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Special Issue: Conservation Behaviour

A simple statistical guide for the analysis of behaviour when data are constrained due to practical or ethical reasons

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Keywords: bias bootstrap confidence interval effect size hierarchical data structure nonparametric statistics null hypothesis testing precision statistical power study design Here, I provide a practical overview on some statistical approaches that are able to handle the constraints that frequently emerge in the study of animal behaviour. When collecting or analysing behavioural data, several sources of limitations, which can raise either uncertainties or biases in the parameter estimates, need to be considered. In particular, these can be issues about (1) limited sample size and missing data, (2) uncertainties about the identity of subjects and the dangers posed by pseudoreplication, (3) large measurement errors resulting from the use of indicator variables with nonperfect reliability or variables with low repeatability, (4) the confounding effect of the within-individual variation of behaviour and (5) phylogenetic nonindependence of data (e.g. when substitute species are used). I suggest some simple analytical solutions to these problems based on existing methodologies and on a consumable language to practitioners. I highlight how randomization and simulation routines, generalized linear mixed models, autocorrelation models, phylogenetic comparative methods and Bayesian statistics can be exploited to overcome the inefficient performance of some conventional statistical approaches with typical behavioural data. To enhance the accessibility of these methodologies, I demonstrate how they can be brought into practice in the R statistical environment, which offers flexible statistical designs. Although the primary motivation behind this discussion was to help animal behaviourists who address questions in relation to conservation, I also hope that researchers working on the evolutionary ecology of behaviour will also find some material useful.

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In different scientific disciplines, the investigated research topics and the attributes of the studied subjects set up specific constraints for study design and the statistical analysis of available data. Here I aim to discuss some of difficulties that can typically emerge in the study of animal behaviour and to offer some statistical approaches that can be used to alleviate the limitations embedded in behavioural data. According to the theme of this Special Issue, I will principally focus on issues that emerge in association with species of conservation concern (i.e. those that can be characterized by low or rapidly declining abundance, by high level of specialization to extreme environments, or by having a specific position on the phylogenetic tree). However, as study designs relying on behavioural observations on marked individuals impose some general challenges for the analysis of data independently of the particular research questions, most discussed topics can be viewed more broadly and easily applied to studies with

* Correspondence: L. Z. Garamszegi, Department of Evolutionary Ecology, Estación Biológica de Doñana-CSIC, c/Americo Vespucio, s/n, 41092, Seville, Spain. *E-mail address:* laszlo.garamszegi@ebd.csic.es. ecological or evolutionary focus. The first three topics discuss concrete problems (limited sample size, the use of surrogate variables when noninvasive studies, unknown identity of subjects) that may typically emerge when working with behavioural data that are constrained for ethical or practical reasons. In the last section, I bring into the focus other approaches (mixed modelling, phylogenetic comparative methods, Bayesian statistics) that could, in general, be more broadly applied in conservation studies.

Given the target audience and the purpose of this paper/journal volume, I provide a superficial overview on a broad array of approaches rather than cover only a few topics with the appropriate statistical deepness (i.e. with complex equations and simulations). This is also because I present nothing new here: all of the methodologies I touch on are already well established in the statistical literature. By maintaining a focus and language that are comprehensible to practitioners, my sole aim is to initiate the spread of a diversity of methodologies that are currently underexploited in the study of animal behaviour and conservation. However, I do emphasize the importance of the scientific foundations for any methodology being implemented in practice. Hence, for the more interested readers, I give pointers to the primary sources that

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contain the corresponding mathematical background. For those who wish to try the methodologies with their own data, I provide an electronic supplement that includes several executable statistical scripts written in the R statistical environment (R Development Core Team, 2015) for the simplest scenarios (i.e. those that are covered in the first three sections). For demonstrative purposes, I use illustrations and examples that rely on elementary statistical situations (e.g. correlations, linear regression with a single predictor), but most of the recommended methodology can be easily tailored to more complex statistical designs. Note that this overview is not intended to be exhaustive, it merely reflects the perspective and knowledge of the author. Problems and solutions that are not discussed here are possible.

LIMITED SAMPLE SIZE

Limited sample size is one of the most obvious constraints that confronts animal behaviourists (Taborsky, 2010), especially when working on conservation-related issues (Bradshaw & Brook, 2010; Martinez-Abrain, 2014). For a variety of reasons that arise from the special characteristics of the studied species, in combination with the difficulty of assaying behaviours and ethical policies, it is impossible to acquire an ideal sample that would be representative of the real world. This is a general problem in the study of animal behaviour, but it is particularly important when working with species of conservation concern. These are typically those species that are at low abundance, difficult to observe in nature, impractical or even illegal to capture and unable to be brought into the laboratory for experimentation. Furthermore, most conservationrelated questions target population-specific parameters (e.g. abundance, species composition) and their temporal or spatial patterns. These tasks necessitate comparisons across higher group levels with a sample size that is equal to the number of groups being compared. Therefore, effective sample size in conservation studies is severely curtailed, and conservationists occasionally have to work with an extremely small sample size.

