

Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning

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Abstract

Minimum convex polygons (convex hulls) are an internationally accepted, standard method for estimating species' ranges, particularly in circumstances in which presence-only data are the only kind of spatially explicit data available. One of their main strengths is their simplicity. They are used to make area statements and to assess trends in occupied habitat, and are an important part of the assessment of the conservation status of species. We show by simulation that these estimates are biased. The bias increases with sample size, and is affected by the underlying shape of the species habitat, the magnitude of errors in locations, and the spatial and temporal distribution of sampling effort. The errors affect both area statements and estimates of trends. Some of these errors may be reduced through the application of α -hulls, which are generalizations of convex hulls, but they cannot be eliminated entirely. α -hulls provide an explicit means for excluding discontinuities within a species range. Strengths and weaknesses of alternatives including kernel estimators were examined. Convex hulls exhibit larger bias than α -hulls when used to quantify habitat extent and to detect changes in range, and when subject to differences in the spatial and temporal distribution of sampling effort and spatial accuracy. α -hulls should be preferred for estimating the extent of and trends in species' ranges.

INTRODUCTION

Extent of habitat is one of the most important pieces of information for assessing the conservation status of species (e.g. Millsap *et al.*, 1990; IUCN, 1994; Lunney *et al.*, 1996). Often, the only data available for estimating habitat area are presence records, the result of opportunistic records, sightings and specimen collections. One of the most influential of the protocols, the IUCN (1994, 2001) rules, defined the extent of occurrence as the area contained within the shortest continuous boundary that encompasses all sites of present occurrence of a taxon. The measure may exclude discontinuities or disjunctions within the overall distributions of taxa, such as large areas of obviously unsuitable habitat.

To measure habitat area, IUCN (1994) recommended a minimum convex polygon (also called a convex hull). It is the smallest polygon in which no internal angle exceeds 180 degrees and which contains all sites. The minimum convex polygon is easy to compute from coordinate data and it is appropriate for presence-only data.

Area estimates from minimum convex polygons are used in two ways. The first is in the evaluation of thresholds for extent of occurrence. For example, the IUCN (1994, 2001) rules classify a species as critically

endangered if its extent of occurrence is less than 100 km². The second use is for inferring trends in range. For example, a species is classified as critically endangered under the IUCN (1994) rules if data suggest a reduction in extent of occurrence of more than 80% in the last 10 years.

Because minimum convex polygons are constructed around the most extreme points in a space, it is possible that area estimates derived from them may be sensitive to errors in location. Surveys for plants and animals intended to detect trends are often somewhat opportunistic and depend on contributions from volunteers. Thus, design variables such as the temporal and spatial distribution of sampling effort are not always under the control of the managing agency or scientist. The purposes of this study are:

- to explore, by simulation, the effect on estimates of habitat area of variation in spatial accuracy, and spatial and temporal sampling effort;
- to evaluate the adequacy of the convex hull for quantifying habitat area;
- to evaluate biases likely to affect conservation assessment protocols.

METHODS

Three hypothetical species ranges were constructed (Fig. 1), representing a range of spatial forms including 'horseshoe', square and linear habitat patches. Each

species had a notional linear range of 300–400 km, although the actual scales were unitless. The sampling area was divided into 10,000 grid squares (notionally, 10,000 km²) and the three shapes were set on a 1 × 1 square grid (notionally, a 1 × 1 km grid). An additional area bounded the three shapes by at least 50 km on all sides.

In the simulations, grid squares were occupied with some frequency (probability) within the specified bounds of the habitat. Grid squares were selected at random and sampled by a hypothetical observer. For example, in many scenarios,

