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Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants

SUSAN J. MAZER[1]* and NATHANIEL T. WHEELWRIGHT[2]
[1]*Department of Biological Sciences, University of California, Santa B*[illegible]

[illegible] spherical fruits of equal [illegible] fitness is enhanced by seed dispersal by many individuals and species of birds, natural selection should favour increasing fruit elongation with increasing fruit size in bird-dispersed plants. According to thi[illegible] view, this allometric pattern would be adaptive. Alternatively, fruit shape in bird-dispersed plants may be constrained by development or phylogeny. To dete[illegible] whether there was any support for the adaptive allometry hypothesis, we exa[illegible] allometric relationships between length an[illegible] diameter in fruits and seeds in a group of neotropical bird-dispersed plant species. Using the major ax[illegible] technique, we regressed ln(diameter) on ln(length) for fruits and seeds at various tax[illegible] [illegible] expected by chance. Esti[illegible]ated slopes of the regressions of fruit length on fruit diameter were < 1 within 15 of the 19 individual *O. tenera* trees, among tree means within *O. tenera*, among [illegible] slopes estimated by major axi[illegible] [illegible]

[illegible] Monteverde; tropical ecology

Introduction

Fruits have evolved to promote seed dispersal by a variety of means. A fruit's form can ofte[illegible] reveal whether its seeds are [illegible] taxo[illegible]mic [illegible]

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* To whom correspondence should be addressed

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affiliation. Fruits of bird-dispersed plants tend to be characterized by [illegible] size, rounded shape, soft and nutritious pericarp, conspicuous colour, obvious and accessible presentation, persistence on the plant and the abs[illegible]

[illegible] [illegible]mann, 1989; Will[illegible]

1989) [illegible]

evolution of fruit traits. Birds discriminate between fruits within and among species on th[illegible] of a variety of features (e.g. size, colour, phenology, nutritional value, accessibility and ri[illegible] and as a result the[illegible]

[illegible]uence of producing a large seed. What adjustme[illegible] in fruit or seed shape are favoured in order to reduce the negative impact of [illegible] fruit size on seed dispersal?

[illegible]

interspecific variation in [illegible] found that fruit length and diameter of vertebrate-dispersed plants of the Iberian Peninsula [illegible] emphasizes the importance of considering alterna[illegible] hyp[illegible] 1992). For example, Herrera (1992) demonstrated that phylogeny (tax[illegible]omic membership) was more high[illegible] correlated with fruit shape than dispersal mode and argued that [illegible] morphogenetic and physical [illegible] such as [illegible]

[illegible] among species of the Lauraceae [illegible] among [illegible] plant [illegible]

[illegible] Rica, from the 10 000-hectare Monteve[illegible] Forest Reserve and from surrounding woodlots (10° 18′ N, 84° 48′ W; Holdridge, 1967; see Wheelwright (1985) for a more [illegible] complete description of the [illegible]).

Detection of allometric relationships

Using the major axis [illegible]

[illegible] least-squares linear regression; in the case of this [illegible] a more conservative test of the hypothesis of negative [illegible] major axis regression produced confidence intervals that [illegible] produced by either reduced [illegible] more positive) regression sl[illegible] study, major axis regression prov[illegible] allometry of fruit shape. In our ana[illegible] averaged 5 [illegible] and the rationale for preferring major axis regression in studies of allometry, see Harvey and Pagel (1991).

In ge[illegible] [illegible] length < 1 indicated negative [illegible]metry. We used the 95% confidence interval (CI) of the regression slope (α) to evaluate whether allometric coefficients were statistically significantly different from 0 or 1 (the lower limit of the 95% CI of the regression slope exceeded 0 or the upper limit was < 1 [illegible]

[illegible] the CI of the slope included both 0 and 1, a result that occurred when sample size was small or when variation about the regression line was high, the slope was n[illegible]idered to be statistically significan[illegible] from [illegible] several cases, the CI was undefined due to small sample size and low r^2; in these instances [illegible]

[illegible] statistics represent mean (x) ± [illegible]

[illegible] the co[illegible]

[illegible] fruit and seed shape at two levels in *O. tenera*: among mature fruits within each tree and among individual trees within the population, using tree means.

