

Modelling the rate of successful search of red foxes during population control

Tom A. Porteus^{A,D,E}, Jonathan C. Reynolds^B and Murdoch K. McAllister^C

^ADepartment of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC, V6T 1Z4, Canada.

^BGame & Wildlife Conservation Trust, Burgate Manor, Fordingbridge, SP6 1EF, UK.

^CInstitute for the Oceans and Fisheries, University of British Columbia, AERL, 2202 Main Mall, Vancouver, BC, V6T 1Z4, Canada.

^DPresent address: Game & Wildlife Conservation Trust, Burgate Manor, Fordingbridge, SP6 1EF, UK.

^ECorresponding author. Email: tporteus@gwct.org.uk

Appendix S1. Reanalysis of fox distance sampling data.

Survey procedure

Heydon *et al.* (2000) used driven line transects to estimate fox densities in three regions of Britain: a) mid-Wales, b) east-Midlands and c) East Anglia. We summarise their survey procedure to highlight similarities between this and how gamekeepers lamp across estates using vehicles on tracks; see the original study for further details. Surveys were carried out on minor public roads at night using spotlights to detect fox eye-shine during autumn 1995 and 1996, and spring 1996 and 1997. Transects were driven at an average speed of 15 km h⁻¹, slowing down and stopping at gaps in hedges as necessary. Surveys were carried out by two people (an observer and a driver) who exchanged places every hour. The observer stood on a raised platform mounted on the back of the vehicle and scanned fields on the left side of the road with a hand-held, 1-million candlepower halogen spotlight. Both observer and driver scanned the road direction ahead.

The perpendicular distance of each fox detection location from the centre of the road line was recorded. Transects were repeated up to four times over ten days to ensure enough detections for reliable density estimation. Half of each 160-180 km transect route (a transect section) was surveyed during a single night, with the start point varied to ensure that individual sections were surveyed at different times. In total, there were 73 transect sections. Surveys were conducted between 20:00 and 06:00 and the total time taken for each transect section was recorded.

Density estimation

Heydon *et al.* (2000) analysed their detection data to estimate fox density in each region (a, b, c), study year (1995-96, 1996-97) and season (autumn, spring), and further

analysis details can be found there. However, detection probability was not reported. As the original analysis files were unavailable, we sought to recreate the analyses to obtain similar density estimates to Heydon *et al.* (2000), in addition to estimating detection probability for each region and season combination. Analyses were conducted in program Distance 6.0 release 2 (Thomas *et al.* 2010). Following Heydon *et al.* (2000), the data were grouped into intervals of 50 m to improve estimator robustness due to evidence of heaping (Buckland *et al.* 2001). Heydon *et al.* (2000) did not report truncation distances so we right-truncated data at distance w such that the fitted detection function or probability of an individual fox being detected at w , $\hat{g}(w)$, was approximately 0.15 (Buckland *et al.* 2001). Given that the transect line was a road, we assumed that $g(0)$, the detection probability of an individual fox on the line, was 1. Heydon *et al.* (2000) adjusted the survey effort to account for sections of transect where visibility beyond 10m was zero because of substantial roadside obstructions (e.g. high hedges and buildings). Compared to no left-truncation of the data, we examined whether left-truncation at 10 m improved detection function fit. This may produce density estimates more representative of the survey region due to the potential for a non-random distribution of foxes on or near roads, e.g. the area closest to the road may be avoided (Buckland *et al.* 2001).

For each region, the detection function was estimated separately for each season but pooled across study years as it was assumed that while vegetative cover varied seasonally, other factors affecting fox detection (e.g. type of agriculture, topography, presence of hedges) would be constant between years. To account for the use of one-sided transects, we specified a sampling fraction of 0.5 using a density multiplier (Buckland *et al.* 2001). Alternative detection function models considered were half-normal, uniform and hazard-rate

key functions with cosine adjustment terms, which were constrained to be monotonically non-increasing. Akaike's Information Criterion (AIC) was used for model selection. The fit of models to the data was assessed using χ^2 goodness-of-fit tests and visual inspection of the distance frequency histograms, with the strength of the fit being used to guide the choice of right-truncation distance and whether to use left-truncated data. The variance of the density estimates was calculated by assuming that observations were Poisson-distributed, i.e., foxes were distributed randomly with no aggregation.

