Abstract: Context: Little is known about the importance of bait-site selection during lethal fox-baiting programmes. Improved bait placement may increase the efficacy of baiting and help reduce fox impacts on wildlife and livestock. Aims: To determine whether bait uptake by the red fox (Vulpes vulpes) differed among five landscape elements (roadsides, fence lines, open paddocks, creek lines and remnant vegetation) and at sites with high or low habitat (ground cover) complexity. Methods: We measured bait uptake at 300 bait stations distributed evenly among the landscape elements in agricultural landscapes in northern Victoria, Australia. Bait uptake was also compared between sites with low and high habitat complexity in districts subject to no fox control and annual fox control. Key results: Among landscape elements, bait uptake was significantly higher in roadside vegetation and along vegetated creek lines than it was along fence lines and in open paddocks (P < 0.05 in each case). Within roadside vegetation, bait uptake was significantly (P = 0.001) lower at sites with a high habitat complexity than at sites with low complexity, particularly in areas subject to annual fox control. Conclusions: Bait placement influences bait-uptake rates considerably and greater consideration should be placed on bait-site selection during fox-baiting programmes. Habitat complexity limited bait uptake, which may indicate a reduced capacity of foxes to find baits in complex habitats. Implications: Our results should help improve bait-site selection in agricultural landscapes and may increase the efficacy of fox baiting to the benefit of native fauna and livestock.

DOI: http://dx.doi.org/10.1071/WR12169

URL: http://researchoutput.csu.edu.au/R/-?func=dbin-jump-full&amp;object_id=52240&amp;local_base=GEN01-CSU01

CRO Number: 52240
Title: Fox baiting in agricultural landscapes: preliminary findings on the importance of bait-site selection

Running head: Bait uptake by foxes in farmland

Author names and affiliations: Andrew Carter\textsuperscript{a}, Gary W. Luck\textsuperscript{a}\textsuperscript{*}

\textsuperscript{a} Institute for Land, Water and Society; Charles Sturt University; Albury, New South Wales, AUSTRALIA

*Corresponding author

PO Box 789
Albury, New South Wales, AUSTRALIA 2640
Ph: +61 2 6051 9945
Fax: +61 2 6051 9897
Email: galuck@csu.edu.au

Type of paper: Original research paper (5333 words + 3 tables, 4 figures and supplementary material).
Abstract

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To determine whether bait uptake by the red fox (*Vulpes vulpes*) differed among five landscape elements (roadsides, fence-lines, open paddocks, creek-lines, and remnant vegetation) and at sites with high or low habitat (ground cover) complexity.

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We measured bait uptake at 300 bait stations distributed evenly among the landscape elements in agricultural landscapes in northern Victoria, Australia. Bait uptake was also compared between sites with low and high habitat complexity in districts subject to no fox control and annual fox control.

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Among landscape elements, bait uptake was significantly higher in roadside vegetation and along vegetated creek-lines compared to fence-lines and open paddocks (*P* < 0.05 in each case). Within roadside vegetation, bait uptake was significantly (*P* = 0.001) lower at sites with a high habitat complexity compared to sites with low complexity, particularly in areas subject to annual fox control.

Conclusions
Bait placement influences bait-uptake rates considerably and greater consideration should be placed on bait-site selection during fox-baiting programs. Habitat complexity limited bait uptake, which may indicate a reduced capacity of foxes to find baits in complex habitats.

Implications
Our results should help improve bait-site selection in agricultural landscapes and may increase the efficacy of fox baiting to the benefit of native fauna and livestock.
Introduction

The red fox (Vulpes vulpes) is a well-established exotic pest in Australia. Through predation, it reduces agricultural production (the sheep industry primarily: Gong et al. 2009) and threatens the survival of more than 100 native fauna species (Coutts-Smith et al. 2007). Currently, the most widespread and effective method of fox management in Australia is lethal baiting, whereby meat-based baits impregnated with poison are distributed in areas requiring fox control (West and Saunders 2007; Mahon 2009). The principal toxicant used in Australia is sodium monofluoroacetate (1080), although an alternative, para-aminopropiophenone (PAPP) (cf. Marks et al. 2004), is also likely to be available for use in the near future (Saunders et al. 2010).

For a lethal fox-baiting program to be successful, baits must: (i) be encountered; (ii) be consumed; and (iii) contain sufficient poison when ingested. The attractiveness and/or palatability of canid baits has been the subject of considerable research in Australia (e.g. Allen et al. 1989; van Polanen Petel et al. 2001; Gentle 2005), as has the issue of 1080 degradation in baits (e.g. McIlroy et al. 1988; Wong et al. 1991; Saunders et al. 2000). Yet, there has been very little research on bait placement in Australia (Carter et al. 2011) even though bait-site selection has been shown to affect bait uptake by foxes elsewhere (e.g. in urban England; Trewhella et al. 1991). This lack of research is surprising given the heavy reliance on baiting and the fact that ultimately, the attractiveness and toxicity of any bait is irrelevant if it is not encountered by a fox.

In Australia, fox baits are distributed via aerial baiting or ground baiting. Aerial baiting involves dropping baits onto the ground from aircraft at regular intervals along transects or selected linear features (e.g. sand dunes) (e.g. Thomson et al. 2000; Claridge and Mills 2007; Moseby et al. 2009). The objective of aerial baiting is generally to distribute baits uniformly over vast tracts of land to increase the likelihood that foxes will encounter a bait. Due to the increased labour associated with ground baiting, baits typically are placed at a limited number of selectively-chosen locations rather
than uniformly over the entire area where fox control is desired. Bait-site selection is therefore an integral aspect of ground-baiting programs and the locations selected for baits may impact on the effectiveness of this fox-control measure.

