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# Appendix: A critical examination of rainfall variability measures used in behavioral ecology studies

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In these pages, Dunbar (1992) proposed two measures of rainfall variability for use in behavioral ecology models. Bronikowski and Altmann (1996) similarly recognized the need to quantify rainfall variability in a behaviorally meaningful manner in variable environments. In this note, we first present results from a simulation study exploring various metrics of annual rainfall distribution in an attempt to identify measures most appropriate for behavioral studies. We then show how the choice of measure affects the interpretation of the importance of rainfall variability to behavioral variability by using the data presented in Bronikowski and Altmann (1996).

The metrics analyzed herein include annual measures of rainfall evenness (the spread of rainfall across the months of a given year), the annual coefficient of variation across months (Sokal and Rohlf 1981), the standard deviation of mean monthly rainfall, and the number of dry months in a given year. We treat the evenness variables first and then analyze the other variability measures.

## Evenness of rainfall

For rainfall evenness, formulas were used from the species diversity literature. These measures reflect both the number of species and the relative abundance of these species (Magurran 1988). To apply diversity measures to rainfall, the number of species is analogous to the number of months in a year (i.e., a constant 12) and the proportion of the total sample in each species is analogous to the proportion of total annual rainfall in each month. A diversity index equal to one implies complete evenness (i.e., equivalent amounts of rain in each month) and an index equal to zero implies complete unevenness (i.e., all rain in 1 month). The diversity measures analyzed include dominance measures (Simpson, McIntosh, and Berger-Parker indices) and information theory measures (Shannon and Brillouin indices) (Table 1). Dominance measures weight the diversity index towards the dominant month (i.e., the month with the most rainfall). In practice, this means that as the amount of rainfall increases in one month, and the amounts in all the other months stay constant, a dominance diversity index decreases faster than a non-dominance measure (i.e., the more uneven rainfall will appear). Information theory measures use the natural logarithm of monthly proportional rainfall. Both dominance and information measures account for the

**Table 1** Diversity indices used in the simulation study ($n_i$ = rainfall per month, $N$ = rainfall per year, $p_i$ = proportion of rainfall per month, $S$ = number of months = 12)

| Index | Formula |
|---|---|
| Shannon | $D = \frac{-\Sigma(p_i \ln(p_i))}{\ln(12)}$ |
| Brillouin | $D = \frac{\ln(N!) - \Sigma \ln(n_i)}{\ln(N!) \quad \{(S-r)\ln[(N/S)!]\} - \{r \ln[(N/S)+1]!\}}$ where $N/S$ = integer($N/S$) and $r = N - S(N/S)$ |
| Simpson | $D = 1 - \Sigma(p_i^2)$ |
| McIntosh | $D = \frac{N - (\Sigma n_i^2)^{0.5}}{N - N^{0.5}}$ |
| Berger-Parker | $D = 1 - (n_{max}/N)$ |

Appendix to the article by Bronikowski and Altmann (1996) Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. Behav Ecol Sociobiol 39:11–25

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number of months and the proportion of the total amount of rainfall in each month.

Ideally for behavior studies, one would choose an index based on how well it correlated with either an animal's behaviorally critical physiological state in the case of a direct meteorological effect or, in the case of an indirect effect, how well it correlated with the availability of resources for the animals in question. In the absence of such information, we tested each index under varying rainfall regimes for the spread and sensitivity of its distribution (Table 2). We wanted to identify a measure that was sensitive to slight changes in rainfall and that had the largest spread under various rainfall regimes. These test cases included completely even rainfall (all 12 months had equal amounts of rain), completely uneven rainfall (only 1 month had rain), and scenarios in between (2 months had equal amounts of rain, 3 months had equal amounts of rain, etc.) We tested two additional scenarios: 12 months of unequal amounts of rain assigned with a random number generator, and 12 months of increasing amounts of rain.

Of the evenness measures, the Shannon and the Brillouin indices had the best properties. For the test cases described above, the Shannon index had a better spread than the Simpson or the Berger-Parker indices. (Note that for the Shannon index, in months with no rainfall, a small number must be used because the natural logarithm of 0 does not exist, an artifact of having a set number of "species" equal to 12). The spread of the McIntosh index was dependent on the total amount of rainfall, a problem circumvented by the indices that use proportional rainfall. The Brillouin index had a spread similar to the Shannon index and it also ranged from 0 to 1, but it was not well-suited to large amounts of rainfall, was less simple to calculate, and had no obvious benefit over the Shannon index.