Results

The fitted detection functions are shown in Fig. S1. For each region and season combination, left truncation at 10 m was applied as this resulted in higher P -values from χ^2 goodness-of-fit tests. However, we found minimal effects on density and detection probability estimates with or without this data filter. Right truncation distances varied between regions but were always greatest for spring transects. Detection probability estimates were similar in each region in autumn but were more variable in spring (Table S1). The fox density estimates for each region and season combination (Table S2) were all within either 0.05 fox km⁻² or 10% of those obtained by Heydon *et al.* (2000), the differences reflecting truncation choices and use of an updated version of the analysis software. These densities were used in calculating the empirical rate of successful search estimates.

Table S1. Regional estimates of detection probability in autumn and spring.

Region	Autumn	Spring
Wales	0.50	0.41
Midlands	0.52	0.68
East Anglia	0.50	0.58

Table S2. Total survey effort, number of foxes detected and densities of foxes estimated by line transect surveys in the three study regions, during 1995-1997. The precision of the density estimates is shown by the coefficient of variation (CV).

Region	Season	Year	Total effort (hours)	Foxes detected	Density (foxes km ⁻²)	CV
Wales	autumn	1995	26.3	29	0.76	0.20
		1996	46.4	74	0.97	0.15
	spring	1996	39.7	35	0.40	0.25
		1997	40.0	39	0.49	0.24
Midlands	autumn	1995	32.1	131	2.93	0.10
		1996	26.5	114	2.57	0.10
	spring	1996	5.8 [†]	13	0.71	0.30
		1997	29.6	74	1.02	0.14
East Anglia	autumn	1995	35.4	32	0.57	0.20
		1996	51.5	62	0.60	0.16
	spring	1996	50.4	18	0.11	0.28
		1997	49.0	25	0.16	0.24

[†]Partial survey due to adverse weather.

