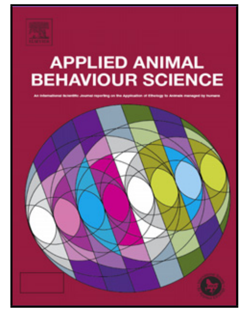

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Calculating association indices in captive animals: controlling for enclosure size and shape

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Highlights

- *Studies using an association index often fail to account for enclosure size and shape*
- *We propose a correction for such indices which controls for enclosure size and shape*
- *Our simple R script can be used to determine chance encounters in any area*
- *Shape did not affect the probability of a chance encounter in large areas*

Abstract

Indices of association are used to quantify and evaluate social affiliation among animals living in groups. Association models assume that physical proximity is an indication of social affiliation; however, individuals seen associating might simply be together by chance. This problem is particularly pronounced in studies of captive animals, whose movements are sometimes severely spatially restricted relative to the wild. Few attempts have been made to estimate – and thus control for – chance encounters based on enclosure size and shape. Using geometric probability and Geographic Information Systems, we investigated the likely effect of chance encounters on association indices within dyads (pairs of animals), when different distance criteria for defining associations are used in shapes of a given area. We developed a simple R script, which can be used to provide a robust estimate of the probability of a chance encounter in a square of any area. We used Monte Carlo methods to determine that this provided acceptable estimates of the probability of chance encounters in rectangular shapes and the shapes of six actual zoo enclosures, and we present an example of its use to correct observed indices of association. Applying this correction controls for differences in enclosure size and shape, and allows association indices between dyads housed in different enclosures to be compared.

Key words: behaviour modelling; geometric probability; index of association; social behaviour.

1. Introduction

Indices of association were originally developed by ecologists to analyse how often plant species were found in proximity to one another (Southwood, 1968) but have also been used since at least the 1970s to quantify social relationships between individual animals living in groups (e.g. lions (*Panthera leo*): Schaller, 1972; feral cats (*Felis catus*): Rees, 1982; spider monkeys (*Ateles geoffroyi*): Chapman, 1990; spotted hyenas (*Crocuta crocuta*): Szykman et al., 2001; Spix's disc-winged bats (*Thyroptera tricolor*): Vonhof et al., 2004; cheetahs (*Acinonyx jubatus*): Chadwick et al., 2013). Association indices assume that physical proximity is an indication of social affiliation (Bejder et al., 1998; Knobel & Du Toit, 2003; Whitehead, 2008) and calculate the proportion of time individuals in dyads are seen together (Whitehead & Dufault, 1999; Godde et al., 2013).

The association index, however, masks the extent to which individuals have come into proximity for reasons other than attempting to associate for social purposes. It has formerly proven difficult to calculate how often individuals are seen associating together simply by chance. The random gas model (Equation 1; Schülke & Kappeler, 2003) has been used to calculate expected encounter rates in wild populations (Waser, 1975; Schülke & Kappeler, 2003; Hutchinson & Waser, 2007; Leu et al., 2010), where the expected frequency of encounter (*f*) is dependent on the density (*p*) of a species, the velocity of the animals (*v*), the group spread (*s*) and the distance criterion that defines association (*d*).

$$f = \frac{(4pv)}{\pi(2d + s)} \quad (1)$$

However, this method relies on variables that can be difficult to measure, such as group spread (dispersion) and the velocity (rate of movement) of the animals.

Whilst the majority of studies using indices of association have been conducted on wild populations (Whitehead & Dufault, 1999), some authors have used association indices to investigate social behaviour in captive animals. An association index was used by Knobel and du Toit (2003) to document the social structure of a pack of captive African wild dogs (*Lycaon pictus*), and Romero and Aureli (2007) calculated association indices in a group of zoo housed ring-tailed coatis (*Nasua nasua*). Neither of these studies took into account chance encounters. The problem of chance encounters is more pronounced in a captive environment, where the space available to animals is limited relative to the wild and where enclosure sizes (and shapes) vary across facilities, making direct comparison of association indices difficult. For instance, animals housed in an enclosure measuring 100 m^2 are more likely to be observed in proximity simply by chance than animals housed in an enclosure measuring 2000 m^2, and animals in a square enclosure measuring 100 m^2 are more likely to be found together by chance than animals in a rectangular enclosure of the same area.

Despite the spatial confinement of captive animals rendering their free movement limited, relative to cage mates, few attempts have been made to estimate – and thus control for – chance encounters based on enclosure size and shape. Stricklin et al. (1979) investigated spacing relationships in square, circular and triangular pens using computer simulations and actual observations of cattle (*Bos taurus*). The results of their simulations demonstrated the effects of pen size and shape on the mean nearest-neighbour distance, with greater distances in the triangle than in the square or the circle when pen size was held constant. Although this study used a different measure of spatial arrangement (distance to nearest neighbour rather than an index of association), the work highlighted the effects of pen size and shape on spacing arrangements and the importance of adequate pen size in ensuring the welfare of group-housed animals.

In a recent paper, we devised a simple Monte Carlo-based simulation to ascertain the effects of chance encounters on indices of association among captive cheetah pairs (Chadwick et al., 2013). Monte Carlo simulations have been used in studies of wild animals to test whether or not individuals have preferred associates (Bejder et al., 1998; Carter et al., 2013) by producing randomly generated data sets for comparison with real data sets. Using data generated by our simulation, we were able to produce corrected indices of association that took into account chance encounters based on enclosure size (Chadwick et al., 2013). However, our calculations of the probability of a chance encounter were limited to hypothetical square enclosures.

