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SUMMARY. Studies which measure animals' positions over time are a vital tool
in understanding the process of resource selection by animals. By comparing
a sample of locations used by animals with a sample of available points, the
types of locations preferred by animals can be analysed using logistic regression.
Random effects logistic regression has been proposed to deal with the repeated
measurements observed for each animal, but we find that this is not feasible
in studies where the sample of available points cannot readily be matched to
specific animals. Instead, this paper investigates the use of marginal logistic
models with robust variance estimators, using a study of Australian bush rats as
a case study. Simulation is used to check the properties of the approach and to
explore alternative designs.

KEY WORDS: Animal tracking; Compositional analysis; Huber-White; Logistic
regression; Radio-tracking; Spool-and-line method.

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1. Introduction

1.1 Motivation

There are many situations in which knowledge of the habitat preferences of organisms would be useful and where one means of studying them would be to compare points used by animals with points available for use. The preferences that drive organisms' selection of resources are of great importance in much ecological, behavioural and conservation research. These preferences have an important role in the spatial dynamics of animal populations (Stapp & Horne, 1997; Turchin, 1991; Loretto & Vieira, 2005). Design and implementation of conservation measures also requires information about the factors which influence animals' movements and resource use. This is of particular relevance for species threatened by habitat fragmentation. It is therefore important to understand how animals choose where to move and which resources to use, relative to the locations and resources available to them.

This paper is concerned with studies where:

(i) A sample of animals is selected in some way and a sample of "used points", traversed or used by these animals, is selected. Generally this sample is selected by trapping animals and following their path using radio-tracking or the "spool-and-line" method.

(ii) The animals collectively use a broader habitat or region. Points in the region are assumed to be available for use by the animals. A sample of

these available points is selected.

(iii) A number of variables are measured for each of the sampled used and available points. Comparison of these variables between used and available gives information on how animals choose resources or locations.

This is essentially design 2 in Manly et al. (2002, page 6). We call our scenario an unmatched design, because while each used point is associated (or matched) with a specific animal, the available points are not matched to particular animals.

This scenario was motivated by a study of habitat use exhibited by the bush rat (*Rattus fuscipes*), an Australian native small mammal. The movement patterns of these animals in regions adjacent to powerlines were under investigation, in an attempt to evaluate and then mitigate some of the negative ecological effects of powerline easements[1]. The spool-and-line technique (e.g. Loretto & Vieira, 2005) was used to give a sample of used points for a number of animals. In this method, animals are captured and released with a miniature thread spool attached. The spools unravel and ultimately detach and the animals' paths can be retraced by following the thread. A sample of available points was selected using a regular grid and five variables were measured for the available and used points. The objectives and design of this study will be discussed in more detail in Section 3.

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[1]Powerline easements are corridors of land, typically ranging from 25m to 100m, that feature power cables and their supporting power poles, and are subject to regular mowing to restrict regrowth of vegetation.

1.2 Matched Designs

An alternative approach would be to use a matched design. A sample of animals would be selected, and a sample of points used by these animals would be measured. A habitat or home range for each animal would then be determined and a sample of available points selected from the home range for each animal. Unlike the unmatched design described in 1.1, both the used and available points are matched to specific animals.

The matched design is only feasible if (a) each sampled animal's home range can be determined (at least approximately) and (b) the home ranges do not substantially overlap. The former requires enough observations taken over a long enough period to identify each animal's home range. This would usually be feasible with radio-tracking which can be used to provide a minimum convex polygon for each animal (e.g. Gillies et al., 2006), but spool-and-line data often only covers a short period of each night's movement for each animal. Requirement (b) is satisfied for some animals but not for communally nesting species such as bush rats and many other small mammals.

In previous studies, repeated tracking of the same individual, typically using radio telemetry, has been used to develop an understanding of home range (see Laidlaw et al., 1996; Leung, 1999; Jedrzejewski et al., 2001). Radio telemetry was not used in the case study discussed in this paper, primarily because of the cost of the equipment and the extremely dense nature of the habitat which would have impeded swift pursuit of the fast-moving bush rats. Another approach would

be to repeatedly apply the spool-and-line method to each animal to estimate their home range. Repeated spooling was avoided both to avoid the possibility of injuring the animals and also because of the difficulty of capturing the same animal repeatedly. This restricted the generation of conclusive home range data for each individual.

1.3 Analyzing Clustered Data

One approach to analyzing resource selection data with multiple measurements from each animal is compositional analysis (Aebischer & Robertson, 1993). In this approach, the data is aggregated to the animal level by taking the proportions of points falling into particular habitat types for each animal as the dependent variables. Logarithms of ratios of these proportions are analyzed as multivariate normal. The use of log transforms mean that zero values are difficult to manage and this can result in inflated type 1 errors (Bingham & Brennan, 2004); also, the method is difficult to apply when habitat type does not naturally fall into a fairly small number of categories. For some examples of the application of this method, see Pendleton et al., 1998; Bos & Carthew, 2003.

A more convenient and flexible method of analysis is logistic regression using a dataset consisting of both used and available points (Manly et al., 2002, Chapter 5, Gillies et al., 2006). The type of point (used vs available) is the dependent variable and the variables measured for each point are explanatory variables. In both cases, there are repeated measurements for each animal and this needs to be taken account of in some way. Otherwise, variances may be severely under-

estimated due to high correlations between observations from the same animal. Alternatively, studies may be designed so that correlations are negligible, by selecting few and distant points from each animal, however this is likely to be an inefficient approach.

One way of incorporating the clustered nature of the data into a logistic regression is by a random effects logistic model (e.g. Pendergast et al., 1996), where the linear predictor includes a random effect or effects for each animal. This approach was recommended by Gillies et al. (2006) for matched studies, because it explicitly models the heterogeneity between animals, which is useful for predicting future behaviour of a group of animals. Moreover Gillies et al. show that the method efficiently handles the case of varying numbers of observations per animals.

Another possible approach suggested by Gillies et al. (2006) is marginal logistic regression. A robust variance estimator should then be used to allow for the clustered nature of the data. Two common alternatives used in logistic regression modelling of clustered data are the Huber-White (HW) variance estimator (Pendergast et al., 1996), and the bootstrap estimator where the bootstrap resamples are constructed by resampling spools and taking all observations in the selected spools (Efron & Tibshirani, 1993).

Gillies et al. (2006) recommended the random effects approach rather than marginal logistic regression. However, only matched studies were considered. For matched data, there is a sample of used points and available points for each ani-

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mal. A logistic regression is conducted with dependent variable given by type of point, and with a random effect for the animal. However, for unmatched data, the available points are not tied to any animal in particular, so that no the animal-level random effects cannot be used for the available points. A work-around solution would be to assign every individual available point its own random effect/s, or to have only a fixed effect model for available points. The interpretation of such a model would be very unclear, and it is difficult to fit this model using standard methods, because many of the random effects would be associated with only one observation.