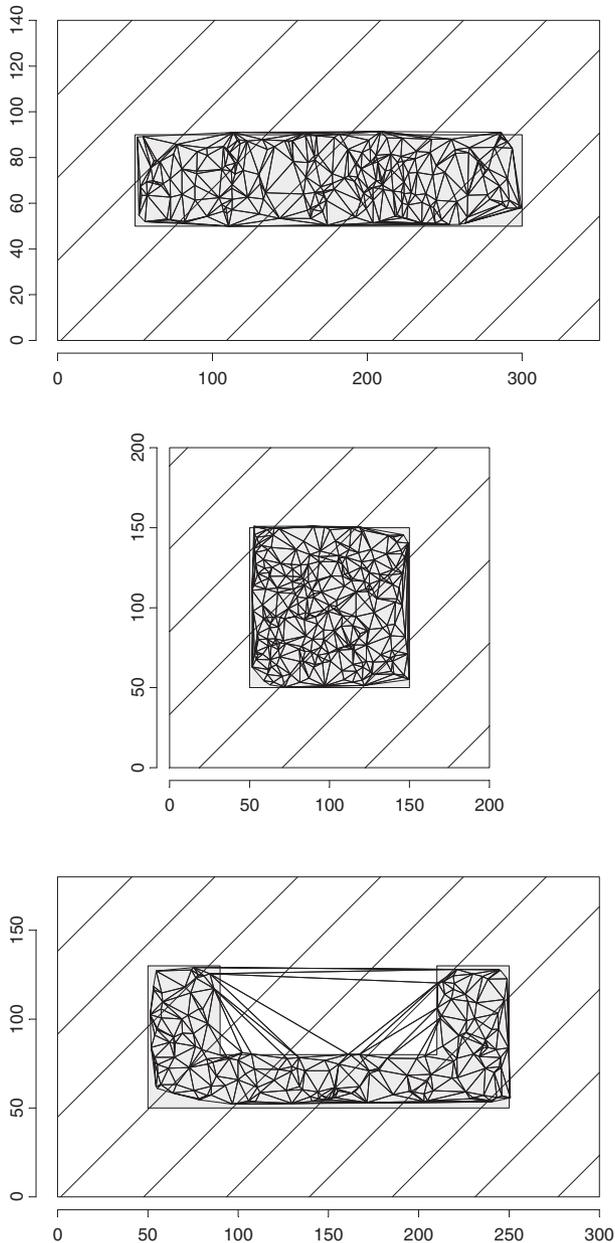


Fig. 1 Hypothetical linear (top), square (middle) and horseshoe (bottom) habitat shapes as used in simulations. Each shape is bounded by a 50 km buffer. The total area within which hypothetical observations were made is hatched. The Delauney triangulation resulting from 2000 spatially uniform samples subject to small spatial error is also shown. The areas of convex hulls were calculated as 9691.3, 9542.8 and 14,730.0 for the line, square and horseshoe compared to known notional areas of 10,000 km².

species occupied half of the potential habitat cells, and when present they were detected only 50% of the time when the hypothetical observer visited a square within the habitat. The probability of detecting a species outside of the habitat area was 0 in all scenarios. This implies that the habitat boundaries were clearly defined, there were no vagrants and there were no false positive sightings.

The number of samples and the spatial distribution of observations were varied within plausible limits. In addition, circumstances were modelled in which there were real trends in both the density of the species (with no reduction in range) and the range of the species (with no reduction in density) (Table 1). This simulation environment was used to represent circumstances in which a fauna survey was conducted, and later repeated to detect trends in species.

The hypothetical species ranges were sampled, and different levels of the features outlined in Table 1 was introduced one at a time. A total of 500 replications was used for every level of the simulation to provide acceptable estimates of the mean and 95% confidence intervals (Manly, 1997). Three levels for each of shape, range and density resulted in 27 combinations. These 27 possible combinations were sampled 500 times each, yielding 13,500 examples, 4500 for each shape of habitat. Each of these hypothetical ranges consisted of a grid (in the shape of square, line or horseshoe) of 1s and 0s corresponding to the presence of a species at each grid intersection, and bounded by a grid of 0s, 50 squares (km) wide. These surfaces represented 500 realizations of 27 different, true underlying processes.

Sampling hypothetical species ranges

In the next stage, the 13,500 ranges were sampled by a hypothetical observer and various sampling artefacts were introduced to mask the true distributions. The artefacts included changes in the intensity of sampling, variation in the spatial accuracy of samples and variation in the intensity of sampling across the range (Table 1). They represent the kinds of deviations from balanced survey designs that are part of large-scale and extensive surveys, such as those conducted for the Birds Australia atlas (Garnett & Crowley, 2000), and that underlie the presence-only data maintained by museums and herbariums. For each level of sampling intensity, observations

Table 1. Habitat features and sampling attributes used in the simulations

Habitat features	Levels
Shape	Horseshoe, square, linear
Range trend	None, 25% reduction, 50% reduction
Density trend	None (sighting rate 0.5), 20% reduction (sighting rate 0.4), 50% reduction (sighting rate 0.25)
Sample attributes	
Number of observations	500, 2000, 20,000
Spatial accuracy	Small, half-small and half-large, large
Spatial uniformity	Uniform (50%–50%), non-uniform (20%–80%)
Area estimation	Convex hull, a-hull

were distributed (uniformly) randomly on the two-dimensional surface.

GPS (global positioning systems) have improved the spatial accuracy of field sampling relative to traditional, map-based methods. The level of spatial accuracy in sampling was varied between two levels that represent the scale of accuracy that might be associated with 1:100,000 maps (large errors) and with GPS units (small errors). A small spatial error was generated by sampling a normal distribution with a mean of zero and standard deviation of 1, and then relocating each sighting by adding this error to its x and y coordinates. For this level of uncertainty, roughly 66% of observations would be located within one grid cell of the true location. A large spatial error was generated by sampling a normal distribution with a mean of zero and standard deviation of 10. These spatial errors were added to the x and y coordinates of the hypothetical species ranges generated in the first stage. The examples in which half the samples were loaded with small errors and half with large errors reflect surveys in which a proportion of participants use GPS units and others do not.

Because of differences in geographical accessibility, the intensity of sampling in most real, uncontrolled surveys is not consistent across a study area. Samples are likely to be concentrated in more accessible areas such as those serviced by roads, compared to more remote areas where access is difficult. Opportunistic records and volunteer sampling are more likely to be closer to large human populations. To reflect this property of samples, two levels of spatial uniformity were used. In the first, samples were distributed uniformly across the study area. In the non-uniform design, 80% of samples were concentrated in one half of the region and 20% in the other half.

Each of the 13,500 hypothetical ranges generated in the first stage were sampled using the 18 ($3 \times 3 \times 2$) different levels of sampling, resulting in 243,000 sampled species ranges.

Estimating the area of species ranges

The next step was to estimate the area of each sampled range, before comparing these estimates to the underlying, true range. The convex hull for a set of points in space generates a minimum convex polygon about the points. It is the smallest polygon that contains all points in which no internal angle exceeds 180 degrees, i.e. concave structures are excluded on the outer surface (Rapoport, 1982; O'Rourke, 1998). The constraint of convexity on the outer surface yields a hull with a very coarse level of resolution on its outer surface that will depart from the actual species range. This is particularly the case for irregularly shaped species ranges (such as the horseshoe), resulting in a substantial overestimate of the range. There are no explicit rules outlined in the methods for assessing conservation status that would suggest a means for establishing when the hull should be split to exclude uninhabitable regions.

To improve the match of the hull to the true habitat shape, the α -hull, a generalization of the convex hull (Edelsbrunner, Kirkpatrick & Seidel, 1983) was applied.

