A novel modelling framework to explicitly simulate predator interaction with poison baits

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Abstract

Context. Management of human–wildlife conflicts is of critical importance for both wildlife conservation and agricultural production. Population models are commonly used to simulate population dynamics and their responses to management actions. However, it is essential that this class of models captures the drivers and mechanisms necessary to reliably forecast future system dynamics.

Aims. We aimed to develop a flexible modelling framework with the capacity to explicitly simulate individual interactions with baits (with or without the presence of other management tools), for which parameter estimates from field data are available. We also intended for the model to potentially accommodate multi-species interaction and avoidance behaviours.

Methods. We expanded an existing spatially explicit, individual-based model to directly simulate bait deployment, animal movements and bait consumption. We demonstrated the utility of this model using a case study from Western Australia where we considered two possible exclusion-fence scenarios, namely, the completion of a landscape-scale and smaller-scale fences. Within each of these proposed cells, using data obtained from a camera-trap study, we evaluated the performance of two levels of baiting to control wild dogs (*Canis familiaris*), in contrast with the option of no control.

Results. The present study represents a substantial step forward in accurately modelling predator dynamics. When applying our model to the case study, for example, it was straightforward to investigate whether outcomes were sensitive to the bait-encounter probability. We could further explore interactions between baiting regimes and different fence designs and demonstrate how wild dog eradication could be achieved in the smaller cell under the more intense control scenarios. In contrast, the landscape-scale fence had only minor effects unless it was implemented as a preventive measure in an area where wild dogs were not already established.

Conclusions. The new component of the model presented here provides fine-scale control of single components of individual–bait interactions.

Implications. The effect of management actions (e.g. lures) that affect this process can be easily investigated. Multi-species modelling and avoidance behaviours can readily be implemented, making the present study widely relevant for a range of contexts such as multi-species competition or non-target bait uptake.

Additional keywords: conservation biology, introduced species, pest control, population dynamics, population modelling, species interactions, wildlife management.

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Introduction

Human–wildlife conflicts are one of the frequent challenges faced by managers around the world (Madden 2004). Of these conflicts, direct interactions between predators and humans, or human assets such as livestock, are of greatest public concern (Haque *et al.* 2015; Olson *et al.* 2015; Trinkel and Angelici 2016). A range of tools is employed to mitigate these impacts and population models are often used to improve planning efforts and test possible intervention strategies (Himes Boor 2014).

We previously developed an individual-based, spatially explicit model in HexSim (Schumaker and Brookes 2018) to investigate predator population dynamics and their response to various management strategies (Pacioni *et al.* 2018). Although this model was useful, it had limitations. For example, the mortality owing to a baiting regime was constant regardless of the population size because additional mortality was applied as a percentage, based on the toxic bait rate. This was unrealistic because the probability of a bait being encountered, and, therefore, eaten, is proportional to the number of animals in the area where the bait is being deployed. Hence, in high-density populations, the same baiting regime is likely to be more effective than it is in low-density populations.

Likewise, in the original model, the risk that an individual was exposed to a bait was dependent on the area of the landscape that the animal explored (i.e. home range), which was parameterised with home-range values obtained from radio-tracking data collected over a year in the same region. Baits can be effective for over a year, but generally their lifespan is much shorter as a result of consumption by non-target species or degradation (Kreplins *et al.* 2018). The original model did not explicitly take into account that some of the baits deployed were removed by non-target species and, therefore, not available to the target species, and did not remove baits once they were consumed. Hence, the mortality as a result of control activities was overestimated by the previous model. Pacioni *et al.* (2018) applied a conservative mortality rate to baiting so as to prevent overestimating the effect of the simulated management control. However, a model that more closely reflects real dynamics will improve management plans and targets.

Last, the original model did not allow for competition among different species exposed to the same baiting regime, and it could not account for learnt behaviours, which may affect management outcomes. To address those issues, and because we anticipate that aspects such as species interaction and avoidance behaviour may have important implications for management programs, we modified the model of Pacioni *et al.* (2018) to more accurately simulate the mechanics of bait deployment and consumption so that it would be possible to more precisely evaluate the likely effects of different management strategies. We were further motivated by the aim of developing a more flexible tool to investigate responses to various control regimes that has parameters that can be easily obtained from field data. For example, the probability of bait encounter, and then the probability of bait uptake given an encounter (parameters in the new model), can be reliably estimated using motion-activated cameras, whereas correctly estimating the overall mortality rate resulting from a specific baiting regime is more challenging. Although our initial work, and the case study we applied the new model to, are

focussed on wild dog populations, given the generality of the new modelling framework, we consider the present work broadly relevant and transferable to other predator species as well.

We used a case study from Western Australia (WA) to demonstrate the utility of the new modelling approach. In Australia, dingoes, free-living domestic dogs and their hybrids (*Canis familiaris*), collectively referred to as 'wild dogs', pose a significant threat to livestock enterprises, particularly small stock (sheep and goats). Nationally, annual total economic losses to the livestock industry resulting from wild dogs have been estimated at AU\$89 million (McLeod 2016). Anecdotal evidence has indicated that in the southern rangelands in WA, wild dog density has increased in recent years and has contributed to the decline of small-stock enterprises in the region. A recent estimate of the economic impact of wild dogs on WA rangeland goat and sheep industries identified annual losses of approximately AU\$25 million (Bell 2015) and wild dogs account for over 75% (>AU\$1.3 million) of the annual expenditure on pest plant and animal control by recognised biosecurity groups in the southern rangelands (DPIRD, unpubl. data).

A suite of techniques is available for the control of wild dogs, including trapping, ground and aerial baiting, and exclusion fencing. Best-practice wild dog management promotes a community-based approach regardless of individuals' land use (i.e. nil-tenure approach; Allen 2011), but this requires planning and a high level of participation by landholders and there are limitations to this approach because of the mix of enterprise choice, absentee landholders and variable attitudes towards bait use (Allen 2017). Alternative methods of wild dog control include the use of 'cell-fencing' (multiple properties fencing their collective outer boundaries with wild dog-proof fencing), which prevents immigration. Here, we considered the development of two possible exclusion fences in the Murchison Region, WA, namely, the completion of a landscape-scale fence to enclose a large area, or a smaller-scale cluster-fence (Fig. 1). Within each of these proposed cells, we evaluated the performance of two levels of baiting, in contrast with the option of no control. By simulating wild dog population dynamics, we predict possible changes that would occur under the proposed management plans.