1.4 Outline of this Paper

In matched resource selection designs, there is a sample of available points and used points for each animal in the study. In unmatched designs, there is a sample of used points for each animal, and a sample of available points from the overall region. Logistic regression models with random effects can be used to analyse matched data, but this is not an option for unmatched designs. This article develops a marginal logistic regression approach with robust variance estimators to handle unmatched resource selection studies. Section 2 describes the logistic model and the Huber-White variance estimator in more detail. Section 3 is a case study where the approach is applied to a study of bush rats in south east Australia. Section 4 describes a simulation study to confirm that logistic regression can give consistent estimates and inferences for studies of this type, and to explore design alternatives. Section 5 is a summary.

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2. Logistic Regression using the Huber-White Variance Estimator

2.1 Logistic Regression Model

Manly et al. (2002, Section 5.4) supposes that there is a sample of available units of size N, with the i-th unit having a vector of values $\mathbf{x_i}$ summarising the characteristics of the unit. In our case, units are locations or points. The probability of a point i being used in a period of time by any animal in the population is assumed to equal

$$w^* \left(\mathbf{x_i} \right) = exp \left(\alpha + \beta^{\mathbf{T}} \mathbf{x_i} \right) \tag{1}$$

where α is sufficiently large and negative that this quantity is always less than 1. This would usually be the case as there would normally be a very large number of available points since this is limited only by the resolution at which points are defined.

The coefficients β reflect the attractiveness of different characteristics. For example, if the k-th element of $\mathbf{x_i}$ measures the level of shrub cover, then a high value of β_k means that a high level of shrub cover is attractive to the animal. A negative value of β_k means that locations with shrub cover tend not to be selected by animals. A zero value means that shrub cover does not influence animals' choices. Continuous covariates, factors and interactions can all be included in the model by appropriate definition of $\mathbf{x_i}$. The intercept parameter α is generally not of interest.

Available points are assumed to be sampled with probability P_a. Used points

are assumed to be sampled from all used points (excluding any points selected in the available sample) with probability P_u. Hence the probability of a point being selected in the available sample is P_a, and the probability of a point being selected in the used sample is $P_u(1 - P_a)$ conditional on the point being used. Let s_a and s_u be the available sample and the used sample respectively. The probability of point i being used given that it is sampled is

$$
\begin{aligned}
Pr\left[\text{i used}|\text{i sampled}\right] &= \frac{P\left[i \in s_u|\text{i used}\right] P\left[\text{i used}\right]}{P\left[i \in s_u|\text{i used}\right] P\left[\text{i used}\right] + P\left[i \in s_a\right]} \\
&= \frac{P_u\left(1 - P_a\right) exp\left(\alpha + \beta^{\mathbf{T}}\mathbf{x_i}\right)}{P_u\left(1 - P_a\right) exp\left(\alpha + \beta^{\mathbf{T}}\mathbf{x_i}\right) + P_a}.
\end{aligned}
$$

Letting $\alpha^* = \alpha + log\left(P_u\right) - log\left(P_a^{-1} - 1\right)$, this can equivalently be written as

$$
\begin{aligned}
Pr\left[\text{i used}|\text{i sampled}\right] &= \frac{exp\left(\alpha^* + \beta^{\mathbf{T}}\mathbf{x_i}\right)}{exp\left(\alpha^* + \beta^{\mathbf{T}}\mathbf{x_i}\right) + 1} \\
&= logit^{-1}\left(\alpha^* + \beta^{\mathbf{T}}\mathbf{x_i}\right) \quad\quad (2)
\end{aligned}
$$

which is a logistic model (Manly et al., 2002, pp.99-100). Result (2) implies that the used and available points can be combined into one dataset, and that a logistic regression with type of point (used vs available) as dependent variable will yield estimates of β in (1).

2.2 Robust Variance Estimation for the Marginal Logistic Regression

Observations taken from the same animal would be expected to be positively correlated. One reason is that different animals may have varying preferences for different types of areas, so that points chosen by the same animal will tend to be more similar than points chosen by different animals (Gillies et al., 2006).

Another reason is that animals are often only tracked for a short period so that the observed points for an animal will be close in distance and possibly in character. (See Otis & White, 1999 for a discussion of autocorrelation in the analysis of radiotracking data.)

Ignoring correlations, the maximum likelihood estimators of the parameters of interest, β, are obtained by solving the score equations

$$\mathbf{0} = \sum_i \mathbf{U_i} \tag{3}$$

with respect to α^* and β, where $\mathbf{U_i} = \left\{ Y_i - logit^{-1}\left(\alpha^* + \beta^{\mathbf{T}}\mathbf{x_i}\right) \right\} \mathbf{x_i}$. The approach taken is to choose β to solve (3), i.e. the score equations ignoring correlations. Even when there are non-zero correlations, this gives consistent estimators of β.

The aim is then to use an estimator of $var\left[\hat{\beta}\right]$ which allows for correlations. The Huber-White method is one alternative. It is assumed that observations i can be grouped into clusters g such that observations from different clusters are independent. In our case, i are observations and the clusters g are animals for the used points. For the available points, each observation is assumed to be independent, so g can be defined to be the same as i, i.e. each available point forms its own cluster. The HW method is based on obtaining a robust estimator of the variance of the right hand side of (3). Using Taylor Series, the variance of $\hat{\beta}$ can be obtained in terms of this variance. The variance estimator is sometimes called the "sandwich estimator" because a robust estimator of $var\left[\sum_i U_i\right]$ is sandwiched

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in between two other terms in the Taylor Expansion. See for example Pendergast et al. (1996).

Hypotheses about the parameters in β can be tested using a robust estimator of $var\left[\hat{\beta}\right]$ via a Wald test. The HW estimation method for logistic regression, and the associated Wald test, have been implemented in a number of statistical packages including Sudaan (Shah et al., 1997), STATA (StataCorp, 2005), the svyglm function (Lumley, 2004) in the R survey package (R Development Core Team, 2006), and PROC SURVEYLOGISTIC in SAS (SAS Institute Inc, 1999).

Another alternative is bootstrapping. Boostrap variance estimators are calculated by creating a large number of resamples from the original data. Each resample is a sample with replacement from the original dataset, of the same size as the original dataset. The estimator of interest, $\hat{\beta}$ is calculated for each resample, resulting in R replicates of $\hat{\beta}$ where R is the number of resamples. The sample variance of these R observations of $\hat{\beta}$ is used to estimate $var\left[\hat{\beta}\right]$. For data with correlations, a robust bootstrap estimator can be calculated by resampling clusters rather than individual observations. Each resample is obtained by taking a simple random sample with replacement of the original clusters, and taking all observations from the selected clusters. See for example Efron and Tibshirani (1993).

3. Case Study: Foraging Behaviour of Bush Rats in New South Wales

3.1 Aims of Study

Data used here were obtained from a study of habitat use exhibited by the bush rat (*Rattus fuscipes*), an Australian native small mammal. The study was conducted in the Conjola National Park in south east Australia. The bush rat, a terrestrial rodent, is a common mammal of the closed, tall and open forests of Australia, with a very wide but disjunct coastal distribution from Cape York in Queensland, southwards and westwards to Western Australia (Robinson, 1987).