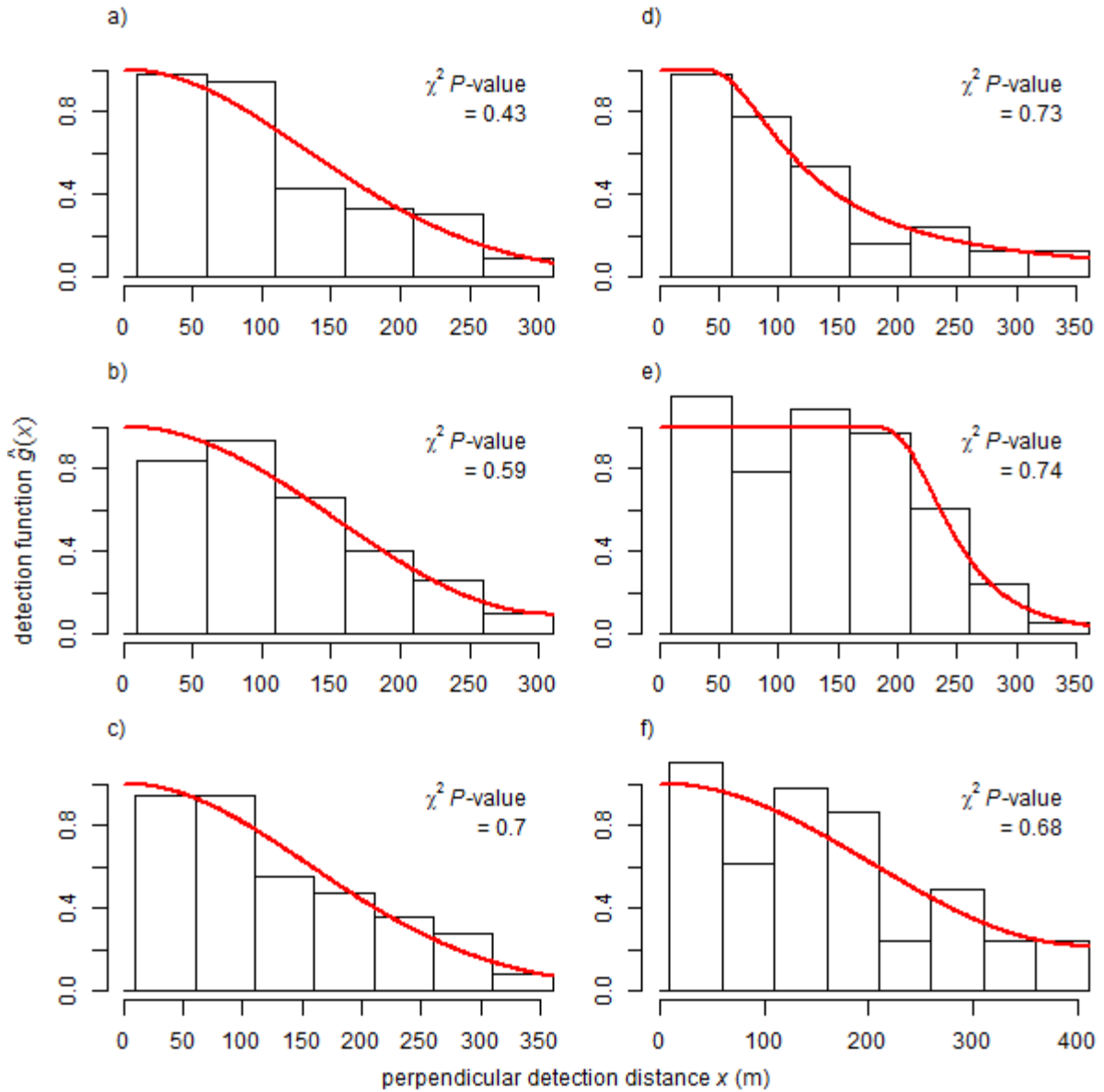


Fig. S1. Histograms of grouped distance data with fitted detection functions fits to distance sampling data, showing χ^2 goodness-of-fit P -value. a) Wales – autumn survey ($n = 101$ fox detections); b) Midlands – autumn ($n = 232$); c) East Anglia – autumn ($n = 92$); d) Wales – spring ($n = 72$); e) Midlands – spring ($n = 81$); f) East Anglia – spring ($n = 39$).

Appendix S2. Derivation of the Holling disc equation for partitioning search and handling time

The relationship between fox detections and fox density described by Eq. 3 means that an increase in survey effort leads to a linear increase in the number of detections at a given fox density. A key assumption in using Eq. 3 to estimate fox density from fox detections is therefore that the handling time is zero, i.e. that search time is equal to the total survey effort. If the handling time is greater than zero, the relationship becomes asymptotic as the search time is limited by the number of detections that can be handled with a given survey effort. A smaller number of detections is thus expected to result from a given fox density and survey effort. This non-linearity could potentially lead to biased fox density estimates. Instead of assuming that handling time is zero, it is instead possible to continue from Eq. 3 and derive the Holling disc equation in the gamekeeper-fox system to partition total lamping effort into search time and handling time. This can then be used to estimate fox density from the number of detections, provided that handling time can either take an assumed value or can be estimated from data. Deriving the disc equation for the gamekeeper-fox system also enables the functional response of gamekeepers to foxes to be examined, i.e. the number of foxes killed as a function of fox density.

