

Fruit size in a tropical tree species: variation, preference by birds, and heritability

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Keywords: *Ocotea tenera*, Lauraceae, Seed dispersal, Frugivory, Plant reproduction

Abstract

Ocotea tenera (Lauraceae), an understory bird-dispersed tree, produces single-seeded fruits that vary in diameter from 1.4 to 2.4 cm. Much of the variation within a population at Monteverde, Costa Rica occurred within individual trees. The relative size of fruits produced by different trees remained generally constant over an 11-year period despite slight differences between years in the average size of fruits produced by a given tree.

Fruit-eating birds could thus express their preferences for particular fruit size characteristics by choosing among trees that have distinct distributions of fruit diameters, and between individually variable fruits within trees. In a field study of individually marked fruits, birds removed 46.2% of fruits; the rest of the fruits were destroyed by invertebrate (25.3%) and vertebrate (4.3%) pulp-feeders or aborted by the plant after remaining ripe but uneaten for as long as 100 days (24.2%). The four major avian seed dispersers of *O. tenera* each have gape widths exceeding all but the largest fruits. Birds preferred plants with greater-than-average-sized fruits; within trees, they favored larger fruits, apparently because net pulp mass increases with fruit diameter. Fruits that ripened early in the season were more likely to be removed and were removed more quickly than late-ripening fruits.

Based on mother-offspring regressions of mean fruit size, the phenotypic variation in fruit diameter in *O. tenera* is highly heritable, indicating the potential for an evolutionary response to selection by birds. Nonetheless, directional selection on fruit size or shape is likely to be inconsistent, constrained by genetic correlations, and weak compared to selection on traits like fecundity or phenology.

Introduction

When flocks of emerald toucanets (*Aulacorhynchus prasinus*) forage through the lower montane forests of Costa Rica, they encounter a diversity of fruits. On a given day, the birds might stop to feed on the clustered orange fruits of *Urera elata*, which measure only 3 mm in diameter, then move on to eat a few 22-mm diameter black drupes of *Beilschmeidia pendula* before swallowing 6-mm *Sapium oligoneuron* seeds covered by

red arils (Wheelwright *et al.* 1984). In a temperate-zone forest the variety of fruits seen by birds is less than in the tropics, but nonetheless birds such as American robins (*Turdus migratorius*) consume fruits as distinct as the 3-mm furry scarlet drupes of *Rhus copallina* and the 10-mm watery fruits of *Pyrus* sp. (Wheelwright 1986a; White & Stiles 1991).

Fruit variation within species, though less extreme than variation between species, can also be striking. Individual plants of the same species

often produce fruits that differ from those of other members of the population (Gorchov 1985). Even within a plant, fruits may vary. Fruit-eating birds must therefore make a series of choices at different scales: between plant species, between individual plants of a single species, and between individual fruits within the canopy of a particular tree.

Most recent research on fruit-eating birds and fruiting plants has tried to make sense of these choices by describing variation in plant reproductive traits and evaluating how different traits affect fruit selection and handling by birds (Willson 1986; Jordano 1992). The problems of fruit variation and avian preferences have implications for understanding the diversity of diets among fruit-eating birds, particularly dietary specialization versus generalization, as well as the degree of mutual dependence between birds and plants, and the strength of their interaction. Birds' choices translate into different rates of fruit removal from plants and influence seed dispersal patterns. Therefore, birds may affect plant fitness and direct the evolution of certain plant traits, but only when the following conditions are met. There must be variation in a particular reproductive trait within plant populations, birds must pick or handle fruits non-randomly with respect to that trait, their preferences must influence the probability of successful seed dispersal and seedling establishment, and at least some of the variation in the plant reproductive trait must be heritable. Once we determine to what extent these conditions apply in natural populations, we will have a much better understanding of the diversity of plant reproductive features and the degree to which they have been influenced evolutionarily by interactions with seed dispersers.

Of these conditions, recent work has clearly documented variation in fruit traits at various levels – between species, between populations, between individuals, and within individuals (Herrera 1981; Howe & Vande Kerckhove 1981; Janson 1983; Wheelwright *et al.* 1984; Gorchov 1985; Johnson *et al.* 1985; Pratt & Stiles 1985; Dowsett-Lemaire 1988; Foster 1990). We have also learned a great deal about the bases of birds'

preferences, specifically the role of plant features such as fruit size, coloration, structure and fecundity, as well as extrinsic, non-heritable features such as habitat or the characteristics of neighboring plants (Howe 1983; Gautier-Hiön *et al.* 1985; Wheelwright & Janson 1985; Denslow 1987; Jordano 1987a; Debussche & Isenmann 1989; Sargent 1990). We know far less about where birds drop seeds and how seed dispersal patterns influence seedling survival and establishment (Estrada & Fleming 1986, Murray 1988), much less plant fitness or the interaction between preferences and patterns of dispersal. With respect to the genetic basis of variation in fruit traits, we know next to nothing about non-commercial, long-lived plant species.