To estimate an α -hull;

- (1) Make a Delauney triangulation of the points in a sample. The triangulation is created by drawing lines joining the points, constrained so that no lines intersect between points (O'Rourke, 1998).
- (2) Measure the lengths of all of the lines, and calculate the average line length.
- (3) Delete all lines that are longer than a multiple (a) of the average line length. The value of a can be chosen with a required level of resolution in mind (see below). The smaller the value of a , the finer the resolution of the hull. This process results in the deletion of lines joining points that are relatively distant, the space between which is unlikely to represent good habitat.
- (4) Calculate the area of habitat by summing the areas of all remaining triangles.

The outer surface of the Delauney triangulation is identical to the convex hull, but this is just one of many possible representations of habitat that can be derived from the triangulation. The advantage of the α -hull is that it provides a more detailed description of the habitat's shape, is capable of breaking the hull into several discrete hulls when it spans an uninhabitable region, and yields a hull unconstrained by convexity on its outer surface (Okabe *et al.*, 2000).

The α -hull is mathematically well defined (Moran & Wagner, 1994; Edelsbrunner, 1995) and consists of a family of hulls of differing levels of resolution on their external surface dependent on the value of the parameter α . Put simply, α -hulls are constructed by retaining only those vertices of the Delauney triangulation that are shorter in length than a chosen value of the parameter α . More formally, they are constructed by preserving sections of the Delauney triangulation corresponding to the union of balls of radius a (Edelsbrunner, 1995). The α -hull is the outer surface of this new subgraph of the Delauney triangulation. Varying the value of α between zero (finest level of resolution, i.e. a set of discrete points in space) and infinity (coarsest level of resolution, i.e. a convex hull) generates different configurations of the hull, and perhaps provides a more reliable estimate of habitat extent when the shape of the range is irregular.

Rapoport's (1982) seminal work proposes the 'maximum propinquity tree' (a minimum spanning tree) for generating an area-based estimate of species extent. The method uses a buffer about the minimum spanning tree with a radius based on the mean or standard deviation of the distance between points. The total area of this buffer is summed to provide an estimate of species range. Similar to the α -hull, the minimum spanning tree is also a subgraph of the Delauney triangulation (Aurenhammer & Klein, 2000) constructed as a single-line graph with minimum total edge length. Rapoport's minimum spanning tree was investigated in this study but quantifying area was relatively difficult in a standard geographic information system. Various buffering

algorithms common in geographic information systems were capable of generating an area estimate, but more formal, computationally efficient methods were lacking (De Floriani, Magillo & Puppo, 2000). The α -hull was deemed preferable as it is geometrically well defined and its area can be computed exactly and efficiently.

Kernel density estimators are applied in ecology to estimate the home ranges of animals from radio-tracking data (Worton, 1995). The method works by placing a two-dimensional probability density over each spatial record of a species. A grid is superimposed on the resulting surface and an estimate of density is obtained at each grid intersection. A parameter termed a 'bandwidth' (Seaman & Powell, 1996) determines the relative contributions of close and distant points to the density estimates. Range estimates based on kernel estimators depend sensitively on the choice of bandwidth (Seaman & Powell, 1996) and are subject to bias, particularly when sample sizes are small, although these biases may be less than those from minimum convex polygons (Seaman & Powell, 1996; Hansteen, Andreassen & Rolf, 1997; Ostro *et al.*, 1999). The advantage of the convex hull and tree methods over kernel estimators is their simplicity of application, and kernel estimators are not considered further here.

When applying α -hulls, rather than selecting arbitrary values of the parameter a , we used a multiple of the mean line length between points to select hulls with the appropriate level of resolution. This was implemented practically using a simple rule whereby triangles were deleted from the triangulation when their mean edge length exceeded some multiple of the overall mean edge length. This effectively removes triangles spanning regions where there are relatively few observations. Three

values for the parameter a were trailed. Triangles were removed when the mean Delauney edge length exceeded two, three, and four times the average overall edge length, respectively. The areas of the remaining triangles were summed to provide estimates of habitat area.

Implementation

The simulation study was implemented using S+. A single function was written that could be called for a particular combination of shape, density and range, which was then sampled using a particular combination of sampling intensity, spatial accuracy and sampling uniformity. This function included a loop that repeated the process 500 times. The function generated four area estimates corresponding to the convex hull and the three α -hulls for each of the 500 iterations. S+ code for implementation of α -hulls is available on request.

RESULTS

Area estimates

Of the three rules for defining α -hulls with differing levels of resolution, rule 2 (triangles removed when the mean edge length exceeded three times the average overall edge length) was consistently the most robust to sampling artefacts introduced by differing sampling intensities, spatial accuracies and spatial uniformities. Subsequently, only the α -hull defined using rule 2 is shown here.