Such a derivation continues from Eq. 3 by assuming that the gamekeeper attempts to shoot all foxes detected, so the number of detections Y over a time interval (time subscripts are removed here for clarity) is also the number of foxes that get shot at. However, the gamekeeper may be successful in killing only some proportion of the foxes detected with probability k , so the number of foxes killed C is:

$$C = kY = ksE_sD \quad \text{Eq. S1}$$

where s is the rate of successful search, E_s is search time and D is fox density. When all foxes that are seen are killed, i.e., if the gamekeeper has perfect conditions for making a shot and is an expert marksman, then k will equal 1. British gamekeepers lamping foxes on shooting estates kill on average only about 30% of the foxes seen on each lamping occasion (GWCT, unpubl. data). Given estimated detection probability is about 0.5, the lamping

efficiency (efficiency = detection probability \times killing probability) is therefore 0.15, i.e. 15% of foxes present on an estate will be killed during one complete pass of the estate area.

The next step is to separate the total lamping survey effort E_a into two defined components i) time spent searching for foxes E_s , and ii) time spent shooting and collecting dead foxes, i.e., the handling time E_h per fox. This will allow an expression for the time spent searching to be found in terms of both the total time available for lamping and the handling time. As the gamekeeper spends more time killing foxes, less time is available to be allocated to searching for other foxes. This trade-off in time allocation can be expressed as:

$$E_s = E_a - E_h C \quad \text{Eq. S2}$$

Note that by this definition the total time lamping is simply partitioned into time spent searching and time spent killing foxes, where the handling time is proportional to the number of kills. By substituting in Eq. S1, this can also be written as:

$$E_s = E_a - E_h k Y \quad \text{Eq. S3}$$

Substituting E_s from Eq. S3 into Eq. 3 for survey effort gives a new equation for the number of foxes seen per total survey effort available (i.e. search time plus handling time):

$$Y = sD(E_a - E_h k Y) \quad \text{Eq. S4}$$

To complete the derivation this needs to be solved for Y :

$$Y = sE_a D / (1 + ksE_h D) \quad \text{Eq. S5}$$

This equation is the same as the Holling disc equation (Holling 1959a; Holling 1959b; Holling 1965) which has been widely used in ecology to describe the functional responses of predators to their prey and to predict catch rates of prey by predators. It should be noted that Eq. S5 collapses to Eq. 3 when E_h goes to zero.