The issue of bait placement during ground-baiting programs is particularly relevant in the agricultural landscapes of south-eastern Australia because aerial baiting is not permitted there (Saunders and McLeod 2007). In these areas, it is mandatory to bury 1080 baits, which is thought to limit access to baits by non-target native species (Allen et al. 1989; Thomson and Kok 2002). Despite the reliance on ground baiting in south-eastern Australia, essentially the only guidance given to baiting practitioners regarding bait placement relates to minimum distance restrictions around dwellings, watercourses, property boundaries and public roadways (cf. Saunders and McLeod 2007). At present, bait-site selection is largely ad hoc.

Previous research has shown that on farmland in northern Victoria most fox baits were placed close to fences (Carter et al. 2011), which is consistent with baiting programs in other agricultural areas (e.g. Saunders et al. 1999; Greentree et al. 2000). However, it is unclear whether these locations represent the best sites to maximise bait exposure to foxes. Here, we examine bait uptake by foxes in two contexts. First, a ‘landscape’ experiment was conducted to determine how bait uptake varied in relation to large-scale features common to agricultural landscapes: open paddocks, fence-lines, creek-lines, roadside vegetation and remnant vegetation patches (separate from creek-lines and roadsides). Secondly, we conducted a ‘habitat complexity’ experiment to determine whether ground-layer habitat complexity influences bait uptake. Maintaining complex ground cover is important for ground-dwelling native species that use this substrate for shelter or nest sites. Variation in ground cover may also alter predation rates (Arthur et al. 2003) thus influencing bait uptake. Our results have implications for improving fox control and managing fox impacts on livestock and threatened fauna in agricultural landscapes.
Materials and methods

Study area

Our study was conducted in a region that supports likely the highest density of the bush stone-curlew (*Burhinus grallarius*) in south-eastern Australia (Carter 2010). Throughout this region, the curlew occurs primarily on private farmland and predation of eggs and chicks by foxes is regarded as a primary cause of the species’ decline and a significant threat to its persistence (Johnson and Baker-Gabb 1994; Gates and Paton 2005; DEC NSW 2006). The curlew is a flagship species in our study region and is used to encourage landholder participation in fox-baiting programs (Kubeil and Castles 2007). Therefore, our results have direct management implications for landholders’ attempts to improve curlew conservation in this region and broader implications for fox control in agricultural landscapes generally.

Bait uptake experiments were conducted across 78 000 ha of farmland in the Northern Plains region of Victoria, Australia (36°03’S, 145°10’E; Figure 1). The region consists mostly of privately-owned farmland used for mixed enterprises including cereal cropping and livestock. The area is a predominantly flat riverine plain, with an elevation of 100–110 m above sea level, and contains many watercourses including the Murray River, Goulburn River and Broken Creek (*cf.* Carter 2010).

[Landscape experiment]

Bait placement

Baits were located at 30 different sites representing six replicates of the following five landscape elements: roadsides, fence-lines, open paddocks, creek-lines, and remnant vegetation (not along
roadsides or creek-lines) (for further details see Carter 2010). These elements were selected because they are thought to be used by foxes for movement or hunting (Saunders et al. 1995), are bait locations used commonly in current fox-baiting campaigns (Carter et al. 2011), or are prominent features of agricultural landscapes. The replicates of each landscape element were inter-dispersed across the study area. Each site was separated by a straight-line distance ≥1.5 km (the approximate width of an average fox home range in the study area: Carter 2010; Carter et al. 2012), but sites where bait uptake was measured concurrently (see below) were ≥5 km apart to reduce the likelihood of individual foxes accessing baits at more than one site.

It was not logistically possible to bait all sites simultaneously so the experiment was conducted during four separate sampling periods in January–February 2006 (seven to eight baiting sites per period). Experiments were conducted during these months because the highest population densities of adult and sub-adult foxes occur at this time in Australia (Marlow 1992; Banks 1997) and it is an opportune time to conduct fox baiting for curlew conservation as juvenile curlews are most likely to be present and commencing dispersal (Marchant and Higgins 1993). Ten bait stations were placed at each baiting site, spaced at an average interval of 275.3 m (± 68.1 m SD, n = 300). Occasionally, landscape factors (e.g. presence of a dam, road, etc.) resulted in some baits being placed 200–400 m apart, although this did not occur in one landscape context more than another so there was no systematic bias in the distances baits were placed across sites or contexts. At each bait station, which was used once only, one bait was buried 50 mm below the soil surface. Bait stations were kept as visually inconspicuous as possible (i.e. no sand pads or raised soil) to avoid providing visual cues to foxes and non-target species. Bait station locations were marked only with a global positioning system (GPS; Garmin GPSmap 60C, Olathe, Kansas).

It was possible that some resident foxes in our study area may have developed aversive conditioning or neophobic behaviours from past exposure to 1080 baits (cf. Saunders et al. 1999;
Saunders et al. 2000; van Polanen Petel et al. 2001). Consequently, we used a novel, non-toxic bait (chicken ‘wingettes’: the wing section containing the ulna and radius bones) to reduce the likelihood of foxes avoiding baits. Baits were checked after eight days as this was deemed the optimal sampling period for such experiments (cf. Carter 2010).