Materials and methods

Study area

As study sites, we used a proposed large-cell fence and an inset smaller cell, both of which were partially complete (Fig. 1). The large cell comprised an area of ~88 000 km^2 and included pastoral properties, unallocated crown land and conservation estate. The proposed large cell is bordered on one side by the existing State Barrier Fence and on another by the existing Murchison Vermin Fence (previously known as the No. 1 Rabbit Fence). The north-western side of the cell has not been constructed. The inset small cell is ~2600 km^2.

The focus of the study was the area inside the large cell. However, we also included an area of ~80 000 km^2 surrounding the large cell as a source area for wild dogs entering the cell, so that there was ~20 km between the fence and the limit of this area. Together the large-cell area and the surrounding area formed the total study site (176 000 km^2). The study area was
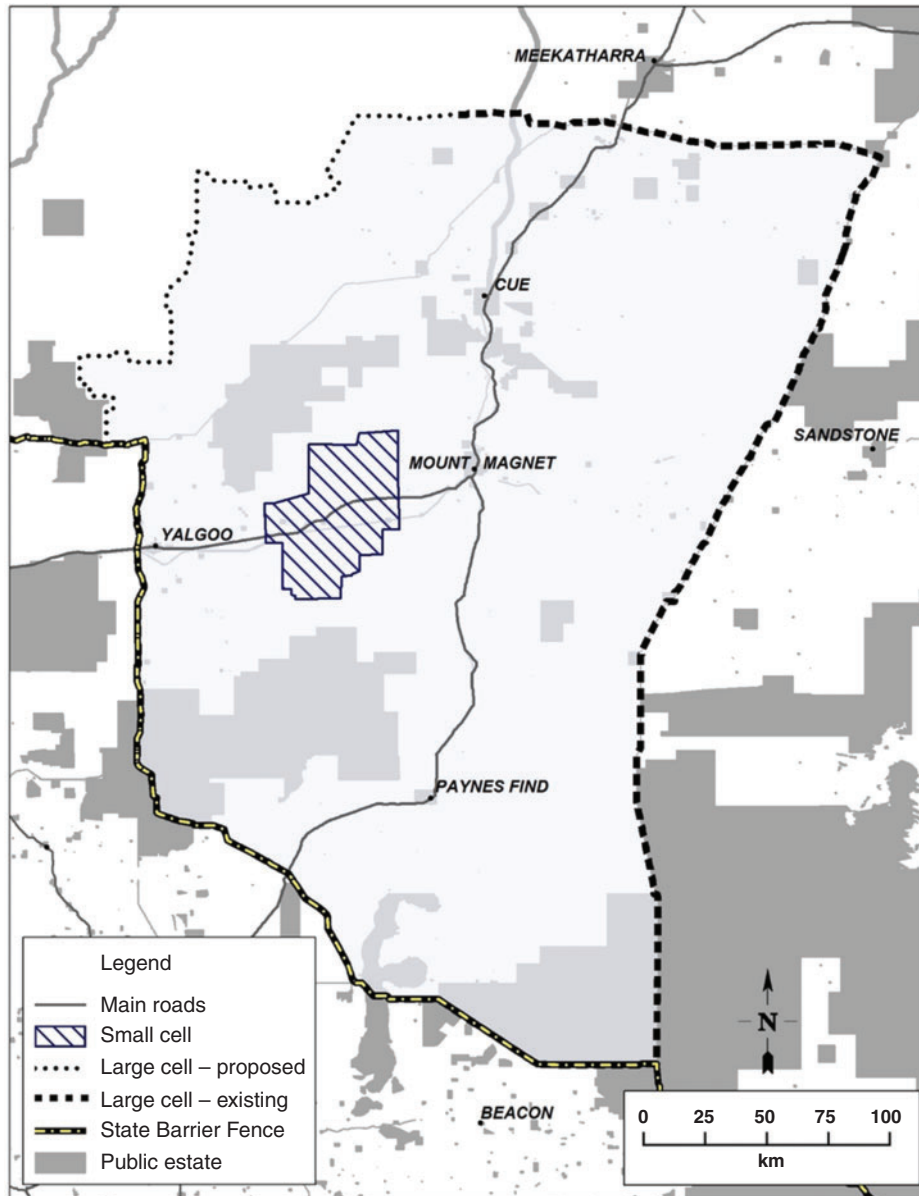
Fig. 1. Map of the study area delineating existing and proposed fences in the rangelands in Western Australia.

mapped as a raster image comprising square pixels of 1.3 km on each side. Pixel values were used to represent resource availability (a unit-less parameter), which was determined by the minimum straight-line distance to land systems containing rocky outcrops. Because the study area is in an arid environment, we used rocky outcrops as the primary habitat resource. A maximum resource value of 75 was assigned to pixels falling within the first 500 m of land systems containing rocky outcrops, and resource value declined as the distance to those land systems increased, reaching a lower bound of 45. Urban areas were assigned a resource score of 15 and pixels comprising salt lakes had a resource value of zero.

HexSim was then used to convert this raster map into a vector array of space-filling hexagonal cells, each having an area of

11.2 km^2 and a width of 3.6 km (measured between parallel sides). Each hexagon enclosed a set of raster pixels, often including partial pixels along the hexagon edges. The hexagons were assigned a score equal to the area-weighted mean of the pixel resource-availability values falling within their bounds.

Model structure and parameters

We started with the model developed by Pacioni *et al.* (2018). This model, also developed in HexSim (Schumaker and Brookes 2018), was a spatially explicit, individual-based model, and it simulated wild dog dynamics with yearly time steps. Simulation parameters were drawn from published research on biology and ecology of dingo populations in the WA northern rangelands, as described in Pacioni *et al.* (2018), and the model included

important elements of the social behaviour such as pack aggregation, pack territoriality, and it linked reproduction to pack composition (for details, see Pacioni *et al.* 2018; Appendix S1 Model description, available as Supplementary material to this paper). To adapt the model to simulate more realistic dingo–bait interactions, we first changed the time-step unit from 1 year to 2 months (Fig. S1, available as Supplementary material to this paper). The 2-month time-step choice was based on the realistic length of life of baits in this environment (Kreplins *et al.* 2018). This time step was also convenient because we had movement data for wild dogs over an approximate 2-month period (Thomson 1992). Accordingly, we adjusted the movement parameters in the model to align these with the new time step. We rounded the average area explored by each wild dog (from Thomson 1992) to the nearest integer number of hexagons (5 hexagons for loners, and 1 hexagon for pack members).

