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Abstract

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Disciplines

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A simulation study to quantify drift fence configuration and spacing effects when sampling mobile animals

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Abstract. Drift fences with traps are commonly used for ecological research and survey. Field studies have examined the effectiveness of selected fence layouts, but comprehensive field testing is impractical. We applied a simulation approach to investigate how the interaction of fence layout and animal movement type influence fence encounter rates. A range of fence layouts, varying in spacing and configuration, were chosen based on common field practices and recommendations in the literature. Animal movement patterns ranged from meandering (Brownian) to highly directional over distances of 10 to 500 m. We found that fences in short, straight, widely spaced arrangements would be encountered more frequently by highly mobile animals than the same amount of fence in complex or continuous configurations. The dispersed arrangement was encountered just as often by animals with more limited movement patterns as were closer spaced fences. Consequently, for broad-scale surveys, as opposed to studies on individuals' movements and microhabitat use, we recommend spacing trap/fence units in relation to the movement abilities of the most mobile species being sought. For studies that require intense point sampling, additional fencing should increase the total rate that animals encounter fences at a point but the increase will not be proportional to the additional fencing used. The software is provided to allow for other configurations of fences and movement patterns to be investigated.

Key words: biological survey; drift fence length; encounter rate; sampling intensity; survey design; trapping efficiency.

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Introduction

Part of the consideration when planning a field study is the optimal layout of traps to answer the question being considered. Many types of traps used for terrestrial vertebrates and invertebrates are used with drift fences constructed of various materials of various lengths laid out in a range of patterns. Fences are thought to increase capture rates by acting as barriers to animal movement, directing them towards the traps (Braithwaite 1983, Morton et al. 1988, Friend et al. 1989). For species that have a simple, known movement pattern, such as frogs migrating to and from a breeding pond, it is easy to intercept many individuals by placing fences across their path (e.g., Hardy and Raymond (1980) fully encircled their study pond). Where the movement is complex, pathways are unknown or where there are numerous species with different movement patterns, it is less obvious how to design a layout of fences that would produce an efficient sampling regime. Field studies require considerable logistical input and biologists need to

maximize their detection rates to answer the ecological questions they are investigating in a cost effective way by choosing an appropriate design.

There has been a growing number of studies of the effectiveness of different survey configurations using drift fences, for both invertebrates (e.g., Ward et al. 2001, Brennan et al. 2005) and vertebrates (e.g., Cockburn et al. 1979, Read 1985, Morton et al. 1988, Friend et al. 1989, Hobbs et al. 1994, Thompson et al. 2005, Ribeiro-Júnior et al. 2011). These studies often also compare trap types, such as different size pitfalls, at the same time (e.g., Morton et al. 1988, Friend et al. 1989, Maritz et al. 2007, Ribeiro-Júnior et al. 2008, Ellis 2013), and one study examined optimal trapping effort in terms of sampling duration and repetition (Moseby and Read 2001). Success has been defined in three ways: total number of animals caught by each arrangement or per trap; captures versus time required to set up and run the arrangement; or species accumulation rates for different configurations. However, field studies of the many possible trap and fence configurations across a broad range of species are so expensive and time consuming as to be impossible.

Studies of the optimal fence configuration follow on from a long history of studies using unfenced baited traps to investigate whether line transects, grids or webs are more effective for answering ecological questions (e.g., Dice 1938, Stickel 1948, Read et al. 1988, Parmenter et al. 2003, Pearson and Ruggiero 2003). The movement pattern of animals, be it across a cruising range, home range or unconfined wandering, was expected to have impacts on the success rate of different trap arrangements and on how the data could be interpreted (Dice 1938). Attention has also focused on what trap spacing should be used to overcome perceived biases of different arrangements (e.g., Stickel 1954, Flowerdew 1976, Read et al. 1988, Tew et al. 1994, Bowman et al. 2001). Tew et al. (1994) recommended that trap spacings should differ for different species but did not specify distances. Once again, logistic constraints mean that these types of field studies only considered a few species and trap configurations at any one time.

Overall there is a relative paucity of data on what drift fence arrangement is best for a given situation and those that exist have often given contradictory results (e.g., Friend et al. 1989 versus Ellis 2013). When existing studies are viewed collectively, they suggest that the optimal arrangement of traps and associated fences is likely to vary across target species and with the type of question being asked. Equally clear, is it is logistically impossible to conduct pilot studies to determine the optimal trap arrangement for each field study.

Simulation modeling allows us to more comprehensively explore questions associated with selecting trap arrangements. In this study we aimed to use a simulation approach to: (1) investigate the effectiveness of different fence configurations to intercept animals with a range of different movement patterns; (2) draw recommendations for field surveys from the results of the simulations; and (3) suggest how a simulation approach can be extended to consider other aspects of survey design in relation to animal movement behavior.

Methods

Modeling framework

We developed a simple modeling framework to perform the simulations in this study (the Java source code and user manual are available as supplementary material). The model simulated animal movements within a homogeneous, two-dimensional landscape. The spacing and layout of drift fences was depicted as a set of line features specified by the user. An input parameters file allowed an orthogonal combination of movement patterns and fence layouts to be specified, together with the number of replicate simulations to run for each combination. Each simulation involved generating a given number of animal movement paths, each of which was tested for intersection with a drift fence as it proceeded. Tabular results were written to an SQL database while paths could be optionally saved as ESRI shapefiles. Data analysis and graphing was performed using the R statistical package (R Development Core Team 2011).

Simulating animal movement abilities

We modeled movement paths as correlated random walks (Codling et al. 2008) to represent a range of behaviors in terms of distance travelled and variability of direction. Each path was gener-

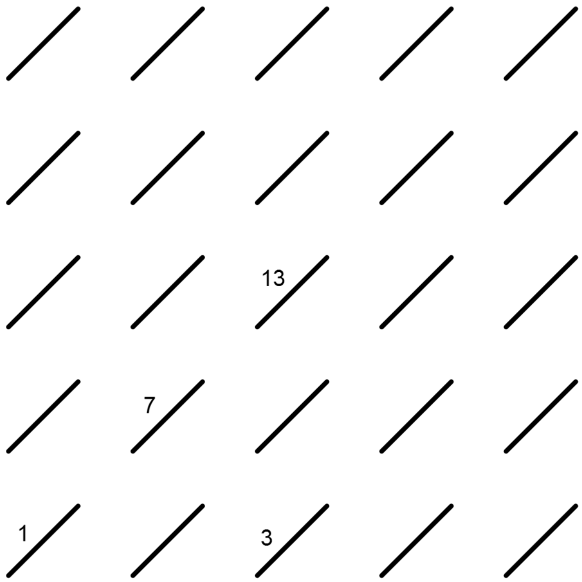

Fig. 1. The layout of the study grid, in this case for the 12.5 m grid spacing, with the identity numbers of the fences referred to in the text. Each fence section is 10 m long.

ated as a series of steps of constant length (1 m or 5 m), with a limit set on the maximum path length (10, 25, 50, 100, 250 or 500 m). Each path began at a random location within a circular neighborhood enclosing the specified fence layout, with a random starting direction. The direction of each subsequent step was derived by summing the current direction with a turning angle, expressed in degrees, drawn from a user-specified continuous probability distribution. We used Laplace distributions centered on 0° (straight ahead) and a constant value for the scale parameter (selected from 2, 10, 30, 60 or 90°). Small values of the scale parameter simulate animals with highly directional movements, while large values simulate meandering movements. Turning angles outside the range −180° to 180° were rejected and a new value drawn, effectively truncating the distributions. To simulate extreme meandering we used a Uniform distribution of turning angles between −180° and 180° to produce random (Brownian) movement. These settings combined to generate 72 movement types of varying lengths and tortuosity (Appendix: Table A1).

Offset distance is the straight-line distance between the starting and final locations of a simulated walk and characterize the tortuosity of a movement type. Deriving expected offset distances analytically for correlated random walks based on truncated distributions is difficult (Byers 2001, Codling et al. 2008), but deriving them from simulations is straightforward. Consequently, we calculated offset distances for 1000 unconstrained random walks for each combination of step size, turning angle distribution, and maximum path length.

