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Commentary

World-wide tiger beetle mandible length ratios: was something left unmentioned?

Jari Niemelä & Esa Ranta[1]

Niemelä, J. & Ranta, E., Integrative Ecology Unit, Department of Zoology, Division of Ecology, P.O. Box 17 (P. Rautatiekatu 13), FIN-00014 University of Helsinki, Finland

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In tiger beetles (*Cicindela*), mandible length correlates with prey size (Pearson & Mury 1979, Pearson 1980) and prey often appears to be a limiting factor (Hori 1982, Pearson & Knisley 1985). These, together with the observation that tiger beetles tend to co-occur with relatively few organisms with a similar resource use (Pearson 1988) make them well-suited for analyses of species packing and assembly of communities, one of the pertinent questions in ecology. Recently, Pearson & Juliano (1991), using world-wide data on tiger beetle communities, addressed the problem of morphological similarity of co-occurring species. Their data included 32 tiger beetle assemblages (77 species) around the globe in five distinct habitats (rain forest, open forest, sand, desert grassland, pond edge). As a measure of species-packing they used mandible length ratios (larger species over the smaller one). When an assemblage had more than two species, the average of the S–1 size ratios was used as an index of morphological closeness of the S species. That was by no means a novel approach (Hutchinson 1959), nor was that of using randomly constructed assemblages for comparisons with real ones (Simberloff & Boecklen 1981, Colwell & Winkler 1984, Mac Nally 1988, are key references).

Pearson & Juliano (1991) concluded that there were no good indications (in statistical terms) for larger than expected ratios in mandible sizes. Moreover, with the help of a linear model that corrected for species numbers they attempted to prove that the five habitats scored differing mandible size ratios. We now argue that their results are affected to a great extent by the strong coupling between the number of species and size ratios in species assemblages. Further, while using the linear model, Pearson & Juliano (1991) were not loyal to the rules of common statistical practice. Finally, we claim that they overlooked some ecologically interesting patterns readily visible in their data. The data we use here are available in Pearson & Juliano (1991).

Species richness vs. mandible size ratios

As a default, the average size ratio in an assemblage is a negative function of the number of species, a point made also by Pearson & Juliano (1991). For this reason (and the practice of calculating the mean of the size ratios among species) larger ratios tend to become increasingly rare with increasing species richness. Obviously, the outcome also depends on the total size range covered by all the species in the appropriate species pool.

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Using linear models, Pearson & Juliano (1991) examined the relationship between species richness and average mandible size ratio in species assemblages in the five habitats. For such comparisons to be of any value, homogeneity of the slopes is a necessity. Their table 3c demonstrates that the slopes vary a lot: rain forest, –0.089; open forest, 0.051; sand, –0.117; grass 0.223; pond edge, –0.056 (Fig. 1). Using analysis of covariance (ANCOVA) the null hypothesis of no differences among slopes is rejected ($F_{4,22} = 3.754$, $P = 0.018$). The significant interaction term simply means that different regression models between the two variables are needed for the different habitats (Sokal & Rohlf 1981:525). This result was known to Pearson & Juliano (1991: table 3a), yet they proceeded by calculating mean size ratios adjusted by the average number of species, this being $S = 3.1$ when calculated over all the 32 assemblages. Adjusting the number of species to the grand mean is just a convenience adopted in the ANCOVA algorithm. This procedure works well when the regression lines are parallel (in fact adjustment for any other number within the observed limits of the covariate works well with homogeneity of the slopes), but when the slopes are different it produces habitat rankings depending on the value of the species richness value adopted (Fig. 1).

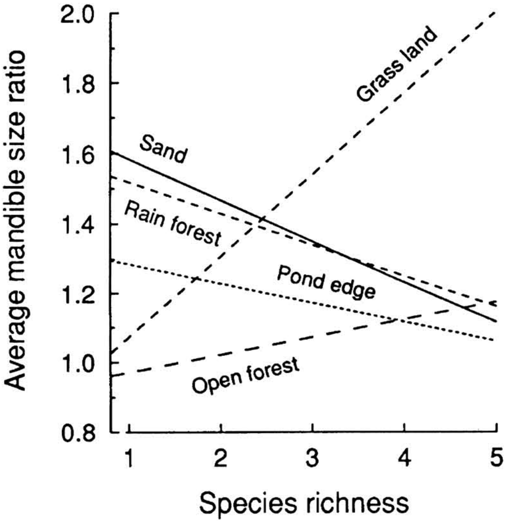

Fig. 1. Linear models for mean mandible length ratio as a function of species richness in the five different habitats. Model parameter values are from table 3c by Pearson & Juliano (1991). Depending on the value of the species richness adopted differing rankings of the five habitats are achievable in terms of the mandible size ratio!