Last, we implemented a framework that explicitly simulates the interaction between wild dogs and baits (see below). It is important to recognise that this framework can be extended to simulate interaction among any species (discussed in more detail below), providing these can be correctly parameterised in the model. Hence, this approach provides a tool to simulate competitive dynamics among predator species or between predators and non-target species.

Wild dog interactions with baits can be thought of as a probabilistic process that includes several components. First, a wild dog needs to encounter a bait, which occurs with a probability of $P(E)$. Once the bait is encountered, whether the wild dog consumes the bait is determined by the conditional probability of bait consumption, given it has been encountered, namely $P(B|E)$. Moreover, because a wild dog can encounter a bait multiple times within the 2-month life span of the bait, it was necessary to determine how many times the same individual would encounter the same bait, repeating, for each time, the process described above. If a wild dog consumes a bait, it will die with probability $P(M_c|B)$.

We used data from Kreplins *et al.* (2018) to obtain several parameter values for the newly developed model. Kreplins *et al.* (2018) monitored the fate of ~936 baits with heat-in-motion camera traps and sand pads during three baiting rounds in an area within the large cell that we simulated. Even though we could explicitly model each non-target species, we did not implement this because of computational constraints and because it fell outside the scope of the study. However, to account for the deployed baits that were unavailable to wild dogs because of removal by non-target species, we calculated the average percentage of baits that were removed in autumn and spring and applied a fixed percentage in each of these seasons in the model. This is equivalent to assuming that the non-target species have the same abundance and that they interact in the same way with poison baits in each baiting round.

We assumed that a wild dog's area of activity (A) over each 2-month time step was fixed, having a centre of activity s and dispersion σ (e.g. Ramsey *et al.* 2005). We expected that when a bait location coincides with the centre of activity s within the 2-month period, the number of encounters ($n_{i,j}$) between the bait i and the wild dog j will follow a Poisson distribution, with a rate λ_0 (i.e. mean number of encounters per 2 months), as follows:

$$n_{i,j} \sim Poisson(\lambda_0) \tag{1}$$

Because HexSim simulates each wild dog's movements, the model is then able to establish whether an individual is in a hexagon with a bait present. We further assumed that $n_{i,j}$ would progressively decrease with the distance between the bait and the activity centre s, following a half-normal distribution, as follows:

$$n_{(i,j)} \sim Poisson\left(\lambda_0 \times e^{-d_{i,j}^2/2\sigma_s^2}\right) \tag{2}$$

where $d_{i,j}$ is the distance between the bait i and the activity centre s and σ is the standard deviation of the half-normal distribution and is proportional to the area of activity A. For each wild dog, the value of σ was selected on the basis of its social status (i.e. whether a pack member or loner) by using the upper and lower limit of the distribution of σ (see below), so that the model would take into account that loners tend to have wider areas of activity. Note that when $d_{i,j} = 0$, Eqn 2 simplifies to Eqn 1. Otherwise, $n_{i,j}$ decreases as d increases. The coordinates of s within a hexagon were randomly drawn from a uniform distribution, in each baiting event and each time step, in such a way that the final location was constrained to be within the circle bound by the hexagon. Bait locations were assigned similarly.

The parameter values for λ_0, σ and $P(B|E)$ were estimated from the camera-trap data of Kreplins *et al.* (2018). Kreplins *et al.* (2018) detected 325 wild dog-bait encounters. Of these, only four baits were consumed by wild dogs. Therefore, we set $P(B|E) = 0.0123$. Using wild dogs' unique morphological features, several individuals could be identified and, therefore, it was possible to fit a spatial mark–resight model for a partially marked population to estimate λ_0 (which is equivalent to the camera detection rate) and σ from Eqn 2 (Chandler and Royle 2013; Forsyth *et al.* 2019). We defined a bait encounter as the co-occurrence of a wild dog and a bait in the same image and used a binary covariate in the analysis to indicate whether the bait was available or not (that is, whether it was already removed), under the expectation that the detection rate could vary depending on the presence of the bait. We limited this analysis to the first baiting round and included data only for the baits with a known fate. Furthermore, we assumed that within the 2-month period, bait consumption was uniformly lethal (that is, $P(M_c|B) = 1$). We also removed the baits at the end of each simulated time step; therefore, baits that were not consumed did not accumulate in the environment. However, it is important to point out that the model is able to include bait accumulation, should this feature be required in future research.

A few additional minor changes were made to the model of Pacioni *et al.* (2018) to adjust for the new time-step units, and smaller movements. During the simulations, HexSim kept track of the resources available within the home range of each individual. These were potentially available to individual wild dogs, although multiple individuals within the same territory would compete for the same resources. Within the same social status (dominant or subordinate animals and pack members or loners) and age class, resources are stochastically assigned to individuals, but dominant and adult animals have priority over subordinates and younger wild dogs (see details on the competition parameters below for resource acquisition of loners). A resource category (low, medium, high) was assigned to each

individual, on the basis of the percentage of their resource target that they were able to obtain (Pacioni *et al.* 2018; Appendix S1 Model description). Resource targets represent the resources required by each individual, which were set to 40 for adults and yearlings and five for juveniles. These resource categories are linked to different levels of mortality so that individuals that lack resources have a higher mortality rate. The modified model differs from that of Pacioni *et al.* (2018) in that individuals in the high-resource category have the same mortality rate as do those in the medium class. This was undertaken so that the population is more responsive to reaching carrying capacity. That is, when the population overshoots carrying capacity, it more quickly returns below carrying capacity, whereas, in Pacioni *et al.* (2018), there was a relatively longer time lag.

We adjusted the minimum resource required for individuals to join a pack in comparison to Pacioni *et al.* (2018), which was set to 80 (that is, the resource required by two individuals). This was done because, as the landscape explored is smaller when the time unit is set to 2 months, no pack formation would be otherwise possible.

Concurrently, we also adjusted the competition parameter, which was set to 50%. As explained in more detail in Pacioni *et al.* (2018), competition between loners and pack members to access resources is controlled by this parameter, and we had to ensure that loners could access a minimum amount of resources, given that a lower resource requirement is applied to pack formation, and pack members have priority in accessing resources in HexSim (see Appendix S1 Model description).