The convex hull provides a consistent and substantial overestimate of range (Fig. 2). Box and whisker plots are used in Fig. 2 to indicate the mean and 1.5 times the

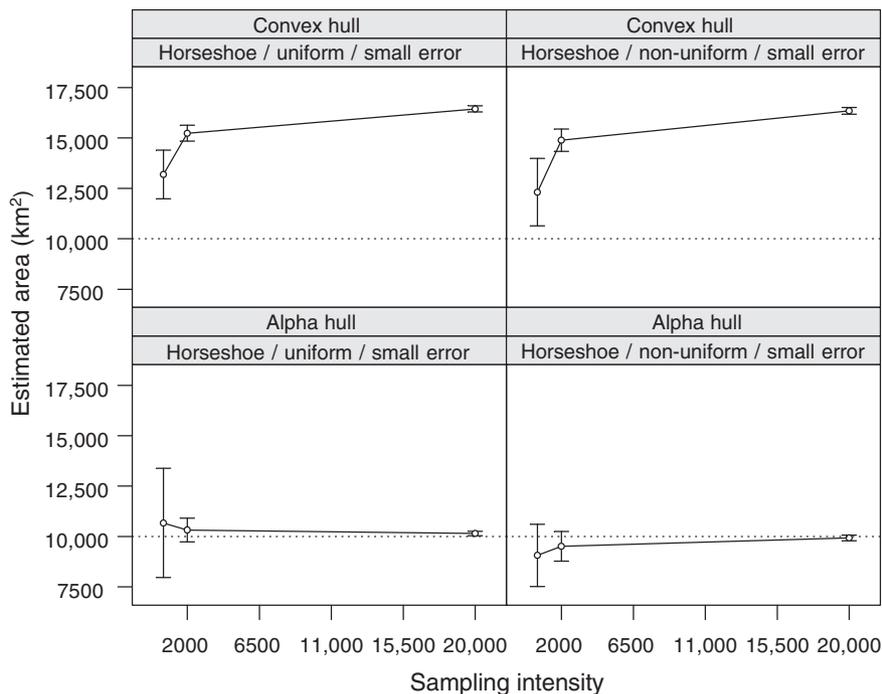


Fig. 2 Performance of the convex hull and α -hull (rule 2) for estimating a known area of 10,000 km². The dotted line represents the correct value. The samples were uniform and non-uniform (unbalanced). In the non-uniform samples, 20% of observations were made in the left half of the areas, and 80% were made in the right half of the areas represented in Fig. 1.

interquartile distance of area estimates, or the extreme value, whichever is less (for 500 replicates). The convex hull has the unappealing property that the range estimate diverges from the truth as the sample size increases, whereas the α -hull converges with increasing sample size. As shown in Fig. 2, an uneven spatial distribution of sample effort has little effect on both the convex and α -hull, although the range of effort is only two- to three-fold for this factor.

The convex hull and the α -hull defined using rule 2 are shown for the horseshoe in Fig. 3. The convex hull is sensitive to irregular, concave habitat shapes for which it substantially overestimates the correct range of 10,000 km². The α -hull prevents this overestimate by removing triangles from the large concave inner region of the horseshoe where no observations were made. When habitat shapes are linear or square (Fig. 1) the results are less sensitive to the choice of hull. As the sample size increases the α -hull converges on the exact habitat extent, with increasing resolution on its exterior surface (Fig. 3).

Influence of spatial errors

Large spatial errors result in substantial overestimates of range (Fig. 4). The definition of large spatial errors in this study was that the locations were sampled from a normal distribution with a standard deviation of 10. This translates to an error in which roughly 95% of the observations are within about 20 cells of the correct cell, or a standard error that is approximately 10% of the species linear range (for the horseshoe-shaped habitat). Errors of this magnitude resulted in substantial overestimation of species ranges and in reduced precision in estimates of species ranges. For both methods (convex and α -hulls), the problem became worse as the sample size increased. Larger samples increase the likelihood of extreme values that result in larger estimates of ranges. The α -hull was least affected. The degree of overestimation was largest for the horseshoe, and smallest for the square.

The results for mixtures of small and large spatial errors were intermediate between the results for small and large errors applied independently (results not shown). Non-uniform sampling effort resulted in poorer resolution for the affected area. Non-uniform spatial accuracy resulted in overestimation of habitat extent for the affected area. When combined, these two artefacts tended to offset one another. Thus, small and non-uniform sample efforts and large spatial errors may introduce compensating biases (see Fig. 4). The degree to which they cancel one another will vary from case to case and will not be measurable in any instance without substantial additional information.

Changes in range of the order of 25–50% are detected reliably when spatial errors are small (Figs 5 & 6 for the horseshoe and square). The ability to detect changes of these magnitudes was not greatly diminished, even in the presence of relatively large spatial errors. Range estimates in the presence of large spatial errors are biased but the bias is consistent and trends are detectable. Generally, larger numbers of samples result in improved likelihood of detection of reductions in species ranges.