To argue further that the number of species together with the minimum mandible size to a great extent governs the results obtained by Pearson & Juliano (1991) we refer to the data in their table 2. There the observed mandible ratio is listed with the number of species and the results of randomisation tests. For the null models Pearson & Juliano used four different species pools: world real, world distribution, regional real, and habitat real (Pearson & Juliano 1991: 227–229). Observed size ratios were compared with those of the four randomizations. Their statistical tests generally agreed over the four null models. However, there is a negative correlation between the number of species and observed size ratio ($r = -0.38$, $P < 0.05$), which becomes even more pronounced if controlled for minimum mandible size (partial correlation $r = -0.63$). We scored observed ratio greater than expected by 1 (*G*, in table 2 in Pearson and Juliano 1991) and smaller than expected by 0 (*L*). This is our response variable, our other variables being number of species (*S*) and minimum mandible size (*MI*). The logistic regression model predicting the likelihood for observing a greater than expected mandible size ratio, $\pi(S,MI)$, is (using world real randomizations)

$$\pi(S,MI) = \frac{\exp(\alpha + \beta_1 s + \beta_2 MI)}{1 + \exp(\alpha + \beta_1 s + \beta_2 MI)},$$

where $\alpha = 39.7(SE = 17.2)$, $\beta_1 = -3.18(1.49)$, $\beta_2 = -14.0(6.1)$, with a reasonably good fit ($\chi^2 = 12.11$, $df = 29$, $P = 0.998$). The negative signs of the β coefficients indicate that the likelihood of scoring greater than observed size ratio decreases both with the number of species and with the increasing mandible size of the smallest species in the assemblages (the outcome is not substantially affected by using data on the other three null models). This, we suggest, has very little to do with species interactions, rather it is a mechanical consequence of the effect of the limited size range from which species' morphologies are drawn. However, the potential for ecology being involved calls for analyses of patterns in mandible sizes. For example, why is there such a great variation in the smallest mandible length (1.41–3.20 mm) among assemblages in the USA? Unfortunately, this is beyond the data we have at our disposal.

Unmentioned patterns in mandible sizes

An interesting point that Pearson & Juliano (1991) did not examine is that the mandible sizes of certain species differ between habitats. To demonstrate this we use species identity and the mandible lengths presented in table 1 in Pearson & Juliano (1991). Two open forest sites in the USA (assemblage no. 6, $S = 2$ and no. 7, $S = 4$) share species. In no. 7, *Cicindela purpurea* has 95 % confidence limits for mandible length from 3.13 to 3.27 mm, while in no. 6 the values (2.98–3.10 mm) do not overlap with those in no. 7. Furthermore, in no. 7, *C. tranquebarica* (3.30–3.44 mm) is the largest species of four, while in no. 6 it is the smallest one (2.89–3.13 mm) of two and does not overlap in mandible size with its conspecifics in assemblage no. 7. Of the two other species in no. 7 *C. scutellaris* is 3.17–3.29 mm, while in Fox Valley, Canada (no. 15), it is clearly smaller (2.77–2.93 mm). Similar examples of non-overlapping mandible sizes within species between assemblages can be found from two water edge habitats which both had the same species composition (assemblages no. 10 and no. 11; measurements in mm) in the USA:

Assemblage:	no. 10		no. 11
C. togata	2.13–2.27	*	1.94–2.04
C. circumpicta	2.48–2.60		2.39–2.55
C. nevadica	2.59–2.77		2.54–2.62
C. fulgida	2.67–2.81	*	2.33–2.45
C. willistoni	2.76–2.90	*	2.55–2.63

In statistical terms the non-overlapping values (*) differ at $\alpha = 0.05$. Note also that all the species were smaller in assemblage no. 11. Uncovering reasons for these patterns would certainly be ecologically fruitful but is beoynd the data available to us.

Another aspect of the data worth inspection is species richness vs. species packing. The mean mandible length in the assemblages of from 2 to 5 species are plotted in Fig. 2. In two-species assemblages the smallest species has an average mandible size of 2.1 mm, while that of the larger one is roughly 2.7 mm. Adding the third species expands the range up to 3.2 mm and somewhat reduces the mandible lengths of the two smaller species (Fig. 2). In assemblages with four or five species no size-range expansion is observed. Rather, the new species pack within these limits. Accepting that mandible length correlates positively with the size of food particles used by tiger beetles, the shifts from $S = 2$ assemblages to assemblages of $S = 3$, and from $S = 3$ to assemblages with four or more species are interesting, indeed. This implies that in assemblages with ≤ 3 species new particle sizes are taken into use, while in assemblages with > 3 species, available resources are shared. Unfortunately, progress along these lines can be made only with original data, and not without considering species' abundance relationships. In fact, taking species abundances into consideration when examining morphological patterns in species assemblages was