Appendix S3. Supplementary figures

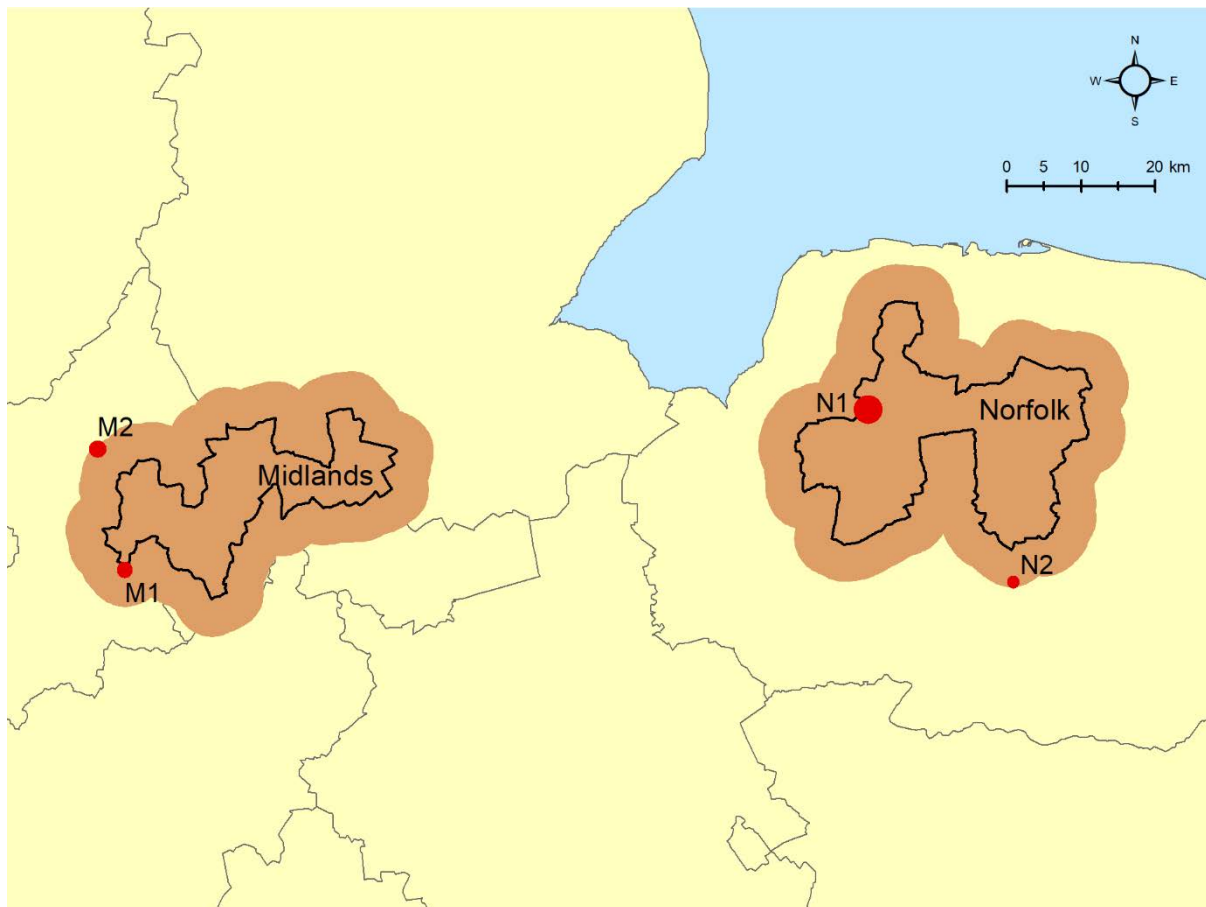


Fig S2. Map showing the location of estates which contributed data to the Fox Monitoring Scheme (red dots) within a 5-km buffer (orange) of the Midlands and Norfolk transect routes used in the 3-region study (black lines). The Wales transect route is not shown as there were no FMS-contributing estates nearby. Numbers relate to estate codes used in the text and estate symbol size reflects estate area.