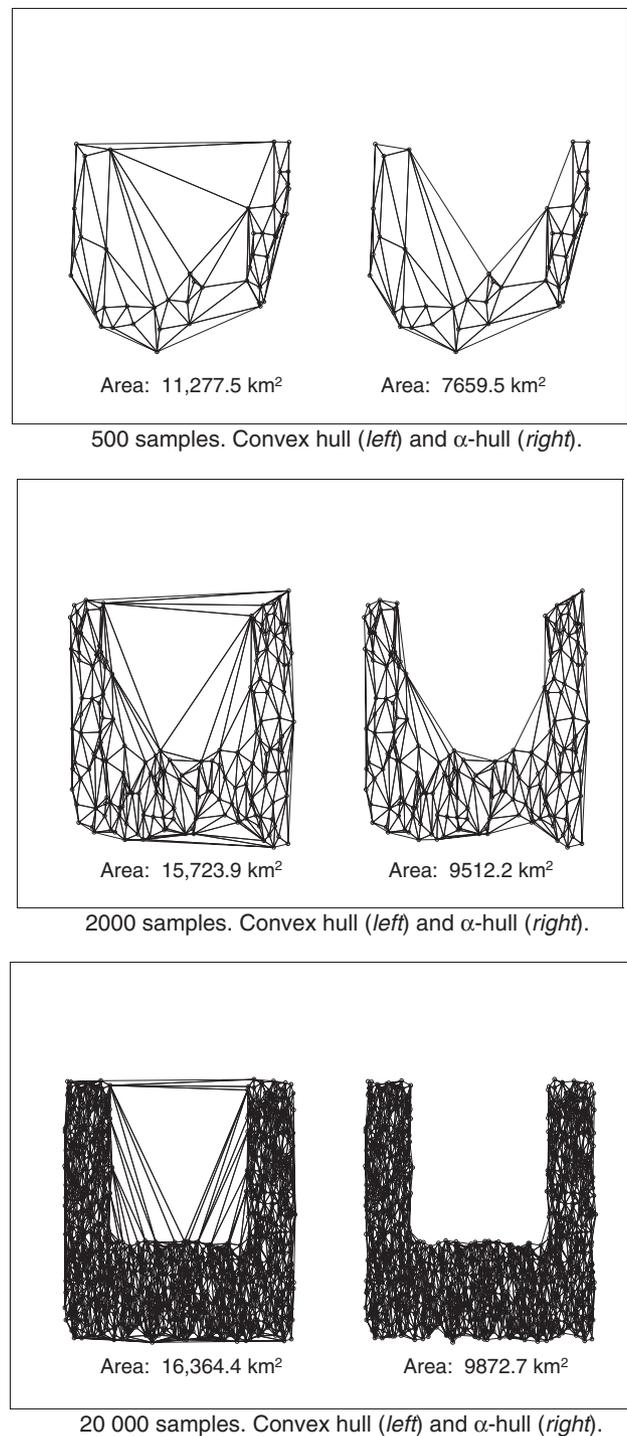


Fig. 3. Comparison of convex and α -hulls for the horseshoe when subject to differing sampling intensities.

Comparing temporal samples when sampling attributes differ

As observed in Figs 5 and 6, when sampling intensity, spatial accuracy and spatial uniformity are consistent across two temporal sampling efforts, trends in range reduction are observed reliably. However, when sampling attributes differ across two temporal sampling periods, the underlying trends in range reduction can become obscured by sampling artefacts (Fig. 7). If the magnitude of spatial

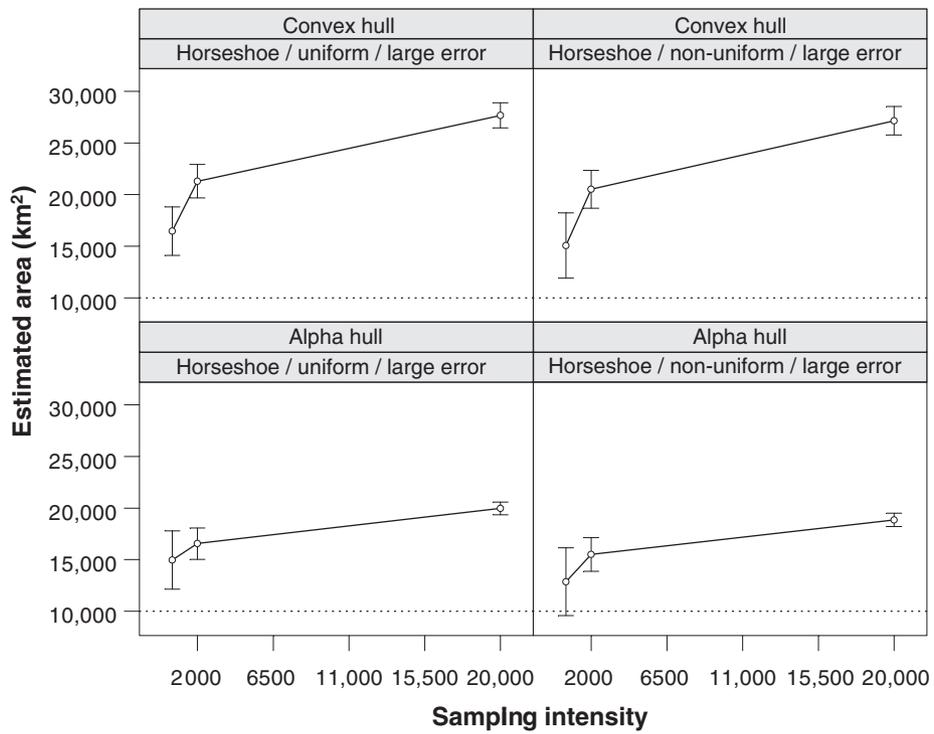


Fig. 4 Performance of the convex hull and α -hull (rule 2) for estimating a known area of 10,000 km² in the presence of large spatial errors.

