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Commentary

Behaviour accumulation curves: a method to study the completeness of behavioural repertoires

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Along with field observations, ethograms allow for the analysis of biological, ecological and evolutionary contexts of behaviour (Lehner 1979). Most frequently, researchers focus on specific behavioural subsamples, usually labelled as catalogues or repertoires. Such is the case of studies that have described the activity budgets (e.g. *Ilhaia cuspidata*: Pereira et al. 2004), positional behaviour (e.g. *Ardeotis kori*: Lichtenberg & Hallager 2008), or sexual behaviour (e.g. *Cebus apella*: Carosi & Visalberghi 2002) of several animal species.

In species with a high diversity of behavioural acts (Fagen & Goldman 1977), a compromise must be reached between sampling effort and the completeness of the catalogues. Fagen & Goldman (1977) and Fagen (1978) have proposed methods for analysing completeness of behavioural catalogues based on lognormal Poisson fitting and logarithmic regression procedures, respectively. In this paper we describe and demonstrate how a method used to study biodiversity allows simpler evaluations of the completeness and efficacy of behavioural repertoires.

Description of the Method

Biodiversity inventories

Floristic and faunistic inventories have been frequently analysed through the construction of species accumulation curves (or collector's curves), where some measure of sampling effort (e.g. number of traps, hours) is plotted against the cumulative number of species observed (Colwell & Coddington 1994; Gotelli & Colwell 2001). In asymptotic species accumulation models, the curves reach an asymptote when the probability of observing new species approaches zero (Soberón & Llorente 1993), thus allowing for an estimation of inventory completeness.

Behaviour accumulation curves

Preparing data for analysis. In the case of behavioural patterns, the observation of new acts can be represented as a function of the observation effort. Specifically, it can be expected that the addition of new behaviours to a repertoire decreases as effort increases.

The first step to project a behaviour accumulation curve (BAC) is to calculate the number of behaviours observed per unit of effort, or

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sampling unit (e.g. animal-focal periods, instantaneous recordings; Altmann 1974). These data must be gathered in a matrix (saved as plain text, tab-delimited), in which the rows represent the observed behavioural acts (scored as 1 for presence and 0 for absence) and the columns represent the sampling units (e.g. Table 1). This matrix should then be loaded in EstimateS, a free software application for Windows and Macintosh available at http://viceroy.eeb.uconn.edu/EstimateS (Colwell 2006). EstimateS allows calculating the mean number of new behavioural acts observed for each sampling unit accumulated up to the total sample size (named 'Sobs' in the output window of the program). Note that the form of the accumulation curves may be affected by temporal biases in sampling effort. This effect may be eliminated by controlling the order in which samples are collected through the randomization of the data. EstimateS allows programming analysis for 50 or more randomizations.

BAC and the Clench equation

Asymptotic models are particularly useful for describing the relationship between sampling effort and the observation of behaviours (i.e. accumulation curves). Such is the case for the Clench equation, which is appropriate when the probability of adding new acts to the repertoire decreases with the number of behaviours already observed, but increases over time (Soberón & Llorente 1993), as is expected to occur with some behavioural patterns, such as social interactions.

Soberón & Llorente (1993) proposed the following derivation of the Clench equation: $S(t) = at/(1 + bt)$; where $S(t)$ is the predicted number of behaviours at t, t is a measure of effort, a is the rate of increase at the beginning of sampling, and b represents the accumulation of behavioural acts. This function must be adjusted to the Sobs through a nonlineal estimation, which is available in statistical software packages.