Nonetheless, there is abundant (albeit indirect) evidence that plant reproductive traits have responded to natural selection by birds and other animals. In this paper I concentrate on one such trait, fruit size, in an attempt to illustrate phenotypic variation in natural populations at different scales and show how seed dispersers potentially influence the evolution of fruit traits. The justification for focusing on fruit size is that, of the variety of traits that have been investigated, fruit size seems to affect handling and profitability directly and to bear a relatively predictable relationship to the feeding behavior and morphology of birds. Birds in nature and in captivity vary in how they select or handle fruits of different sizes. The reasons are various, but they include the physical difficulty of picking or swallowing large fruits because of gape limitations (Pratt & Stiles 1985; Wheelwright 1985a; Jordano 1987b; Lambert 1989), differences in profitability between large and small fruits due to differences in pulp:seed ratios (Herrera 1981; Howe & Vande Kerckhove 1981; Howe 1983; Jordano 1987; Snow & Snow 1988) or handling rates (White & Stiles 1991), and digestive problems associated with large versus small seeds (Levey 1987; Murray *et al.* 1992). Most of the studies cited above examined birds' fruit size preferences between plant species, but a few have shown that birds respond to fruit size variation between populations (Herrera 1981) or individual plants (Howe 1983; Wheelwright

1985a; Piper 1986; see also Bonaccorso 1979). In several temperate zone studies the relationship between a bird's gape or body size and the number or size of fruits that it ate was weak or non-existent (Johnson *et al.* 1985; Malmberg & Willson 1988, but see Jordano 1987b), presumably because temperate zone fruits tend to be small relative to birds' gapes, and because the range of fruit sizes is limited compared to tropical habitats (Wheelwright 1988a). In general, though, most studies agree that fruit size alone is one of the surest predictors of whether or not a bird will consume a fruit and disperse its seeds (Jordano 1992).

Within habitats, the distribution of gape widths of fruit-eating birds often mirrors the size distribution of the fruits on which they depend for food, further evidence that fruit size is an important feature of plants, one that could direct co-evolution between species and determine community-wide patterns (Wheelwright 1985a; Pratt & Stiles 1985; Dowsett-Lemaire 1988). Moreover, the allometry of fruit form – specifically, the tendency for larger fruits to be more elongated than smaller fruits (Mazer & Wheelwright, 1993) – indicates that the evolution of fruit shape may be constrained by the ability of potential seed dispersers to swallow fruits.

The common interpretation of such patterns of size and shape in the fruits of bird-dispersed plants is that they reflect mutual adaptation with contemporary seed dispersers. Such patterns could be influenced by selection at the level of species as well as genotype. For example, parallel distributions of fruit sizes and gape widths of fruit-eating birds, as well as upper limits on fruit size, could be the result of a process of species selection producing broad patterns. Contemporary fruit forms may have arisen in response to historical dispersers (Janzen & Martin 1982; Wheelwright 1988b). Furthermore, fruit size and shape conceivably could have evolved in response to selection on genetically correlated characters such as flower or leaf traits (Primack 1987).

To understand the evolution of traits such as fruit size, it is important to 1) quantify phenotypic variability among and within individual plants; 2)

measure correlations between fruit size and other traits of relevance to foraging birds, such as seed characteristics or crop size; 3) evaluate the constancy of the trait in different seasons and throughout the life of individual plants; 4) determine if fruits of distinct size differ in their profitability to potential seed dispersers; 5) show that birds can distinguish and actually choose among fruits on the basis of size at the level of species, individual plants, or individual fruits within a canopy; 6) demonstrate that birds' preferences result in differential survival and recruitment of the seeds of fruits of distinct sizes; and 7) determine how much of the variation is heritable versus induced by environmental factors such as climate or microhabitat. In other words, we need to ask whether fruit size really matters to birds, and if so, whether their choices influence plant fitness.