We assessed whether foxes or non-target species were removing baits using a sub-sample of 50 bait stations (16.7% of 300 stations), which were monitored with passive infrared-triggered digital cameras (TrailMAC D540, Trailsense Engineering, Middletown, Delaware; and FaunaFocus FF120, Faunatech, Bairnsdale, Victoria). Cameras were mounted on portable stands constructed from fallen timber, placed approximately three metres from bait stations (for further details see Carter 2010). The location of cameras was randomised across the different landscape elements to avoid the presence of cameras causing bias in uptake results (e.g. through foxes avoiding bait stations with cameras). We also inspected each bait station for footprints, scats and other signs of visitation. Any baits known or suspected of being taken by non-target species were removed from analysis.

Landscape characteristics

The proximity of each bait station to the five landscape elements was measured to quantify their influence on bait uptake (e.g. were baits closer to roads more likely to be taken than those further from roads?). We also recorded grass height, prevalence of grazing land and presence/absence of stock at each bait station as these may influence bait uptake (Table 1).

[Approximate location for Table 1]

Data Analysis
Sample size varied slightly between landscape elements (Figure 3), so we compared differences in the mean percentage of bait uptake across landscape elements using a one-way analysis of variance (ANOVA). Error variances were equal (Levene’s test) and Tukey’s honestly significant difference (HSD) post-hoc test was used to conduct pairwise comparisons of means. Correlative relationships between bait uptake and the independent variables were examined using logistic regression with uptake included as a binomial response (bait removed or bait not removed). Independent variables were checked for multicollinearity prior to modelling using Spearman’s Rank Correlation, with $r_s \geq 0.5$ considered a suitable criterion for omitting a variable.

We aimed to identify the most parsimonious model, balancing the number of independent variables against the amount of variance explained in bait uptake (Gauch 2003). In logistic regression, Nagelkerke $r^2$ provides an estimate of variance explained, and we employed a manual forward selection procedure whereby once the variable explaining the most variance in bait uptake was identified, subsequent variables were added to the model to test the amount of additional variance explained relative to the global model (the model including all independent variables: Blanchet et al. 2008). Additional landscape variables were included in the model only if they improved the amount of variance explained by $>10\%$ of total variance. Model fit was assessed using the Hosmer-Lemeshow goodness-of-fit test.

**Habitat complexity experiment**

**Bait placement**

Subsequent to the landscape experiment, a further 120 bait stations were placed along roadsides, divided equally between two habitat complexity treatments: low and high. Roadsides were selected because habitat complexity varied substantially compared with other landscape elements in the study area and foxes are known to use roads (e.g. Meek and Saunders 2000; Ramp et al. 2006; Towerton et al. 2011). Habitat complexity was determined initially by visual assessments of fallen
timber (≥1 m long, ≥50 mm large-end diameter) density; areas with limited fallen timber = ‘low complexity’, areas with much fallen timber = ‘high complexity’. After the initial visual assessments, detailed measurements of habitat structure were collected at ‘high’ and ‘low’ complexity sites (see below) and differences in structure were tested using a two-sample unequal variance t-test (t).

Bait stations were then divided further to investigate whether an annual fox-control program may influence the results. In each complexity treatment, half the bait stations were assigned to areas with no recent history of coordinated fox control (i.e. no control since 2005; ‘no fox control’), while the other half were assigned to areas where a coordinated 1080 fox-baiting program had been conducted annually since 2005 (‘annual fox control’: cf. Carter et al. 2011). Vegetation and landscape structure were similar between the two treatments. This experimental design created four baiting treatments (Figure 2).

Bait stations were prepared and marked following the methods of the landscape experiment. A minimum straight-line distance of 1.5 km was maintained between bait stations in the no- and annual fox-control treatments. The average minimum distance between baits within each treatment was 611.2 m (± 149.7 m SD, range = 504–1505 m, n = 120). Baits were checked eight days after deployment and non-consumed baits were collected at this time. The experiment was repeated during three separate sampling periods throughout 2008 (120 baits were laid during each sampling period) to synchronise with an annual four-week community fox-baiting program (Carter et al. 2011). Sampling occurred immediately before lethal baiting commenced (‘pre-1080’), immediately after lethal baiting ceased (‘immediately post-1080’), and six weeks after baiting finished (‘6 weeks post-1080’).
Habitat complexity measures

Habitat complexity was measured for each bait station at a ‘roadside’ scale by measuring fallen timber density (TIMDEN) in a 50 m × 5 m straight-line transect located parallel to the road and 25 m either side of the bait station. We also recorded the width (m) of the roadside containing the bait station (RSWidth) and the predominant overstorey tree species (PREDTREE). Habitat measurements were also taken at a ‘macro’ (5 m × 5 m quadrat) and ‘micro’ (1 m²) scale, but these data did not show any clear relationships between habitat components and bait uptake and are therefore not included (see Carter 2010 for details).

Data Analysis

To determine if bait uptake was independent of fox-control history (annual or no fox baiting), habitat complexity (high or low) or sampling period (pre-, immediately post- or 6 weeks post-1080), data were arranged into a multi-way contingency table (2 × 2 × 3). The table was analysed using log-linear analysis (Tabachnick and Fidell 2007), which uses a model-fitting approach to compare the observed and expected frequencies for each cell in the table and determines the most economical combination of main effects and interactions that best describes variation in the data (Kinnear and Gray 2008). To test for all possible main effects and interactions, we used the ‘backward hierarchical’ approach to model-building with all possible effects and interactions included in the initial model (i.e. the ‘saturated model’). The best-fit model was identified by progressively removing each term in the model (starting with the third-order effect, followed by second-order effects, and so on), until a significant increase in the model’s chi-square value ($\chi^2$) was detected; at which point the final model was obtained.