Dunbar (1992) used the Simpson index to represent the evenness of rainfall in a study of the correlation between meteorological variation and behavioral variation in baboons. Two major disadvantages of the Simpson index are that its potential maximum is always less than one and it is dependent on the number of months with rainfall. Even if rain fell in every month of the year, the range of the Simpson index is not 0 to 1, but 0 to a maximum value of 11/12 or 0.917. Because the Simpson index fails to take dry months into account at all, it actually calculates evenness only across months with rain. For example, in a year with 12 months of equal rainfall, the maximum is 11/12, whereas in a year with 6 months each of equivalent rain and 6 months with no rain, the maximum value of the Simpson index is 5/6 or 0.83.

## Other variance measures

There is no *a priori* reason to expect that a diversity measure will be a truer reflection of the variability of rainfall across months than other variability measures, although some may be more appropriate for different purposes [e.g., diversity measures for primary productivity studies (Coe et al. 1976; Murphy 1975)]. Therefore, in our case study we also consider as variability measures the annual coefficient of variation, the number of months with less than 50 mm of rainfall per year (as in Dunbar 1992), and the standard deviation of mean monthly rainfall in a year (Table 3). After determining that the Shannon index was the most appropriate diversity measure above, the question became

**Table 2** Simulations for each of the diversity indices

| Month | Rain (mm) | Rain (mm) | Rain (mm) | Rain (mm) | Rain (mm) | Rain (mm) | Rain (mm) | Rain (mm) | Rain (mm) | Rain (mm) | Rain (mm) | Rain (mm) | Rain (mm) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| January | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 471 |
| February | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 234 |
| March | 100 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 75 |
| April | 100 | 100 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 30 | 300 |
| May | 100 | 100 | 100 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 339 |
| June | 100 | 100 | 100 | 100 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 322 |
| July | 100 | 100 | 100 | 100 | 100 | 100 | 0 | 0 | 0 | 0 | 0 | 60 | 176 |
| August | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 0 | 0 | 0 | 0 | 70 | 83 |
| September | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 0 | 0 | 0 | 80 | 389 |
| October | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 0 | 0 | 90 | 322 |
| November | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 0 | 100 | 87 |
| December | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 110 | 446 |
| Total | 1200 | 1000 | 900 | 800 | 700 | 600 | 500 | 400 | 300 | 200 | 100 | 660 | 3244 |
| Index | | | | | | | | | | | | | |
| Shannon | 1.00 | 0.93 | 0.88 | 0.84 | 0.78 | 0.72 | 0.65 | 0.56 | 0.55 | 0.44 | 0 | 0.90 | 0.94 |
| Brillouin | 1.00 | 0.93 | 0.90 | 0.85 | 0.80 | 0.74 | 0.68 | 0.60 | 0.49 | 0.33 | 0 | 0.90 | 0.95 |
| Simpson | 0.92 | 0.90 | 0.90 | 0.87 | 0.86 | 0.83 | 0.80 | 0.75 | 0.67 | 0.50 | 0 | 0.88 | 0.90 |
| McIntosh | 1.00 | 0.96 | 0.94 | 0.91 | 0.53 | 0.83 | 0.78 | 0.70 | 0.60 | 0.41 | 0 | 0.93 | 0.95 |
| Berger-Parker | 0.92 | 0.90 | 0.89 | 0.88 | 0.86 | 0.83 | 0.80 | 0.75 | 0.67 | 0.50 | 0 | 0.83 | 0.86 |

Table 3 Rainfall variability measures for the Amboseli case study. (Measures computed from Amboseli rainfall data. See Bronikowski and Altmann 1996, Table 1 and text for details.)

| Year | (*P*) – Rain (mm) | (*I*) Shannon Diversity | (*CV*) Coefficient of Variation | (*SD*) Standard Deviation | (*U*) Dry months <50 mm Rainfall |
|---|---|---|---|---|---|
| 1982 | 349 | 0.667 | 152 | 44.3 | 9 |
| 1983 | 376 | 0.615 | 145 | 45.4 | 10 |
| 1984 | 132 | 0.525 | 201 | 24.2 | 10 |
| 1985 | 297 | 0.681 | 134 | 33.2 | 10 |
| 1986 | 317 | 0.671 | 112 | 29.7 | 10 |
| 1987 | 250 | 0.733 | 121 | 25.2 | 10 |
| 1988 | 408 | 0.717 | 113 | 38.6 | 7 |
| 1989 | 488 | 0.756 | 109 | 44.3 | 7 |
| 1990 | 326 | 0.704 | 113 | 30.7 | 10 |
| 1991 | 407 | 0.605 | 129 | 43.9 | 10 |