The movement patterns of these animals in regions adjacent to powerlines were under investigation, in an attempt to evaluate and then mitigate some of the negative ecological effects of powerline easements. These easements, which are regularly mowed to control vegetation growth, have been found to inhibit the movement of small mammals between adjacent regions of forest (Goosem & Marsh, 1997; Strevens, 2007). The main consequence of reduced dispersal of individuals is greater susceptibility of isolated populations to extinction (Fahrig & Merriam, 1985), as a result of lower immigration rates. Effective design of measures to counteract easement crossing-inhibition first requires a clear understanding of how the animals move within their habitat.

3.2 Data Collection Issues

The spool-and-line technique was used for this study. The spool-and-line technique was used by Breder (1927), and later by Stickel (1950) in tracking movement patterns of turtles (*Terrapene c. carolina*). Miles et al. (1981) was

the first to apply the spool-and-line technique to small mammals, as part of a parasitological study in Amazonia. Most recently Loretto and Vieira (2005) have used the spool-and-line technique to measure the intensity of habitat use and the daily movement areas of the black-eared opossum (*Didelphis aurita*).

Trapping was conducted over a 25 by 125m area in September and November 2004 and in February and April 2005. Two rows of 12 traps were inspected approximately two hours after dark. Animals discovered in the traps were removed, marked and fitted with a miniature thread spool using cyanacrolyte (superglue). The end of the thread line was tied to a nearby tree or shrub and the bush rat gently released. The site of release was marked with flagging tape to facilitate identification of the start of the thread path the following day. After a short period of flight, the released animal returns to foraging for the remainder of the night. (The first few measurements of each spool are sometimes excluded from analysis as they may represent flight rather than foraging, but in our case no systematic difference was found between these and subsequent measurements, so all data were used.) The spools unravel from the inside, so that as the spooled animal proceeds through the vegetation, the thread is dispensed without inhibiting the animal's movement. When the thread is fully unravelled, or before, the spool detaches harmlessly from the animal's back.

The following day, the white thread trail dispensed by the spooled animal was traced through the habitat. Points at 3m intervals along this trail were scored for five variables (Table 1) based on the vegetation and cover in a 1m radius of each

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data point. There was a potential for some of these 1m radius circles to overlap, but in practice this occurred very rarely. A total of 26 animals were tracked. An average of 10.7 points per animal were measured, with a range of 3 to 28 points, for a total of 278 "used" points.

The spool-and-line technique was used because this method provides high resolution spatial data. Radio-tracking is a popular alternative because of the temporal component to the information it provides, but it is more expensive (Anderson et al., 1988), offers poorer spatial resolution (Macdonald & Amlaner, 1980), is difficult to use in dense forest, and is not always feasible for small animals.

The second stage of the study was the measurement of "available" points. Rows of points at 3m intervals were surveyed, with each row spaced 6m apart amounting to a total of 396 points covering the study area.

3.3 Exploratory Analysis

Figure 1 shows the frequency distributions of variables for used and available points. Only 50% of used locations fell into the category of No Logs, compared to the 80% of available points which were in this category. This indicates avoidance behaviour by the animals of regions with no logs present (Fig. 1(a)). Conversely, results show that the animals select for areas with the two largest size categories of logs, approximately 10% more frequently than logs of those sizes occur in the available points.

Discrepancies between the used and available points were less pronounced

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for Leaves (Fig. 1(b)), although there is some suggestion that animals avoided locations with the lowest leaf density.

Animals preferred areas of habitat with medium and high densities of Branches, compared to habitat that offered very few branches (Fig. 1(c)), though the margin of this preference was just 8% and 5% greater, respectively, than feature availability. A more marked contrast was found for the lowest Branch density category. Results reveal that animals traversed these areas approximately 25% less than would be expected based on availability in the habitat (Fig. 1(c)).

A strong aversion to regions with very low ground vegetation was apparent, as only 40% of used points were at the lowest ground vegetation category compared to 80% in the available points (Fig. 1(d)).

Finally, animals' preferences for greater densities of Shrub Vegetation were apparent (Fig. 1(e)). For example, there are 19% fewer records of selection for areas with very low values for Shrub Vegetation than there were records of this category in the sample of available points. This pattern is also true for the second lowest density of Shrub Vegetation, though to a lesser degree (7%) (Fig 1(e)).

3.4 Logistic Regression Model

A model was constructed by backward selection starting with the model containing all five main effects. Table 2 shows the results of omitting one effect at a time from the full model. The variable Leaf was not significant but all other variables were. Both the naive variance estimators (i.e. ignoring correlations) and the HW variance estimator gave the same finding, but the naive test was

more statistically significant in all cases, suggesting that this test has higher type 1 error rates than the robust HW method. After omitting Leaf, the other four variables were still statistically significant (details not shown).

Two-way interactions were also considered. These were problematical because the small cell sizes led to infinite parameter estimates, and the Wald test is known to perform poorly in this case (e.g. Hosmer & Lemeshow, 1989). Robust quasi-score tests were used instead (Rao et al., 1998). Details are omitted here, because none of these interactions turned out to be significant at the 0.05 level.

Visual inspection of the estimated coefficients suggested that there was a distinct difference between the lowest level of Ground Vegetation, Logs and Branches, and the other levels of these variables. In contrast, the parameters for Shrub Vegetation appeared to increase fairly smoothly over the levels of this variable. This suggested that perhaps each main effect could be replaced by just one parameter. Table 3 shows the results of testing these simplifications using the robust HW Wald tests. The table shows that the model fit is not significantly worsened by these simplifications, either taken individually or all together.

Table 4 summarises the final model. Bush rats were more likely to move through areas containing more ground vegetation, logs, branches or shrub vegetation. For Ground Vegetation, Logs and Branches, the mammals tended to choose points which had at least some of these (odds ratios of 6.1, 3.1 and 3.4) but were indifferent to whether there was a little or a lot. For example, the odds of a point being visited by a bush rat were increased by a factor of just over 6

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if the point contained ground vegetation, compared to a point without ground vegetation, all else being equal.

The animals also tended to prefer points with shrub vegetation and the more shrubs there were, the more likely a position was to be chosen, with the odds increasing by a factor of 1.6 for every increase of 1 in the level of Shrub Vegetation (all else being equal). No significant association between Leaf and animals' presence was found.

The naive standard errors in Table 4 were appreciably lower than the robust standard errors, suggesting a severe negative bias in the former.

It is worth noting that the robust variance estimators are only approximately unbiased if observations from different animals are independent. This may not be correct due to spatial correlations and some form of spatial modelling would be worth considering to test this assumption. This has not been attempted in habitat selection studies to our knowledge, but is worth considering in future studies. We conducted a very partial check for spatial correlations across animals by including the capture location (North or South) as a predictor in the logistic model. This variable was not significant (Table A1 in Clark & Strevens, 2008). As a further protection, the case study was restricted to the Conjola region which is reasonably homogenous in terms of topography and vegetation.