Here, we use geometric probability and Geographic Information Systems (GIS) to build on the model devised by Chadwick et al. (2013) and explore the effects of area and shape on the probability of chance associations. Our aim was to produce a simplified method of determining the likely effect of chance encounters on association indices when particular distance criteria for defining associations were used in shapes of a given area. Such a method would allow enclosure size and shape to be taken into account in studies using an association index.

2. Methods

2.1 Theoretical background

If the location of animal A in two-dimensional space is x_a, y_a and the location of animal B is x_b, y_b, the Euclidean distance between these points is calculated using Pythagoras' Theorem:

$$\textit{Distance}\ (d) = \sqrt{(x_a - x_b)^2 + (y_a - y_b)^2} \qquad (2)$$

If this value (d) is less than the threshold (l) which defines association ($d < l$) then the animals will be deemed to be associating together.

Probability distributions for random line picking are known for various geometric shapes (Solomon, 1978; Mathai, 1999; Weisstein, n.d.) and can be used to determine the probability of a chance encounter. The probability ($\Pr\{d < l\}$) that any two points randomly picked within a square are less than l (the threshold which defines association) apart can be calculated using Equations 3 – 5 (Weisstein, n.d.). This is known as the Square Line Picking problem, and the probability is given directly by the distribution function of the distance between two points randomly picked within the square.

Let d = the distance between two points chosen at random, l = the threshold which defines association and L = the length of the side of the square. If $0 < l < L$:

$$\Pr\{d < l\} = \frac{1}{2}\left(\frac{l}{L}\right)^4 - \frac{8}{3}\left(\frac{l}{L}\right)^3 + \pi\left(\frac{l}{L}\right)^2 \qquad (3)$$

If $L < l <$ the length of the diagonal of the square:

$$\Pr\{d < l\} = -\frac{1}{2}\left(\frac{l}{L}\right)^4 - 4\left(\frac{l}{L}\right)^2 \tan^{-1}\left(\sqrt{\left(\frac{l}{L}\right)^2 - 1}\right) + \frac{4}{3}\left(2\left(\frac{l}{L}\right)^2 + 1\right)\sqrt{\left(\frac{l}{L}\right)^2 - 1} + (\pi - 2)\left(\frac{l}{L}\right)^2 + \frac{1}{3} \qquad (4)$$

If $l >$ the length of the diagonal of the square:

$$\Pr\{d < l\} = 1 \qquad (5)$$

In calculating the probability of a chance association, we assume that resources are evenly distributed throughout the area, that animals make use of the whole area, and that each consecutive location plotted for each individual in the dyad is independent of the previous location. Similar assumptions have been made in previous studies. Schülke and Kappeler (2003) and Leu et al. (2010) used the random gas model to calculate expected encounter rates based on random movement of individuals. The gas model has also been used to estimate mating success in males, defined as the number of females fertilised in an average reproductive cycle, assuming that mate searching is random (Dunbar, 2002). Despite their assumptions, such models still have value because they provide an estimation of minimal possible outcomes for comparison with observed values; in this case, the minimum number of times spatially restricted animals would theoretically be seen together by chance based on the size and shape of their enclosure.

2.2 Procedures

The probability of a chance encounter in hypothetical square shapes was calculated using Equations 3 – 5 (Weisstein, n.d.). The effect of altering the distance criterion on the probability of a chance encounter was examined by varying the value of l from 1 unit through 10 units.

To investigate how robust the analytical method for calculating the probability of chance associations was to differences in length:width ratios, we first conducted a Monte Carlo randomisation test for a significant departure from the analytic estimate based on a square of the same area, using R. In this test, for any combination of length and width representing an enclosure, 200 pairs of random points within the enclosure were generated and the probability of a chance association was calculated by dividing the number of obtained associations by the number of pairs of points. The simulation was repeated 10,000 times and the probability of chance associations for each replication was compared to the analytic solution for a square of the same area to give the randomisation test. The test was one-tailed because the probability of an encounter in a rectangle can never be higher than the probability of an encounter in a square of the same area. A significant P-value (<0.05) suggests that the analytic solution for a square does not adequately estimate the probability of chance encounters in a rectangle of the specified length and width. Optimisation with respect to the absolute difference between 0.05 and the output of the randomisation test was used to estimate the maximum length:width ratio of a rectangle that can be adequately estimated by the analytic square method. The optimisation was carried out using rectangles of total area 100 units^2, with lengths ranging from 1 unit to 10 units and a distance criterion of 5 units.

In order to investigate the probability of a chance encounter in irregular shapes, we used Geographic Information Systems to generate 200 pairs of random points within images of real zoo enclosures. This equated to 200 observations and was considered to represent a reasonable sampling effort in a field study.

Ordnance Survey MasterMap™ data for six actual zoo exhibits in the UK (Figure 1) were downloaded using the EDINA Digimap Ordnance Survey Service (http://edina.ac.uk/digimap). These enclosures were used in a study of cheetah association patterns by the first author (Chadwick, 2014). Aerial photographic images of the enclosures (Google Earth, 2012), detailing the enclosure boundaries, were geo-corrected using ERDAS Imagine® 2010. The geo-corrected images were then imported into ESRI (Environmental Systems Resource Institute) ArcGIS™ 9.3.1, along with the OS MasterMap™ data, and vector-based polygons were digitised representing the boundaries of each enclosure. The 'Generate Random Points' tool, found in Hawth's Analysis Tools for ArcGIS™ (Beyer, 2004), was used to generate 200 pairs of random points within each polygon. Since the polygons were combined with the Ordnance Survey data in the GIS, every generated point had real-world co-ordinates and the distances between them could be calculated.