Because life-history events (e.g. pack formation, breeding, natural mortality) are spread across different seasons (Fig. 2), the model needs to run through a few cycles before reaching equilibrium. To speed up the computation time, we let the model with no control run for the equivalent of 6 years. We saved the model steady-state conditions at the end of these shorter simulations and used them to initialise all simulations used for analysis here. Hence, all simulations start with a wild dog density being closer to carrying capacity, except for those scenarios where the large cell was empty (i.e. post-eradication simulations, see below).
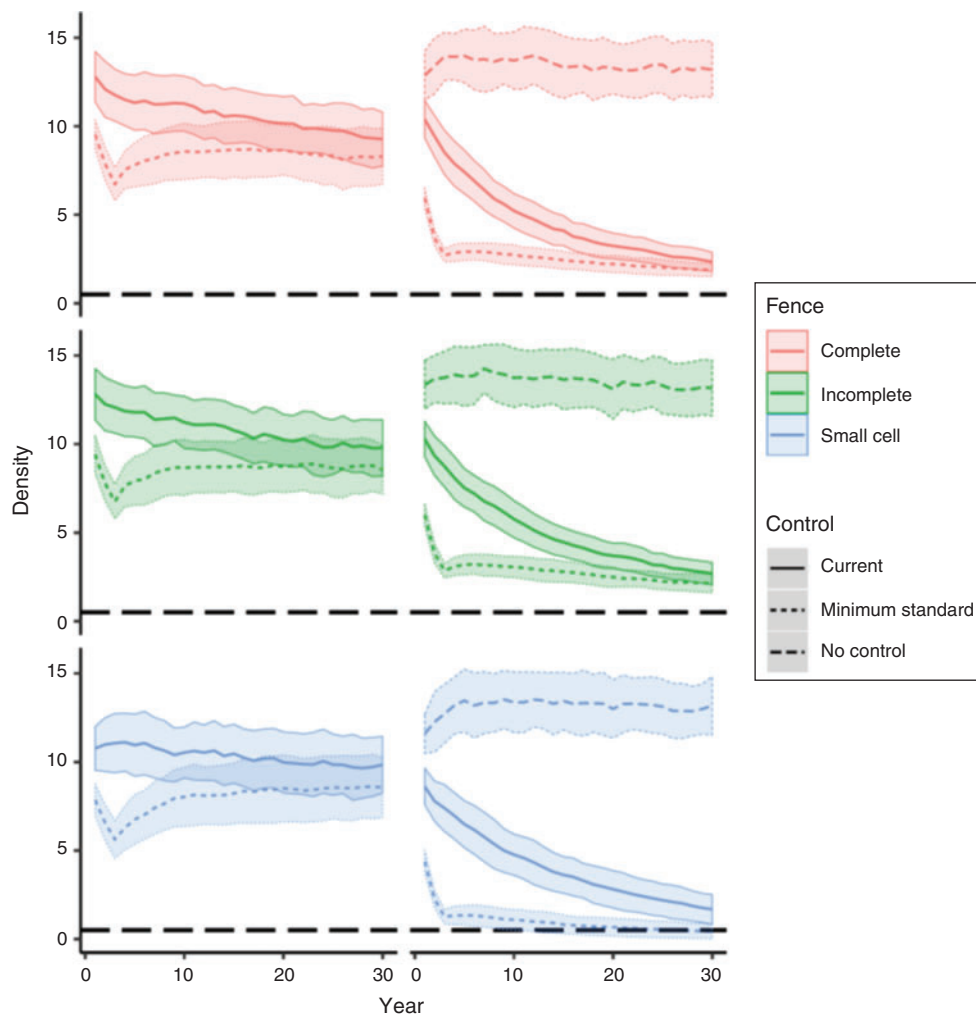

Fig. 2. Mean wild dog density projections (shaded area indicates one standard deviation) from scenarios with different fencing options (by row and colour) and control levels (line types) with $\lambda_0 = 0.4$ (left) or $\lambda_0 = 1.3$ (right). Thick dashed line indicates a density of 0.5 dogs per 100 km^2.

A framework similar to that used for the baiting process could be easily implemented to simulate trapping and shooting. In fact, the efficiency of this control method will similarly depend on the probability of encountering the trap, and then that the wild dog will be trapped, once the trap has been encountered. However, we did not have data for trapping equivalent to those we had for baiting, so we were not able to accurately parameterise these events and decided to maintain the approach used in Pacioni *et al.* (2018; that is, to apply a fixed percentage mortality as a function of the landscape used by the wild dog where trapping and shooting occur). The final model is available in Appendix S1.

Management scenarios

Wild dogs are generally controlled in the study area by using a combination of baiting, trapping and shooting. Trapping and shooting were simulated by applying 5% additional mortality in all scenarios that implemented control.

The following three baiting regimes were modelled:

- No Control
- Current Control: intended to simulate the current control implemented in the area, which is characterised by two baiting events, one in autumn (pre-breeding) and one in spring (post-breeding). For each baiting event, the selected properties where baits were deployed and the bait rate (either 3 or 10 baits km^{-1}) were based on records collected for 2015 by the Meekatharra Rangeland Biosecurity Association (MRBA) biannual coordinated baiting (MRBA, unpubl. data, see below).
- Minimum Standard: a baiting regime designed to resemble the proposed management approach inside of the large cell, as identified in the Meekatharra Rangeland Biosecurity Association Wild Dog Management Plan 2014–2019 (MRBA 2014). In this regime, the whole cell is baited (with the exception of salt lakes) at 10 baits km^{-1} every 6 weeks (i.e. eight sessions per year, four before breeding and four after). We simulated this option by developing scenarios where the new minimum standard control was applied for the first 3 years and then reversed back to the Current Control as for the proposed management plan.

We used the records of the Meekatharra Rangeland Biosecurity Association to calculate the number of baits that were deployed, on average, during 2015 (the year for which we had data) and, by using ArcGIS (ESRI 2011), we obtained the length of the roads in the properties included in the large cell. We then computed the mean bait rate on each road in each property, and, eventually, the total number of baits within each hexagon that would be deployed in each of the baiting regimes in the cell under the Current Control and the Minimum Standard, assuming 10 baits km^{-1}.

All control options described above were modelled with three possible fencing solutions, which are summarised below.

- Incomplete: without the completion of the large-cell fence. Following on from Pacioni *et al.* (2018), the existing fence was assumed to have 2% permeability.
- Complete: with the completion of the large-cell fence with 2% permeability.
- Small cell: completion of the small cell (2600 km^2). Given the small size of the fence, we assumed that it was possible to maintain the permeability of the fence at zero.