4. Simulation Study

4.1 Introduction

The logistic model (1) and the derivation of (2) from it involved strong assumptions. In addition, the HW and bootstrap variance estimators assume that there are no correlations between observations between different animals, and no correlations between observations from the used and available points. Any of these assumptions could fail to hold, for example spatial correlations may occur between measurements of points which are close together, even when these points were recorded from different animals.

A simulation study was conducted to test the approach. To give a realistic evaluation, a hypothetical landscape consisting of a 1000*1000 grid was simulated, and animal movements across this landscape were simulated using a Markov Chain model. Samples of available points, animals and used points from each animal were then simulated. The target of inference was the logistic model fitted using the whole population of available and used points.

4.2 Generation of Landscape and Population of Available Points

The first step was to generate a variable X, representing characteristics of points, for the 1000*1000 grid. This was done by firstly generating standard normal variables Z over the grid using the GaussRF function in the RandomFields (Schlather, 2006) package in the R statistical language. Two grids were generated. Firstly, the variable Z was generated as independent standard normal variables, corresponding to uncorrelated values across the region. Secondly, Z were

spatially correlated standard normals with an exponential spatial autocovariance function with scale 2. The approximate circulant method (Wood & Chan, 1994) was used as it was computationally unfeasible to generate variables with exactly the required covariance matrix. X was generated by taking the inverse normal distribution function of Z and then rescaling so that X was distributed uniformly on [-1,1]. Finally, X was discretised to one decimal place to reduce computation.

The next step was to generate the paths of a population of animals over this region. Paths consisting of 1500 steps were generated for each of a population of 1500 animals. For each animal, a startpoint was randomly generated from the 1000*1000 grid. A Markov chain model was then used to determine each animals' step conditional on their current location. Each point had 4 neighbours (up, down, left and right) and the probability of choosing a point from this set was proportional to $exp\left(\gamma x\left(1+\sigma A\right)\right)$ where x represents the value of X at that point, γ is a slope parameter measuring the effect of x on the animal's choice, and A is an animal-level random slopes term. The parameter σ controls the correlation of choices made by the same animal. An animal-level random effect was used to give a realistic evaluation, since the robust HW and bootstrap variance estimators should be able to handle any correlation structure between observations from the same animal.

Four populations were generated:

Population (1): uncorrelated grid of values of Z, with $\sigma = 0$ (uncorrelated

region data and uncorrelated choices within animal).

Population (2): uncorrelated grid of values of Z, with $\sigma = 0.1$ (somewhat correlated choices within animal).

Population (3): correlated grid of values of Z with scale of 2, with $\sigma = 0.1$ (correlated region data and somewhat uncorrelated choices within animal).

Population (4): correlated grid of values of Z with scale of 2, with $\sigma = 0.5$ (correlated region data and highly correlated choices within animal).

The extent to which the values of a variable tend to be similar within groups can be measured by the intraclass correlation, which lies between -1 and 1 (see definition (1) in Koch, 1982). The intraclass correlations of X within animal were 0.003, 0.038, 0.113 and 0.294 respectively. Population (3) was most similar to the case study described in Section 3 in terms of the intraclass correlation. Population (1) was included to show a case where there was negligible correlation between observations from the same animal, and population (2) has some intra-animal correlation but no spatial correlation in the values of X across the region. Population (4) was included to show the effect of very high correlation within animal. The value of γ was set to 0 in all four populations, since the properties of inferences for small values of the parameter of interest are usually considered the most important. Simulations with larger values of γ were also conducted and results are described in Clark and Strevens (2008) with similar conclusions.

The values of β for populations (1)-(4) were 0.001, 0.003, 0.018 and 0.013, respectively. Note that the values of β are not identical to the values of γ, because the parameters of a marginal logistic model are not in general the same as those of the conditional logistic model fitted to the same data (e.g. Breslow & Clayton, 1993).

To illustrate the simulation further, Figure 2 shows the path of a particular animal for a 20*20 square within the grid. The background shade indicates the value of X with high values shaded darker. The arrows indicate the animals path over a number of steps. It can be seen that the animal often retraces its path.

4.3 Simulation of Samples from this Population

The next step was to conduct a large number (1000) of simulations of samples from this population. Each sample consisted of a simple random sample without replacement of n_a available points, to simulate the regular grid sampling of the available points from the region which is used in field studies. The sample also consisted of a simple random sample without replacement of m animals, and $\bar{n}_u$ successive points from each animal, to simulate the trapping and tracking of m animals. The simulation was conducted for the four different populations defined in Section 4.2, with m set to 30, 60 and 120, $\bar{n}_u$ set to 5, 10 and 25, and $n_a = 400$. Values of n_a equal to 50, 100, 200, 800 and 1000 were also trialled with $m = 30$ and $\bar{n}_u = 10$, and values of $\bar{n}_u$ equal to 2 and 50 were trialled with $m = 30$ and $n_a = 400$.

A variable Y was set to 1 for used points, and to 0 for available points. For

each sample, the logistic regression model was fitted, with X as a continuous variable. Confidence intervals for β with 90% nominal coverage were calculated using the naive, Huber-White and bootstrap variance estimation methods. The bootstrap was applied with clusters defined as animals for the used points, and with each cluster being an individual point for the available points.

4.4 Results

Tables 5 and 6 show the bias and standard error (SE) of $\hat{\beta}$ for the four populations. The bias is negligible compared to the SE in all cases. The SE decreases as m increases, and decreases at a slower rate as $\bar{n}_u$ increases. The SEs are increasing in order of population (1-4) with population 1 giving the lowest SEs and population 4 the highest. This is because the intra-animal correlation is increasing from populations 1 to 4, and there is less gain from repeated sampling of the same animal as this correlation increases.

Table 7 shows the non-coverage of confidence intervals for β for populations 1 and 3. The naive variance estimator gives non-coverage of 13%-18% for population 1 which is higher than the nominal 10% but not dramatically. For population 3, the naive variance estimator performed very poorly with noncoverage of 23%-44%. The HW and bootstrap estimators had non-coverage close to the nominal 10% in all cases.

Considerable effort is required to measure the characteristics of the sample of available points, so it is of interest to determine how large a sample of points is needed to give good results. Table 8 shows the standard errors of $\hat{\beta}$ for $m = 30$

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and $\bar{n}_u = 10$ for different numbers n_a of available points, for populations 1-4. For populations 1 and 2 (the least clustered), n_a of 200 or 400 both seem like reasonable choices, although the gains from increasing from 200 to 400 are not large. For population 3, $n_a = 200$ or perhaps even $n_a = 100$ seems appropriate, as there is only minor gain from further increasing n_a. For population 4 (which is highly clustered), n_a of 100 or even 50 would seem to be suitable; virtually no gain is seen for increasing n_a beyond 200. Overall, setting n_a to about half of the number of used points seems sensible, and would usually be preferable to having equal numbers of used and available points. If values are highly clustered within animals, then a smaller value of n_a could be used, but this would be a risky strategy unless there is some data to support this belief. Even if there is no clustering, n_a equal to half of the number of used points is not too bad, so this seems to be a good all-round strategy.