The probability of a chance association was calculated by dividing the number of simulated associations by the number of pairs of points (200). The simulation was repeated 1000 times for each enclosure (Bejder et al., 1998) and the mean probability of a chance encounter (and standard deviation) was calculated. The results of the simulation were compared to the analytic solution to examine differences in the probability of a chance association between actual zoo enclosures and hypothetical squares of the same area.

3. Results

The probability of a chance encounter, calculated using geometric probability for squares of up to 2000 units^2, is shown in Figure 2.

The optimisation of the randomisation tests showed that the analytic solution for squares accurately estimates the probability of a chance encounter until the length of the rectangle is more than ~3.2 times the width. Above this ratio, the analytic solution is significantly different from the Monte Carlo solution for the rectangle (Figure 3).

The probability of a chance encounter calculated using Monte Carlo simulations in GIS for actual zoo exhibits was compared with the analytic solution for squares of the same area. The probability calculated using GIS was within one standard deviation of the analytic solution in all cases (Figure 4).

As would be expected, increasing the distance criterion that defined association through 1 unit to 10 units resulted in an increase in the probability of a chance encounter (Figure 5).

4. Correcting observed indices of association

Given that the analytic solution accurately estimates the probability of a chance encounter in irregular shapes, we developed a simple R script using the analytic solution (available as electronic supplementary material) which can be used to calculate the probability of a chance encounter. The output of the script can also be used to correct observed indices of association (Chadwick et al., 2013). First, the expected number of chance encounters can be obtained by multiplying the probability of a chance encounter by the number of field observations made. An index of association based on the number of chance encounters can then be calculated, and subtracted from the index calculated using field observations (e.g. Table 1; Chadwick, 2014). An observed number of associations that is lower than the simulated number of chance encounters (thereby resulting in a corrected association index with a negative value) would indicate avoidance, rather than association (Leu et al., 2010).

For example, in a recent study of cheetah association patterns, 143 recordings were made of a pair of males in enclosure 1 at Chester Zoo (Figure 1a; Chadwick, 2014). This dyad was seen in proximity (within 5 m) 86 times. A simple ratio index of association was calculated (Equation 7: Ginsberg & Young, 1992), where x is the number of separate occasions when A and B are observed together, y_A is the number of separate occasions when only A is observed, y_B is the number of separate occasions when only B is observed, and y_{AB} is the number of separate occasions when A and B are observed not associated. Although here we have used the simple ratio index, our correction can be applied to any index of association (see Whitehead (2008) and Godde et al. (2013) for discussions of alternative association indices).

$$\mathrm{I_A} = \frac{x}{(x + y_{AB} + y_A + y_B)} \tag{6}$$

The observed index of association for this dyad was calculated as follows:

$$\mathrm{I_A} = \frac{86}{(86 + 54 + 3 + 0)} = 0.601 \tag{7}$$

The area of the enclosure was 497.06 m^2. For a hypothetical square of the same area, the side length (L) is 22.295 units ($\sqrt{497.06}$). Using our R script (consisting of the analytic solution given by Equation 3 above (Weisstein, n.d.)) and a threshold for association (l) of 5 units, the probability of a chance encounter was calculated as follows:

$$\Pr\{d < 5\} = \frac{1}{2}\left(\frac{5}{22.295}\right)^4 - \frac{8}{3}\left(\frac{5}{22.295}\right)^3 + \pi\left(\frac{5}{22.295}\right)^2 = 0.129 \tag{8}$$

Thus, the expected number of chance encounters in 143 recordings is:

$$143 \times 0.129 = 18 \tag{9}$$

and the index of association based on chance encounters is calculated as follows:

$$\mathrm{I_A} = \frac{18}{(18 + 125 + 0 + 0)} = 0.126 \tag{10}$$

The index of association based on chance encounters is then subtracted from the index calculated using field observations to give the corrected index:

$$0.601 - 0.126 = 0.475 \tag{11}$$

During the study, the space available to the animals varied and they were given access to different combinations of enclosures 1, 2 and 3 on different observation days (Figure 1a).

Thus, corrected indices of association were also calculated for this dyad in each combination of enclosures to which they had access (Table 1), enabling direct comparisons of association indices between the three enclosures to be made (Chadwick, 2014).

5. Discussion

Our results demonstrate that captive studies using an association index to quantify social relationships should take into account chance encounters. In captive animals, the probability of a chance encounter is affected by enclosure size and shape. However, there have been few attempts to estimate – and thus control for – the effects of enclosure size and shape on chance encounters and indices of association. Here, we used geometric probability and Geographic Information Systems to produce a simplified method of calculating the probability a of chance encounter when particular distance criteria for defining associations were used in shapes of a given area.

The probability of a chance encounter in a square of a given area can be determined analytically (Solomon, 1978; Mathai, 1999; Weisstein, n.d.). However, it is unlikely that space-restricted animals will be limited to square-shaped areas. The effect of shape on the probability of chance encounters was investigated by applying a Monte Carlo simulation to rectangular shapes and spatially-referenced images of actual UK zoo enclosures. The analytic solution for squares accurately estimates the probability of chance encounters in a rectangle until the length of the rectangle is ~3.2 times the width. This suggests that the analytical method is robust to fairly large variations in shape. Furthermore, the probability of a chance encounter within all of the actual zoo enclosures investigated was within one standard deviation of the calculated probability for a square of the same area. Geometric probability can therefore be used to approximate the number of chance encounters in irregular, non-geometric shapes.