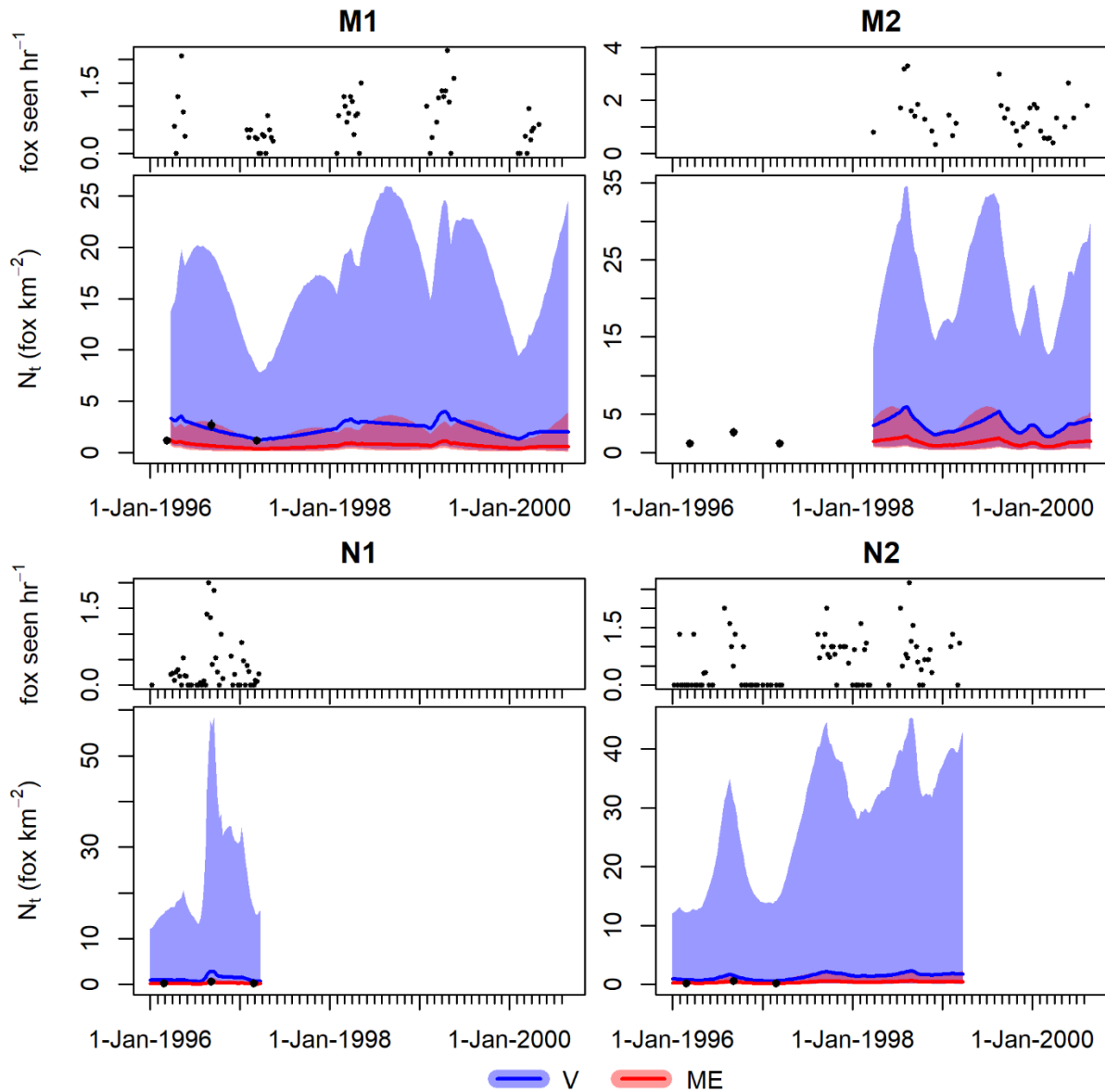


Fig. S3. Weekly fox lamping effort and sighting data (top subpanels) and estimated fox density (bottom subpanels) from four estates in two regions: Midlands (M1, M2) and Norfolk (N1, N2). Posterior median fox density estimates are from models using either a vague (V) or a mechanistic-empirical (ME) prior on the rate of successful search. 95% credible intervals are shaded respectively blue and red; mix of colours shows overlap. Regional density estimates from the distance sampling study are shown for spring 1996, autumn 1996 and spring 1997 (mean and 95% confidence interval) for comparison, plotted (black dots) in the middle of each 7-10 day survey period.