Testing spacing influences on drift fence encounters

To study how the spacing of drift fences affects the rate at which animals encounter them, a 5 by 5 grid of 10-m fences was simulated with the grid spaced at 12.5, 25, 50 or 100 m. When setting up fences in the field, their orientation is often dictated by local constraints such as vegetation and rock outcrops, but in the simulations we neglected such complications and instead orientated all fences at 45° to the alignment of the grid to maximize the separation between fences at the smallest grid spacing (Fig. 1). The fence length of 10 m for surveying small vertebrates was used in the simulations because it matched published recommendations such as those of Friend et al. (1989) and Hobbs et al. (1994), and fence sizes used in field studies such as Ribeiro-Júnior et al. (2011) and Ellis (2013). Varying the fence length would affect the outcome by altering not only what the animals could encounter but the spaces through which they could pass undetected. Even so, the results of our simulations should be scalable to smaller animals with less movement abilities surveyed on smaller grids. Individual fences were numbered from left to right starting in the south west corner (Fig. 1).

Testing configuration effects on drift fence encounters

To study the impact of fence arrangement, we simulated sections of drift fence 10 m long arranged in six configurations: (1) one fence ("1"); (2) two fences aligned in an L shape ("2 L"); (3) three fences radiating from a central point at 120° ("Y"); (4) three fences aligned continuously end to end ("3 I"); (5) four fences radiating from a central point at 90° ("+"); and (6) four fences aligned continuously end to end ("4 I").

These configurations match some of the variety of non-linear arrangements reported in the literature from field studies such as Ribeiro-

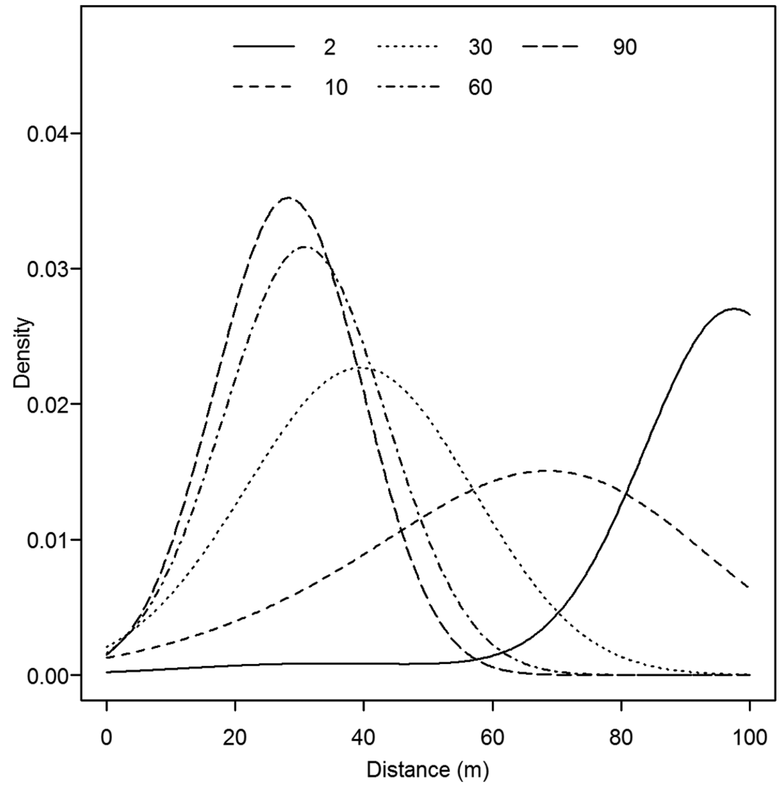

Fig. 2. Density plot of the achieved offset distance from their point of origin for 1000 animals obeying each of five Laplace turning functions (2, 10, 30, 60, 90°) for total walk distances of 100 m.

Júnior et al. (2011) and Ellis (2013), as well as different lengths of straight fencing.

Running the simulations

In each simulation the grid or other arrangement of fences was centered within a bounding circle of radius 800 m, area 201.06 ha, which ensured that all fences were further from the edge than the maximum path length tested (500 m). One hundred replicate simulations were run for each combination of turning angle, step distance and maximum path length. In each replicate, 20,106 animal movement paths were generated with each starting from a random position within the bounding circle. Thus, on average, 100 independent walks were initiated for each hectare of the bounding circle. To generate each random starting point, the square root of a uniform random number from the unit interval was multiplied by the study area radius (in our case 800 m) to calculate its displacement from the center, while angular position was drawn uniformly from the interval −180 to 180°. Animals were allowed to move until they encountered a fence (an absorbing barrier (Codling et al. 2008)) or reached the maximum path length. Movement paths were permitted to leave the study area and (possibly) re-enter it, but any such paths would terminate at their maximum path length and therefore not reach the fences in the middle of the study area. When a movement path encountered a fence a hit was scored against the unique identifier for the fence. For paths that did not encounter a fence, the offset distance was recorded.

Results

Offset distances of movement types

The offset distances generated to characterize each movement type ranged from 3 to 490 m, representing 4–100% of the maximum path distance (Appendix: Table A1). Examples of the achieved offset densities for a 100-m path distance and various turning functions are shown in Fig. 2.

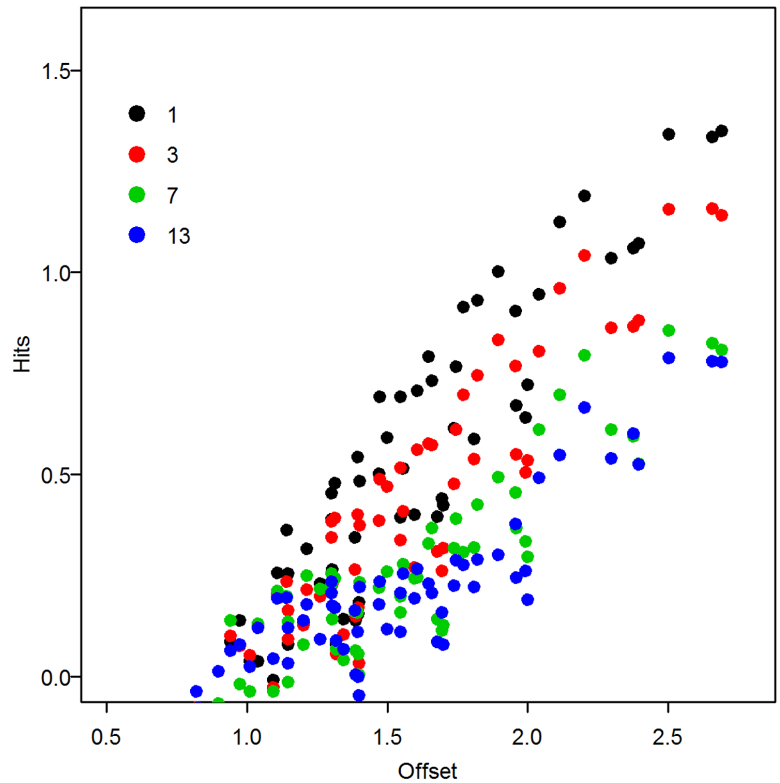

Fig. 3. Mean number of hits for four fence positions in a 5 by 5 grid at 12.5-m spacing plotted against the mean achieved offset distance for each of the 72 walk types simulated. Fence locations and identity numbers within a grid are shown in Fig. 2. Each set of four vertically aligned points represents the results for four the fences as encountered by one movement type. Log-log scales.

Effects of spacing on fence encounter rates

The number times that individual fences in a 5 × 5 grid were encountered by simulated animal movement paths varied with location of the fence within the grid (Figs. 3–6), spacing between fences (Figs. 3–12), and movement behavior (Figs. 7–13). As expected from field studies (e.g., Tew et al. 1994), the fences at the outside of the grid were encountered more often than those inside, with the corners being most frequently encountered (Figs. 3–6). The pattern of fence encounters in relation to movement behavior is complex, particularly at the smallest grid spacing, with the total path distance travelled by an animal and the tortuosity of its path producing relatively large differences in the rate at which they encountered fences in different parts of the grid. At the 12.5-m spacing there was a wide variation in fence encounter rates between the corner and edge (fences 1 and 3) of a small grid versus the center (fence 13) (Fig. 3), and only when the grid spacing was greatly expanded did rates become more even across the grid. Whereas paths with the highest offsets showed a 0.6 difference on the log scale, equating to a fourfold difference in raw distance, between encounters with the center and corner fences (Fig. 3), there was almost no difference when spacing was increased to 100 m (Fig. 6).