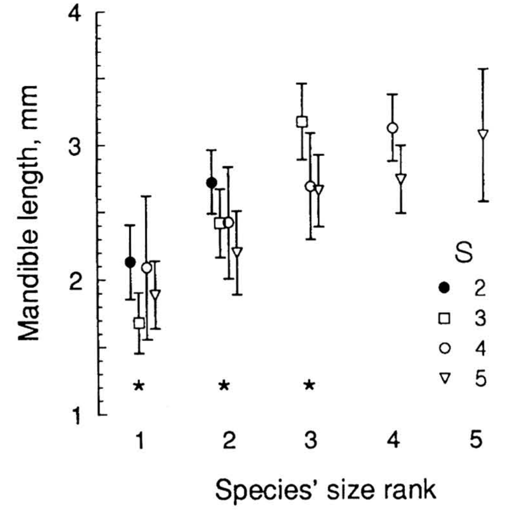

Fig. 2. Mean mandible length of species ranked from smallest ones (rank 1) to the largest ones in assemblages of from 2 to 5 species. Mean with 95% confidence interval is indicated. Asterisks indicate size-rank groups where *a posteriori* LSD-tests suggested differences at $\alpha = 0.05$ between assemblages of different species numbers.

one of the lessons learned in the rise and fall of the research on Hutchinsonian size ratios (e.g. Ranta 1984), which was also acknowledged by Juliano and Lawton (1990).

Conclusions

We have argued that much of the results discussed by Pearson & Juliano (1991) are caused by numerical artifacts only. Namely, the way of calculating the average of the size ratios between adjacent species in the morphological space conceals much of the information about species packing. More critically, the mean size ratio is, as a default, negatively correlated with number of species. Therefore, comparisons over assemblages differing in species richness will be spurious. The other main conclusion of Pearson & Juliano (1991), that there were significant differences between different habitats in the mean mandible ratio, was invalidated because of not obeying the standard usage of covariance analysis. In that analysis the assumption of homogeneity of slopes was not met.

Moreover, Pearson & Juliano (1991) did not discuss the interesting finding that mandible sizes in many species differed between habitats. This was most clearly demonstrated in two five-species assemblages along salt flat water edges in the central USA. These samples had identical species lists, but most species had non-overlapping mandible sizes. Such variation is most relevant when focusing on species packing. Neither did Pearson & Juliano (1991) discuss the observation that there were no morphologically similar small species in any of the 32 assemblages examined. In a similar vein, the pattern that the morphological space used by species in the assemblages did not increase after three species was ignored. It appears that species did not stretch the upper and lower mandible size limits in four and five-species assemblages but packed in between the extreme sizes already visible in assemblages with a smaller number of species. This observation indicates that mandible sizes in cicindelid species are very flexible and that understanding the forces determining their size in any given assemblage (habitat) requires additional research.

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References

Colwell, R. K. & Winkler, D. W. 1984: A null model for null models in biogeography. — In: Strong, D. R., Simberloff, D., Abele, L. G., & Thistle, A. B. (eds), Ecological communities: conceptual issues and the evidence: 344–359. Princeton Univ. Press, Princeton, NJ.

Hori, M. 1982: The biology and population dynamics of the tiger beetle, Cicindela japonica (Thunberg). — Physiol. Ecol., Japan 19:77–212.

Hutchinson, G. E. 1959: Homage to Santa Rosalia or why are there so many kinds of animals? — Am. Nat. 93:145–159.

Juliano, S. A. & Lawton, J. H. 1990: The relationship between competition and morphology. 1. Morphological patterns among co-occurring dytiscid beetles. — J. Anim. Ecol. 59:403–419.

Mac Nally, R. C. 1988: On the statistical significance of the Hutchinsonian size-ratio parameter. — Ecology 69:1974–1982.

Pearson, D. L. 1980: Patterns of limiting similarity in tropical forest tiger beetles (Coleoptera: Cicindelidae). — Biotropica 12:195–204.

— 1988: Biology of tiger beetles. — Ann. Rev. Ent. 33:123–147.

Pearson, D. L. & Juliano, S. A. 1991: Mandible length ratios as a mechanism for co-occurrence: evidence from a world-wide comparison of tiger beetle assemblages (Cicindelidae). — Oikos 60:223–233.

Pearson, D. L. & Knisley, C. B. 1985: Evidence for food as a limiting resource in the life cycle of tiger beetles (Coleoptera: Cicindelidae). — Oikos 45:161–168.

Pearson, D. L. & Mury, E. J. 1979: Character divergence and convergence among tiger beetles (Coleoptera: Cicindelidae). — Ecology 60:557–566.

Ranta, E. 1984: Proboscis length and the coexistence of bumblebee species. — Oikos 43:189–196.

Simberloff, D. & Boecklen, W. 1981: Santa Rosalia reconsidered: size ratios and competition. — Evolution 35:1206–1228.

Sokal, R. R. & Rohlf, F. J. 1981. Biometry, 2nd Edition. — Freeman, New York. NY.