 2018). In our study, estimates of p were very small (mean = 0.006, var = 0.003) and this is likely to explain why many sessions did not converge. In recent times, the density of unmarked populations has been estimated elsewhere with numerous other statistical approaches (e.g. FMP Formula, Stephens et al. 2006; REM, Rowcliffe et al. 2008; SPA Model, Ramsey et al. 2015; REST Model, Nakashima et al. 2018; see also SPIM Model, Augustine et al. 2018; Royle et al. 2014, Chapter 18; Chandler and Royle 2013) and these may warrant further investigation for estimating fox abundance in future studies.

Following the introduction of lethal control, foxes fitted with GPS collars did not survive long enough to enable density estimates to be produced using spatial capturerecapture approaches. Nevertheless, during the first month of baiting, we observed an 89% reduction in the collaredfox population, and, as anticipated, we observed considerable declines in the subsequent indices and abundance estimates using count methods. Values for the Allen-Engeman index from camera-trap data were 85% lower, on average, during the 2 years of lethal control than the pre-control values, whereas the same metric using sand-plot data was 75% lower, on average, during the lethal control period. Estimates of fox abundance using N-mixture modelling from cameratrap data were likewise lower, ranging from 101 to 258 foxes per session, pre-control, compared with 43-130 foxes per session, when fox control was implemented. We were unable to generate abundance estimates using N-mixture modelling from sand-plot data because models would not converge (as discussed above). Combined, these results align with studies published previously that have demonstrated that broad-scale 1080 baiting can be effective at reducing fox abundance (e.g. Thomson *et al.* 2000; Berry *et al.* 2012, 2013; Marlow *et al.* 2015, 2016), and contrast some studies that concluded that baiting did not produce a clear decline in fox activity or abundance (e.g. Towerton *et al.* 2011; Bengsen 2014).

Broadly speaking, when undertaking population monitoring, we advocate for obtaining some marked animals, at least for a subset of sessions. If robust estimates of abundance are available at more than one point in time, they can be used to scale an index of activity if it changes in the same direction as the underlying population density. In this study, prior to the introduction of lethal control, changes in abundance were detected by using methods based on robust methods of density estimation (i.e. spatial markresight modelling augmented with GPS-collar information (SMR–Bayes + GPS)) and simple data collection and analyses (i.e. Allen–Engeman index; Fig. 7). Scaling both data sets showed a measure of agreement and we are confident, that after the introduction of lethal control, zero on the index was at or near zero population density.

Little published information exists on the time demands of camera trapping and sand-plot surveys. In our study, when the two methods were compared on a time-per-unit basis, an individual camera trap (on- and off-road combined) required approximately 60% of the person-hours each month of those that a sand plot did. This is noteworthy given the richness of data that camera traps can provide. Compared with sand plots, cameras can collect meaningful data in all types of weather, they are less dependent on observer skill (Ruykys and Carter 2019), they can operate for extended periods (months) with no human intervention, and they can facilitate estimation of population density (cf. Rovero and Zimmermann 2016). Moreover, in our study, all cameratrap images were viewed and classified manually. As machine learning and artificial intelligence software become more readily available (e.g. Norouzzadeh et al. 2018; Tabak et al. 2019), the time required to review large quantities of camera-trap images will decrease considerably, leading to further increases in the efficiency of camera-trap surveys.

Fox control

During the first 23 days of our lethal control program, we deployed only canid pest ejectors (CPEs), at an average density of 1.03 devices per km² (Fig. 2). During this period, each of the nine foxes fitted with GPS collars had access to multiple CPEs within their home range (range = 4–17), yet no CPEs were triggered. This prompted us to introduce buried fresh-meat baits (mean density = 1.4 baits per km²), which delivered an immediate impact, with four of the nine



Fig. 7. Comparison of abundance estimates (\pm 95% CI) from spatial mark–resight modelling augmented with GPS-collar information (SMR–Bayes + GPS) and the Allen–Engemen index (per trap night) derived from cameras (24 occasions per session).