Thus, grid spacing dramatically influenced the total number of fence encounters that occurred on a grid. Even for the least mobile animals the smallest grid tested was less efficient and that the disparity between various grids widened for more mobile animals (Figs. 3–6). With 50-m spacing the relative difference between the encounter rate for a corner fence and the central fence was reduced (Fig. 5). Overall, the center fence was the least encountered in each simulation, but the relative difference between the

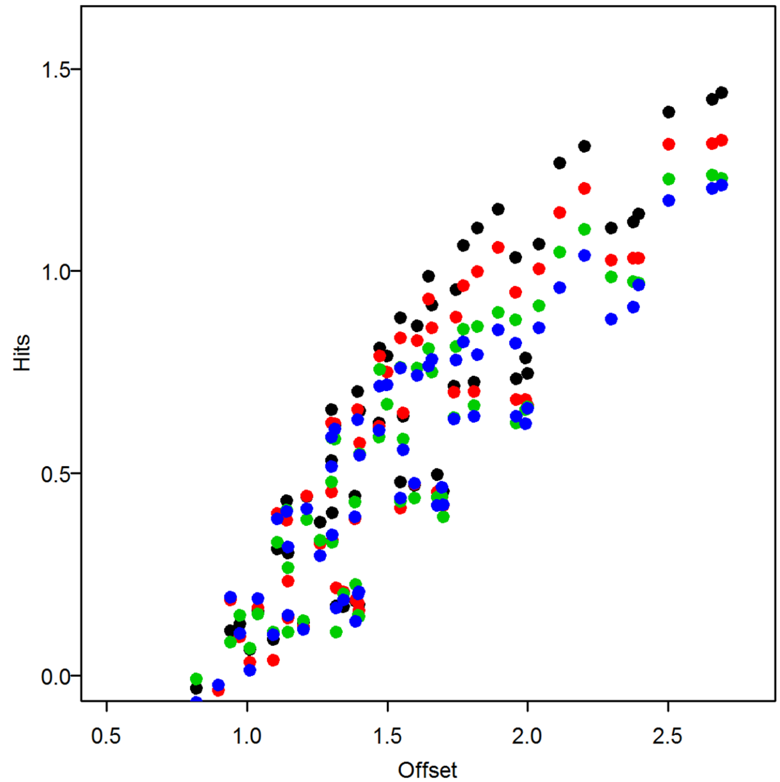

Fig. 4. Same as for Fig. 3 but with a 25-m grid spacing.

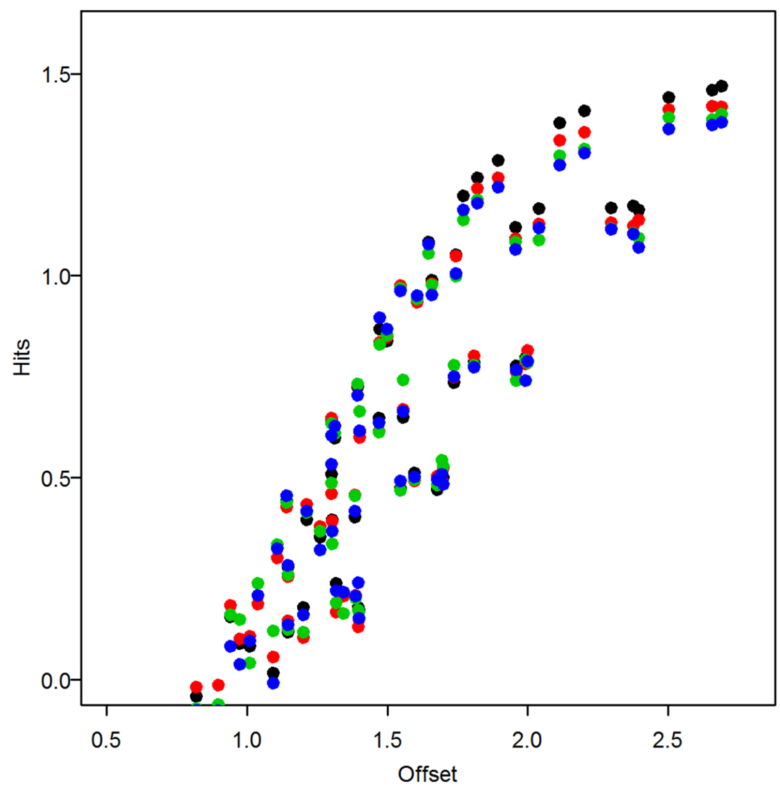

Fig. 5. Same as for Fig. 3 but with a 50-m grid spacing.

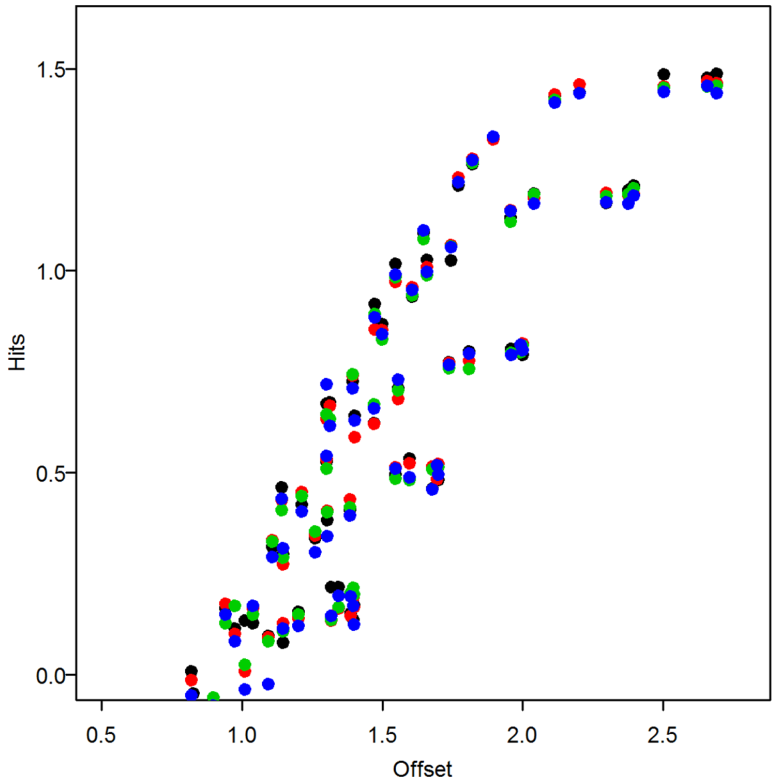

Fig. 6. Same as for Fig. 3 but with a 100-m grid spacing.

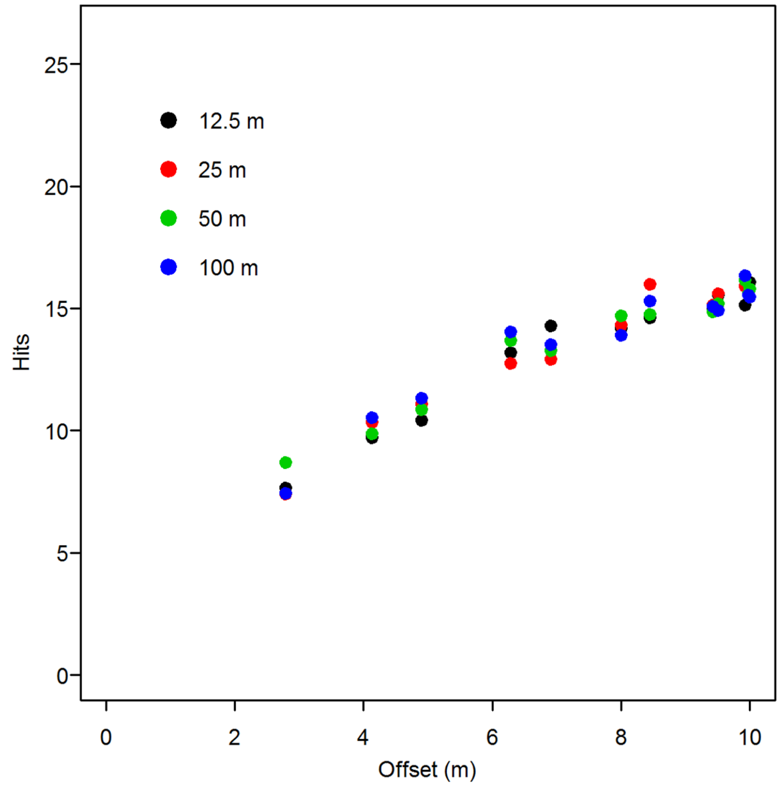

Fig. 7. Mean number of fence hits for an entire grid by animals moving the maximum walk distance of 10-m plotted against the mean achieved offset distance for each of the 12 walk types (step/turn angle combinations) simulated per total distance. Four spacings for the 5 by 5 grid were used: 12.5 m, 25 m, 50 m and 100 m.