As area increased, the probability of a chance encounter decreased. Animals housed in larger enclosures are less likely to be observed in proximity simply by chance than those in smaller enclosures. High corrected indices of association for dyads in large areas may therefore be considered to represent actual associations among individuals. However, associations can occur between animals in confined spaces for reasons other than the animals choosing to be together; for example mutual attraction to resources (Mitani et al., 1991; Pepper et al., 1999; Ramos-Fernández et al., 2009), or, in captive animals, gathering at the entrance to indoor accommodation (Stoinski et al., 2001). Thus, corrected indices of association should be interpreted alongside behavioural observations of affiliative or aggressive interactions, since relationships are not solely based on spatial proximity (Whitehead & Dufault, 1999; Whitehead, 2008). Future work to further validate our proposed correction will incorporate behavioural observations to distinguish between chance encounters and specific social encounters in captive animals.

As would be expected, increasing the distance criterion that defined association through 1 unit to 10 units resulted in an increase in the probability of a chance encounter. It is important for researchers to select a distance criterion that defines an association which is biologically meaningful to their study species. In their review of techniques for analysing vertebrate social structure, Whitehead and Dufault (1999) found large variation in the distances between individuals which constituted an association. Some authors considered animals to be associated if they were within 1 m of each other (e.g. common marmosets (*Callithrix jacchus*): Koenig & Rothe, 1991), and in other studies animals were considered to be associated if they were within 500 m of each other (e.g. giraffes (*Giraffa camelopardalis*): Leuthold, 1979). In our earlier paper, we considered male cheetahs to be associating if the distance between them was 5 m or less (Chadwick et al., 2013). This distance criterion was previously established in field studies of coalitions of wild male cheetahs in the Serengeti (Caro, 1994). The definition of an association will depend upon the interactions and behaviours of the study species and the ease of observing individuals. Nonetheless, our results highlight the importance of selecting an appropriate definition of association that corresponds to both the behaviour of the animals being studied and the size and shape of the area to which they have access.

Given that the probability of a chance encounter calculated using Geographic Information Systems was within one standard deviation of the analytic solution, and that the analytic solution proved robust to quite large changes in shape, geometric probability can be used to estimate the probability of chance encounters between individuals in any confined space. We developed a simple R script which can be used by researchers to calculate the probability of a chance encounter in an enclosure of any shape, and to correct observed indices of association. We have used the simple ratio index to demonstrate how indices of association can be corrected, however the correction can be applied to any index of association (see Whitehead (2008) and Godde et al. (2013) for discussions of alternative association indices), and enables association indices to be compared across different sized – and shaped – enclosures.

Our proposed correction is especially relevant when animals are limited to small spaces and can be applied not only to zoo animals but to any confined animals, for example farm and laboratory animals. However, the concern for overestimating association may not only be limited to captive animals since free-ranging animals, for example animals in managed areas (e.g. sanctuaries or reserves), often have restricted ranges. Indeed, animals in totally wild environments may also be naturally limited in their ranging; for example, territorial species, where an individual’s or group’s movement may be restricted by the presence of neighbours.

In calculating the probability of a chance association, we assume that resources are evenly distributed throughout the area, that animals make use of the whole area, and that each consecutive location plotted for each individual in the dyad is independent of the previous location. We acknowledge that our calculations provide minimal association indices based on enclosure size and shape, and do not include the effects of habitat preference or resource distribution. In addition, we recognise that relationships are not solely based upon spatial proximity and observations of social interactions should be used alongside spatial associations to allow conclusions to be drawn about the social relationships between individuals. A given observation of two animals in close proximity can occur as a consequence of both social motivation and non-social movement of individuals, and our proposed correction may underestimate the true association between individuals when a combination of social and random association occurs. Nonetheless, we have devised the first method for correcting indices of association to take into account chance encounters based on spatial restrictions. Correcting the index in this way controls for enclosure size and shape, and facilitates direct comparisons of association indices for dyads housed in different enclosures.

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7. References

Bejder L, Fletcher D, Brager S (1998) A method for testing association patterns of social animals. Anim Behav 56 (3):719-725. doi:10.1006/anbe.1998.0802

Beyer HL (2004) Hawth's Analysis Tools for ArcGIS. Retrieved from http://www.spatialecology.com/htools

Caro TM (1994) Cheetahs of the Serengeti Plains: Group Living in an Asocial Species. University of Chicago Press, Chicago

Carter KD, Seddon JM, Frère CH, Carter JK, Goldizen AW (2013) Fission–fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. Anim Behav 85 (2):385-394. doi:10.1016/j.anbehav.2012.11.011

Chadwick C (2014) Social behaviour and personality assessment as a tool for improving the management of cheetahs (*Acinonyx jubatus*) in captivity. (Doctoral thesis, University of Salford, Salford, UK)

Chadwick CL, Rees PA, Stevens-Wood B (2013) Captive-housed male cheetahs (*Acinonyx jubatus soemmeringii*) form naturalistic coalitions: measuring associations and calculating chance encounters. Zoo Biol 32 (5):518-527. doi:10.1002/zoo.21085

Chapman C (1990) Association patterns of spider monkeys: the influence of ecology and sex on social organization. Behav Ecol Sociobiol 26 (6):409-414. doi:10.1007/bf00170898

Dunbar RIM (2002) Modelling primate behavioural ecology. Int J Primatol 23 (4):785-819. doi:10.1023/A:1015576915296

