Applied Animal Behaviour Science 169 (2015) 100–106

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

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

Carly L. Chadwick[a,*], David A. Springate[b], Paul A. Rees[a], Richard P. Armitage[a], Sean J. O'Hara[a]

[a] Ecosystems and Environment Research Centre, School of Environment and Life Sciences, University of Salford, The Crescent, Greater Manchester M5 4WT, UK

[b] Centre for Biostatistics, Institute of Population Health, University of Manchester, M13 9PL, UK

ARTICLE INFO

Article history:
Accepted 3 May 2015
Available online 18 May 2015

Keywords:
Behaviour modelling
Geometric probability
Index of association
Social behaviour

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.

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).

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

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 and 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

* Corresponding author. Tel.: +44 161 962 6574.
E-mail address: c.l.chadwick@edu.salford.ac.uk (C.L. Chadwick).

http://dx.doi.org/10.1016/j.applanim.2015.05.001
0168-1591/

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:

$$\text{Distance}\,(d) = \sqrt{(x_a - x_b)^2 + (y_a - y_b)^2} \tag{2}$$

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 $0 < l < L$:

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

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

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

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

$$Pr\{d < l\} = 1 \tag{5}$$

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