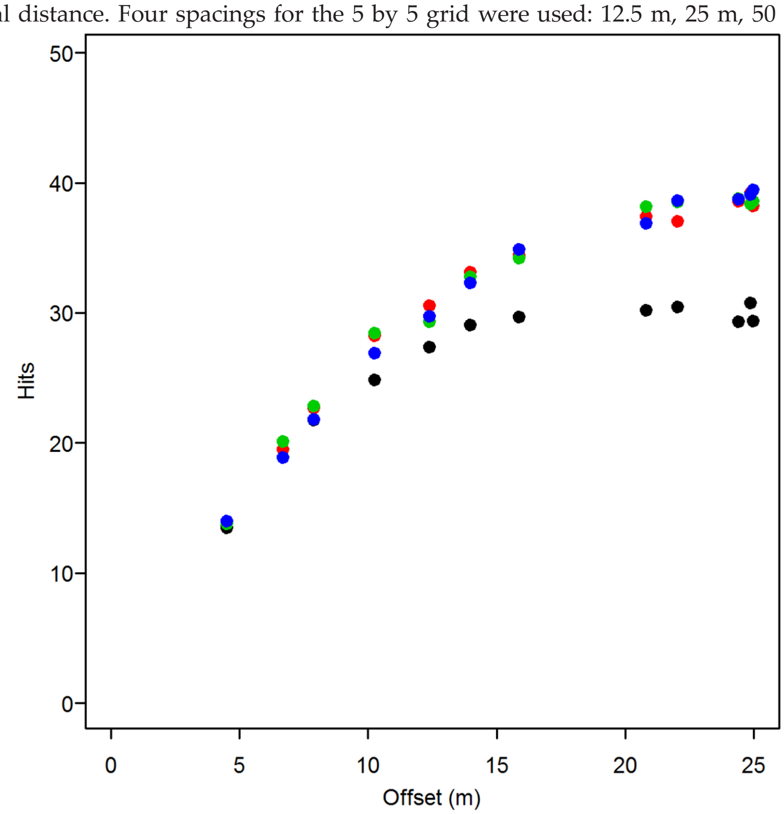

Fig. 8. Same as for Fig. 7 but for the maximum walk distance of 25 m.

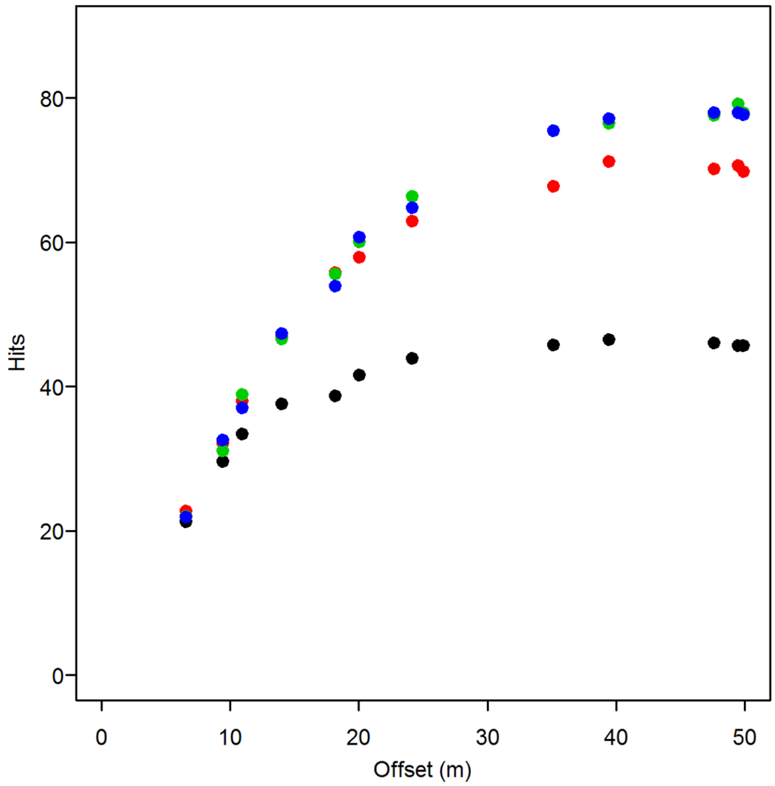

Fig. 9. Same as for Fig. 7 but for the maximum walk distance of 50 m.

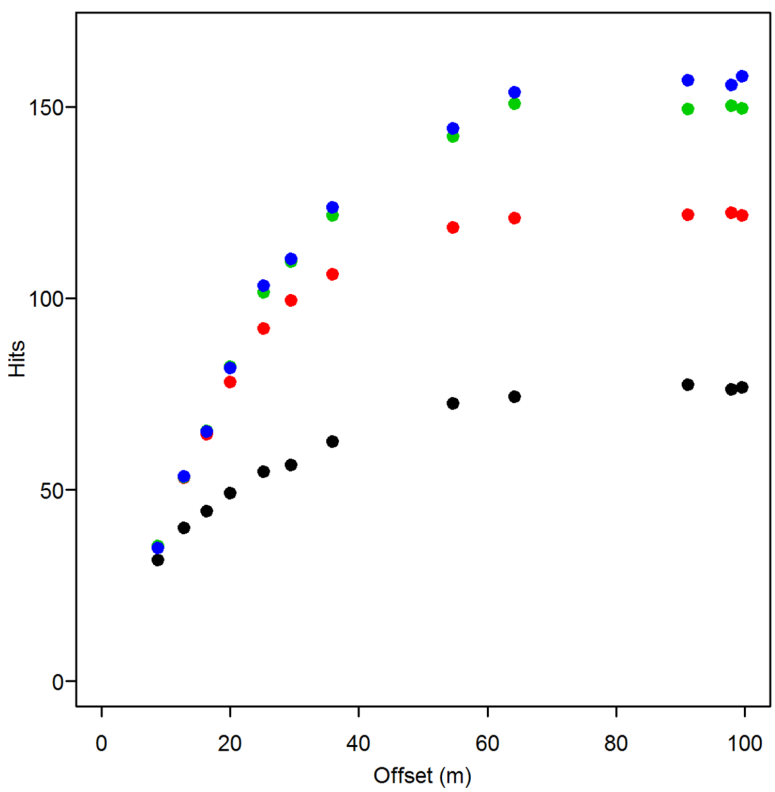

Fig. 10. Same as for Fig. 7 but for the maximum walk distance of 100 m.

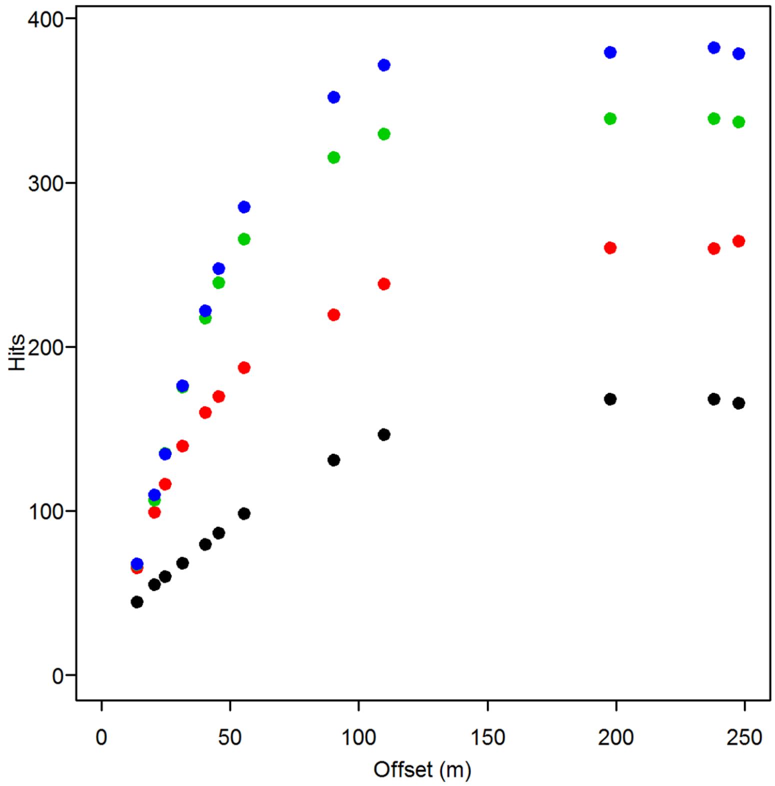

Fig. 11. Same as for Fig. 7 but for the maximum walk distance of 250 m.