Gillam EH, O'Shea TJ, Brigham RM (2011) Nonrandom patterns of roost emergence in big brown bats, *Eptesicus fuscus*. J Mammal 92 (6):1253-1260. doi:10.1644/10-mamm-a-393.1

Ginsberg JR, Young TP (1992) Measuring association between individuals or groups in behavioural studies. Anim Behav 44 (2):377-379. doi:10.1016/0003-3472(92)90042-8

Godde S, Humbert L, Côté SD, Réale D, Whitehead H (2013) Correcting for the impact of gregariousness in social network analyses. Anim Behav 85 (3):553-558. doi:10.1016/j.anbehav.2012.12.010

Google Earth (2012) Google Earth (Version 7.0). Retrieved from http://www.google.com/earth/index.html

Hutchinson JMC, Waser PM (2007) Use, misuse and extensions of "ideal gas" models of animal encounter. Biol Rev 82 (3):335-359. doi:10.1111/j.1469-185X.2007.00014.x

Knobel D, Du Toit J (2003) The influence of pack social structure on oral rabies vaccination coverage in captive African wild dogs (*Lycaon pictus*). Appl Anim Behav Sci 80 (1):61-70. doi:10.1016/S0168-1591(02)00136-3

Koenig A, Rothe H (1991) Social relationships and individual contribution to cooperative behaviour in captive common marmosets (*Callithrix jacchus*). Primates 32 (2):183-195. doi:10.1007/bf02381175

Leu ST, Bashford J, Kappeler PM, Bull CM (2010) Association networks reveal social organisation in the sleepy lizard. Anim Behav 79 (1):217-225. doi:10.1016/j.anbehav.2009.11.002

Leuthold BM (1979) Social organization and behaviour of giraffe in Tsavo East National Park. Afr J Ecol 17 (1):19-34. doi:10.1111/j.1365-2028.1979.tb00453.x

Martin P, Bateson P (2007) Measuring Behaviour: An Introductory Guide. 3rd edn. Cambridge University Press, Cambridge

Mathai AM (1999) An Introduction to Geometrical Probability: Distributed Aspects with

Applications. Gordon and Breach Science Publishers, The Netherlands

Mitani JC, Grether GF, Rodman PS, Priatna D (1991) Association among wild orang-utans: sociality, passive aggregations or chance? Anim Behav 42 (1):33-46. doi:10.1016/S0003-3472(05)80603-7

Pepper JW, Mitani JC, Watts DP (1999) General gregariousness and specific social preferences among wild chimpanzees. Int J Primatol 20 (5):613-632. doi:10.1023/a:1020760616641

Ramos-Fernández G, Boyer D, Aureli F, Vick LG (2009) Association networks in spider monkeys (*Ateles geoffroyi*). Behav Ecol Sociobiol 63 (7):999-1013. doi:10.1007/s00265-009-0719-4

Rees PA (1982) The ecology and management of feral cat colonies, (Doctoral thesis, University of Bradford, Bradford, UK)

Romero T, Aureli F (2007) Spatial association and social behaviour in zoo-living female ring-tailed coatis (*Nasua nasua*). Behaviour 144 (2):179-193. doi:10.1163/156853907779947355

Schaller GB (1972) The Serengeti Lion. University of Chicago Press, Chicago

Schülke O, Kappeler PM (2003) So near and yet so far: territorial pairs but low cohesion between pair partners in a nocturnal lemur, *Phaner furcifer*. Anim Behav 65 (2):331-343. doi:10.1006/anbe.2003.2018

Solomon H (1978) Geometric Probability. Society for Industrial and Applied Mathematics, Philadelphia

Southwood TRE (1968) Ecological Methods, with Particular Reference to the Study of Insect Populations. Methuen & Co. Ltd, London

Stoinski TS, Hoff MP, Maple TL (2001) Habitat use and structural preferences of captive western lowland gorillas (*Gorilla gorilla gorilla*): effects of environmental and social variables. Int J Primatol 22 (3):431-447. doi:10.1023/A:1010707712728

Stricklin W, Graves H, Wilson L (1979) Some theoretical and observed relationships of fixed and portable spacing behaviour of animals. Appl Anim Ethol 5 (3):201-214. doi:10.1016/0304-3762(79)90056-7

Szykman M, Engh AL, Van Horn RC, Funk SM, Scribner KT, Holekamp KE (2001) Association patterns among male and female spotted hyenas (*Crocuta crocuta*) reflect male mate choice. Behav Ecol Sociobiol 50 (3):231-238. doi:10.1007/s002650100356

Vonhof MJ, Whitehead H, Fenton MB (2004) Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. Anim Behav 68 (3):507-521. doi:10.1016/j.anbehav.2003.08.025

Waser PM (1975) Spatial associations and social interactions in a "solitary" ungulate: the bushbuck *Tragelaphus scriptus (Pallas).* Z Tierpsychol 37 (1):24–36. doi: 10.1111/j.1439-0310.1975.tb01125.x

Weisstein EW (no date) Square Line Picking. Retrieved from http://mathworld.wolfram.com/SquareLinePicking.html.

Whitehead H (2008) Analysing Animal Societies: Quantitative Methods for Vertebrate Social Analysis. University of Chicago Press, Chicago

Whitehead H, Dufault S (1999) Techniques for analysing vertebrate social structure using identified individuals: review and recommendations. Adv Stud Behav 28:33-74. doi:10.1016/S0065-3454(08)60215-6

Table and Figure Captions

Fig 1 Shapes and areas of the cheetah enclosures at (a) Chester Zoo (Cheshire, UK); (b) Exmoor Zoo (Devon, UK); (c)(i) and (c)(ii) Port Lympne (Kent, UK); (d) West Midland Safari Park (Worcestershire, UK) and (e) ZSL Whipsnade Zoo (Bedfordshire, UK). Four combinations of the three enclosures at Chester Zoo were used to generate random points as these were the combinations used for husbandry reasons: enclosure 1 alone; enclosures 1 and 2; enclosures 1 and 3; enclosure 3 alone. (Not to scale. Crown Copyright/database right 2013. An Ordnance Survey/EDINA supplied service.)