If eradication was achieved in the large cell, we evaluated the level of control that would be needed to keep the large cell free of wild dogs. This was undertaken by including scenarios where the large cell was initialised with no wild dogs inside. Because the small cell was assumed to have a completely dog-proof fence, we limited the 'post-eradication' simulations to scenarios with and without a completed fence of the large cell, and with and without Current Control.

Statistical analysis

Simulated data were collated and statistical analysis was conducted with the R package HexSimR (Pacioni *et al.* 2018) or custom scripts in R 3.5.2 (R Core Team 2018). We defined immigrant wild dogs as those born outside the fence but whose location was recorded within the fenced area at the end of each time step. The wild dog mean density was calculated considering only extant populations (that is, simulations where the wild dog population went extinct were removed before analysis). We computed the mean probability of eradication as the proportion of simulations where the population size was zero, and the 'functional' probability of eradication as the proportion of simulations where the wild dog density was <0.5 dogs per 100 km^2. The 95% confidence intervals for probability parameters were computed with the function binom.confint, from the R package binom (Dorai-Raj 2014), by using the Wilson method (Brown *et al.* 2001). Pairwise statistical comparisons between mean densities of the scenario were performed computing the strictly standardised mean difference (Zhang 2007) because its significance is not influenced by sample size (which is large in our case).

Results

As expected, estimates of σ were consistent regardless of whether the bait was present in front of the camera or not. Hence, we estimated this parameter by fitting the model without this covariate. The mean estimate was 8500 m, with a 95% upper limit of 9411 m, which was applied to loners, and a lower limit of 7678 m, which was applied to pack members. Surprisingly, the detection rates were lower when the bait was present (that is, $\lambda_0 = 0.4$, 0.2–0.8) than when it was not (1.3, 1–1.6). On the basis of these results, we ran the simulations twice, once with $\lambda_0 = 0.4$ and another with $\lambda_0 = 1.3$, so as to evaluate the sensitivity of the results to this parameter value.

Management scenarios

No Control

Under the No Control option, if a wild dog population was established in the cell, we did not detect any difference in wild dog density, which fluctuated around the carrying capacity of ~12 dogs per 100 km^2, across the three considered fencing solutions (Table S1, available as Supplementary material to this paper, Fig. 2). For this reason, we do not discuss these results further.

Current Control

The value of λ_0 had a strong effect on the results. The Current Control scenarios predicted significantly ($P < 0.001$) lower wild dog densities than did the No Control option in both short-term (Year 5) and long-term (Year 30) trajectories in all fencing options, but only when $\lambda_0 = 1.3$ (Table S1, Fig. 2).
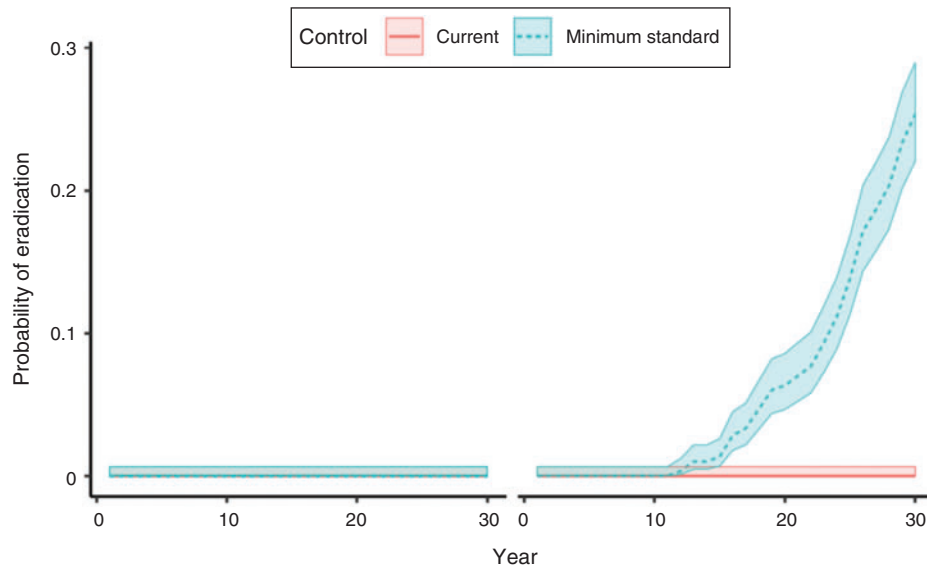
Fig. 3. Mean probability of eradication within the small cell as a function of time (shaded area represents 95% confidence intervals) for scenarios with different control levels (line types and colour) with $\lambda_0 = 0.4$ (left) or $\lambda_0 = 1.3$ (right).

In the short term (5 years), the mean density was <8 dogs per 100 km^2, regardless of the fencing option applied (i.e. complete or not, or the small cell). In the long term (Year 30), the mean density was <3 dogs per 100 km^2 with an incomplete or complete fence, and 1.7 dogs per 100 km^2 when a small cell was simulated (Table S1, Fig. 2).

When $\lambda_0 = 0.4$, the wild dog density under the Current Control scenario was lower than under the No Control option ($P < 0.036$) only in the long term (Year 30) and in the scenario where the fence was completed (Table S1, Fig. 2). With this level of control, the completion of the fence did not change wild dog density significantly compared with the incomplete-fence scenarios. Similarly, although there was a tendency in the simulations with the small cell to have a slightly lower density at Year 30, the density was not significantly lower.

Minimum Standard Control

When the Minimum Standard level of control was simulated, the predicted wild dog densities were significantly lower, in both the short- and long-term trajectories, than were those obtained with the No Control and the Current Control options within the same fence option (Table S1, Fig. 2; $P \leq 0.0003$ when $\lambda_0 = 1.3$, and $P < 0.04$ when $\lambda_0 = 0.4$). Also, the mean wild dog density in the small cell with the Minimum Standard level of control was significantly lower than it was in the other two fence alternatives ($P < 0.001$, except in the comparison with the complete-fence option at Year 30, where $P = 0.017$) when $\lambda_0 = 1.3$ (Table S1, Fig. 2).