Interspecific studies: 21 species in the Lauraceae. Mature fruits were co[illegible] additional species of the Lauraceae (Table 1, number of fruits [illegible]

[illegible] the Lauraceae described above (plus four more species for which sample sizes were too small [illegible]

Table 1. Mean (± 1 SD) fruit and seed dimensions for 21 bird-dispersed tree species in the Lauraceae

[illegible]	*n*	Fruit length (cm)	Fruit diameter (cm)	Fruit slope	Seed length (cm)	Seed diameter (cm)	Seed slope
Aiouea costaricensis	12	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

known. The most recent taxonomic treatment of the Lauraceae of Costa Rica [illegible]

[illegible] genera within the family is [illegible] (R. Foster, [illegible]

Interspecific st[illegible] *plant community.* Fruits from 167 species in 122 genera and 63 plant families were collected in [illegible] mean fruit and seed characters were recorded [illegible] of three fruits per species. Fruits of all of the species were believed to be eaten and [illegible] seeds dispersed primarily by birds (Wheelwright *et al.*, 1984). Examining allometric [illegible]ationships among all bird-dispersed plant species at Monteverde by using species' means could [illegible]ult in a biased estimate [illegible] phylogenetic [illegible] In fact, we found significant differences among families with respect to the m[illegible] fruit [illegible]

[illegible] or capsules with soft pulp in the following taxa: *Centropogon* (Campanulaceae), Ericaceae [illegible] *Blakea*, *Conostegia* (Melastomataceae), [illegible]aceae), *Passiflora* (Passifloraceae), *Phytolacca* (Phytolaccaceae), *Fuchsia* (Onagraceae), *Hoffmannia*, *Xerococcus*, *Coccocypselum*, *Psychotria*, *Hamelia* (Rubiaceae) and [illegible]*anthes*, *Solanum*, *Wi*[illegible]

[illegible]

[illegible] trees (tree [illegible] C). A [illegible] cut down for reasons [illegible] fruits throughout th[illegible]

[illegible] July and 4 August, 1985), fruits were collected from each of two [illegible] third tree (tree B) was sampled on the first three dates, but was the[illegible] unrelated to this study. We could not [illegible] the ontogeny of individ[illegible] de[illegible] developing fruits and seeds required destructive sampling. Instead we measured haphazard sa[illegible]

[illegible] age groups corresponded to the following size classes: (1) fruits less than 3.7 mm in length, (2) fruits 3.7–10.0 mm in length and (3) fruits longer than [illegible]

Results

[illegible]

[illegible] ees, the calculated slope of the major a[illegible]

Figure 1. The relationship between fruit le[illegible]

considered significantly negatively allometric in only se[illegible]

[illegible] [illegible]gher proportion of trees with negatively allometric seed shapes than would [illegible] [illegible]2). The mean slope (omitting two trees in which high variance in seed sha[illegible]

Intraspecific studies: 21 species in the Lauraceae

Within in[illegible] species in the Lauraceae, the [illegible] be more elonga[illegible]

[illegible]

=0.46). h on fruit [illegible] man rank, [illegible] species was 0

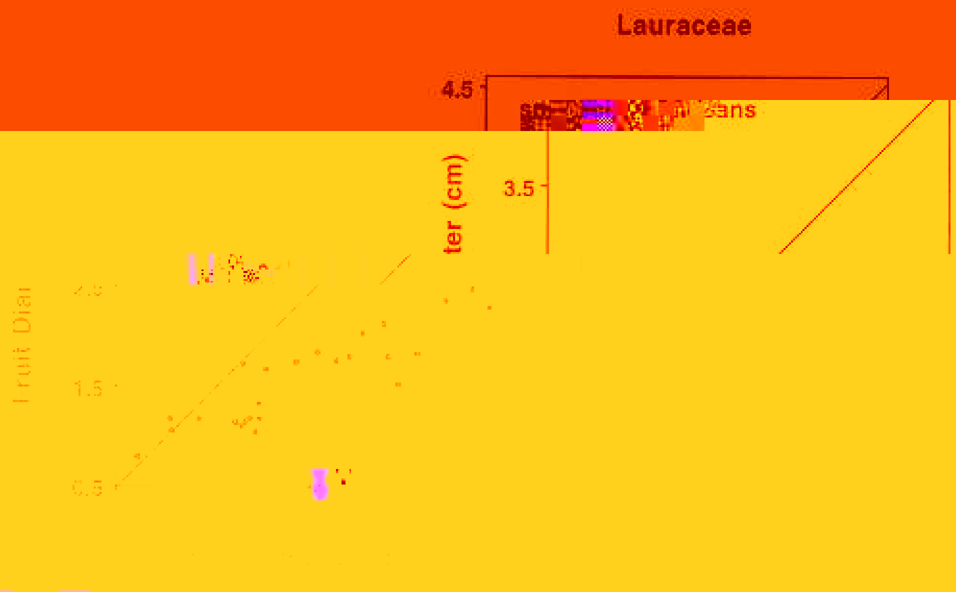
There was a positive correlation between the slope of the regression of fruit len diameter and the slope of the regression of seed length on seed diameter (Sp $r_s=0.67$, $n=21$ species, $p<0.002$).