We determined if the complexity of any particular ground habitat components influenced bait uptake more than others using logistic regression and an Information Theoretic Approach (ITA)
after checking the independent variables for multicollinearity (as per the landscape experiment). We ranked competing models using the second-order variant of Akaike’s Information Criterion, \( \text{AIC}_c: \) Akaike 1974; Buckland et al. 1997; Burnham and Anderson 2002), to select the model best explaining variation in bait uptake by foxes. Before proceeding with modelling, we assessed the fit of the global model to the data with a Hosmer-Lemeshow \( \chi^2 \) goodness-of-fit test (Burnham and Anderson 2002).

We used a random subsets approach to select the model best explaining bait uptake by foxes for each baiting treatment (annual fox control, no fox control); at the roadside scale; and for each sampling period (pre-, immediately post-, 6 weeks post-1080). We then compared the difference in the criterion values of the best ranked model to model \( i \) \( (\Delta_i) \). Models where \( \Delta_i < 2 \) have substantial empirical support; models where \( \Delta_i \) is 4–7 suggest considerably less support; while models where \( \Delta_i \) is >10 indicate essentially no support (Burnham and Anderson 2002). Akaike weights \( (\omega_i) \) were also calculated and these can be interpreted as the probability that any given model is the best model in the suite of candidate models (Burnham and Anderson 2001). To assess the relative importance of individual variables for each baiting treatment, spatial scale, and sampling period, we summed the Akaike weights \( (\omega_i) \) for every model containing the variable of interest. Statistical analyses were performed using SPSS 16.0.2 (IBM Corporation: Chicago, Illinois, USA) and S-PLUS 8.0 (TIBCO Software Inc.: Palo Alto, California, USA).

**Results**

**Landscape experiment**

Overall, 54.9\% \((n = 163/297)\) of baits were removed. There was no significant difference in the mean percentage of bait uptake across the four sampling periods (ANOVA, \( \text{F}_{3,26} = 0.654, P = 0.587 \)). The mean percentage of bait uptake at roadsides and creek-lines was significantly higher than at fence-lines and open paddocks \((P < 0.05\) in each case; Table 2; Figure 3). The most
parsimonious model explaining variation in bait uptake included only the variable ‘distance to road’
(\(\beta = -0.01 \) (SE ± 0.001); \(\chi^2 = 24.63\), d.f. = 1, \(P = < 0.001\)), and this model was not significantly
different from the statistically perfect model (Hosmer-Lemeshow goodness-of-fit \(\chi^2 = 2.09\), d.f. = 3,
\(P = 0.56\)). Bait uptake was higher the closer bait stations were to a road. The Nagelkerke \(r^2\) value
was 0.15 for the global model and 0.11 for the model with roads only.

[Approximate location for Table 2 & Figure 3]

Camera trapping occurred at fifty bait stations (600 camera nights), resulting in 344 photographs of
21 vertebrate species (Supplementary Material, Table S1). Foxes were the only species
photographed removing baits. Moreover, no other bait stations showed signs of bait uptake by non-
target species; hence all baits removed were assumed to have been taken by foxes and were used in
analyses.

Habitat complexity experiment

The percentage of baits removed varied according to baiting treatment and sampling period (Figure
4). Fewer baits were removed from sites with annual fox-control (54.4%; \(n = 98/180\)) compared to
no fox control (82.8%; \(n = 149/180\); Fisher’s Exact Test, two-tailed, \(P = < 0.001\)), and from high
complexity sites (60.6%; \(n = 109/180\)) compared to low complexity sites (76.7%; \(n = 138/180\); \(P =
0.001\)). No significant interactions between fox-control history, habitat complexity and sampling
period were identified using log-linear analysis (\(\chi^2 = 0.70\), d.f. = 2, \(P = 0.71\)) and the most
parsimonious model contained one main effect only (fox-control history) and no interactions (\(\chi^2 =
11.37\), d.f. = 10, \(P = 0.33\)). Fox-control history was the only significant main effect (\(\chi^2 = 10.61\), d.f.
= 1, \(P = 0.001\)), indicating fewer baits were removed from areas subjected to annual fox baiting.
The main effect of habitat complexity suggested a slight but non-significant trend toward the
removal of fewer baits from high complexity habitat (\(\chi^2 = 3.41\), d.f. = 1, \(P = 0.07\)).
Habitat complexity at the high and low complexity sites differed markedly. As expected, high complexity sites contained significantly more fallen timber (Supplementary Material, Table S2). There were no significant differences in the average values of the habitat variables between the no- and annual fox-control treatments (Supplementary Material, Table S2).

At the roadside scale, prior to 1080 baiting, PREDTREE was the highest ranked model in both the no- and annual fox-control treatments ($\omega_i = 0.27$ and 0.19, respectively), yet in both treatments, the top 4–5 models had $\Delta_i < 2$ (Table 3). PREDTREE had the highest summed Akaike weights in both no- and annual fox-control treatments ($\sum\omega_i = 0.72$ and 0.61, respectively). In the no fox-control treatment, all variables were positively related with bait uptake (i.e. as their values rose, the number of baits removed increased), while RSWidth was the only variable positively related with bait uptake in the annual fox-control treatment. Immediately post-1080 baiting, in the no fox-control treatment, two models had $\Delta_i < 2$. RSWidth was the top ranked model ($\omega_i = 0.42$) and received considerably more support than the second ranked model. In the annual fox-control treatment, three models had $\Delta_i < 2$ and RSWidth + TIMDEN was the highest ranked model ($\omega_i = 0.40$). RSWidth had the highest summed Akaike weights in both no- and annual fox-control treatments ($\sum\omega_i = 0.63$ and 0.70, respectively). All variables were negatively related with bait uptake. Similar results were obtained 6 weeks post-1080 baiting (Table 3).