collared foxes succumbing to baits within 7 days of baiting commencing. A further three collared foxes died in the same period and we suspect they too consumed fresh baits, but GPS-collar malfunction prevented confirmation. The high mortality rate of radio-collared foxes during the baiting program supports the findings of two previous studies. In coastal New South Wales, 100% of collared foxes (n = 6)died within 10 days of baiting commencing (Dexter and Meek 1998), whereas in semi-arid Western Australia, mortality rates were 60% (of 45 collared foxes) within 3 days and 100% within 44 days following 1080 baiting (Thomson et al. 2000). Conflicting results were obtained from two other Australian studies that found that most foxes collared survived 1080 baiting programs in mixed farmland (Carter et al. 2011; Bengsen 2014). In our study, one collared fox survived 54 days of the CPE program and a 9-day baiting campaign (at which point its collar released).

Results from field-based trials on the effectiveness of CPEs against foxes in Australia are limited. Of the published data that are available, the success rate of CPEs on foxes (i.e. percentage of 'CPE nights' with triggers) is relatively low, ranging from 0 (from 810 nights; Kreplins *et al.* 2018) to 2.3% (Gil-Fernández *et al.* 2021). Our study is, by far, the largest published study at present and delivered a success rate of 0.01% (i.e. 15 triggers from 105 705 CPE nights) across a 2-year period. Our results follow those of Moseby and Read (2014) in semi-arid South Australia, who also found CPEs to be less efficacious than 1080 baits. The low

success rate of CPEs may stem from the fox's neophobic behaviour, which is supported by observational studies at CPE sites (Moseby and Read 2014; Gil-Fernández *et al.* 2021). Considerable interference with CPEs by non-target species has also been noted (see Kreplins *et al.* 2018) and this too may influence the low success rate by limiting access to, or reducing the appeal of, attractants. The choice of attractants will also certainly influence the efficacy of CPEs, and further investigation into this issue is required, as are evaluations into the overall usefulness of CPEs as a method of fox control (Kreplins *et al.* 2018).

Management implications

Despite the vast impact of foxes in Australia, the development and implementation of fit-for-purpose monitoring programs over large areas remain a challenge (Marlow *et al.* 2015) and, as such, little information exists on fox population densities or abundance in most ecosystems. The results from our study showed that the Allen–Engeman index derived from camera-trap data appears to provide an accurate reflection of change in the underlying fox density. This method provides land managers with an efficient means to detect large shifts in abundance, whether up or down, which may trigger a shift to more precise population monitoring methods. If accuracy is paramount (e.g. for reintroduction programs), then SMR–GPS using a Bayesian framework provides robust estimates, noting that this method is computationally demanding and requires more expertise and resources than an index. Alternatively, within a similar analytical framework, rapidly developing genotyping methods mentioned above can provide density estimates without the need for managers or researchers to have expertise in genetics.

Regardless of the method chosen, our study has provided empirical data to demonstrate that the shorter the survey period is, the greater the likelihood of false absences (i.e. the target species is present, but not detected; cf. Field et al. 2005). From an operational standpoint, if short-term surveys are used to inform assessments of predation pressure, for instance, this could result in adverse outcomes (e.g. Hayward et al. 2012). If limited resources are available, we encourage land managers to prioritise survey duration over survey frequency. In other words, longer surveys conducted less frequently will provide a more accurate reflection of the underlying population than do shorter surveys conducted more often. These findings will help wildlife managers design fit-for-purpose monitoring programs for red foxes and other species with non-distinct pelage or similar behaviour patterns.

Supplementary material

Supplementary material is available online.

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Data availability. The data are archived at the Movebank Data Repository (https://www.datarepository.movebank.org) as 'Carter and Roshier (2019) Red fox (Vulpes vulpes) – Scotia, NSW Australia'. https://doi.org/10.5441/001/1.72hh609t.

Conflicts of interest. The authors declare no conflicts of interest.

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