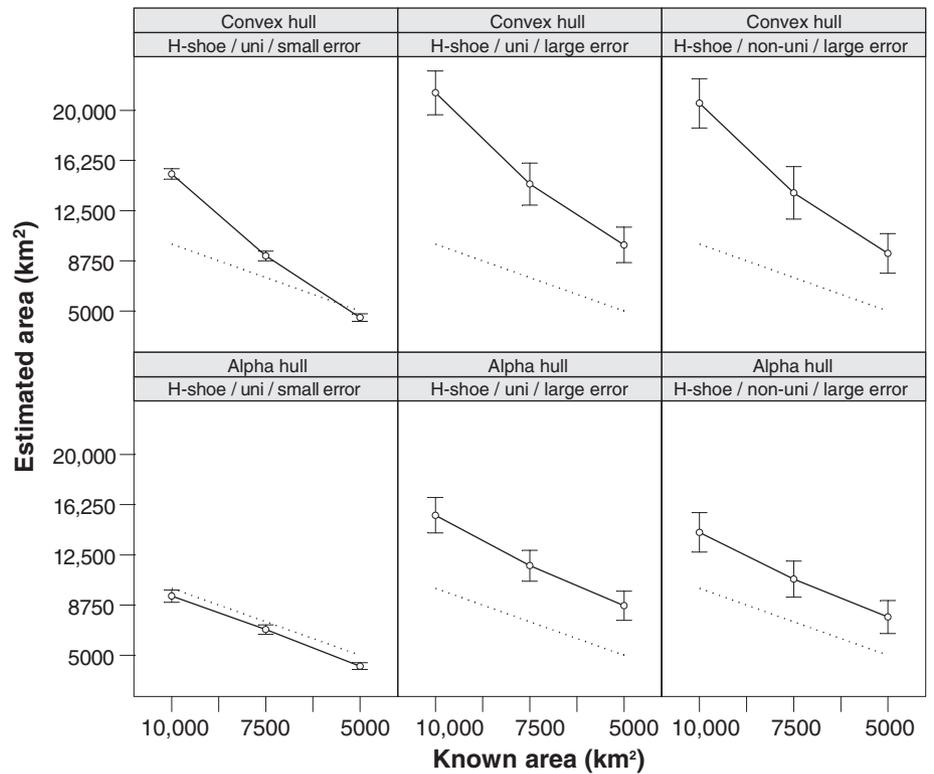


Fig. 5. Ability to detect reductions in range of 25% and 50% for 2000 samples of the horseshoe shape using the convex and α -hull (rule 2)

errors in the first temporal sample was relatively small, and the magnitude of errors in the second sample was substantially larger, a valid comparison of ranges will be unreliable because of the overestimation of the range of

the species in the second sample. The extent of the overestimation in the example here is such that it obscures a 50% range reduction in the second temporal sample. Such a distribution of errors will also lead to the detection

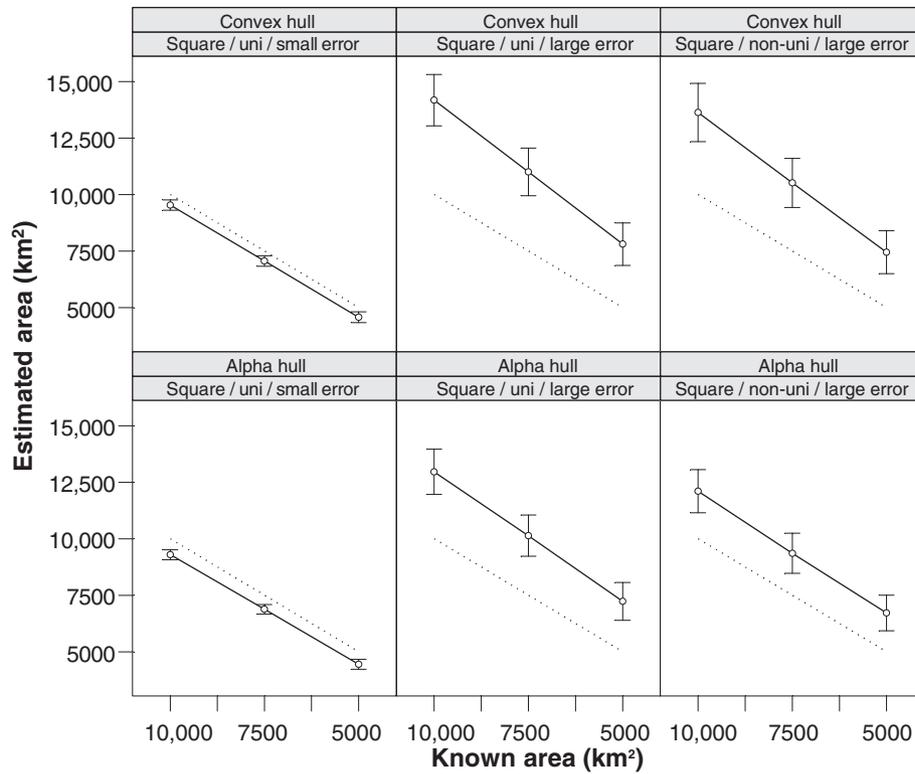


Fig. 6 Ability to detect reductions in range of 25% and 50% for 2000 samples of the square shape using the convex and α -hull (rule 2).