Fig 2 Probability of a chance encounter in squares of up to 2000 units^2. The distance criterion (l) was fixed at 5 units

Fig 3 Relationship between length:width ratio and P value for randomisation tests for significant departure from analytic estimates based on a square. The total area of the rectangle was fixed at 100 units^2. The distance criterion (*l*) was fixed at 5 units

Fig 4 Probability of a chance encounter in actual enclosures, calculated using geometric probability and Monte Carlo simulations in GIS. For the Monte Carlo simulations, the mean probability is plotted and error bars represent one standard deviation. The distance criterion (*l*) was fixed at 5 units

Fig 5 The effect of altering the distance criterion (*l*) on the probability of a chance encounter in squares of increasing area

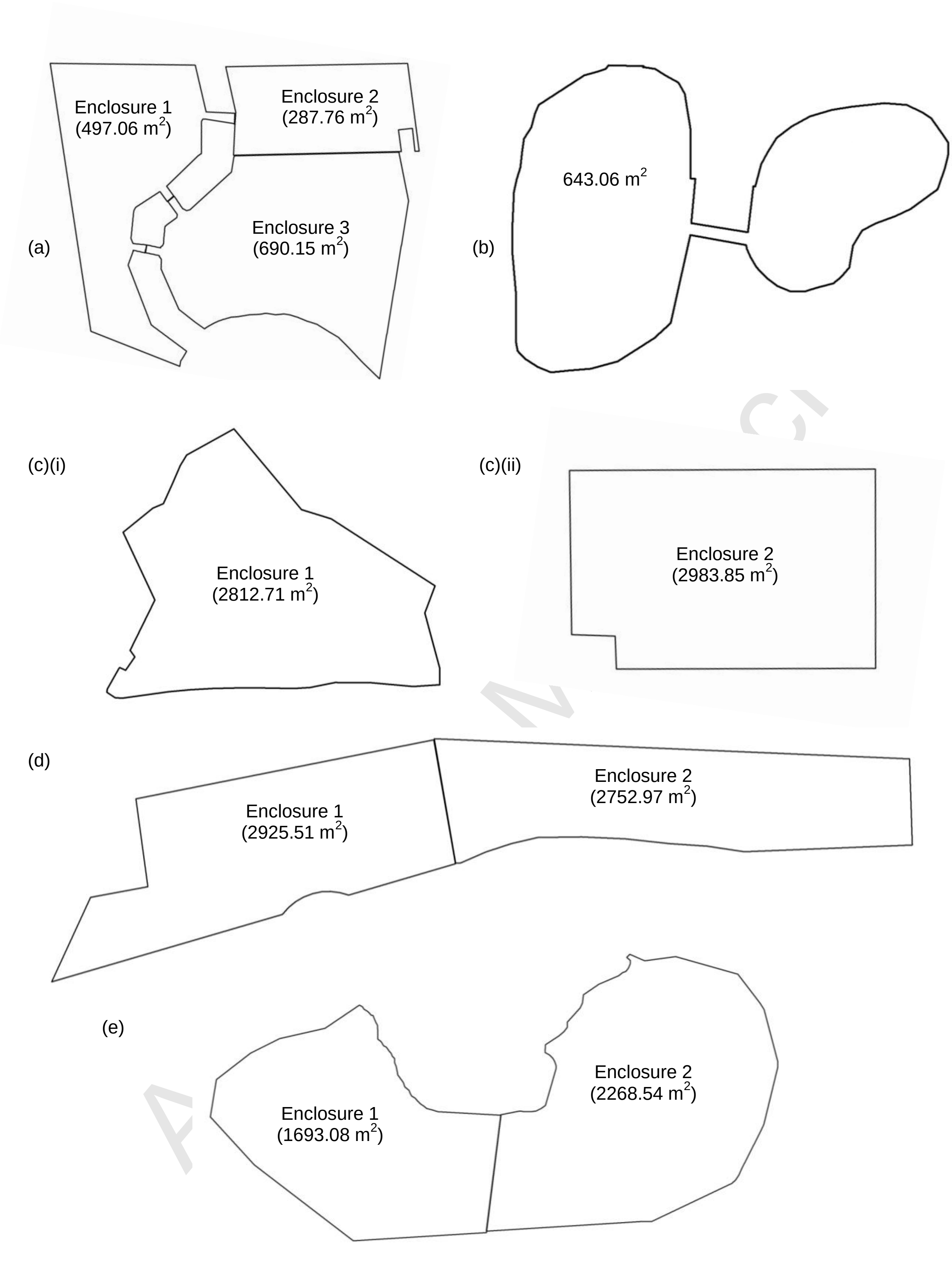
Table 1 Observed and corrected indices of association for a pair of male cheetahs, housed in three combinations of zoo enclosures (Chadwick, 2014)

Electronic Supplementary Material R script used for estimating the probability of a chance encounter in a square of a supplied area with a set distance criterion

Enclosure	Area	No. of field recordings	Pr{d < l}	No. of chance encounters	Observed I_A[1]	Chance I_A[1]	Corrected I_A[1]
Chester 1	497.06	143	0.129	18	0.601	0.126	0.475
Chester 1 & 2	784.82	291	0.085	25	0.605	0.086	0.519
Chester 1 & 3	1187.21	35	0.058	2	0.735	0.057	0.678

[1]Simple ratio index: $I_A = x/(x + y_{AB} + y_A + y_B)$, where x = number of separate occasions A and B observed together, y_A = number of separate occasions only A observed, y_B = number of separate occasions only B observed, y_{AB} = number of separate occasions A and B observed not associated (Ginsberg & Young, 1992).