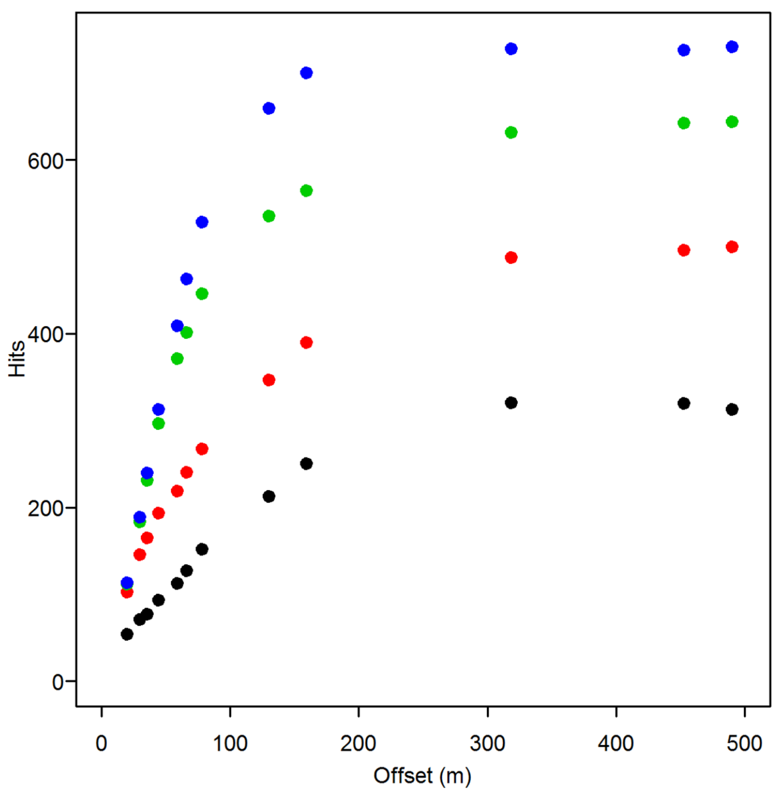

Fig. 12. Same as for Fig. 7 but for the maximum walk distance of 500 m.

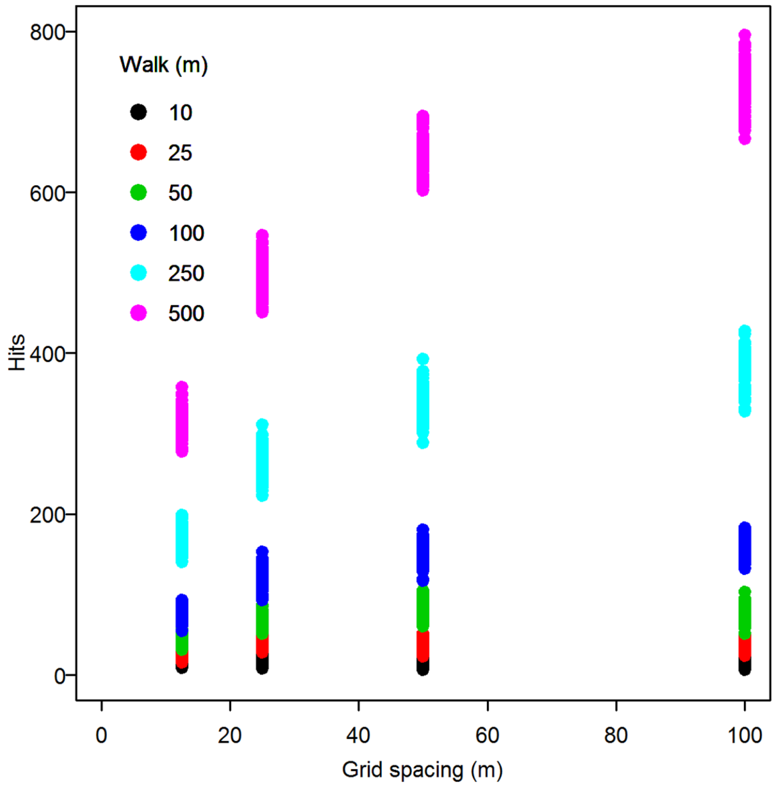

Fig. 13. The number of fence hits in each of 100 replicates for straightest walkers (Laplace 2°) in each total walk distance class showing a trend towards an asymptote as the grid spacing increases, with the asymptote being higher for longer walk distances.

center and an external corner fence was reduced as the grid spacing increased.

Larger spacing generally increased the total number of encounters with fences for an entire grid, particularly for animals with more directed movements (Fig. 7 cf. Fig. 12). Once again the curvilinear pattern of the total number of hits in relation to achieved offset distance is evident in the plots, as is the separation of the curves for each grid simulated. With the most directed movements (turning angle distribution Laplace, scale = 2°) the rate of fence encounters in relation to grid spacing approached a plateau which varied with maximum path distance (Fig. 13).

Effects of drift fence configuration on encounter rates

The arrangement of four fences radiating from a central point consistently had the lowest fence encounter rate per section of fence of any of the simulated arrangements (Figs. 14–19). Three radiating fences and the L shape arrangement performed slightly better but were still generally poorer than fences in straight arrangements. A single fence outperformed all other arrangements overall, with all three straight arrangements having similar results for animals with the most directed movements. Animals with more tortuous or meandering movements were detected less often despite being present at the same density as those with more directed movements (Figs. 14–19).

Discussion

Simulating the interaction of animals with traps has progressed markedly since Stickel (1954) used scale cut-out shapes of home ranges thrown randomly onto a scale drawing of a trapping grid to investigate trapping efficiency. The results of our simulations demonstrate that the rate at which animals encounter drift fences is

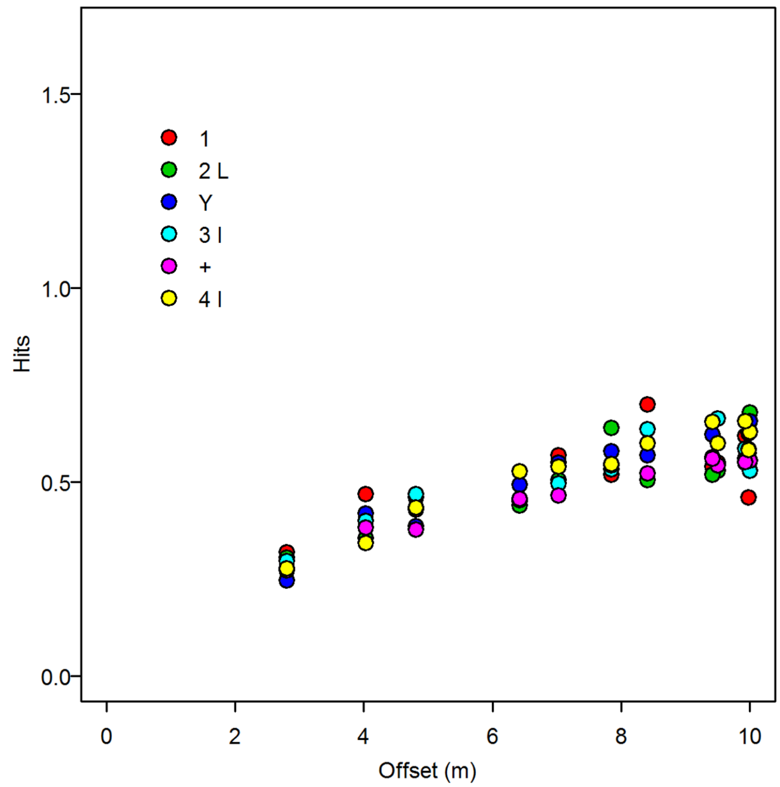

Fig. 14. Mean number of hits per 10-m fence section by animals moving the maximum walk distance of 10 m plotted against the mean achieved offset distance for each walk type for six different arrangements of fences.

highly influenced by both general movement behavior and fence arrangement. Quantifying these effects requires repeated trials across many combinations of fence layout and movement parameters, something that is logistically impractical to undertake in field studies.