Discussion

Landscape experiment
Significantly more baits were taken from roadsides and creek-lines than from fence-lines and open paddocks. This may be because foxes: (a) were more abundant-, (b) spent more time-, and/or (c) were more efficient at locating baits at roadsides and creek-lines. Without an independent measure of fox habitat use or detailed information on fox foraging behaviour, it is difficult to pinpoint the exact cause of the variation in bait uptake between landscape features. Nevertheless, this has little bearing on our most important finding that bait uptake varied across landscape features and this has substantial implications for appropriate bait-site selection in ground-baiting programs.

Saunders et al. (1997) suggested that bait uptake, and therefore fox-control efficiency, could be improved in the United Kingdom by targeting baits at preferred fox habitats. While this is also likely true in Australia, the strategy is currently hampered by the lack of data on fox habitat preferences at appropriate scales. In coastal New South Wales (NSW), Phillips and Catling (1991) tracked three foxes and identified a preference for coastal scrub habitat, while Moseby et al. (2009) used data from four foxes in arid South Australia to identify a preference for dune habitats. Other telemetry data on fox habitat preferences in Australia are limited to urban and peri-urban Melbourne where foxes exhibited a consistent preference for diurnal shelters associated with exotic weed infestations (Marks and Bloomfield 2006; White et al. 2006). Yet, most telemetry data on foxes to date are not at an appropriate spatial resolution to inform assessments of likely preference for particular landscape features such as fence-lines or roadsides.

Despite a poor understanding of fox habitat preferences in Australia, it is clear that foxes do not use space evenly within their home range. Foxes in the current study area used different locations within their home range for different purposes (e.g. feeding, movement between foci of interest, denning, etc.: Carter et al. 2012), which is consistent with telemetry studies on foxes outside Australia (e.g. Maurel 1983; Adkins and Stott 1998). Uneven space utilisation by foxes means that even if a control program delivers baits to a fox’s home range, there is no guarantee those baits will
be encountered or removed (as confirmed by Carter et al. 2011). Nevertheless, our results suggest that distributing baits preferentially along roadsides and creek-lines could increase the likelihood of bait uptake by foxes in agricultural landscapes, which is consistent with Meek’s (1998) recommendation to target these features during fox control in coastal NSW. In most regions this would require alterations to current regulations which prohibit baiting along roadsides and creek-lines (cf. Saunders and McLeod 2007).

Our findings may assist baiting practitioners in the agricultural landscapes of south-eastern Australia who are currently given no guidance on the best locations to maximise bait uptake. Apart from restrictions for baiting near certain features (e.g. property boundaries: cf. Saunders and McLeod 2007), bait placement is entirely ad hoc. In a related experiment, we explored bait-site selection during a typical landholder fox-baiting program, and demonstrated that most baits were placed along fence-lines (Carter et al. 2011). Baiting along fence-lines is also common elsewhere (Saunders et al. 1999; Greentree et al. 2000), yet, in the current study foxes removed fewer baits from fence-lines than from any other landscape feature. This suggests that the efficacy of landholder fox-baiting programs may be reduced by poor bait-site selection, although it is important to confirm our findings with more extensive studies.

Firstly, we measured bait uptake after eight days only, whereas fox-baiting programs occur commonly over 2–4-week periods (e.g. Greentree et al. 2000; Roberts et al. 2006; Carter et al. 2011). Hence, more baits are likely to have been discovered at fence-lines and open paddocks if baits were exposed for longer (although, we also tested for differences in bait uptake over 12 days and these results were very similar to those recorded for 8 days: see Carter 2010). Our shorter exposure period was justified as it is advantageous to maximise uptake of baits in the first few days after deployment to avoid potential problems associated with foxes eating baits containing sub-lethal doses of poison (cf. Saunders et al. 1999; Saunders et al. 2000; van Polanen Petel et al. 2001).
Secondly, some individuals within a fox population may not remove baits (Algar and Kinnear 1990; Thompson and Fleming 1994; Marks et al. 2009), while other foxes may monopolise and cache baits (Marks et al. 2003). Marks and Bloomfield (1999) found evidence of higher consumption of non-toxic baits by yearling foxes in urban Melbourne and suggested baits were either monopolised by young foxes or were less desirable to older foxes. Therefore, it is possible that our bait uptake results are not representative of the broader fox population but instead reflect the foraging activities of a few individuals (Marks et al. 2009) or a particular age class.

Bait uptake results may also vary with seasonality (Gürtler and Zimen 1982; Woodford et al. 2012). Seasonal variation in bait uptake could be influenced by a variety of factors including changes in fox abundance, home-range size, foraging behaviour or food requirements; prey availability (Trewhella et al. 1991); the activity of other bait-consuming species (Woodford et al. 2012); or climatic conditions (Gürtler and Zimen 1982). Our landscape experiment was restricted to January and February to coincide with a period of likely high fox density and the presence of juvenile curlews (see Materials and methods). Given this short time-frame it is unreasonable to extrapolate our results to other seasons when bait uptake may vary. Although logistically challenging, future landscape experiments could test the interaction between season and landscape context on bait uptake by foxes.

While our results may not necessarily hold true at other times of the year or in different environments, they demonstrate clearly the importance of bait-site selection. We argue that the efficacy of lethal fox-baiting programs would improve if bait-site selection was more strategic. This could be achieved by keeping spatial records of bait uptake and, during subsequent baiting programs, concentrating baiting at locations where baits were removed previously and re-locating bait stations where bait uptake was less prevalent. Over time, this approach should improve bait
encounter rates by foxes. This may require practitioners to place baits at locations that are less convenient to check (e.g. away from fence-lines), but the likely benefits include fewer wasted baits, less risk to non-target species and improved fox control.

