



Research paper

The relevance of host overcrowding in wildlife epidemiology: A new spatially explicit aggregation index



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ABSTRACT

Species distribution and population abundance are keystone patterns in ecology, and currently also in epidemiology. The aggregation of individuals in the population is closely related to distribution and abundance, but they are not totally equivalent patterns. Despite the great efforts made in recent decades to harmonise the sampling protocols used to collect distribution and abundance data, studies regarding the development and testing of aggregation indices are scarce, even when individuals' aggregation is quite relevant and necessary for the design of effective wildlife management policies. One of the most popular aggregation indices is the overcrowding index (m^*), which quantifies the number of individuals per group, and does not, therefore, take into account how the individuals and groups are distributed in a given territorial unit. In this study, we describe and assess a new spatially explicit aggregation index (SAI) in which the distribution of individuals within the group and the groups in the territorial units are included in the formulation. A comparative evaluation of the proposed index was carried out in relation to m^* , including a specific assessment of the biological meaning of these indices by relating aggregation indices with pathogen prevalence in a multi-host epidemiological scenario. Our results showed that SAI – but not m^* – responded to changes in the aggregation level of individuals in the population in both theoretical scenarios and with real data obtained from a case study. Spatial information is, therefore, required to quantify individuals' aggregation and the processes that are associated with it. This is particularly relevant when our understanding of processes needs to be addressed on a fine local scale, as is the case when working in epidemiology. Our results reinforce this idea, since the capacity of SAI to explain the prevalence of animal tuberculosis at a community level was significantly higher than that observed for m^* , the latter being to a great extent based in the abundance of individuals in the area. We concluded that SAI has a great potential for wildlife monitoring in general and for epidemiological studies in particular and may, together with abundance data, provide practical information to evaluate wildlife management actions and define effective policies for diseases control.

1. Introduction

Species distribution and population abundance are keystone topics in ecology, and currently also in epidemiology (e.g. Hassell and May, 1974). From an epidemiological perspective, the relevance of this kind of studies has grown in the last few years, and this has principally been motivated by: (i) the recurrent evidence on the association between the emergence and persistence of pathogens and the presence of complex ecological communities (e.g. Frölich et al., 2002; Gortázar et al., 2016), and (ii) the usually strong relationship between host abundance and

sanitary status (e.g. Gortázar et al., 2006). Overall, the transmission and maintenance of most pathogens increase in situations of high host population abundance and individuals' aggregation (McCallum et al., 2001; Vicente et al., 2004; Gortázar et al., 2006). The aggregation of individuals in the population is closely related to distribution and abundance patterns, but they are not totally equivalent. What is more, the relationship between the rates of pathogens (transmission, prevalence, etc.) and host aggregation is closer than that observed between these rates and host population abundance (Acevedo et al., 2007; Vander Wal et al., 2012). Whereas abundance assumes a probability of

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contact among individuals that is proportional to the number of individuals, the animals' aggregation determines the probability of contact by considering how close the individuals are (Drewe et al., 2013).

Measuring the patterns of population distribution and abundance and individuals' aggregation requires an intensive sampling effort, since they may be modulated by not only abiotic and biotic factors, but also by human-mediated ones (Etherington et al., 2009; Acevedo et al., 2011). The degree of individuals' aggregation is, in part, an intrinsic ecological trait of each species that is, for instance, expressed in the form of gregariousness, territoriality and polygyny (Shuster and Wade, 2003; Pérez-González and Carranza, 2011). However, wildlife management can alter the natural behaviour of the species, and consequently their distribution, abundance and aggregation patterns, by actions such as the introduction of animals, fencing territories, and/or food and water supplementation, among others (Vicente et al., 2007; Pérez-González et al., 2010a; Forristal et al., 2012). The research efforts made in recent decades have been focused on developing and validating methods that can be used to determine population distribution and abundance (e.g. Acevedo et al., 2010; Engeman et al., 2013). However, studies aimed at developing and testing aggregation indices are scarce, even when they are quite relevant for management and are required for the design of effective disease control management programs (Boadella et al., 2011).

Lloyd (1967) developed a statistical framework for quantifying the individuals' distribution in natural populations in relation to overcrowding and competition. He defined m^* as an overcrowding index that measures the degree to which the individuals are grouped around key resources. Shuster and Wade (2003) subsequently used the m^* index to quantify females' aggregation during the breeding season in a spatial context (see also Pérez-González et al., 2010b). Lloyd (1967) index quantifies the mean number of individuals per group in the following manner:

$$m^* = \left(\sum_{g=1}^M mg(mg - 1) \right) / n \quad (1)$$

Where M is the number of groups in a given territorial unit, m_g is the number of individuals in the group, and $n = \sum m_g$, that is, the number of individuals in the territorial unit. In this index, the aggregation is based on the number of individuals in each group (m_g), and on the number that are in the territorial unit (n). In m^* the population abundance is, therefore, considered when quantifying individuals' aggregation but it does not take into account how the individuals and groups are distributed within the territorial unit.