Figure 1



(a)
Enclosure 1
(497.06 m2)
Enclosure 2
(287.76 m2)
Enclosure 3
(690.15 m2)
(b)
643.06 m2
(c)(i)
Enclosure 1
(2812.71 m2)
(c)(ii)
Enclosure 2
(2983.85 m2)
(d)
Enclosure 1
(2925.51 m2)
Enclosure 2
(2752.97 m2)
(e)
Enclosure 1
(1693.08 m2)
Enclosure 2
(2268.54 m2)

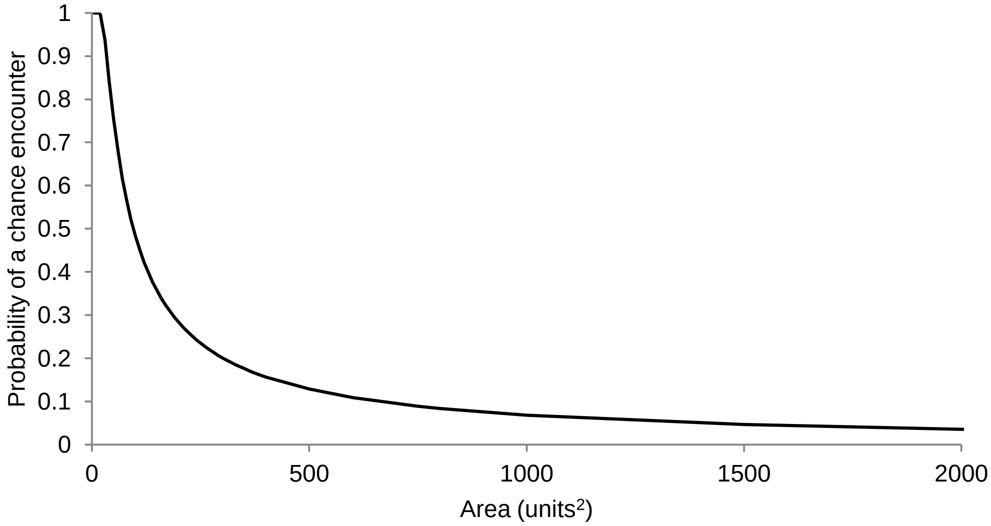
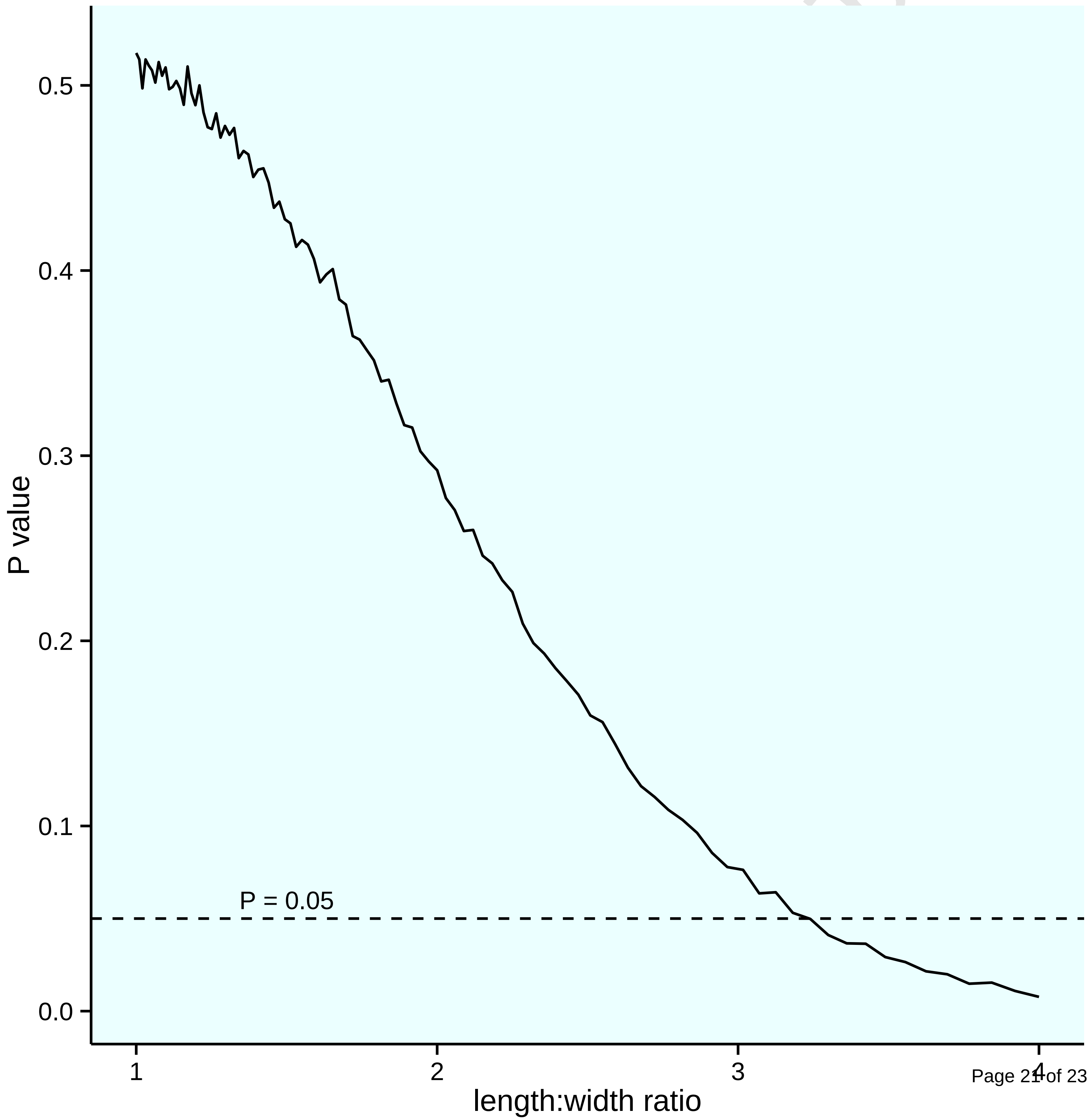
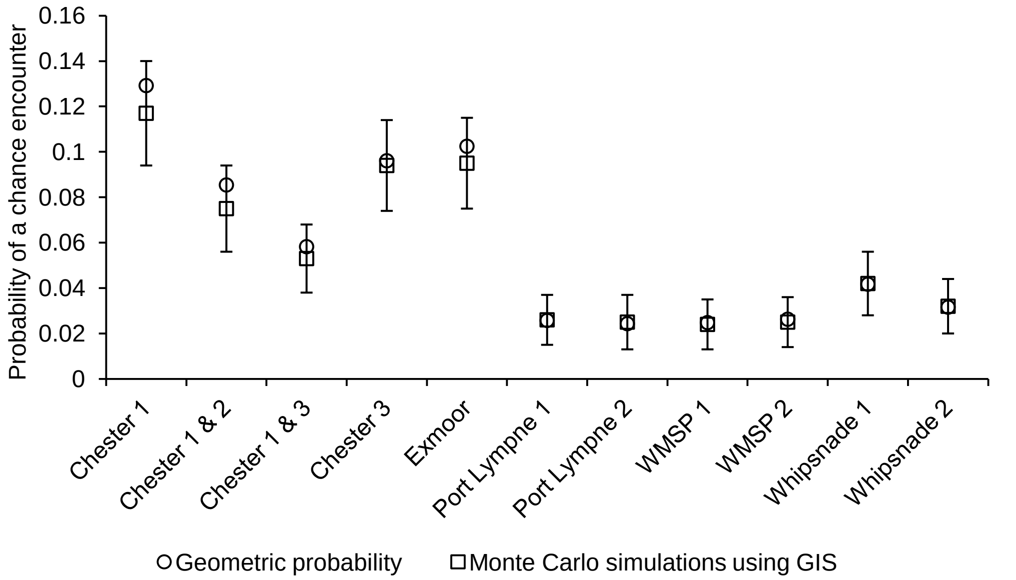
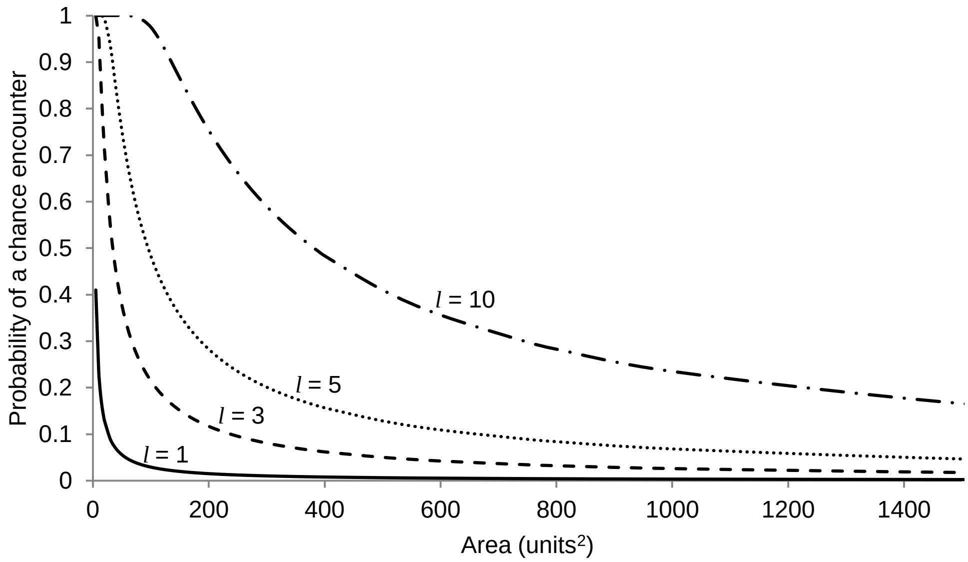

Probability of a chance encounter
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
500
1000
1500
2000
Area (units²)

Figure 3




0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Probability of a chance encounter
Chester 1
Chester 1 & 2
Chester 1 & 3
Chester 3
Exmoor
Port Lympne 1
Port Lympne 2
WMSP 1
WMSP 2
Whipsnade 1
Whipsnade 2
Geometric probability
Monte Carlo simulations using GIS


1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Probability of a chance encounter
0
200
400
600
800
1000
1200
1400
Area (units²)
l = 10
l = 5
l = 3
l = 1