Calculating repertoire completeness

The results from the nonlineal estimation include a value for the fitting of the model to the observed data (r^2), and the parameters intercept (a) and slope (b), which will be used to study repertoire completeness and research planning. First, the asymptote of the curve, which represents the predicted total number of behavioural acts, is calculated as a/b. Second, the proportion of observed behavioural acts (calculated from the predicted asymptotic repertoire size) is calculated as: $P_{Sobs} = T_{Sobs}/(a/b)$; where P_{Sobs} is the proportion of observed behaviours, and T_{Sobs} is the total number of observed behaviours. Third, the sampling effort required to reach a 90% level of completeness (a conservative level suggested by Moreno & Halffter 2000), is calculated as: $t_{0.90} = 0.90/(b \times (1 - 0.90))$. Note that as the total number of behaviours in a repertoire is reached, the effort required to record a new act is expected to be increasingly higher. Therefore, by definition, an infinite effort would be necessary to observe 100% of the behaviours.

A Practical Example of the BAC Method

The social interactions of black howler monkeys (Alouatta pigra)

To exemplify the application of the BAC method to primate behaviour, we will use data on the social interactions of black howlers observed in the Mexican state of Campeche. We recorded the social interactions of adult individuals belonging to six groups using the focal animal sampling method with a continuous recording technique during 1 h periods (our sampling effort unit). Each time that we observed a new type of social interaction (operationally defined as the way the behaviour of one individual was affected by the presence or behaviour of another, excluding vocalizations; Whitehead 2008; Table 1), we described it and recorded its time of occurrence. We collected a total of 1320 h of systematic data.

Table 1
Partial view of the matrix of social interactions of black howler monkeys

Social interactions*	Unit of effort†									
	S1	S2	S3	S4	S5	S6	S7	S9	…	S1106‡	…
Grooming	0	0	0	1	1	0	0	1	…	0	…
Contact	0	0	0	1	1	0	0	0	…	0	…
Finger stroking	0	0	0	1	1	0	0	1	…	0	…
Hand-holding	0	0	0	1	0	0	0	0	…	0	…
Touching	0	0	0	1	1	0	0	1	…	0	…
Grooming solicitation	0	0	0	0	0	0	0	1	…	0	…
Approach-avoiding	0	0	0	0	0	0	0	0	…	0	…
Supplanting	0	0	0	0	0	0	0	0	…	0	…
Tail embracing	0	0	0	0	0	0	0	0	…	0	…
Smelling	0	0	0	0	0	0	0	0	…	1	…
Scratching	0	0	0	0	0	0	0	0	…	0	…
Avoiding	0	0	0	0	0	0	0	0	…	0	…
Submissive position	0	0	0	0	0	0	0	0	…	0	…
Playing solicitation	0	0	0	0	0	0	0	0	…	0	…
Playing	0	0	0	0	0	0	0	0	…	0	…
Fleeing	0	0	0	0	0	0	0	0	…	0	…
Chasing	0	0	0	0	0	0	0	0	…	0	…
Punching	0	0	0	0	0	0	0	0	…	0	…
Fighting	0	0	0	0	0	0	0	0	…	0	…
Running towards	0	0	0	0	0	0	0	0	…	0	…
Hugging	0	0	0	0	0	0	0	0	…	0	…
Slapping	0	0	0	0	0	0	0	0	…	0	…
Threatening	0	0	0	0	0	0	0	0	…	0	…
Ignoring	0	0	0	0	0	0	0	0	…	0	…
Lay on top	0	0	0	0	0	0	0	0	…	0	…
Blocking	0	0	0	0	0	0	0	0	…	0	…
Intervening	0	0	0	0	0	0	0	0	…	0	…
Pushing	0	0	0	0	0	0	0	0	…	1	…

* Interaction types are ordered by moment of first observation.
† 1 h samples.
‡ Session where the last social interaction (pushing) was observed for the first time.