In general, compared to fruits, seeds did not show less [illegible]ngation with increa [illegible] cies, the mean slope of the regression [illegible] fruit diameter on [illegible] ength (two-tailed [illegible] fruit length did not differ significantly from that of seed diameter on see paired t-test, $p=0.76$).

s than did [illegible] meter) on

Interspecific studies: Lauraceae

Among 25 species in the Lauraceae, large-fruited species produced more elongate fr small-fruited species (Fig. 3). The among-species slope of the regression of ln(fruit d ln(fruit length) was 0.63 ($r^2=0.83$), which was slightly less than the mean for 21 s [illegible]



[illegible]

[illegible] length) for all 167 available Monteverde species had a slope of 0.81, which was significantly <1 (Fig. 4; $r^2=0.73$, $p<0.0001$). However, when family means were used to reduce the potential bias due to unequal numbers of species per family, the relationship became indistinguishable from isometric (Fig. 5; $s=1.03$, lower bound of the CI =0.87, upper bound of the CI=1.22, $r^2=0.76$, $p<0.0001$). Among 63 bird-dispersed plant families at Monteverde, large-fr[illegible]

[illegible] species eaten piecemeal had a mean fruit length : diameter ratio of 1.17 ± 0.70, which was significantly smaller than that of fruits swallowed whole (1.25 [illegible]; Mann Whitney U test [illegible]

Interspecific [illegible] bird-dispersed plants from Monte[illegible]

[illegible] Monteverde, Costa Rica. Each point represents [illegible]

Devel[illegible]mental allometry: within- and bet[illegible]

[illegible] on ln(length[illegible]