**Habitat complexity experiment**

Ground-layer habitat complexity made little difference to bait uptake where foxes were not controlled, yet bait uptake was lower at high complexity sites where foxes were controlled annually; especially immediately after a month-long lethal baiting program (see Figure 4). Hence, the maintenance of complex ground cover appeared to limit the success of foxes in finding baits, but only in areas where annual control programs were conducted. Lower bait uptake in complex habitats may indicate that ground-cover complexity disrupts fox foraging behaviour, as has been demonstrated for aquatic predators (e.g. Hemminga and Duarte 2000; Manatunge *et al.* 2000), or alternatively, that foxes prefer more open ground cover (cf. Ruette *et al.* 2003).

Frequency of predation events vary regularly between different habitats (e.g. Hebblewhite *et al.* 2005; Hopcroft *et al.* 2005; Kauffman *et al.* 2007), but the reasons for this are often unclear (Andruskiw *et al.* 2008). In our study, bait uptake variation between the annual- and no fox-control treatments may reflect differences in fox abundance and/or age structure. Several researchers have used non-toxic bait uptake as an index of fox abundance (Thompson and Fleming 1994; Banks 2000), but recent research demonstrated that bait indices fail to reflect fox abundance accurately (Marks *et al.* 2009). We did not measure fox numbers directly so we cannot confirm that fox abundance was lower in the annual fox-control treatment. Nevertheless, short-term reductions in fox abundance have previously been recorded in this area (by spotlighting) immediately after baiting ceased (Kubeil and Castles 2007) and the effectiveness of 1080 baiting at reducing fox abundance in Australia is recognised widely (e.g. Dexter and Meek 1998; Thomson *et al.* 2000;
Körtner and Watson 2005). It is therefore reasonable to assume that the 1080-baiting program produced at least a short-term reduction in fox abundance in our annual fox-control area.

In the annual fox control–high complexity treatment, bait uptake immediately after 1080 baiting ceased was the lowest recorded in any treatment (23.3%) and was 50% lower than pre-control uptake for the same treatment. Across the same period, the reduction in bait uptake in the annual fox control–low complexity treatment (and in both no fox-control treatments) was marginal. The difference in bait uptake between high and low complexity sites in the annual fox-control treatment cannot reflect a disproportionate reduction in fox numbers between these sites, as high and low complexity bait stations were interspersed. Instead, it would appear that where fox abundance was likely reduced, foxes were either less efficient at locating baits in areas with high habitat complexity or avoided such areas.

In the eastern highlands of Victoria, Marks et al. (2003) demonstrated that areas subjected repeatedly to lethal fox control contained progressively fewer adult foxes and higher ratios of yearlings (<1-year old) to adults (>1-year old). Similar results have been obtained elsewhere (cf. Harris 1977). Hence, in our study, the area baited annually may have had a higher proportion of young foxes. In numerous species, young individuals are less efficient at foraging than older conspecifics (e.g. Goss-Custard and Le V. Dit Durell 1987; Smith and Metcalfe 1997; Bertellotti and Yorio 2000). If this is also true for foxes, our results may indicate that young foxes were less efficient at detecting baits in areas where ground-layer complexity was high. Alternatively, when competition for resources was likely reduced (following 1080 baiting) foxes may have devoted less effort (i.e. spent less time) to foraging in high complexity areas because they were less energetically rewarding than low complexity areas. Further research is required to discriminate between these alternative interpretations.
When habitat complexity was analysed in greater detail, certain variables appeared important influences of bait uptake. Roadsides from which baits were removed were considerably narrower, on average, than roadsides where baits were not taken. Bait uptake was also lower where roadside fallen timber density was high, but only in the annual fox-control treatment. Without detailed information on the foraging behaviour of foxes we cannot determine why these variables were related to bait uptake. Nevertheless, our results support the hypotheses of other researchers that predation by mammalian predators is affected by habitat width (Jackson et al. 1975; Shalaway 1985; Seymour et al. 2004) and ground-layer habitat complexity (Thompson and Harestad 1994; Arthur et al. 2003; Andruskiw et al. 2008).

Management implications

Our results demonstrate that bait-site selection, at both large and small scales, is an important consideration for fox-baiting programs in agricultural landscapes. At a large scale, narrow strips of linear vegetation appear favourable baiting sites for increasing bait uptake by foxes. Moreover, baits placed in areas with a simple ground layer appear more likely to be removed than baits placed at sites with heterogeneous ground cover. Equipped with this information, landholders within our study area can refine bait-station placement to improve bait uptake by foxes. This may advance their efforts to conserve the bush stone-curlew throughout the region. More refined bait placement in agricultural landscapes may also benefit other threatened species such as the inland carpet python (Morelia spilota metcalfei) and malleefowl (Leipoa ocellata), and help reduce fox impacts on livestock.

We recognise that bait uptake does not equate to bait consumption as some baits are cached by foxes and never retrieved (Saunders et al. 1999; Jackson et al. 2007), hence higher bait uptake may not reflect increased baiting effectiveness. Consequently, there is still a great need for additional research to investigate strategies to limit bait caching and monopolisation of baits by individual
foxes. Fixed devices, such as the M-44 ejector, deliver toxicants that cannot be moved or cached (Marks et al. 1999) and these devices may be used increasingly in the future. Our results could help guide the placement of M-44 ejectors and other management tools such as ‘Sticky Wicket’ or ‘Poly Pipe’ hair-sampling devices which provide a non-invasive method for collecting DNA to identify individual foxes (cf. Garretson et al. 2008; Berry et al. 2012). This information can facilitate accurate assessments of fox-control efficacy, population size and ranging behaviour to improve fox management further.