The experimenter must decide whether to put their efforts into capturing more animals, or whether to capture fewer animals but collect more data for each animal. A factor in this decision is the time involved in capturing and releasing animals, relative to the time taken to collect additional points from each animal. To make this trade-off effectively, it is important to understand the effect on statistical efficiency of varying m and $\bar{n}_u$. Figure 3 shows how the standard error of $\hat{\beta}$ varies with these design parameters, for populations 1-4. A sample of $n_a = 400$ available points was assumed. The figure shows diminishing returns as $\bar{n}_u$ increases, and suggests that it is not worthwhile collecting much

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more than 20 points per animal for populations 2, 3 and 4.

These results suggest that fewer available points (150-200) should have been used in the study in Section 3, and the resources saved should have been used to sample more animals. It should be noted, however, that time saved by these changes cannot necessarily be easily redirected into increasing m, for several practical reasons. The measurement of used and available points takes place during the day whereas trapping occurs at night. Furthermore, animal sampling was constrained by the number of individuals that could be trapped and released each night. This number can depend on factors such as site location, species abundance, difficulty of trapping, habitat type and season. Moreover, multiple spool trails in a confined section of habitat can confuse the recording of used points owing to entangled or entwined trails from different individuals (although this can be reduced through the use of different colours of spool thread).

5. Discussion and Conclusions

Logistic regression is a flexible and efficient method for analysing resource selection data consisting of separate samples of used and available locations. For a case study of bush rats in Australia, we found that:

- Marginal logistic regression was an option but random effects logistic regression was not.

- Robust variance estimators gave considerably higher values than non-robust variance estimators, indicating that the latter are severely biased.

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A simulation study further demonstrated that:

- parameter estimates from marginal logistic regression had low bias and were reasonably precise for the corresponding population parameters.

- confidence intervals based on robust variance estimators had close to nominal coverage, whereas nonrobust variance estimators resulted in seriously flawed inferences.

The simulation was also used to evaluate alternative designs. The number of available points should only be around half the number of used points, and 20 or less used points per animal should be measured provided that these points are well-spaced. These results are based on our bush rat dataset and could differ somewhat in other situations depending on the level of correlation between measurements from the same animal.

Overall, marginal logistic regression is an effective analysis tool for resource selection studies where available points are not tied to specific animals.

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Table 1: Key Habitat Features and Classes Recorded at 3m Intervals of the Spools and at Points of the Habitat Grid

Variable	Level	Explanation
Logs	1	No Logs Seen at All
	2	Logs present with maximum width 0-10cm
	3	Logs present with maximum width 10-20cm
	4	Logs present with maximum width 20-50cm
	5	Logs present with maximum width ¿50cm
Leaves	1	0-20% of ground (1m radius) covered with leaf litter
	2	20-40% of ground covered with leaf litter
	3	40-60% of ground covered with leaf litter
	4	60-100% of ground covered with leaf litter
Branches	1	Zero or just a few branches (<10cm diameter) present
	2	Several branches present
	3	Network of branches / fallen tree
Ground.Veg	1	0-20% of Ground (1m radius) has vegetation [1]
	2	20-40% of Ground has vegetation
	3	40-60% of Ground has vegetation
	4	60-100% of Ground has vegetation
Shrub.Veg	1	0-20% of Ground (1m radius) covered with shrubs [2]
	2	20-40% of Ground has vegetation covered with shrubs
	3	40-60% of Ground has vegetation covered with shrubs
	4	60-100% of Ground has vegetation covered with shrubs

1. Ground Vegetation defined to be plants less than 30cm across.
2. Shrub Vegetation defined to be plants 30cm or more across.

Figure 1: Frequency Distributions of Variables for Used and Available Points[1]
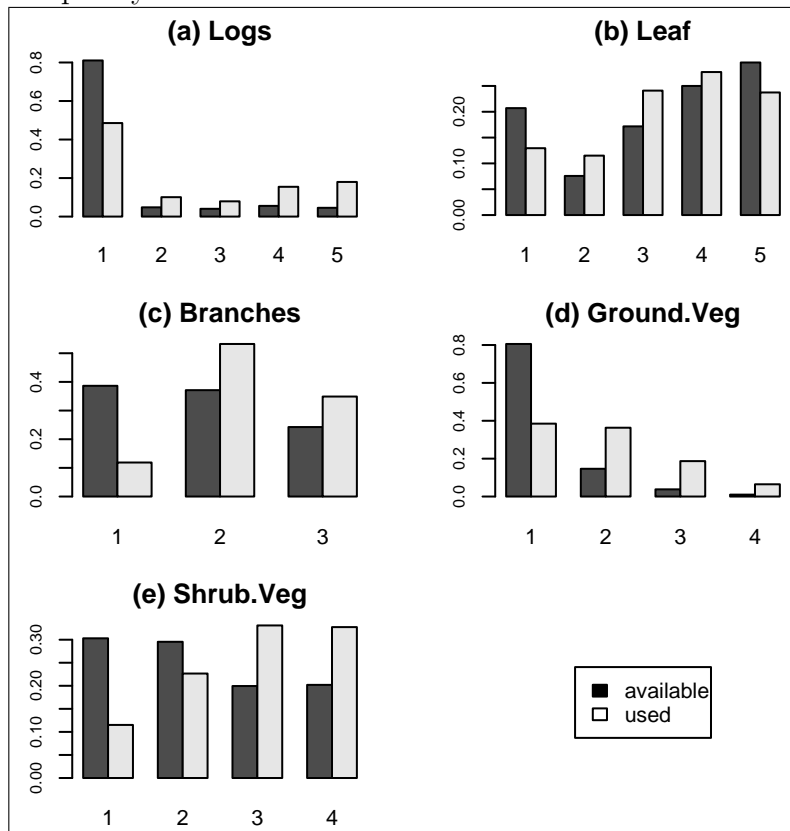
1. E.g. the black bars in (a) are the proportion of available points which have
Logs=1, Logs=2, etc. and the grey bars are the proportion of used points
which have Logs=1, 2 etc.

Table 2: Backward Selection of Main Effects for Conjola Bush Rat Data using
Wald Tests (Wald χ^2 statistics shown with associated p-values in brackets)

Variable [1]	d.f.[2]	Naive Variance Estimates	Robust HW Variance Estimates
-Logs	4	29.58(0.000)	22.67(0.000)
-Leaf	3	1.82(0.610)	1.19(0.756)
-Branches	2	22.84(0.000)	12.94(0.002)
-Ground.Veg	3	74.83(0.000)	29.97(0.000)
-Shrub.Veg	3	22.26(0.000)	14.16(0.003)

1. "-Logs" means the test results for dropping Logs from the full model; "-Leaf"
gives the test results for dropping Leaf from the full model; etc.
2. degrees of freedom

Table 3: Model Simplification for Conjola Bush Rat Data

Term	d.f.	Robust H-W Wald χ^2 (p-value)
Logs $\rightarrow$ (Logs $\geq$ 2) [1]	3	0.31(0.96)
Branches $\rightarrow$ (Branches $\geq$ 2) [2]	1	0.03(0.86)
Ground.Veg $\rightarrow$ (Ground.Veg $\geq$ 2) [3]	2	3.77(0.15)
Shrub.Veg $\rightarrow$ continuous [4]	2	0.51(0.78)
all [5]	8	4.70(0.79)

1. Test results for replacing the Logs variable by a new variable which is equal to 1.
   if Logs $\geq$ 2 and 0 otherwise.
2. Test results for replacing Branches by "Branches $\geq$ 2".
3. Test results for replacing Ground.Veg by "Ground.Veg $\geq$ 2".
4. Test results for using Shrub.Veg as a continuous covariate rather than as a factor.
5. Test results for making changes 1, 2, 3 and 4 simultaneously.