This paper addresses some of these questions by describing the nature of fruit variation in *Ocotea tenera*, a tree species which I have studied in Costa Rica since 1979. Diameter is used as the measure of fruit size most meaningful to avian seed dispersers (Pratt & Stiles 1985; Wheelwright 1985a; Lambert 1989). I describe variation at two levels: within a natural population and within individual plants. I also present the results of a study of fruit removal as a function of mean fruit size within plants and individual fruit size. Finally, I provide estimates of the heritability (h^2) of fruit diameter based on parent-offspring regressions.

Methods

Study species

Ocotea tenera (Lauraceae) is a small, dioecious, bird-dispersed tree which reaches a maximum height of 12 m and diameter-at-breast-height (DBH) of 20 cm. *O. tenera* occurs in clumped distributions along forest edges and in small light gaps, although once established, saplings can survive for many years in dense shade in the understory (Fig. 1). Endemic to Costa Rica, the species' range extends from an elevation of 1700 m

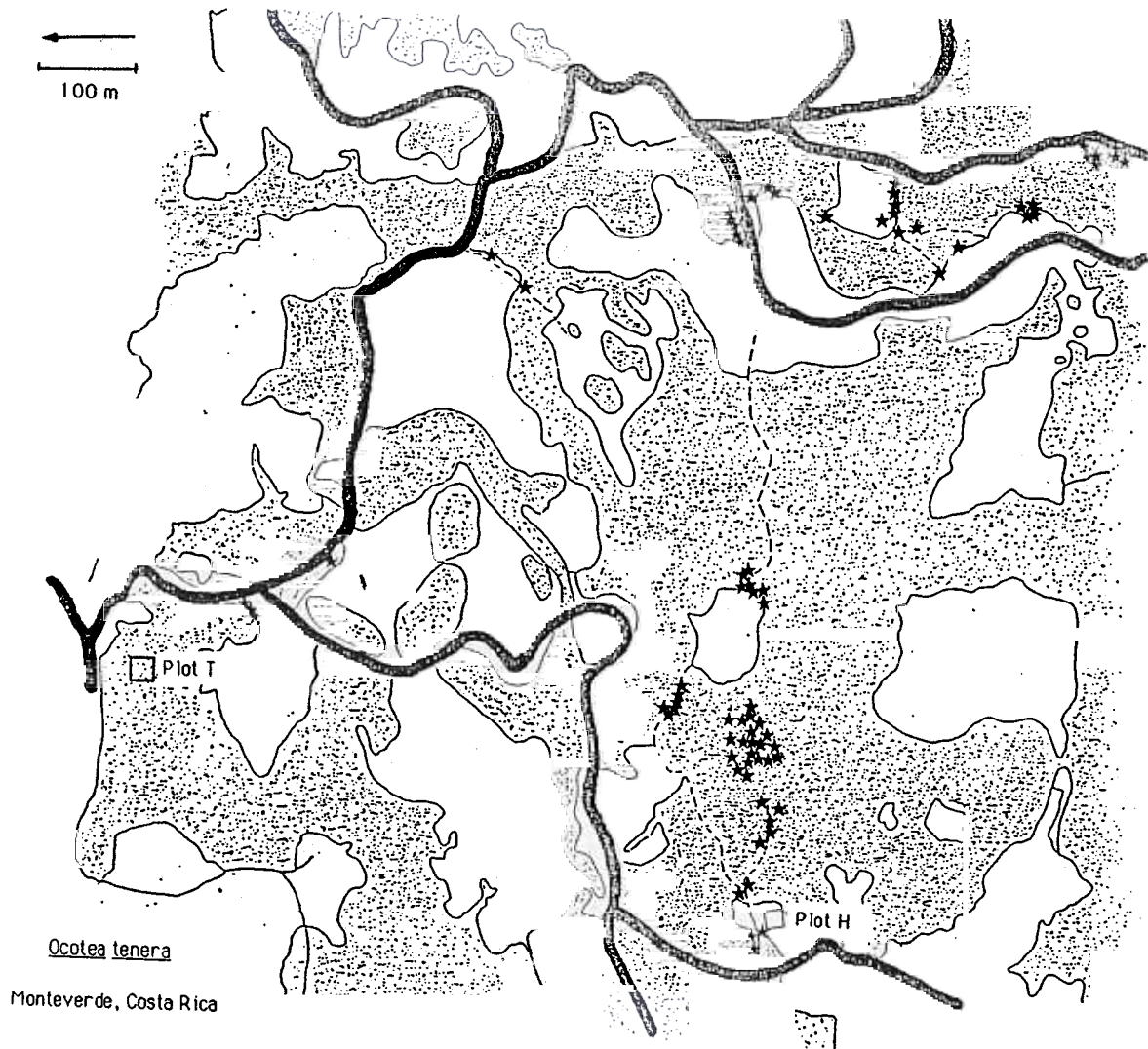


Fig. 1. Map of the study site. Stars indicate the locations of all reproductively mature *Ocotea tenera* trees known in 1980. Dark lines indicate dirt roads or major trails; dashed lines indicate minor trails. Open areas designate pastures, and stippled areas, forests. Plot T and Plot H were established in 1981 and 1984, respectively; in each plot, 32 trees of known maternity survived to reproductive maturity.