Our simulations indicate that scattered short fences would be more often encountered than the same length of fence in a continuous arrangement (Figs. 14–19), and support the findings of Brennan et al. (2005) who concluded from their spider captures that multiple smaller fence arrangements would catch more than fewer longer fence arrangements. Ribeiro-Júnior et al. (2011) found that the arrangement of fences in straight lines or Y shaped layouts at each trapping site had no effect on species detection in terms of species richness or rank abundance order. However, their straight arrangements, using the same number and type of pits and the same length of fencing for the same amount of time, caught 1.64 times as many individuals as their Y shaped layouts. Our simulations support this outcome, with Y shaped layouts being encountered less frequently than the same amount of fence arranged in a straight line (Figs. 14–19). Similarly, Ellis (2013) found that pit traps with four fences radiating out from them only caught 1.4 times the number of animals that pits with two fences radiating from them did, but used twice as much fencing; a pattern also reflected in the simulations (Figs. 14–19). At a larger scale, Hobbs et al. (1994) found that their various crossed long fence and multiple pit arrangements produced little improvement in terms of trap success over straight arrangements, and withdrew the recommendation previously published in Morton et al. (1988) for their use.

Our results are contrary to those of Bury and Corn (1987), who found that capture rates depended on the total amount of fencing rather than its arrangement. There are several possible explanations for our different findings. Fence encounter rate, the primary focus of our simula-

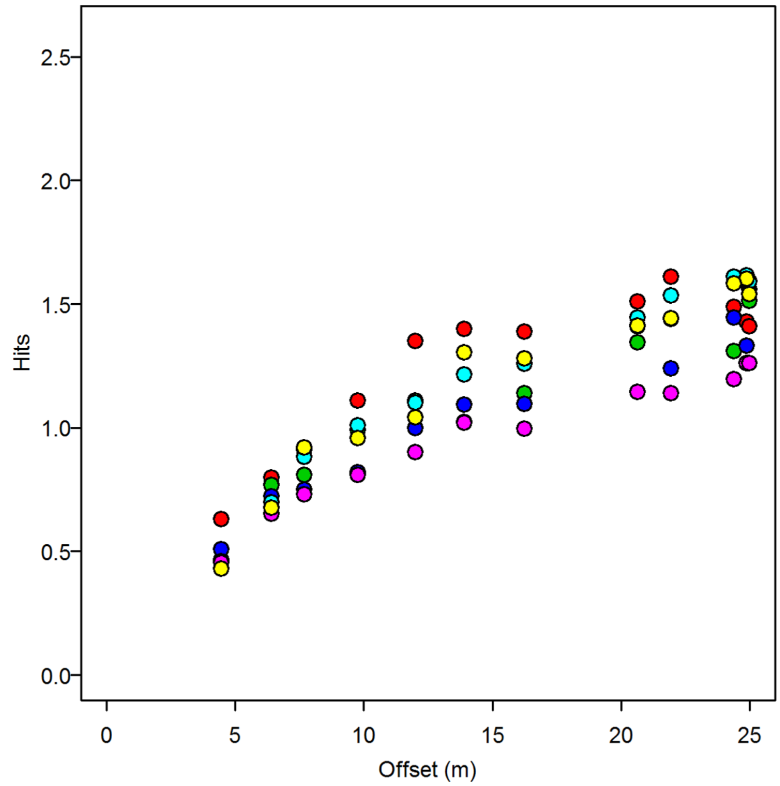

Fig. 15. Same as for Fig. 14 but for the maximum walk distance of 25 m.

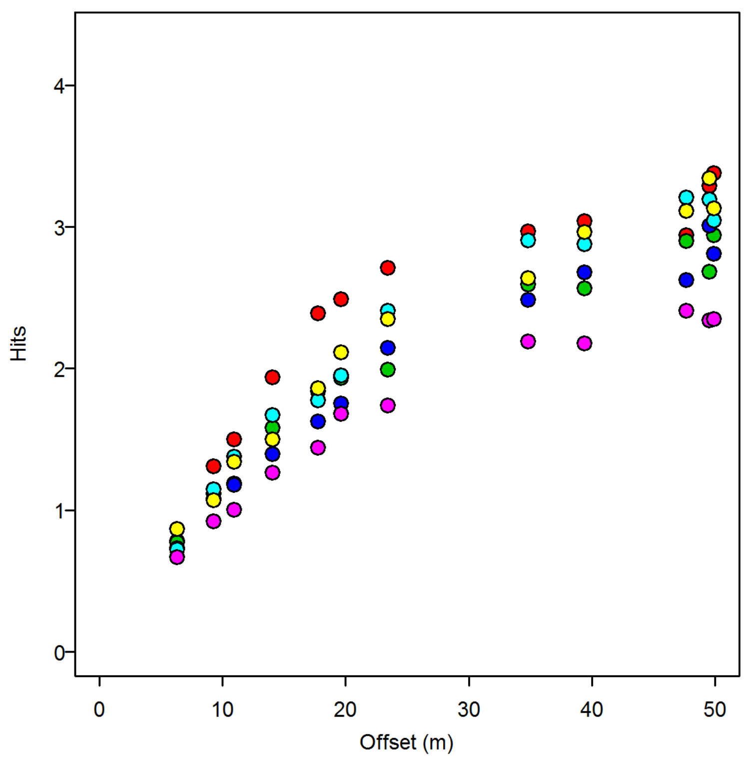

Fig. 16. Same as for Fig. 14 but for the maximum walk distance of 50 m.

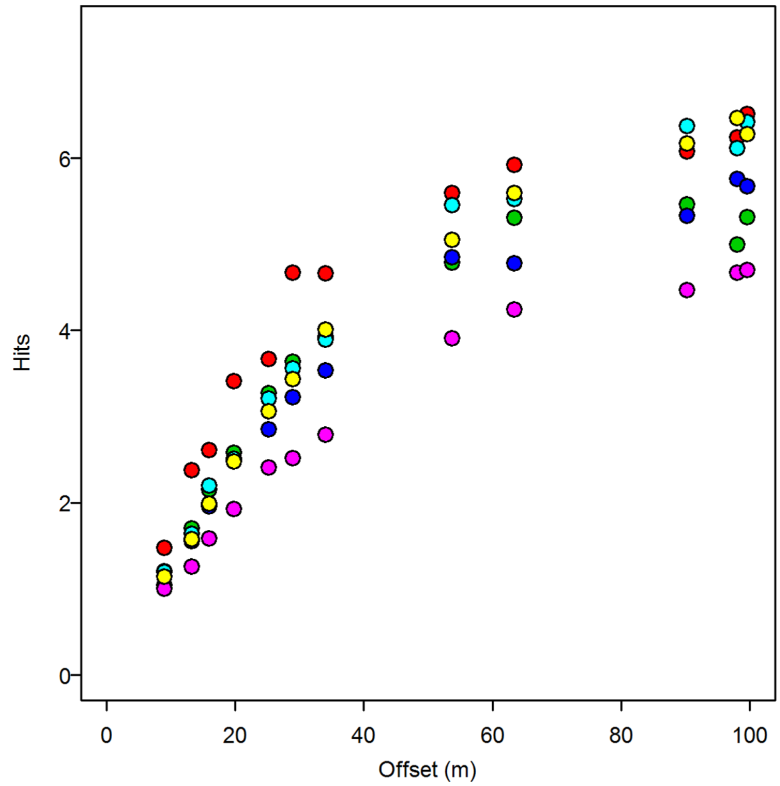

Fig. 17. Same as for Fig. 14 but for the maximum walk distance of 100 m.

tions, may not be proportional to capture rate for some species. Also, variation in topography, vegetation etc., not considered in our simulations, may have interacted with fence arrangement and the location of traps to influence capture rates. Some of these effects could be investigated by further development of our simulation model.