Table 4: Summary of Final Model

Variable	Coefficient	Naive SE	Robust SE	Odds Ratio
(Intercept)	-3.08	0.28	0.45	
Logs $\geq$ 2	1.14	0.20	0.25	3.14
Branches $\geq$ 2	1.23	0.24	0.41	3.41
Ground.Veg $\geq$ 2	1.80	0.20	0.33	6.06
Shrub Veg. (cts[1])	0.45	0.09	0.14	1.58

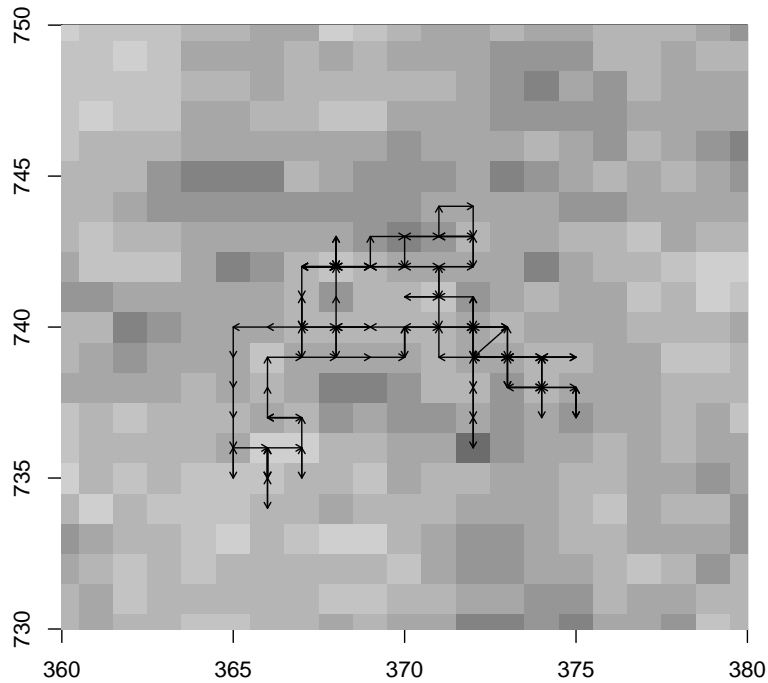1. Shrub.Veg is used as a continuous covariate in this model.

Figure 2: Example of Simulated Animal Path

Table 5: Bias of $\hat{\beta}$ in Simulation Study

#animals (m)	#obs/animal ($\bar{n}_u$)	Population 1 (no spatial, $\sigma = 0$)	Population 2 (no spatial, $\sigma = 0.1$)	Population 3 (spatial, $\sigma = 0.1$)	Population 4 (spatial, $\sigma = 0.5$)
30	5	-0.0082	-0.0056	-0.0027	0.0025
60	5	0.0084	0.0015	-0.0048	-0.0043
120	5	-0.0015	-0.0012	-0.0034	-0.0039
30	10	-0.0048	-0.0041	-0.0057	0.0037
60	10	0.0106	0.0009	-0.0058	-0.0054
120	10	-0.0026	-0.0010	-0.0024	-0.0042
30	25	-0.0045	-0.0033	-0.0026	0.0042
60	25	0.0097	0.0013	-0.0047	-0.0059
120	25	-0.0008	-0.0030	-0.0009	-0.0068

Table 6: SE of $\hat{\beta}$ in Simulation Study

#animals (m)	#obs/animal ($\bar{n}_u$)	Population 1 (no spatial, $\sigma = 0$)	Population 2 (no spatial, $\sigma = 0.1$)	Population 3 (spatial, $\sigma = 0.1$)	Population 4 (spatial, $\sigma = 0.5$)
30	5	0.177	0.183	0.271	0.277
60	5	0.140	0.139	0.196	0.208
120	5	0.119	0.117	0.150	0.146
30	10	0.146	0.154	0.248	0.264
60	10	0.121	0.124	0.184	0.190
120	10	0.107	0.106	0.143	0.140
30	25	0.123	0.134	0.222	0.239
60	25	0.105	0.109	0.161	0.175
120	25	0.097	0.098	0.131	0.130

Table 7: Confidence Interval Non-Coverage (%)[1] for Populations 1 and 3 in Simulation Study

#animals (m)	#obs/animal ($\bar{n}_u$)	Population 1 (no spatial, $\sigma = 0$)			Population 3 (spatial, $\sigma = 0.1$)		
		Naive	Huber-White	Bootstrap	Naive	Huber-White	Bootstrap
30	5	13.4	10.1	10.6	33.0	11.2	9.9
60	5	13.9	10.4	10.8	29.9	11.0	9.7
120	5	14.0	11.8	11.4	23.4	10.5	10.5
30	10	15.0	9.5	9.1	39.0	11.3	10.3
60	10	14.6	10.9	10.3	33.9	11.1	10.6
120	10	13.5	10.9	11.1	27.5	10.9	10.7
30	25	17.5	10.8	10.5	44.1	12.1	10.6
60	25	15.0	11.2	11.8	36.6	9.7	10.5
120	25	14.3	11.4	12.3	27.9	10.9	10.5

1. The percentage of confidence intervals with nominal coverage of 10% which do not cover the true values is shown in each case. These values should be close to 10.