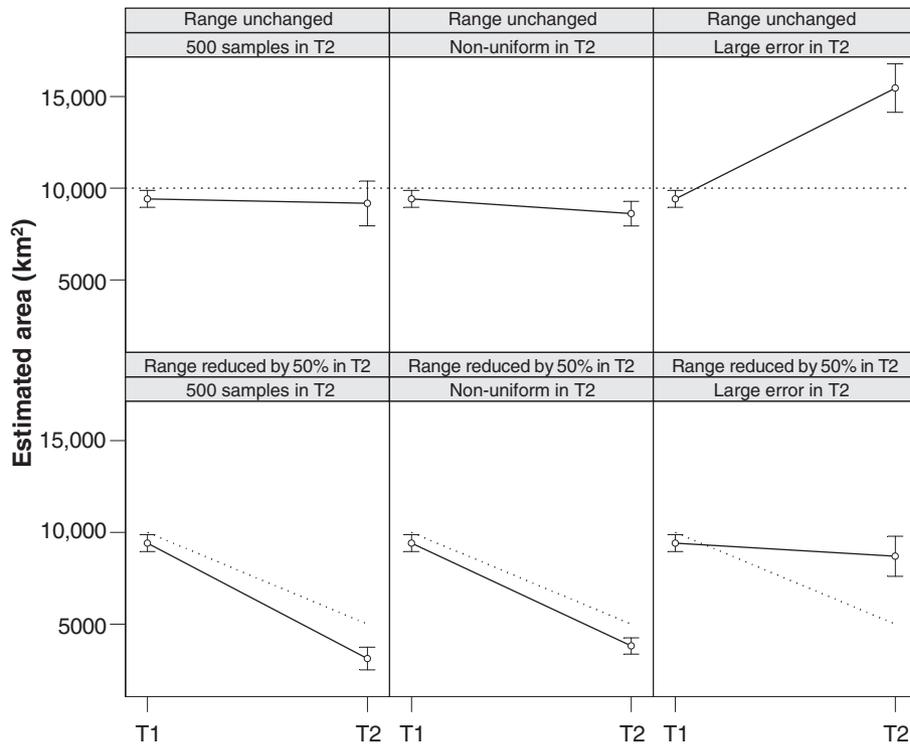


Fig. 7 Comparing range estimates from two temporal samples when sampling attributes differ. For all estimates the horseshoe shape and α -hull (rule 2) were used. Sampling attributes for T1 were 2000 samples, subject to uniformity and small spatial errors.

of apparent trends that are sampling artefacts (Fig. 7). These biases were even greater for convex hulls (not shown) than for α -hulls. For instances when a non-uniform sampling effort or a reduction in sampling intensity is introduced in time 2, comparisons of range will be affected by a consistent underestimate (by 10% or more) of species range in time 2, irrespective of the shape of the patch of habitat (Fig. 7). If both artefacts are introduced in time 2, an even greater bias can be expected. When large spatial errors are added to the problem, range estimates are substantially overestimated by 20–30% (Fig. 7).

Overall, comparisons of range size are unreliable when sampling attributes vary between times. The only way to standardize when this is so, would be to conduct a series of simulations, such as those outlined here, and correct each of the estimates to eliminate the expected biases.

Application of convex and α -hulls

Convex and α -hulls were applied to data for the locations of observations of Richard's pipit in the Birds Australia atlas data, from Field Atlas records collected between 1977 and 1981 (Fig. 8) and New Atlas records collected between 1998 and 2000 (Fig. 9). The finer resolution provided by the α -hull (rule 2) resulted in areas of ocean such as the Great Australian Bight and Gulf of Carpentaria correctly excluded from the triangulation. The improved resolution provided by the α -hull yields range estimates almost half of those generated using convex hulls. Another advantage of the α -hull is that outliers are also excluded from the hull when their distance from other records exceeds three times (rule 2) the average overall edge length. From the results of the simulation study, the estimates of habitat extent from the α -hull should more accurately reflect the actual extent of Richard's pipit.

Inferences based on changes in range are highly sensitive to which hull is used and to differences in the spatial and temporal distribution of sampling effort and spatial accuracy. To test for the significance of changes in habitat extent, randomization tests can be performed by resampling the combined new and old records. However, these tests assume that the observations are independently and randomly drawn from the distribution of the species, that the spatial intensities of the samples are approximately the same in both sampling periods, and that the errors associated with the locations of the samples are roughly equal in both sampling periods. The simulations performed in this study provide an indication of the importance of each of these assumptions.

For the Birds Australia atlas data, sampling effort was almost equivalent in the two time periods. However, the errors associated with locations were much smaller in the New Atlas records owing to the widespread use of hand-held GPS. This temporal difference in the spatial accuracy of samples may be capable of producing artefacts such as apparent range reductions when the underlying range is unchanged (Fig. 7). In addition, the first survey included observations collected over 5 years. The data for the second survey, which was ongoing, were over 2.5 years. The first survey may integrate over a broader array of climatic conditions, and if the birds track these conditions on a continental scale then apparent differences in range may dissipate as sampling continues through time. To some extent, conclusions about 'real' trends may be tempered by the magnitude of methodological biases relative to observed changes. For example, errors in map-read locations compared to GPS locations are likely to be small, relative to the range size of the pipit.

When the range of Richard's pipit is based on the Field (Fig. 8) and New Atlas records (Fig. 9) and the convex

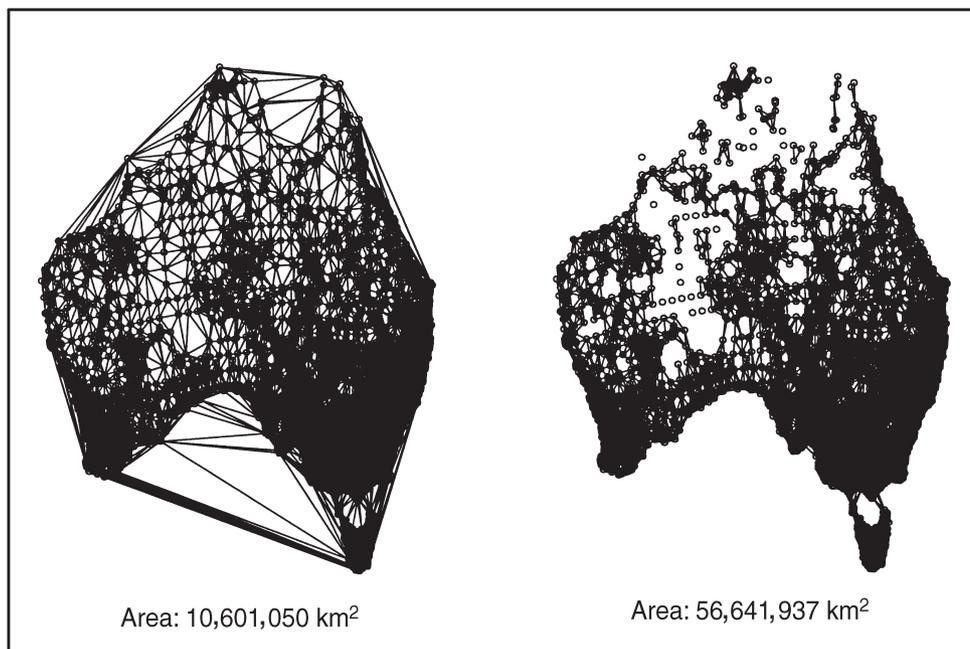


Fig. 8 Convex (*left*) and α -hull (*right*) for Field Atlas records collected between 1977 and 1981.