Probability of eradication

The only scenario that had a probability of eradication higher than zero was where the small cell was modelled and when lethal control was applied as planned in the proposed new management

(i.e. Minimum Standard, Fig. 3) with $\lambda_0 = 1.3$. Implementation of the Minimum Standard of 6-weekly baiting (effectively quadrupling the Current Control level of baiting) resulted in a rapid decline of wild dog abundance, with a ~50% decline in the first year compared with the No Control option. The population continued to rapidly decline, with the probability of eradication becoming significantly larger than zero at Year 12 and progressively increasing over the 30 simulated years to reach 25% (95% confidence intervals: 22–29%). Consistent with this pattern, the inspection of the probability of functional eradication profiles further demonstrated that the small cell and Minimum Standard is the most efficient combination between fencing and control (Fig. 4). This was the only fencing solution where the Current Control level was effective in achieving functional eradication. When the small cell was implemented, the probability of functional eradication was significantly larger than zero at Year 23, with the Current Control reaching 2.3% (95% confidence intervals: 1.4–3.9%) at the end of the simulations. Results were more optimistic when the Minimum Standard baiting regime was implemented. In this case, the probability of functional eradication was larger than zero at Year 3, reaching 59.7% (95% confidence intervals: 55.7–63.5%) at the end of the 30-year simulations.

Immigrants

Immigrants did not account for more than 2% of the population in all the simulations with a complete fence, whereas the proportion of immigrants in scenarios where the fence was incomplete was highly variable across the 30 simulated years (although always being relatively small, Fig. 5). Somewhat counterintuitively, the proportion of immigrants was higher in simulations where the Minimum Standard baiting regime was implemented and smaller when No Control was simulated (<2.5%), with the Current Control being somewhere in between (~4–8%).
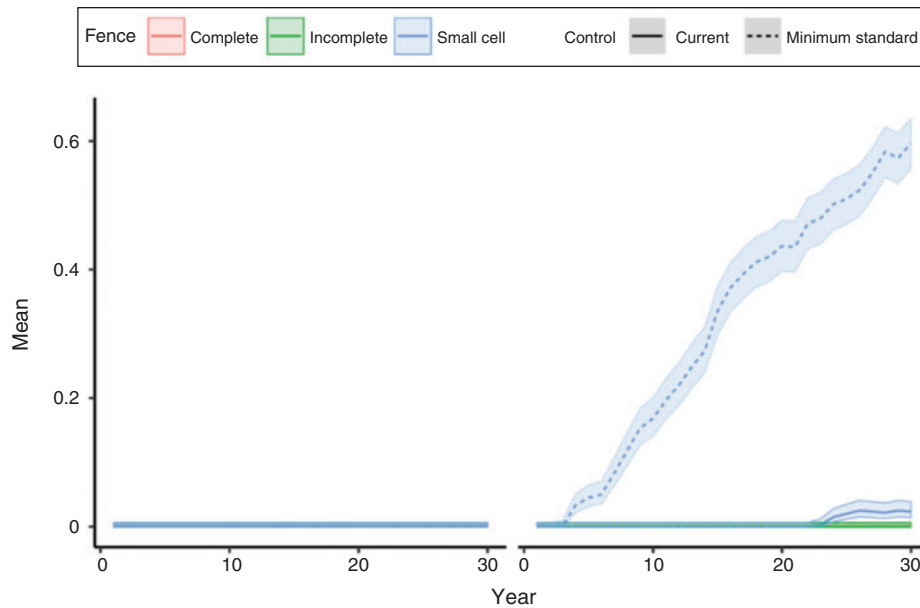
Fig. 4. Mean probability of functional eradication (that is, the probability of wild dog density to be <0.5 dogs per 100 km^2) as a function of time (shaded area represents 95% confidence intervals) for scenarios with different fencing options (colour) and control levels (line types) with $\lambda_0 = 0.4$ (left) or $\lambda_0 = 1.3$ (right). Note that results vary only for Current and Minimum Standard Control levels different with $\lambda_0 = 1.3$ in the small cell. For all other fence and control combinations, results overlap.

Post-eradication scenarios

The small-cell scenarios were simulated with a permanent fully wild dog-proof fence; thus, post-eradication simulations were limited to the large cell (Table S1, Fig. 6). Broadly speaking, if eradication is achieved, the role of the fence is more substantial. If control is suspended after eradication is achieved, the wild dog population will gradually recover reaching a mean density of 5–7 dogs per 100 km^2 at the end of the 30-year simulations, with no statistical difference depending on whether the fence was completed or not. However, in the short term, the completion of the fence will maintain the mean wild dog density at <0.5 dogs per 100 km^2, for ~10 years, whereas in the scenarios without a complete fence, the wild dog density will go above this threshold within 3 years and will be significantly ($P < 0.001$) higher in Year 5.

Our results indicated that ongoing control activities at the Current Control level, after achieving eradication, will maintain the population at a density of <0.5 dogs per 100 km^2 for all of the simulated years in the model with $\lambda_0 = 1.3$, and the first 20 years when $\lambda_0 = 0.4$ and the fence is completed. Without completion of the fence, the wild dog density is predicted to go above this threshold within the first 10 years (Table S1, Fig. 6).

Discussion

We have demonstrated how our model can be used to test management scenarios by simulating different levels of control within a large cell with and without a completed fence, or, alternatively, limiting the exclusion fence to a smaller cell of producers. We first discuss the management implications of this work, and, then, the general benefits of the improved modelling

framework that we have developed, as well as indicate areas of further expansion.

Management of wild dogs within a large cell

The main principles underpinning the establishment of the large cell are as follows: (1) the control of the wild dog population in the cell is necessary to re-establish small-stock enterprises in the area and (2) immigration of wild dogs prevents effective wild dog control in the cell. Preventing immigration with a fence should facilitate effective control and allow livestock enterprises to re-establish. However, the primary finding of our study was that, once wild dogs are established, there are only minor differences in population trajectories between scenarios with and those without the completion of the fence. Reproduction of the wild dog population is clearly of greater contribution to the growth in the wild dog population than is immigration from outside the cell. For example, under the Current Control scenarios without the fence completed, average immigration is between 2% and 6%, which we argue is insufficient to cause a drastic change in population trajectories. However, interestingly, in the absence of a complete fence, a more intense baiting regime is responsible for a higher proportion of the population inside the cell being immigrants. We argue that this is because the removal of resident individuals frees up resources that facilitate the survival of immigrants. In contrast, with a stable population, pack members defend the territory and deter access to resources by immigrants (Thomson 1992; Corbett 1995).