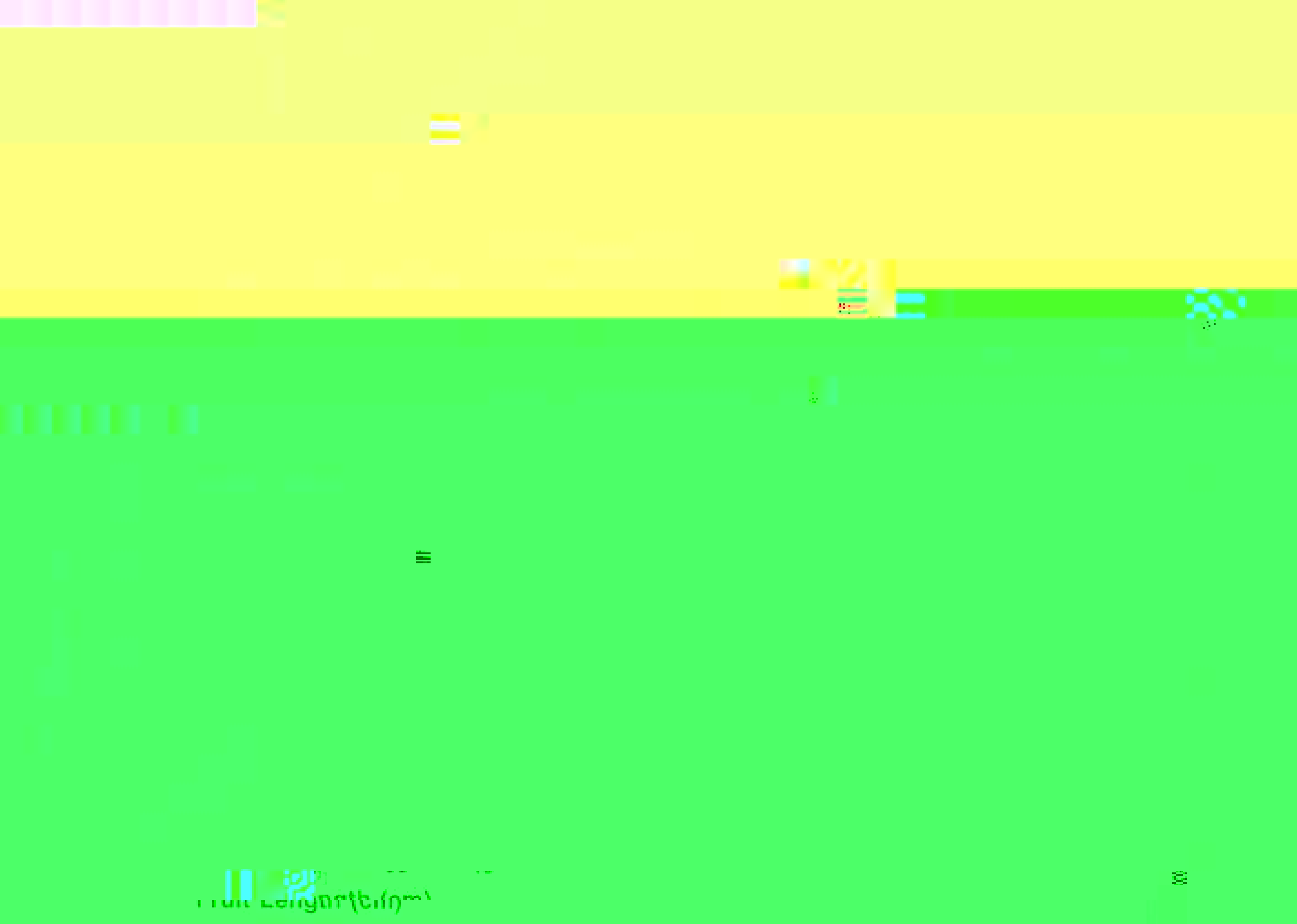


Figure 6. The relationship between fruit length and diameter among bird disp[illegible] species in the upland forests of Malawi. Each poin[illegible]

<1 in all trees, indicating a period of elongation (mean $s = 0.71$, $p < 0.0001$, $n = 46$ fruits). Late in development, when fruit length was > 10 mm, the slope of the regression was slightly > 1, significantly so in two trees (mean $s = 1.16$, $p < 0.0001$, n = [illegible] fruits; Fig. 7). There was a significant association between fruit size and elongation but no tree effect on fruit elongation (two-way ANOVA, $p < 0.0001$).

Unlike fruits, seeds tended to be elongate rather than spherical early in development (mean seed length [illegible] = 1.55). Nonetheless, the slope of the regression of ln(seed diameter) on ln(seed length) [illegible] significantly [illegible]

[illegible] seed diameter increased more rapidly than seed length, indicating [illegible] ontogenetic shift in the [illegible] of seed length and diameter.

clearly show that, for the Lauraceae at least, large fruits are not simply

fruits. The mature fruits of *Ocotea tenera* (Lauraceae) showed a

tion with size within individual trees, as fruit length increased more

although the [illegible] produced by major axis

difficult to rule out isometry in individual cases in all but seven trees, the fact

slopes were < 1 in 15 of the 19 individual trees provides strong evidence for

observed [illegible] fruits within trees of *O. tenera*.

scaled-up versions of sm

pattern of increasing elon

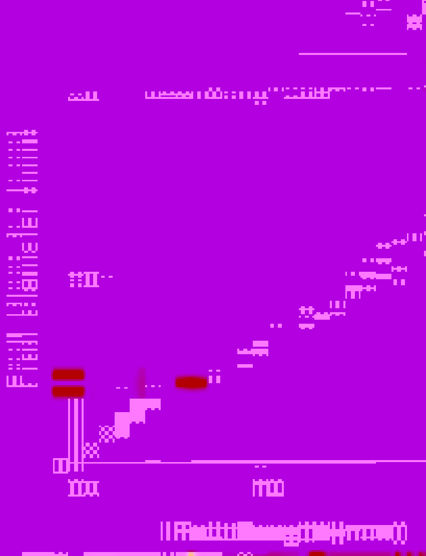
rapidly tha [illegible]

regression made

that estimated

negative allometry [illegible]