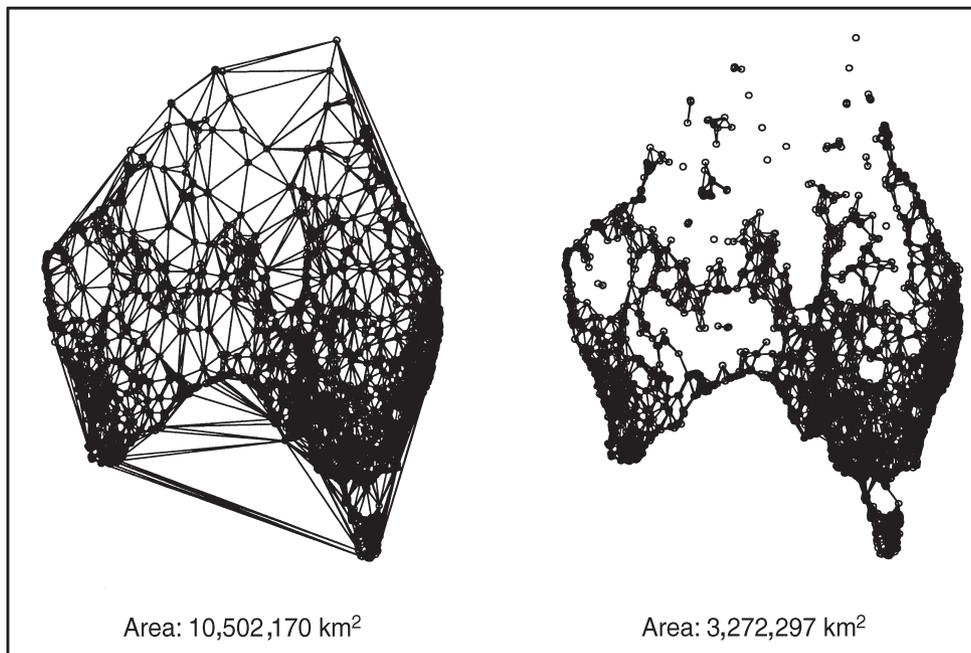


Fig. 9 Convex (*left*) and α -hull (*right*) for New Atlas records collected between 1998 and 2000

hull is used to estimate area, the habitat extent appears to have contracted only slightly (by about 1%), and was not statistically significant in the randomization test. The α -hull reveals a much larger contraction in habitat extent (by about 40%) that is significant ($P < 0.0001$). Such a difference would have profound consequences for evaluating species using Millsap *et al.* (1990) or IUCN (1994, 2001) rules. These apparent range reductions need to be treated with caution because of the possibility of sampling artefacts and the influence of climate on observations. The results may best be used to flag potential problems that should be evaluated with independent biological evidence.

DISCUSSION

There is little to recommend convex hulls for range estimation. They have the unpleasant properties that biases increase as sample sizes increase, and that biases may be very substantial, even when errors in the location of observations are small. Important bias may be introduced by the shape of the habitat patch, and by interactions between shape, location errors, and the temporal and spatial distribution of sampling effort. The α -hull seems to be more robust to the kinds of sampling characteristics that are likely to be present in such data sets as bird surveys. Trends in the ranges of bird distributions of the order of 25% or 50% should be detected with samples of several hundred records, even if spatial errors are substantial. However, if the magnitude of errors is substantially different between surveys and is appreciable compared to the ranges of the species in question, then spurious trends may result, and would not be distinguishable from range-wide biological trends.

Trends in range are an important part of state of the

environment reporting and the classification of conservation status (IUCN, 1994, 2001). In most instances, trends are inferred using observational data and simple inferential tools such as range estimates inferred from convex hulls. The most difficult circumstances for detecting trends reliably for these methods are created by unevenness in the temporal distribution of sampling effort and location errors. Large spatial errors will contribute to overestimation of the range in the first sample. Fewer observations will lead to underestimation of range in the second sample. These two factors, taken together, will generate spurious apparent trends in many species.

The importance of this phenomenon depends on the relative magnitude of the differences in spatial errors, and the magnitude relative to the extent of a species distribution. If errors are relatively small, or approximately the same between sampling periods, and sample sizes are generally large, then these sources of bias may be unimportant and the trends detected may have causes other than sampling artefacts. Thus, the interpretation of the reliability of inferences drawn from area estimates will depend critically on the quantification of the magnitude of spatial errors in different surveys. The application of α -hulls to data collected using approaches such as those outlined by Keith (2000) will generate estimates of range and inferences of trends in range that are substantially more reliable than those made currently.

Generalizations are difficult because the sensitivity of a survey to the errors outlined above will depend on unique spatial and temporal characteristics. If species occupy very small spatial scales relative to the errors implicit in location data, such as rare and geographically restricted plants, then the results will be sensitive to location errors. If species have wide geographic ranges, such as many birds, then small location errors will be less

critical. Uniform temporal and spatial sampling effort will matter more if trends are important, and will matter less if area statements are important. Sensitivity may also depend on whether or not a species' range characteristics are close to one of the IUCN's (2001) thresholds. These factors will interact to determine what is important in a survey. The results presented here provide guidance on how to allocate survey effort to minimize important sources of bias.

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