Although substantial control of wild dogs could be achieved through increased control practices, our results also indicate that both levels of control (i.e. the Current Control and the
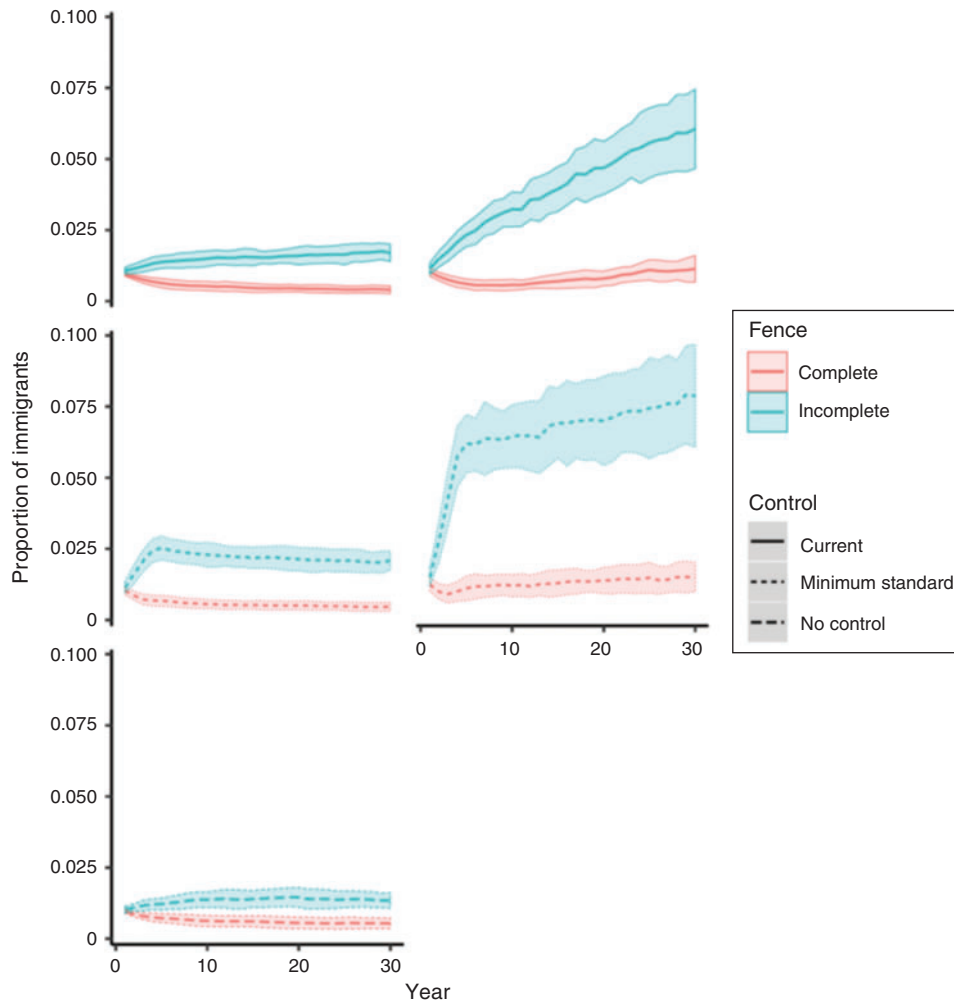
Fig. 5. Mean proportion of immigrants (shaded area indicates one standard deviation) across different fence options (colour) and control regimes (by row and line type) with $\lambda_0 = 0.4$ (left) or $\lambda_0 = 1.3$ (right).

Minimum Standard) in the large cell are inadequate to achieve true eradication of the wild dog population. The proposed Minimum Standard of control as advocated in the Meekatharra Rangeland Biosecurity Association Wild Dog Management Plan 2014–2019 (MRBA 2014) effectively reduces wild dog populations by a third to a half in the first year and a half to two-thirds within 3 years, depending on the value of λ_0. However, it is likely that there would be significant challenges associated with the implementation of 6-weekly baiting in terms of time and provision of meat for baits, bait manufacture and bait deployment. Furthermore, it should be noted that in Kreplins *et al.* (2018), the baits are taken only by juveniles, so it is possible that the modelled mortality owing to baiting is over-estimated. With regard to impacts of wild dogs on livestock, it is important to note that a reduction in wild dog numbers does not guarantee a linear decrease in livestock losses (Fleming *et al.* 2014). Thomson (1986) indicated that prevention of losses for sheep producers is achieved only when there is 100% removal of resident wild dogs within paddocks and reinvasion is prevented.

In contrast, the small-cell option appears to provide a more feasible alternative. We considered the size of this exclusion fence to be small enough to reasonably expect that it could be maintained to be fully wild dog-proof. Scenarios that implemented this fencing solution were the only ones where an absolute eradication could be achieved. Even if not achieved, when the Minimum Standard of control was implemented (and when $\lambda_0 = 1.3$), the mean population density was below 0.5 dogs km^{-2} for most of the second half of the 30 years, which we would expect to provide substantial relief to small-stock producers. However, it is important to note that the threshold of 0.5 dogs km^{-2} we considered is somewhat arbitrary and there is no evidence that, at this density, the economic benefits for the livestock industry are equivalent to those of true eradication. Given the smaller size of the enclosed area, the costs and the logistics involved in implementing such a high level of control are likely to be reduced. Additionally, because all participants have a direct interest in controlling wild dogs, any issues of variable implementation of control measures should be resolved. Moreover, if true eradication is achieved, control
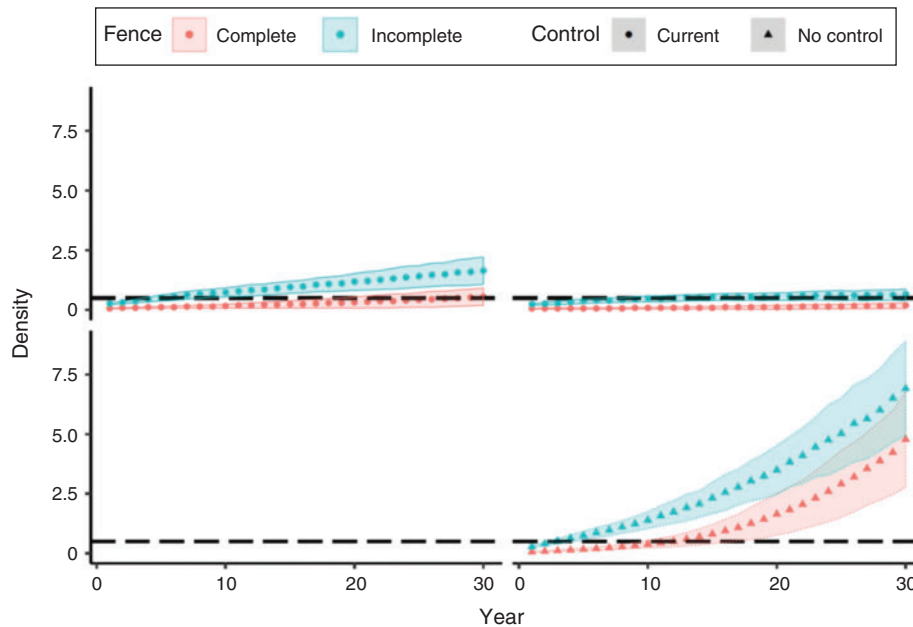
Fig. 6. Mean wild dog density projections (shaded area indicates one standard deviation) of post-eradication scenarios with different fencing options (colour) for the Current Control scenario (top row) with $\lambda_0 = 0.4$ (left) or $\lambda_0 = 1.3$ (right), or the No Control scenario (bottom row). Thick dashed line indicates a density of 0.5 dogs per 100 km^2.