Similarly, we found a st



diameter during development in *Ocotea viridifolia* [illegible] (Lauraceae) in Monteverde, Costa Rica. Each point represents a single fruit ($n = 130$ fruits). Major [illegible]

growth, then positive allometric growth.

the *O. tenera* population: [illegible] tree produced large fruits, its fruits [illegible] tend [illegible] tree [illegible] among individuals with respect to fruit shape, which is a necessary condition for phe[illegible] change in allometry. Preliminary results suggest that variation in fruit form is highly heritable (Wheelwright, 1993). Within [illegible] other bird-dispersed species in the Lauraceae of Monteverde, Costa Rica, the relationship between fruit length and diameter also suggested negative allometry, although [illegible] statistically significantly different from isometry in most species.

Among 25 species within the Lauraceae, large-fr[illegible]

[illegible]

[illegible] ut length and diameter within [illegible] expected to mirror allometric relationships during ontogeny, with differ

[illegible] among species might be [illegible] t fruits, trees or species simply reaching maturity and stopping growth at different points along an ontogenetic curve. On [illegible] hand, if [illegible] choice among fruits is the primary selective force [illegible] influencing [illegible] shape of mature fruits, we might expect [illegible] distinct allometric relationships [illegible] changes in allometric scaling occurring relatively late in fruit [illegible] development.

We found that the [illegible] relative growth rates of fruit diameter and le[illegible]

[illegible]

[illegible] (among Monteverde family means). Similarly, [illegible] Herrera's (1992) and Dowsett-Lemaire's (1988) data showed isometry among species' [illegible] representing a variety of plant families.

[illegible] (1981) and [illegible] and Harvey (1988) have suggested that the taxon-level effect could [illegible] be a statistical artifact [illegible] when there are substantial differences [illegible]

[illegible] both [illegible] mean[illegible] Sm[illegible] larg[illegible] in strength or changed direction as one considered progressively less ecologically similar taxa, such as distinct families. The degree of negative allometry between fruit diameter and length is also likely to depend on the degree to which individual plants or species share seed dispersers. For example, if large-fruited species within a plant family are dispersed chiefly by large-gaped birds and small-fruited species are dispersed chiefly by small-gaped birds, allometric scaling may be negative within each species but isometric among species (Fig. 8). Be[illegible] confamilial species are more likely to share dispersers than [illegible] distinct [illegible] gape-limited seed dispersers. Moreover, birds can immediately evaluate fruit diameter but [illegible] seed diameter (except in the rare case of translucent fruits), so their discrimination of fruit shape should have a more important effect on seed dispersal [illegible]

[illegible] relative se[illegible]

[illegible] ic levels not on[illegible]cause of statistical artifacts but also because factors such as developmental constraints, maternal effects, variation in [illegible]llen donors, selection among genotypes, speciation, species selection and [illegible] contrib[illegible] differentially to [illegible]

[illegible] The model of adaptive allometr[illegible] negatively allometric relationship between fruit length and dia[illegible] [illegible] basis of such allometric patterns and it assumes tha[illegible] Finally, a key test of the model of disperser-media[illegible]

assumes that birds benefit by a [illegible] and by upper limits to fruit [illegible] individual trees and species on the [illegible] plants benefit by avian seed dispe[illegible] d selectio[illegible] an under studied aspect of fruits, their shape and to suggest that fruit shape may in fact bear a predictable relationship to fruit size in bird-[illegible] [illegible] Although we do not [illegible] [illegible] negative allometry in fruit shape at the exclusion of [illegible] interpretations, we propose several specific hypotheses to test the proposition that fruit shape reflects adaptation to different dispersers. We also wish to encourage the application of allometry in comparative studies in plant biology, where it has long been neglected. Traditionally reserved for describing morphological relationships among plant parts and crop yields (Bidabe, 1978; Hamid [illegible]

[illegible]

[illegible] land. This work was supported in part by a [illegible] [illegible] to S.J. Mazer from the National Science Foundation to [illegible] S.J. Mazer.

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[illegible] [illegible]ing birds and bird-dispersed plants in the tropics and [illegible]