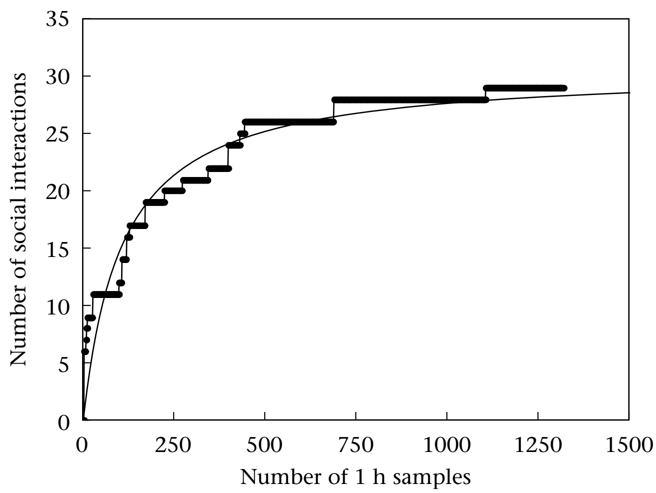

Figure 1. Behavioural accumulation curves of the social interactions of adult black howler monkeys in Campeche (Mexico), with a 1320 1-hour sampling effort: original (●) and fitted (–) data.

Results

Our behavioural data fitted well to the Clench model's function ($r^2 \geq 0.98$). During the 1320 1-hour samples we observed 29 different social interactions, and the estimated asymptotic repertoire size was 30.43 ($a = 0.283$, $b = 0.0093$); thus, the observed proportion of the total repertoire was 95%.

As expected, the number of new social behaviours decreased progressively with increasing sampling effort (Fig. 1). Although we reached the minimum threshold level of completeness (90%), to illustrate the application of this method to the planning of the sampling protocols, we calculated the effort required to observe 99% of the predicted repertoire size. Approximately 10 700 h of observations (9375 h more than those already completed) would be required to increase completeness by only 4%.

Conclusions

Behaviour accumulation curves may be an effective tool for analysing within- and between-repertoire completeness and efficacy, and can be used for calculating completeness of both detailed and simple ethograms, although completeness will be reached at different moments depending on the level of resolution. Additionally, the use of a standardized method allows direct comparisons between studies that describe behavioural repertoires, and lend rigour to those comparisons. For instance, the BAC method could be used to assess behavioural similarities between related taxa, and therefore, to study the influence of phylogeny in repertoire characteristics. Nevertheless, comparisons may only be performed when the level of resolution of repertoires is similar, as minor differences in the operational definition of behavioural categories may lead to significant variation in completeness calculations.

Another important advantage of the BAC method is that it allows planning of sampling protocols that are based on direct estimates of the effort required to obtain complete repertoires. Furthermore, when planning, it is essential that researchers identify contextual or temporal sources of variation in the expression of behaviour (e.g. circadian variation in activity, reproductive seasonality). For instance, black howlers' diet and activity patterns vary seasonally: during periods of increased fruit abundance, they feed mainly on fruits and spend more time moving and less time socializing (Pavelka & Knopff 2004). If our observations concentrated on that period, both the observed and the predicted repertoire size may have been much smaller, as fewer social interactions would have been observed. Therefore, the observation of a new interaction would result in a larger decrease in repertoire completeness.

Although we have described the use of the Clench equation, it is important to consider the specific characteristics of the behavioural repertoire that will be studied before selecting a model to project the accumulation curves. For instance, if a repertoire is composed of few acts, few rare acts, or there is previous research that informs on the total number of acts, other models, such as the linear dependence model, are more appropriate (Soberón & Llorente 1993). The linear dependence model assumes that the probability of observing new acts decreases proportionally to repertoire size. Thus, this model is more appropriate to the study of frequent behavioural acts (e.g. body postures). Independently from the model that is selected, the procedures described here may be applied by adjusting a different function to the nonlineal estimation calculations.

Finally, in addition to the BAC method, there are analytic procedures from the field of ecology, among others, that may be useful to the study of behavioural repertoires. Nonparametric estimators, for instance, may use the proportions of rare behavioural acts to estimate the total repertoire size, based on the assumption that the number of acts not yet observed increases when there are many rare behaviours in a repertoire (e.g. Smith & van Belle 1984; Hortal et al. 2006).

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