Effects size versus costs

Our simulations can be used as a basis for trading off effects sizes (expressed as fence encounter rate) versus the time and expense required to install various fence arrangements and check the associated traps. They showed that increasing the amount of fencing at a sample point is unlikely to produce a proportional increase in encounters or captures, an effect found in field studies (Hobbs et al. 1994, Ellis 2013). However, our analyses did not consider set up costs, and if the cost in time and materials of setting up drift fences is low compared to that for installing the associated trap(s) the increase in total captures may warrant it. Conversely, when the set up time for fencing is long compared to the installation of the associated trap(s) the advantages of adding extra sampling points need to be considered in light of how much time will be available for travelling to and checking them during the study period. For example, Ellis (2013) found that installing a cross arrangement of fencing around a single pitfall was only justified for general fauna survey if it took less than 40% longer than the time required to install a straight arrangement with half the fencing. In an extreme case, Brennan et al. (2005) working on spiders found that a large number of unfenced pitfalls may be easier to install and maintain than a small number of fenced arrangements, yet produce comparable captures.

Edge effects and trapping designs

Our simulations add support to field and theoretical studies showing that the success rate of any given trap in a configuration is influenced by neighboring traps (e.g., Dice 1938, Luff 1975). Flowerdew (1976: Fig. 4.2) expected the capture rate in a grid of baited traps would be uniform

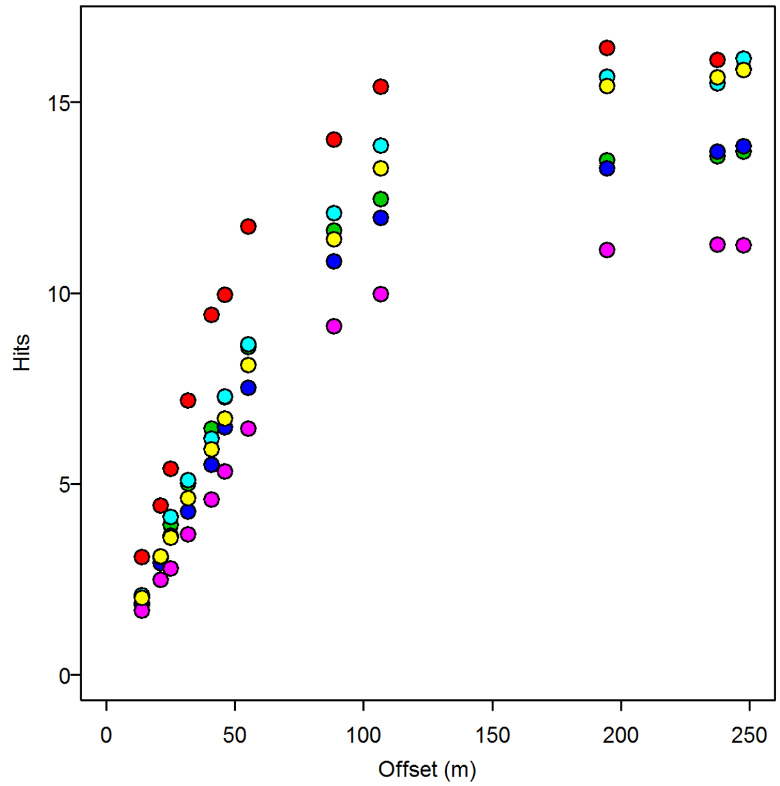

Fig. 18. Same as for Fig. 14 but for the maximum walk distance of 250 m.

away from the edges, and recommended that trap spacings of 15 m or less should be used for population studies of small mammals. However, based on the asymptotes evident in Fig. 13, the gridded fence arrangements we examined needed to be spaced by at least half of the offset distance moved by an animal during a trapping period. This will maximize the encounter rate with the fences by maximizing the trappable area and the independence of each element of the grid. Further simulations could be applied to investigate this effect for any particular layout and length of fencing. Similarly, other movement models such as Lévy walks or empirical data on turn angles and step lengths, such as from GPS tracking, could be used.

For most animal species we currently do not know the minimum, or optimum, spacing between traps because the magnitude and tortuosity of their movements are unknown. Up to now, suggested trap spacings often have been made without any field testing (e.g., 10–0 m spacing for surveying reptiles in arid Australia; Friend et al. 1989, Hobbs et al. 1994). Fortuitously, these suggested spacings fitted with subsequently reported movement distances for some arid-zone fauna, e.g., mean recapture distances of <35 m for skinks and geckoes (Read 1998, 1999), although James (1991) found some individuals moving over 600 m. Our simulation approach provides a step forward for trapping design as it can be used to determine credible spacings for a particular study based on existing knowledge of the movement behavior of target species.

In the case of grid spacing, the time required for a researcher to traverse the grid needs to be considered against the increased likelihood of capture when selecting a layout. It is clear from Figs. 7–12 that for many of the movement behaviors simulated, doubling the grid spacing did not produce a doubling of the encounter rate, but it would definitely double the distance that needs to be traversed to inspect each element in the grid arrangement. For our 100-m grid spacing case, this distance would be at least 2.4 km to do the complete check and return to the starting point, requiring a significant amount of time. This would obviously not be warranted

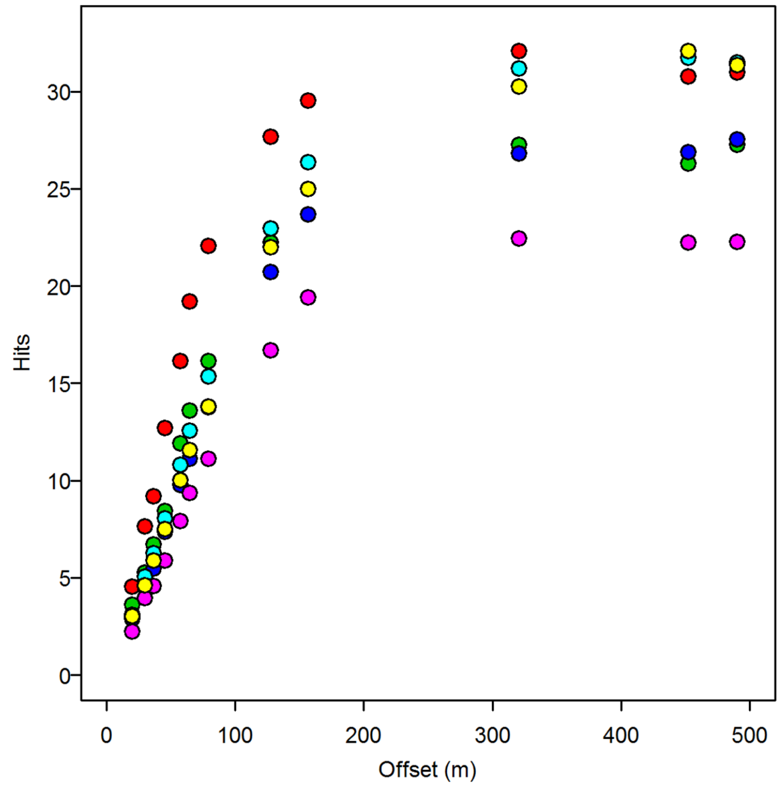

Fig. 19. Same as for Fig. 14 but for the maximum walk distance of 500 m.

when studying animals with limited mobility.

Potential to extend the simulation framework

The simulation approach used here could be adapted to consider the case where animals are attracted or repelled by fences (e.g., the arboreal skink *Cryptoblepharus carnabyi* in Ellis 2013). Another possibility would be to simulate captures, as opposed to fence encounters, by modeling individual animal movements upon reaching a fence. Complicated fence arrangements, such as X or Y shapes, are expected to funnel certain animals towards a trap once they encounter a fence (Morton et al. 1988), although several field studies (Hobbs et al. 1994, Ribeiro-Júnior et al. 2011, Ellis 2013) as well as our simulations indicate that simple straight fences are likely to give higher encounter rates per unit length of fence. The choice of placement of traps along a fence (middle or ends), spacing between traps, and length of fences may all depend on the behaviors of different species on encountering a fence and require further study.

Recommendations

Measures of trap success such as captures per trap day may not be sufficient to allow data from studies using different trap layouts to be combined or compared. The impacts of these methodological variations can be explored in a simulation framework to aid in interpreting such data combinations.