Acknowledgements

We are most grateful to the many landholders that provided access to their properties for baiting, Ron Jepson for logistical support throughout the study, Prue Laidlaw and Andy Carter for fieldwork assistance, Simon McDonald (Spatial Data Analysis Network, Charles Sturt University) for support with statistical analyses, and David Watson for providing comments on the research. All procedures relating to the study were approved by the Charles Sturt University Animal Care and Ethics Committee (approval numbers 06/104; 05/077; 04/021), and the Department of Sustainability and Environment/Parks Victoria (research permit numbers 10003556; 10002399). This research was supported by grants from the NSW Department of Environment and Conservation, Stuart Leslie Bird Research Award, Broken–Boosey Conservation Management Network, Goulburn–Broken Catchment Management Authority, Moira Shire, Birding NSW and the Nature Conservation Working Group. This manuscript was improved greatly by suggestions from three anonymous reviewers.

References


Table 1. The variables measured at each bait station during the landscape experiment.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Method of measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance to nearest road, fence-line, creek-line, remnant vegetation and water</td>
<td>Visual estimation to nearest 10 m when ≤25 m away; thereafter to nearest 100 m.</td>
</tr>
<tr>
<td>Grass height</td>
<td>Visual estimation of mean grass height (nearest 100 mm) within a 1 m² quadrat surrounding the bait station.</td>
</tr>
<tr>
<td>Prevalence of grazing land</td>
<td>Visual estimation of percentage (nearest 10%) of land used for grazing within a 100 m radius of the bait station.</td>
</tr>
<tr>
<td>Presence/absence of stock</td>
<td>Visual determination of the presence of sheep and/or cattle with access to the area within a 100 m radius of the bait station.</td>
</tr>
</tbody>
</table>
Table 2. ANOVA test of between-subject effects after 8 days.

<table>
<thead>
<tr>
<th>Source</th>
<th>Type III sum of squares</th>
<th>df</th>
<th>Mean square</th>
<th>F</th>
<th>Sig.</th>
<th>Noncent. parameter</th>
<th>Observed power(^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corrected Model</td>
<td>10508.395(^a)</td>
<td>4</td>
<td>2627.099</td>
<td>8.328</td>
<td>.000</td>
<td>33.313</td>
<td>.994</td>
</tr>
<tr>
<td>Intercept</td>
<td>70190.782</td>
<td>1</td>
<td>70190.782</td>
<td>222.517</td>
<td>.000</td>
<td>222.517</td>
<td>1.000</td>
</tr>
<tr>
<td>LANDSCAPE ELEMENTS</td>
<td>10508.395(^a)</td>
<td>4</td>
<td>2627.099</td>
<td>8.328</td>
<td>.000</td>
<td>33.313</td>
<td>.994</td>
</tr>
<tr>
<td>Error</td>
<td>7886.008</td>
<td>25</td>
<td>315.440</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>88585.185</td>
<td>30</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corrected Total</td>
<td>18394.403</td>
<td>29</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)R Squared = 0.571 (adjusted R Squared = 0.503)

\(^b\)Computed using alpha = 0.05
Table 3. Logistic regression model selection summary for no- and annual fox-control treatments at the roadside scale. K, number of parameters; AICc, Akaike’s Information Criterion adjusted for small sample sizes; Δi, difference in AICc; ωi, Akaike weights. The Hosmer-Lemeshow χ² goodness-of-fit test for the global model (χ², d.f., P). Only models with Δi ≤ 2 are shown (with the exception of the global model). Summed Akaike weights (∑ωi) for each parameter from all models are also provided, with symbols in parentheses indicating the direction of the relationship between parameters and bait uptake based on Spearman’s Rank Correlation Coefficients (rₛ).

<table>
<thead>
<tr>
<th>Sampling period</th>
<th>Model</th>
<th>−2 log likelihood</th>
<th>K</th>
<th>AICc</th>
<th>Δi</th>
<th>ωi</th>
</tr>
</thead>
<tbody>
<tr>
<td>P</td>
<td>PREDTREE</td>
<td>41.52</td>
<td>3</td>
<td>47.95</td>
<td>0</td>
<td>0.27</td>
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<tr>
<td></td>
<td>RSWidth + PREDTREE</td>
<td>40.09</td>
<td>4</td>
<td>48.82</td>
<td>0.87</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>RSWidth</td>
<td>44.70</td>
<td>2</td>
<td>48.91</td>
<td>0.96</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>TIMDEN + PREDTREE</td>
<td>40.31</td>
<td>4</td>
<td>49.04</td>
<td>1.08</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>GLOBAL</td>
<td>38.67</td>
<td>5</td>
<td>49.78</td>
<td>1.83</td>
<td>0.11</td>
</tr>
<tr>
<td>χ² = 5.16, d.f. = 8, P = 0.74</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summed Akaike weights (Σωi)</td>
<td>RSWidth: 0.52 (+)</td>
<td>TIMDEN: 0.38 (+)</td>
<td>PREDTREE: 0.72</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| I              | RSWidth                | 61.59             | 2 | 65.80| 0  | 0.42|
|                 | TIMDEN                 | 62.57             | 2 | 66.78| 0.98| 0.26|
|                 | GLOBAL                 | 61.46             | 5 | 72.57| 6.77| 0.01|
| χ² = 6.91, d.f. = 8, P = 0.55 |
| Summed Akaike weights (Σωi) | RSWidth: 0.63 (-)    | TIMDEN: 0.45 (-)  | PREDTREE: 0.18 |