The aim of our study is, therefore, to describe and assess a new spatially explicit index that accounts for the distribution of individuals within the group and the groups in the territorial units in the formulation. The proposed index is evaluated in comparison to m^* , including a specific assessment of their biological meaning of these indices by relating aggregation indices with pathogen prevalence in a multi-host epidemiological scenario.

2. Methods

2.1. The spatially explicit aggregation index (SAI)

The abundance of animals, in addition to the location of both the animals within the group and the groups in the territorial unit, are parameters that should be considered when quantifying aggregation, since they notably affect the overcrowding of the animals. Two ratios have, therefore, been incorporated into the new 'Spatially explicit Aggregation Index' (SAI) in order to take into account the spatial location of individuals and groups (see Fig. 1). First, the new index requires the estimation of the ratio between the maximum observed distance among individuals in the group and the spatial scale of the pattern (D_{ind}). The spatial scale of the pattern (d^*) is the spatial

resolution at which the aggregation in a point pattern study should be analysed (Ripley 1981). This parameter is used to determine what animals are in a group (see below). The d^* can be determined mathematically when no priors regarding the cohesiveness of the "points" are available (see e.g. Pérez-González et al., 2010b), but it can also be inferred from observational evidence when working with well-known species. Second, SAI also considers the ratio between the mean distance between groups in the territorial unit in relation to the maximum possible distance between two groups in the territory (D_{gr}). SAI is formulated as follow:

$$SAI = \log_{10} \left(\frac{\sum_{g=1}^M (mg/D_{ind})}{D_{gr}} \right) \quad (2)$$

Where $D_{ind} = 1$ for isolated individuals, and $D_{gr} = 1$ for territories with a single group.

In this study, the aggregation indices $-m^*$ and SAI – were first assessed in theoretical scenarios in which the number of individuals and the distribution of both individuals within the groups and groups in the territorial unit were manipulated. Secondly, a case study was carried out to illustrate the differences between m^* and SAI with real data, and including the assessment of their capacity to explain pathogen prevalence at a community level.

2.2. The case study: ungulates in Doñana National Park

2.2.1. The study area

In order to comparatively assess m^* and SAI in a natural scenario, we carried out a study on the community of ungulates in Doñana National Park, DNP (37°09 N, 6°309 W; 54,000 ha), a nature reserve located on the Atlantic coast of south-western Spain and one of the most important biodiversity reserves in Europe. The complexity of the epidemiology of tuberculosis (TB) in the ungulate community of DNP has been intensively studied (e.g. Romero et al., 2008; Gortázar et al., 2011; Barasona et al., 2014a). A traditional breed of cattle (locally known as "marisemeña") cohabits with a diverse and abundant community of wild ungulates, including wild boar (*Sus scrofa*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*). The incidence of TB in cattle is high (9.23% per year), and TB prevalence in wild boar (52–54%), red deer and fallow deer (14–19%) are among the highest found in natural populations worldwide (zar et al., 2008, 2011; zar et al., 2008, 2011).

2.2.2. Unmanned aircraft systems methodology

We used Unmanned Aircraft Systems (UAS, also known as drones) to collect information on animal distribution in the study area. During the summer (August and September) of 2011, 15 aerial tracks (of a length of ≈ 4 km and a width of ≈ 0.1 km) were conducted between 17.30 h and 21.00 h local time (Fig. 2). The sampling design responded to the period of maximum expected aggregation of the animals (reproductive season) in the study area (Braza and Alvarez 1987; Barasona et al., 2014b). We used a radio-controlled model Easy Fly plane (St-models, China) propelled by a brushless electric engine. The plane carried a video camera used for First Person View Flight, a GPS (Mediatek, model FGPMMOPA6B), an Ikarus autopilot which provides flight stabilisation, an On Screen Display, and a Panasonic Lumix LX-3 digital photo camera 11MP to take the photographs. The UAS was programmed to fly at an altitude of 100 m above ground level and at an average speed of 40 km/h. Further details on the sampling, the system and the image processing can be found in Barasona et al. (2014b) and Mulero-Pázmány et al. (2015).

Once the animals had been identified on the images gathered by the UAS in the sampling area, 100 m \times 100 m grid squares were overlapped in order to define the territorial units for estimating the inter-specific aggregation indices. The objective of this analysis was to illustrate the potential differences between the indices rather than focusing on a particular ecological question. In this case, study the data

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