Table 8: SE of $\hat{\beta}$ for Various Sample Sizes (n_a) of Available Points (30 animals, 10 observations per animal)

n_a	$SE\left[\hat{\beta}\right]$			
	Population 1 (no spatial, $\sigma = 0$)	Population 2 (no spatial, $\sigma = 0.1$)	Population 3 (spatial, $\sigma = 0.1$)	Population 4 (spatial, $\sigma = 0.5$)
50	0.263	0.266	0.325	0.314
100	0.205	0.210	0.284	0.283
200	0.172	0.172	0.261	0.264
400	0.146	0.154	0.248	0.264
800	0.140	0.144	0.247	0.265
2000	0.127	0.141	0.235	0.257

Figure 3: SE of $\hat{\beta}$ for Different Numbers of Observations per Animal $(\bar{n}_u)$ with m=30
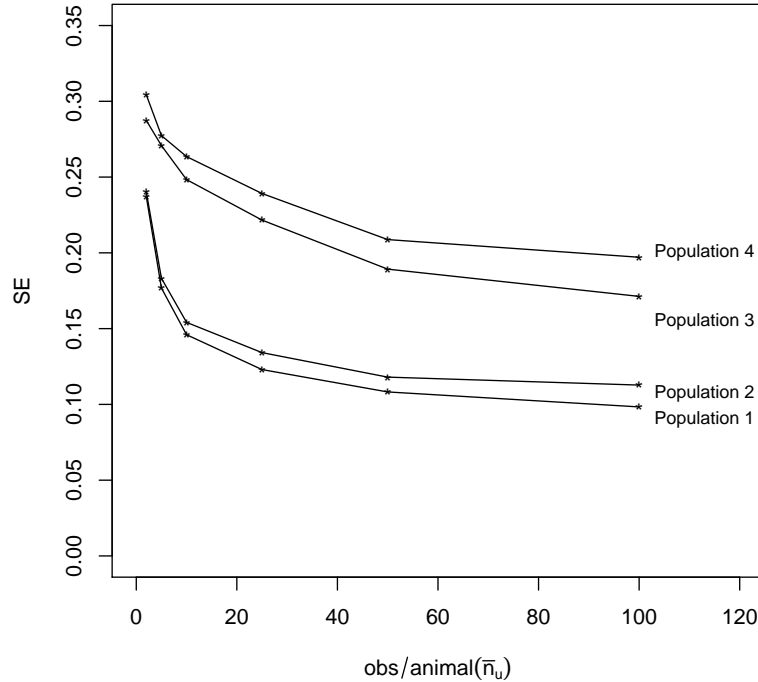
Appendix 1: Additional Empirical Results from Case Study

The robust variance estimators discussed in this paper are robust to dependencies between measurements to the same animal, but still rely on observations from different animals being independent. It is possible that there are spatial correlations, or other effects, that would cause correlations between measurements from different animals. Ideally, spatial coordinate data should have been used to test for spatial correlations across animals, however this data was not available for the Conjola study. However, the side of the region (North or South) to which each point belonged was available. This was tested by fitting the main effects model including the variable "North", and testing the significance of each effect using the robust Huber-White Wald test. Table A1, which is similar to Table 2 in the main report except for the inclusion of North, shows the results. The variable North was not significant.

Appendix 2: Additional Simulation Results

Populations 1-4 shown in the body of the paper all used $\gamma = 0$. Four additional populations were generated with $\gamma = 1$. This corresponds to an odds ratio of $e^{2\gamma} = e^2 = 7$ between the smallest and largest possible values of X, which represents quite a large effect of X on animals' choice of path. The four new populations are otherwise similar to populations 1-4:

Population (5): uncorrelated grid of values of Z, with $\sigma = 0$ (uncorrelated region data and uncorrelated choices within animal).

Population (6): uncorrelated grid of values of Z, with $\sigma = 0.1$ (somewhat correlated choices within animal).

Population (7): correlated grid of values of Z with scale of 2, with $\sigma = 0$ (correlated region data and uncorrelated choices within animal).

Population (8): correlated grid of values of Z with scale of 2, with $\sigma = 0.5$ (correlated region data and highly correlated choices within animal).

The values of β for populations (5)-(8) were 0.992, 0.970, 1.43 and 1.19, respectively. Populations 5-8 are in increasing order of intra-class correlation, as are populations 1-4.

Tables A2 and A3 show the bias and standard error of $\hat{\beta}$ in all 8 simulations. The bias is negligible relative to the standard error in all cases. The standard errors are decreasing with m and $\bar{n}_u$. The standard errors are increasing over populations 5-8 as the intra-class correlation increases.

Table A4 shows the non-coverage of confidence intervals based on the naive variance estimator, and Table A5 shows the non-coverage of confidence intervals based on the Huber-White variance estimator. Conclusions are similar to those in the body of the paper.

Table A6 is similar to Table 7 in the main paper, except that an additional variance estimator has been included. The grouped bootstrap is given by grouping the available points into random non-overlapping sets of 50 points, and calculating the bootstrap using these sets of points. In contrast, the bootstrap was

calculated by dropping out individual random points. The grouped bootstrap was considered because it saves considerable computation time. Table A6 shows that this is a viable approach, as the coverage properties of the grouped bootstrap are very similar to those of the bootstrap.

Table A1: Backward Selection of Main Effects (including North Side) for Conjola Bush Rat Data using Robust Huber-White Wald Tests

Variable	d.f.	χ^2 Statistic	p-value
-Logs	4	19.63	0.001
-Leaf	3	0.80	0.849
-Branches	2	12.79	0.002
-Ground.Veg	3	45.68	0.000
-Shrub.Veg	3	13.94	0.003
-North.Side	1	1.04	0.308

Table A2: Bias of $\hat{\beta}$ in Simulation Study: Populations 1-8

m	$\bar{n}_u$	Population							
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
30	5	-0.0082	-0.0056	-0.0027	0.0025	0.0069	0.0214	0.0472	0.0979
60	5	0.0084	0.0015	-0.0048	-0.0043	0.0093	0.0090	0.0322	0.0534
120	5	-0.0015	-0.0012	-0.0034	-0.0039	0.0004	0.0068	0.0156	0.0240
400	5	-0.0058	-0.0041	0.0043	0.0041	-0.0010	-0.0047	0.0035	-0.0137
30	10	-0.0048	-0.0041	-0.0057	0.0037	0.0056	0.0185	0.0383	0.0752
60	10	0.0106	0.0009	-0.0058	-0.0054	0.0079	0.0039	0.0249	0.0330
120	10	-0.0026	-0.0010	-0.0024	-0.0042	0.0005	0.0038	0.0104	0.0005
400	10	-0.0046	-0.0050	0.0037	0.0028	-0.0015	-0.0056	0.0044	-0.0260
30	25	-0.0045	-0.0033	-0.0026	0.0042	0.0015	0.0119	0.0240	0.0379
60	25	0.0097	0.0013	-0.0047	-0.0059	0.0088	0.0055	0.0149	0.0071
120	25	-0.0008	-0.0030	-0.0009	-0.0068	0.0017	-0.0003	0.0073	-0.0185
400	25	-0.0041	-0.0053	0.0038	0.0021	-0.0022	-0.0060	0.0035	-0.0360
30	50	0.0023	0.0030	0.0009	0.0002	0.0021	0.0088	0.0190	0.0164
60	50	-0.0007	0.0003	-0.0070	-0.0049	0.0069	0.0031	0.0111	-0.0104
120	50	-0.0020	-0.0044	0.0020	-0.0014	0.0020	-0.0033	0.0072	-0.0262
400	50	-0.0042	-0.0051	0.0055	0.0018	-0.0024	-0.0052	0.0061	-0.0380