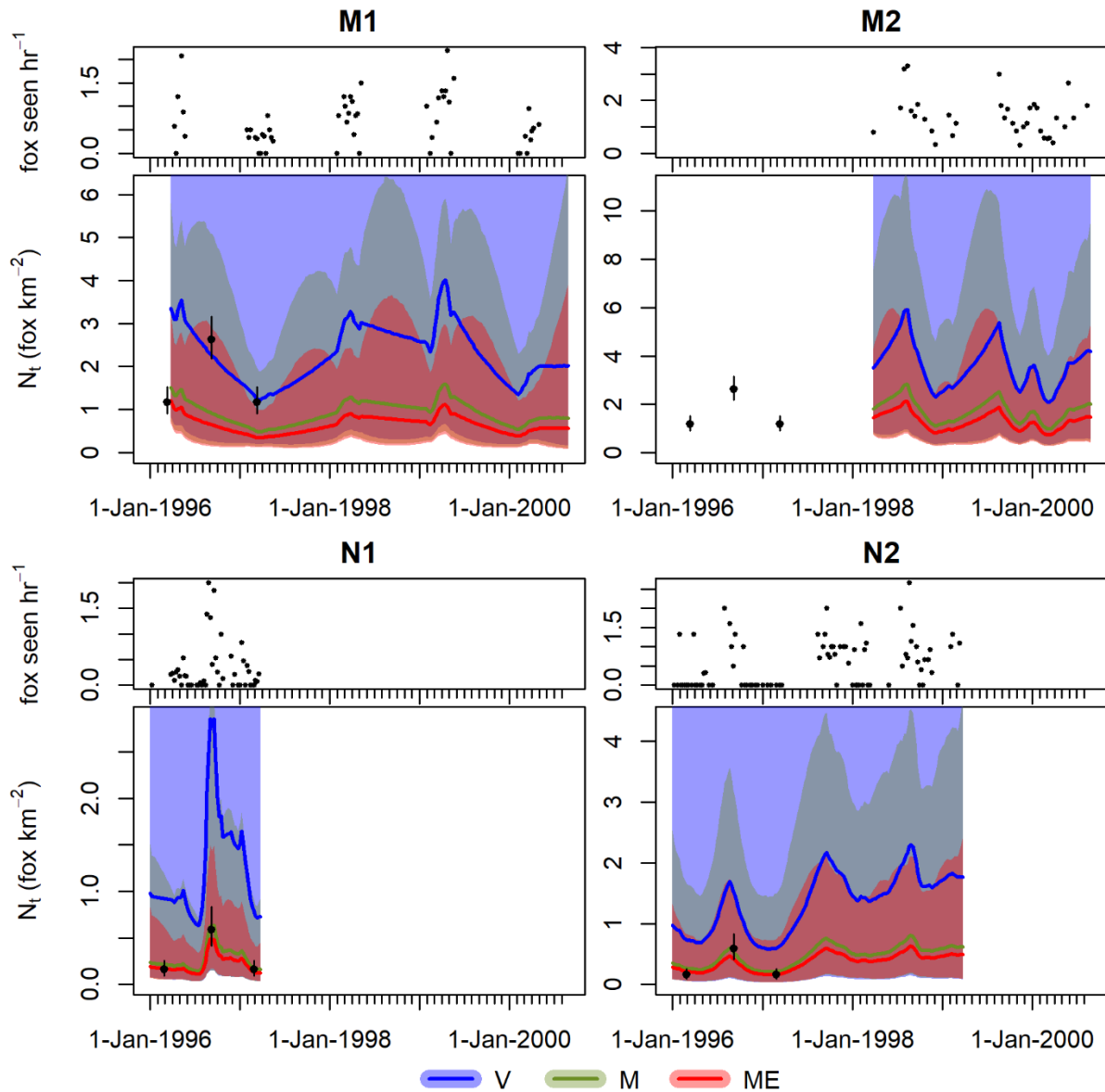


Fig. S4. Weekly fox lamping effort and sighting data (top subpanels) and estimated fox density (bottom subpanels) from four estates in two regions: Midlands (M1, M2) and Norfolk (N1, N2). Posterior median fox density estimates are from models using different priors on the rate of successful search: vague (V), mechanistic (M), or mechanistic-empirical (ME). 95% credible intervals are shaded respectively blue, red, and green; mix of colours shows overlap. The full extent of the vague prior model credible intervals are not shown (see Fig. S3). Regional density estimates from the distance sampling study are shown for spring 1996, autumn 1996 and spring 1997 (mean and 95% confidence interval) for comparison, plotted (black dots) in the middle of each 7-10 day survey period.

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