| S              | RSWidth                | 52.16             | 2 | 56.38| 0  | 0.26|
|                 | PREDTREE               | 50.06             | 3 | 56.49| 0.11| 0.25|
|                 | TIMDEN                 | 53.42             | 2 | 57.63| 1.25| 0.14|
|                 | RSWidth + TIMDEN       | 51.58             | 3 | 58.01| 1.63| 0.12|
|                 | RSWidth + PREDTREE     | 49.35             | 4 | 58.08| 1.70| 0.11|
|                 | GLOBAL                 | 49.10             | 5 | 60.21| 3.84| 0.04|
| χ² = 10.92, d.f. = 8, P = 0.21 |
| Summed Akaike weights (Σωi) | RSWidth: 0.52 (-)    | TIMDEN: 0.38 (-)  | PREDTREE: 0.49 |
### Table 3. Continued...

#### ANNUAL Fox Control

<table>
<thead>
<tr>
<th>Sampling period</th>
<th>Model</th>
<th>$-2 \log$ likelihood</th>
<th>K</th>
<th>AICc</th>
<th>$\Delta_i$</th>
<th>$\omega_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PREDTREE</td>
<td>79.204</td>
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<td>0</td>
<td>0.19</td>
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<td>RSWidth + PREDTREE</td>
<td>77.041</td>
<td>4</td>
<td>85.77</td>
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<td>0.18</td>
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<tr>
<td></td>
<td>RSWidth</td>
<td>81.679</td>
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<td>85.89</td>
<td>0.26</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>TIMDEN</td>
<td>81.832</td>
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<td>86.04</td>
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<tr>
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<td>75.933</td>
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<td>1.41</td>
<td>0.09</td>
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<tr>
<td></td>
<td>$\chi^2 = 11.51$, d.f. = 8, P = 0.17</td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

**Summed Akaike weights ($\sum \omega$)**

| RSWidth: 0.51 (+) | TIMDEN: 0.46 (-) | PREDTREE: 0.61 |

<table>
<thead>
<tr>
<th>Model</th>
<th>$-2 \log$ likelihood</th>
<th>K</th>
<th>AICc</th>
<th>$\Delta_i$</th>
<th>$\omega_i$</th>
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<tbody>
<tr>
<td>RSWidth + TIMDEN</td>
<td>74.89</td>
<td>3</td>
<td>81.31</td>
<td>0</td>
<td>0.40</td>
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<tr>
<td>RSWidth</td>
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<td>82.46</td>
<td>1.14</td>
<td>0.22</td>
</tr>
<tr>
<td>TIMDEN</td>
<td>78.99</td>
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<td>83.20</td>
<td>1.88</td>
<td>0.15</td>
</tr>
<tr>
<td>GLOBAL</td>
<td>74.55</td>
<td>5</td>
<td>85.67</td>
<td>4.35</td>
<td>0.04</td>
</tr>
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<td>$\chi^2 = 7.64$, d.f. = 8, P = 0.47</td>
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</tbody>
</table>

**Summed Akaike weights ($\sum \omega$)**

| RSWidth: 0.70 (-) | TIMDEN: 0.68 (-) | PREDTREE: 0.23 |

<table>
<thead>
<tr>
<th>Model</th>
<th>$-2 \log$ likelihood</th>
<th>K</th>
<th>AICc</th>
<th>$\Delta_i$</th>
<th>$\omega_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>TIMDEN</td>
<td>72.58</td>
<td>2</td>
<td>76.79</td>
<td>0</td>
<td>0.31</td>
</tr>
<tr>
<td>RSWidth + TIMDEN</td>
<td>70.76</td>
<td>3</td>
<td>77.19</td>
<td>0.40</td>
<td>0.25</td>
</tr>
<tr>
<td>TIMDEN + PREDTREE</td>
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<td>78.09</td>
<td>1.30</td>
<td>0.16</td>
</tr>
<tr>
<td>RSWidth</td>
<td>74.25</td>
<td>2</td>
<td>78.46</td>
<td>1.67</td>
<td>0.13</td>
</tr>
<tr>
<td>GLOBAL</td>
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<td>5</td>
<td>80.38</td>
<td>3.59</td>
<td>0.05</td>
</tr>
<tr>
<td>$\chi^2 = 7.37$, d.f. = 8, P = 0.50</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Summed Akaike weights ($\sum \omega$)**

| RSWidth: 0.46 (-) | TIMDEN: 0.77 (-) | PREDTREE: 0.31 |

---

a Pre-1080  
b Immediately Post-1080  
c 6 Weeks Post-1080  
d Categorical variable so direction of correlations not provided
Figure captions

Figure 1. Study area within Australia (inset a), Victoria (inset b) and the Northern Plains region (main figure).

Figure 2. A diagrammatic representation of the experimental design of the habitat complexity experiment showing the four baiting treatments: (1) high complexity, annual fox control; (2) high complexity, no fox control; (3) low complexity, annual fox control; (4) low complexity, no fox control.

Figure 3. Mean percentage of baits removed (including 95% confidence intervals) from each landscape element after 8 days. Landscape elements with different letters are significantly different at $P = <0.05$. Each landscape element contained 6 replicates (baiting sites) and 60 baits, except creek-lines ($n = 59$ baits) and open paddocks ($n = 58$ baits).

Figure 4. The percentage of baits removed after 8 days, according to baiting treatment and sampling period. O, overall cumulative percentage of baits removed after all sampling periods; P, pre-1080; I, immediately post-1080; S, 6 weeks post-1080.
Fig. 1
Fig. 2
Fig. 3
Fig. 4

*total baits available = 90

*total baits available = 30