This sample-size limitation brings up statistical issues about precision, accuracy and stability (Quinn & Keough, 2002). Low sample size has the statistical consequence that the chances of obtaining a reliable and appropriate estimate of the central tendency (e.g. mean or median), data spread (e.g. variance or standard deviation, shape of the frequency distribution) and the strength of relationship between variables (correlation, between-group differences, regression slopes) are low. Under these circumstances, the ability to tease pattern and noise apart without bias becomes progressively intractable. In a null hypothesis testing (NHT) framework, this problem is typically manifested as limited statistical power signifying that high type II error rates make it very likely that the null hypothesis cannot be rejected even if it is false (Cohen, 1988). More generally, data limitation translates into imprecise parameter estimates meaning that central tendencies can be obtained with very large confidence intervals, which is a considerable shortcoming even in a non-NHT framework (Nakagawa & Cuthill, 2007). In terms of accuracy, some statistical approaches are known to perform badly and provide parameter estimates with a systematic upward or downward bias when supplied with limited data (Bishara & Hittner, 2015; Gorsuch & Lehmann, 2010). A related point is that, because of the strict relationship between the number of parameters and the sample size that can be entered into a statistical model (Bolker, 2007), an observer cannot achieve full control on several potentially confounding variables when data are limited, which can also generate biases. Finally, questions about stability appear via the relative importance of particular data points, as the influence of a single outlier can be drastic in a small sample. Accordingly, small changes in the data can lead to substantially different results, challenging the reliability of the obtained parameter estimate. Note that errors arising from low sample sizes can reach beyond these traditional problems for accuracy and precision, as sign errors and exaggeration errors can also emerge (Gelman, 2015). Furthermore, low statistical power as caused by limited data has consequences for the reproducibility/replicability of results (Button et al., 2013).

The traditional way to circumvent at least some of the above caveats is to use simple statistical methods (such as *t* tests, correlations, Fisher exact test) that have been demonstrated to perform convincingly well when sample sizes are small (Larntz, 1978; Soper, Young, Cave, Lee, & Pearson, 1917; de Winter, 2013). Furthermore, some textbooks recommend the use of nonparametric statistics in such situations (Siegel & Castellan, 1988). However, these approaches offer practical solutions only, as issues about the precision, the role of influential data points and the need for controlling for other variables are treated only partially or remain completely unresolved.

Effect Size Thinking: towards Separating Strength from Precision

When data are limited, several confusions may arise from the NHT-based inference of results (Cohen, 1994; Stephens, Buskirk, & del Rio, 2007). Most of the weaknesses revolve around the fact that small samples inherently incur low statistical power; thus, it is highly likely that effects of small or intermediate magnitude (which could still be of biological importance) remain nonsignificant. Given that the NHT-framework enforces binary decisions about the existence or nonexistence of effects, nonsignificant results are often interpreted as evidence for no biological relationship between the investigated variables. This misleading scientific conclusion is based on too much attention to P values, which can generate at least two problems for conservation biology. First, if an effect of a small or intermediate magnitude appears nonsignificant in an NHTbased study and is inferred as being biologically unimportant, such a scientific verdict may lead to an omission of an effect from the practical side as well (e.g. a pollutant has no detected effect, thus no actions are needed against it). This is particularly dangerous if the investigation involves a threatened species that is very hard to study. In that situation, the replication of a given study is not warranted, and the same null results can be repeatedly used as a motivation for a wrong conservation action. Second, nonsignificant results are difficult to publish, and thus often remain in file-drawers and generate publication bias (Møller & Jennions, 2001; Rosenberg, 2005). If policy makers rely on published information for their decisions, they will design their action plans following a biased picture from the published material (i.e. the efficiency of a prevention campaign is overestimated if only supportive studies are getting published). Therefore, drawing strong conclusions with practical importance from small samples and based on significance levels should be avoided. Scientists working with species of conservation concern have a high responsibility to publish their results, even if these are not significant.

Effect size thinking may offer a straightforward alternative to the NHT-based inferential approach (Garamszegi, 2006; Nakagawa, 2004; Nakagawa & Cuthill, 2007; Nakagawa & Santos, 2012; Thompson, 2002). The most important drawback of focusing on *P* values is that they combine statistical power and the magnitude of the underlying effect (in extreme scenarios this leads to the problem that everything will appear significant when sample sizes are very large, but nothing will appear significant when sample sizes are very low). Effect size theorem, on the other hand, separates these properties, as it relies on different metrics to describe the strength of the biological effect and the uncertainty by which it can be measured from the available data. Most biological questions

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