When designing broad biological surveys involving large study units such as extensive vegetation types or landforms, as opposed to ecological studies of individuals' movements and home ranges, we recommend spacing simple fence/trap combinations as widely as logistically feasible, in terms of installation and inspection effort, to maximize the rate that wide ranging animals will encounter the drift fences. Such a configuration should also perform equally as well for less mobile animals as a more closely spaced configuration, i.e., the same number of animals on average will be exposed to the fences but from different parts of the population. In this manner, a wide range of species can be most effectively surveyed concurrently. Complicated

fence arrangements may only be justified when sampling at a fine scale, with the aim of capturing high numbers of individuals or measuring the intensity of utilization at specific points.

We encourage people planning field studies to use the simulation software to explore possible trapping layouts, or people who have conducted trapping studies to explore the relative effectiveness of different parts of their trapping layout for animals of different mobility to visualize the impacts that this has on interpreting their results.

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Supplemental Material

Appendix

Table A1. The realized offset distance (straight-line distance between start point and final location) achieved by 1000 replicates of each type of unconstrained walk used in the simulations.

Turn angle	Step (m)	Max path length (m)	Offset distance (m)						
			Min	Lower quartile	Mean	Median	Upper quartile	Max	Variance
laplace 0 2	1	10	9.82	9.97	9.98	9.99	9.99	10.00	0.001
laplace 0 2	5	10	9.92	10.00	10.00	10.00	10.00	10.00	0.000
laplace 0 2	1	25	23.87	24.85	24.87	24.91	24.95	24.99	0.016
laplace 0 2	5	25	24.67	24.97	24.98	24.99	24.99	25.00	0.001
laplace 0 2	1	50	46.82	49.38	49.49	49.62	49.78	49.95	0.203
laplace 0 2	5	50	49.21	49.87	49.90	49.94	49.97	50.00	0.010
laplace 0 2	1	100	81.08	97.35	97.91	98.52	99.12	99.81	3.656
laplace 0 2	5	100	97.57	99.49	99.60	99.73	99.85	99.98	0.136
laplace 0 2	1	250	174.55	234.44	238.02	241.31	244.78	248.62	99.916
laplace 0 2	5	250	225.94	246.78	247.51	248.25	248.98	249.80	5.411
laplace 0 2	1	500	75.01	439.97	452.67	464.81	479.66	495.52	1707.223
laplace 0 2	5	500	433.27	487.13	490.10	492.66	495.98	499.29	71.742
laplace 0 10	1	10	5.95	9.37	9.51	9.69	9.84	9.99	0.262
laplace 0 10	5	10	8.31	9.93	9.93	9.98	10.00	10.00	0.023
laplace 0 10	1	25	5.59	21.24	22.03	22.83	23.78	24.83	6.849
laplace 0 10	5	25	16.74	24.26	24.39	24.66	24.85	25.00	0.611
laplace 0 10	1	50	3.78	35.89	39.44	41.76	45.24	49.14	63.806
laplace 0 10	5	50	27.48	46.95	47.60	48.42	49.20	49.95	6.260
laplace 0 10	1	100	6.21	50.12	64.21	68.94	80.51	95.95	420.644
laplace 0 10	5	100	44.41	88.33	91.12	93.56	96.21	99.72	58.992
laplace 0 10	1	250	6.74	71.22	109.70	110.36	147.40	220.93	2358.934
laplace 0 10	5	250	29.29	181.18	197.63	209.47	225.85	244.05	1466.893
laplace 0 10	1	500	5.60	99.95	159.39	154.79	210.63	384.72	6066.468
laplace 0 10	5	500	5.58	251.46	318.19	344.62	403.81	476.28	11616.483
laplace 0 30	1	10	0.36	5.73	6.91	7.45	8.55	9.89	4.330
laplace 0 30	5	10	0.60	9.37	9.42	9.81	9.97	10.00	1.102
laplace 0 30	1	25	0.07	8.23	12.38	12.51	16.60	23.14	28.212
laplace 0 30	5	25	1.65	19.12	20.82	22.23	23.75	24.97	16.688
laplace 0 30	1	50	0.40	11.82	18.17	17.70	24.02	42.45	72.384
laplace 0 30	5	50	0.53	29.34	35.11	37.32	43.17	49.76	104.938
laplace 0 30	1	100	1.05	15.24	25.21	23.99	33.22	78.34	169.249
laplace 0 30	5	100	2.91	38.26	54.62	56.76	72.05	96.11	470.203
laplace 0 30	1	250	0.74	24.10	40.24	38.01	53.84	117.30	420.562
laplace 0 30	5	250	0.59	59.08	90.20	87.39	121.05	216.86	1858.006
laplace 0 30	1	500	0.95	35.73	58.78	54.50	78.45	178.78	909.460
laplace 0 30	5	500	1.68	83.45	130.08	124.86	170.03	349.69	4059.705
laplace 0 60	1	10	0.02	3.28	4.90	4.94	6.49	9.42	4.417
laplace 0 60	5	10	0.14	7.90	8.45	9.46	9.89	10.00	4.594
laplace 0 60	1	25	0.40	4.93	7.90	7.51	10.43	20.16	14.872
laplace 0 60	5	25	1.03	11.89	15.87	16.73	20.63	24.98	33.649
laplace 0 60	1	50	0.35	6.68	10.92	10.32	14.63	30.24	30.528
laplace 0 60	5	50	2.47	16.09	24.17	24.38	31.91	47.60	108.594
laplace 0 60	1	100	0.49	9.89	16.32	15.44	22.01	47.06	72.001
laplace 0 60	5	100	1.81	22.55	35.87	34.54	47.26	87.31	302.293
laplace 0 60	1	250	0.60	14.86	24.78	23.45	32.75	72.48	171.405
laplace 0 60	5	250	2.51	35.13	55.33	52.35	71.68	164.06	778.022
laplace 0 60	1	500	2.52	21.71	35.17	32.62	46.72	108.33	338.362
laplace 0 60	5	500	1.42	47.97	78.24	74.09	103.16	224.09	1707.113
laplace 0 90	1	10	0.17	2.62	4.13	4.02	5.55	9.38	3.645
laplace 0 90	5	10	0.04	6.88	8.01	9.09	9.80	10.00	5.847
laplace 0 90	1	25	0.16	4.13	6.70	6.46	8.99	17.31	11.247
laplace 0 90	5	25	0.43	9.86	13.97	14.20	18.46	24.57	33.057
laplace 0 90	1	50	0.15	5.78	9.43	8.76	12.62	29.22	23.073
laplace 0 90	5	50	0.61	12.22	20.06	20.09	27.16	43.88	89.982
laplace 0 90	1	100	0.71	7.81	12.83	11.91	17.11	38.31	43.561
laplace 0 90	5	100	1.75	18.67	29.48	28.31	39.30	78.91	211.676
laplace 0 90	1	250	1.18	12.89	20.53	19.77	27.16	64.32	106.997

Table A1. Continued.

Turn angle	Step (m)	Max path length (m)	Offset distance (m)						
			Min	Lower quartile	Mean	Median	Upper quartile	Max	Variance
laplace 0 90	5	250	0.74	28.46	45.61	43.71	60.76	137.37	536.218
laplace 0 90	1	500	1.23	17.37	29.73	27.93	39.70	93.13	248.809
laplace 0 90	5	500	2.62	41.55	66.01	62.75	85.88	188.24	1111.213
uniform −180 180	1	10	0.09	1.73	2.79	2.65	3.65	8.48	2.116
uniform −180 180	5	10	0.03	3.65	6.28	6.98	9.16	10.00	9.516
uniform −180 180	1	25	0.09	2.80	4.51	4.28	5.89	16.50	5.393
uniform −180 180	5	25	0.33	6.25	10.25	10.01	13.71	24.47	25.018
uniform −180 180	1	50	0.23	4.00	6.58	6.20	8.78	19.24	11.668
uniform −180 180	5	50	0.57	8.60	14.01	13.34	18.90	41.45	50.269
uniform −180 180	1	100	0.29	5.17	8.72	8.34	11.55	24.87	20.828
uniform −180 180	5	100	0.51	11.93	19.94	19.00	26.43	56.23	104.823
uniform −180 180	1	250	0.32	8.25	13.83	13.06	18.67	37.62	52.870
uniform −180 180	5	250	0.24	19.32	31.47	30.23	41.46	102.88	258.239
uniform −180 180	1	500	0.24	11.94	20.04	18.90	26.89	62.89	111.245
uniform −180 180	5	500	3.20	26.34	44.21	41.79	59.03	140.94	522.774

Supplement

Sample files for replicating the simulations in the main text (*Ecological Archives* C005-005-S1).