Table A3: SE of $\hat{\beta}$ in Simulation Study: Populations 1-8

m	$\bar{n}_u$	Population							
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
30	5	0.177	0.183	0.271	0.277	0.192	0.211	0.309	0.317
60	5	0.140	0.139	0.196	0.208	0.157	0.156	0.229	0.241
120	5	0.119	0.117	0.150	0.146	0.124	0.129	0.172	0.168
400	5	0.097	0.098	0.104	0.096	0.102	0.100	0.121	0.115
30	10	0.146	0.154	0.248	0.264	0.161	0.180	0.277	0.295
60	10	0.121	0.124	0.184	0.190	0.134	0.134	0.214	0.228
120	10	0.107	0.106	0.143	0.140	0.111	0.117	0.164	0.159
400	10	0.093	0.092	0.100	0.093	0.097	0.095	0.114	0.111
30	25	0.123	0.134	0.222	0.239	0.132	0.142	0.247	0.267
60	25	0.105	0.109	0.161	0.175	0.113	0.116	0.191	0.207
120	25	0.097	0.098	0.131	0.130	0.099	0.105	0.146	0.144
400	25	0.090	0.089	0.096	0.090	0.093	0.091	0.106	0.104
30	50	0.108	0.118	0.189	0.209	0.117	0.128	0.226	0.249
60	50	0.099	0.103	0.152	0.161	0.103	0.109	0.174	0.190
120	50	0.094	0.095	0.110	0.118	0.095	0.099	0.132	0.136
400	50	0.088	0.088	0.093	0.088	0.090	0.089	0.101	0.100

Table A4: Confidence Interval Non-Coverage (%)[1] for Independence Model Variance Estimator for Populations 1-8 in Simulation Study

m	$\bar{n}_u$	Population							
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
30	5	13.4	16.3	33.0	36.3	13.1	15.7	29.6	34.8
60	5	13.9	13.0	29.9	32.4	14.9	14.4	28.8	31.3
120	5	14.0	13.2	23.4	24.3	12.6	14.9	23.2	25.0
400	5	12.6	13.2	14.7	14.1	12.2	11.9	17.8	19.9
30	10	15.0	18.4	39.0	45.0	15.3	19.7	37.3	43.8
60	10	14.6	15.4	33.9	38.4	15.5	16.2	31.7	39.2
120	10	13.5	14.9	27.5	28.0	14.3	15.6	27.8	29.9
400	10	12.4	13.9	15.9	15.7	13.2	12.7	19.4	21.4
30	25	17.5	21.1	44.1	50.5	16.0	19.4	44.0	51.7
60	25	15.0	16.3	36.6	41.3	14.8	16.4	37.2	45.2
120	25	14.3	14.8	27.9	28.0	13.3	15.3	27.5	33.0
400	25	12.4	13.8	16.4	16.0	13.2	13.4	19.0	22.4
30	50	16.5	18.9	42.3	48.2	16.5	19.8	46.9	52.8
60	50	15.3	17.4	34.2	38.2	14.1	16.9	36.1	44.6
120	50	13.6	14.6	19.8	27.0	13.2	15.9	27.1	32.6
400	50	12.8	13.4	16.2	14.8	13.3	13.1	17.6	22.5

1. The percentage of confidence intervals with nominal coverage of 10% which do not cover the true values is shown in each case. These values should be close to 10.

Table A5: Confidence Interval Non-Coverage (%)[1] for Huber-White Estimator for Populations 1-8 in Simulation Study

m	$\bar{n}_u$	Population							
		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
30	5	0.101	0.105	0.112	0.107	0.094	0.109	0.114	0.105
60	5	0.104	0.091	0.110	0.121	0.109	0.102	0.105	0.119
120	5	0.118	0.102	0.105	0.092	0.103	0.110	0.095	0.089
400	5	0.115	0.122	0.095	0.091	0.109	0.107	0.106	0.114
30	10	0.095	0.101	0.113	0.106	0.091	0.110	0.106	0.105
60	10	0.109	0.096	0.111	0.119	0.104	0.109	0.115	0.121
120	10	0.109	0.104	0.109	0.108	0.106	0.110	0.108	0.084
400	10	0.107	0.123	0.107	0.105	0.119	0.119	0.102	0.126
30	25	0.108	0.117	0.121	0.115	0.100	0.109	0.118	0.110
60	25	0.112	0.098	0.097	0.111	0.094	0.097	0.109	0.116
120	25	0.114	0.113	0.109	0.105	0.106	0.103	0.098	0.090
400	25	0.116	0.131	0.105	0.095	0.123	0.120	0.099	0.119
30	50	0.120	0.096	0.106	0.087	0.111	0.103	0.112	0.114
60	50	0.117	0.101	0.110	0.101	0.095	0.097	0.119	0.124
120	50	0.119	0.118	0.082	0.073	0.117	0.109	0.079	0.097
400	50	0.125	0.127	0.114	0.099	0.128	0.122	0.105	0.124

1. The percentage of confidence intervals with nominal coverage of 10% which do not cover the true values is shown in each case. These values should be close to 10.

Table A6: Confidence Interval Non-Coverage (%)[1] for Populations 1 and 3 in Simulation Study including Grouped Bootstrap

m	$\bar{n}_u$	Population 1 (no spatial, $\sigma = 0$)				Population 3 (spatial, $\sigma = 0.5$)			
		Indep.Model	Robust	Bootstrap	Grp Bootstrap	Indep.Model	Robust	Bootstrap	Grp Bootst
30	5	13.4	10.1	10.6	10.2	33.0	11.2	9.9	
60	5	13.9	10.4	10.8	10.6	29.9	11.0	9.7	
120	5	14.0	11.8	11.4	11.8	23.4	10.5	10.5	
30	10	15.0	9.5	9.1	9.7	39.0	11.3	10.3	
60	10	14.6	10.9	10.3	11.1	33.9	11.1	10.6	
120	10	13.5	10.9	11.1	10.7	27.5	10.9	10.7	
30	25	17.5	10.8	10.5	11.0	44.1	12.1	10.6	
60	25	15.0	11.2	11.8	11.7	36.6	9.7	10.5	
120	25	14.3	11.4	12.3	13.3	27.9	10.9	10.5	

1. The percentage of confidence intervals with nominal coverage of 10% which do not cover the true values is shown in each case. These values should be close to 10.

Table A7: Percentage Biases of Variance Estimators

m	$\bar{n}_u$	Population 1 (no spatial, $\sigma = 0$)			Population 3 (spatial, $\sigma = 0.5$)		
		Indep.Model	Robust	Bootstrap	Indep.Model	Robust	Bootstrap
30	5	-19.2	-0.8	2.7	-65.4	-8.1	-1.4
60	5	-18.0	-2.0	0.1	-58.6	-3.9	-0.7
120	5	-18.9	-7.4	-6.0	-50.3	-4.6	-2.6
30	10	-24.8	1.9	4.2	-74.0	-7.0	-0.6
60	10	-21.8	-1.0	0.8	-66.6	-5.9	-3.6
120	10	-20.8	-7.3	-5.5	-56.0	-5.9	-4.3
30	25	-30.6	-3.6	-1.8	-78.8	-8.4	-2.6
60	25	-21.7	-2.6	-1.1	-67.4	-0.8	1.3
120	25	-18.3	-7.0	-5.5	-55.9	-5.9	-4.6