could be suspended, except to prevent fence breaches, providing a further return on investment.

There was a substantial difference in the results depending on the value used for parameter λ_0. Curiously, the estimation of the encounter rate with camera-trap data was lower when a bait was present in front of the camera. This could be a result of active avoidance of the baits by wild dogs. Indeed, Kreplins *et al.* (2018) observed wild dogs urinating or defecating on or in proximity of the baits, which is a behaviour thought to encourage active avoidance. Alternatively, our finding could be due to a response to the actual human activities related to deploying the baits. Wild dogs could have resumed their normal activities in a few days, but, because most baits were removed by non-target species within a few days (Kreplins *et al.* 2018), our estimates could be biased. Because we could not distinguish between these two alternative hypotheses, we evaluated the effect of baiting by using both values. Regardless of what the true value for this parameter is, the general trend remains unchanged in that only the Small Cell option seems to provide an opportunity for an absolute or functional eradication of wild dogs and possibly allows the control regime to be suspended once eradication is achieved. The difference of the impact of baiting on wild dogs between λ_0 values suggests that, should new or refined tools become available and be effective in increasing the encounter rate, efficacy of control could be greatly increased. Despite the discouraging results from Kreplins *et al.* (2018), our results indicated that there might be value in further exploring the use of lures in future research.

The modelling framework

We extended our previous model to simulate interactions between predators and baiting deployment in the landscape. Whereas we

recognise that the mathematical approach integrated in our framework is well established, as is the modelling environment (HexSim), we argue that the new coding that we implemented, and make available here, will facilitate further research in this field. The new coding is computationally intensive because it explicitly simulates single interactions between predators and baits, but we consider that this cost is minimal compared with the benefits of the model. Being an individual-based, spatially explicit model, this framework allows for a fine control of single components of the dynamics. Moreover, HexSim provides a very flexible module-based platform where further elements can be easily integrated. Coupled with the R package that we developed (HexSimR, Pacioni *et al.* 2018), which facilitates HexSim output-data handling and analysis, simulation results are readily available. We argue that the present study represents a substantial step forward in our capacity to accurately model predator dynamics, and their response to different management options.

HexSim allows multi-species modelling. That is, more than one species can be concurrently modelled. By linking each of the modelled species to the simulation features that we have developed, it will be possible to explicitly evaluate the effect of baiting programs on multiple predators (e.g. wild dogs, cats (*Felis catus*), foxes (*Vulpes vulpes*)), as well as the removal of baits by non-target species. Whereas these aspects were not of primary interest in our case study, they may be an important priority for other research where mesopredator release is anticipated to affect management strategies. Additionally, this approach may be relevant in conservation settings where non-target species may be native, threatened species, and the intent is to deliver a control program that reduces the abundance of introduced predators, while limiting the impact on native species.

Another research area where we envisage that our model can be of substantial assistance is in the investigation of consequences of learnt behaviours. It has been hypothesised that predators that are exposed to sublethal doses of poisonous baits may develop bait-avoidance behaviours because they associate the bait with a negative experience (Allsop *et al.* 2017; Kreplins *et al.* 2018). This acquired knowledge could be transferred either vertically, by teaching young animals to avoid baits, or horizontally to other conspecifics, by marking the baits present in the environment (e.g. by urinating on them) to prompt avoidance (Taylor 2017). A possible important consequence of bait-avoidance behaviours is that the efficacy of baiting programs is progressively reduced (Binks *et al.* 2015; Kreplins *et al.* 2018). Although quantifying the effect of learnt behaviours is challenging in the field, it could be easily implemented within our framework. It would be straightforward to, for example, compare whether the predicted consequences matched measured differences between a naïve versus an experienced population. Implementing this component in our model would involve the flagging of individuals that were exposed to baits but did not die (this clearly implies that the mortality probability when the bait is consumed is less than 100%). For these animals, λ_0 or P(B|E) would be reduced to reflect their knowledge and negative association with the bait. The simulations can keep track of the offspring of these individuals, and pass on this acquired trait. Indeed, HexSim has an inbuilt mechanism for trait inheritance. Horizontal knowledge transfer, instead, can be simulated by flagging the baits that have been successively encountered by individuals that were exposed to sublethal-bait intake. These flagged baits can then have a lower P(B|E) in their successive interactions with other individuals than would be the case for baits that have been urinated or defecated upon. We have already demonstrated a strong sensitivity of the model to the value of the encounter rate, indirectly highlighting how important these dynamics could be in altering the predicted outcome.

Further work

We recommend that future work include monitoring of bait uptake by target and non-target species as a function of their landscape use, so as to further refine the parameter estimates of the model, validate the model outputs and improve its predictive capability. Similarly, monitoring of trapping practices to obtain estimates of the probability of encountering a trap, and the probability of being trapped given a trap encounter, would be beneficial.

Clearly, obtaining predictive trajectories of predator abundance lends itself to become the input of bioeconomic modelling, so that it may be possible to not only evaluate management outcomes from an ecological perspective, but also from a cost–benefit one. We believe that adequate quantification of the per-capita predation on livestock and associated economic costs for the target species (regardless whether this is a threatened or livestock species) is currently often lacking and we suggest that further research in this area will make it possible to take full advantage of the output of the model we have presented here.

Because toxins used for bait preparation as well as methodologies to deliver baits are in continuous development, we envisage that further research should also evaluate the effects of situations where baits may persist through sequential baiting

events (i.e. bait accumulation in the environment), a feature for which the model is already equipped.

Conflicts of interest

The authors declare no conflicts of interest.

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