Table 4 Regression analysis of rainfall variability measures and percent of daytime spent foraging for two social groups, (Alto's and Hook's) of Amboseli baboons. See Bronikowski and Altmann (1996) Table 2 for data. Significant coefficients are boldened

| *Analysis* | | $R^2$ | *F* (*df*) | *P* |
|---|---|---|---|---|
| Alto's percent of time spent feeding plus moving: | | | | |
| Rain and Shannon: | FM = 92 − 0.02 (*P*) − 21.2 (*I*) | 0.23 | 2.21 (2,6) | 0.19 |
| Rain and SD: | FM = 80 − 0.04 (*P*) + 0.10 (*SD*) | 0.20 | 1.98 (2,6) | 0.21 |
| Rain and CV: | FM = 78 − 0.03 (*P*) + 0.02 (*CV*) | 0.19 | 1.93 (2,6) | 0.22 |
| Rain and Dry Months: | FM = 62 − 0.02 (*P*) + 1.58 (*V*) | 0.27 | 2.51 (2,6) | 0.16 |
| Hook's percent of time spent feeding plus moving: | | | | |
| Rain and Shannon: | FM = 45 − **0.04** (*P*) + **62.8** (*I*) | 0.85 | 23.05 (2,6) | 0.0015 |
| Rain and SD: | FM = 89 + **0.05** (*P*) − **0.8** (*SD*) | 0.60 | 6.98 (2,6) | 0.0271 |
| Rain and CV: | FM = 107 − 0.04 (*P*) − 0.1 (*CV*) | 0.33 | 2.98 (2,6) | 0.13 |
| Rain and Dry Months: | FM = 97 − 0.02 (*P*) − 1.52 (*V*) | 0.00 | 0.81 (2,6) | 0.49 |

which one of the Shannon index (*I*), standard deviation (*SD*), coefficient of variation (*CV*), or number of dry months (*V*) was the most appropriate to use in a behavioral study for a rainfall variability measure. Note that the coefficient of variation and the Shannon index were highly negatively correlated ($r = -0.85$) so one would not want to use both. Also, number of dry months was negatively correlated with rainfall evenness measures, but we used it as opposed to number of wet months to remain comparable to Dunbar (1992).

We used the above four variability measures (*I*, *SD*, *CV*, and *V*) and total annual rainfall (*P*) in a series of multiple regressions to predict percent of time spent foraging (feeding plus moving) for the Amboseli baboon social groups (Alto's and Hook's) of Bronikowski and Altmann (1996, Tables 1 and 2 for data). The regressions did not include rainfall variability consistently (Table 4). For Alto's Group, the coefficient of (*I*) was negative, whereas the coefficient for (*V*) was positive, and the coefficients for (*SD*) and (*CV*) were positive and essentially zero. For Hook's group, the coefficient of (*I*) was positive, whereas the coefficients for (*V*), (*SD*), and (*CV*) were negative.

## Discussion

Our goal was to determine how to best represent variability in rainfall and perhaps other meteorological variables such as solar input in studies relating behavioral variation to environmental variation. In our analysis of diversity indices we found that the Shannon index had the best spread and sensitivity under different rainfall regimes. Of the non-diversity variability measures, the number of dry months index is quite problematic (as discussed in Bronikowski and Altmann 1996). But even if we ignore the number of dry months as a measure in the analysis of the Amboseli baboons (Table 4), the Shannon index and the two non-diversity measures of variability were not always consistently informative in regression modeling. If behavioral activity is truly affected by year-to-year differences in the monthly distribution of rain (mediated through vegetation cover), the relationship between activity and variability in precipitation should be robust to the choice among apparently reasonable variability measures. The fact that it was not suggests a problem in the assumed variance-vegetation or vegetation-activity relationships. Until these relationships are better understood and are able to inform the choice of measure, cautious interpretation of results seems appropriate when using one of these measures.

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