in the central highlands to as low as 50 m on the Caribbean slope; it is commonest between 1200 and 1350 m (Burger & van der Werff 1990). In earlier publications (Wheelwright *et al.* 1984, Wheelwright 1986b) the species was referred to as *O. bernouliana* (sic), now considered by Burger & van der Werff (1990) to be a distinct species.

O. tenera begins to flower at a median age of 5 years, height of 1.5 m, and DBH of 2–3 cm (Wheelwright & Bruneau, 1992). Its major polli-

nators are small, generalist wasps, bees, and flies. The fruits, borne in shallow receptacles at the end of enlarged, scarlet pedicels, become full-size about 6 months after pollination. As they ripen, they change in color from green to black over a 2–3 day period. The principal dispersers of *O. tenera* are resplendent quetzals (*Pharomachrus mocinno*), three-wattled bellbirds (*Procnias tricarunculata*), emerald toucanets, keel-billed toucans (*Ramphastos sulfuratus*) and black guan

(*Chamaepetes unicolor*) (Wheelwright *et al.* 1984). Birds swallow the fruits whole and regurgitate the large single seeds after about 50 min (Wheelwright 1991).

Study site and procedures

In 1980, as part of a study of the phenology of the Lauraceae (Wheelwright 1986b), I marked every reproductively mature individual of *O. tenera* encountered in 15 km² of lower montane wet and rain forests around Monteverde, Costa Rica (10° 18' N, 84° 48' W; see Lawton and Dryer (1980) & Wheelwright (1985b) for a more complete description of the site) (Fig. 1). Thereafter, all trees have been measured and their fruits counted individually at least once a year during the peak of fruit production in mid-dry season (mid-February to early March). For most of the female trees, haphazard samples of ripe fruits, sometimes comprising all that were produced by the tree, were collected in 1981, and their dimensions (length and maximum diameter of fruits and seeds) were measured to 0.1 mm using dial calipers; mass was determined to 0.1 g using portable balances. At least 10 fruits were measured per plant, except for those with crop sizes less than 10 fruits. I measured the fruits of several plants in at least 5 different years spanning an 11-year period.

To determine the factors influencing fruit removal by birds, I monitored the disappearance of ripe fruits from 29 trees in 1980–1. For trees with crop sizes less than the median for the population (30 fruits), I observed all fruits; for trees with larger crop sizes, I followed a subset of accessible fruits (those borne at heights lower than 3 m). Fruits were identified by writing a number in black permanent marker on the pedicel. For 524 fruits the diameter at the widest point was measured with calipers, as was the length of the exposed fruit (from the margin of the receptacle to the tip). From late December, 1980 until late May, 1981, 597 fruits were censused at 3-day intervals. The dates of ripening and removal (or damage caused by animals or desiccation) were determined. Because the stages of ripening were signaled by

gradual color changes, 3-day censuses were frequent enough to determine the exact day when fruits became fully ripe. Removal was obvious because of the empty receptacle left on the tree; I checked beneath plants for evidence that fruits had been dropped rather than dispersed. Pulp-feeding animals left characteristic marks of their activity (pericarp disks excised or totally naked seeds left by leaf-cutter ants (*Acromyrmex* spp.), patchy holes in the pericarp excavated by weevils (Curculionidae), and incisor scars produced by arboreal rodents). Virtually all removal of fruits was by birds, as indicated by direct observations of feeding behavior by birds (Wheelwright 1991), negligible fruit removal rates during the night, absence of seeds in mammal feces or beneath bat roosts, and examination of isolated dispersed seeds showing that the pulp had been cleanly removed.

In 1981 and 1984 I established experimental populations consisting of 185 *O. tenera* seedlings grown from seeds of known maternity, representing 11 maternal families; 64 plants survived until 1991. Of those, most proved to be males and a few had not reached reproductive maturity by 1991. For 25 female F₁ plants whose maternal phenotypes were known, fruits were collected and measured. The mean fruit diameters of siblings were then averaged within sibships and regressed against maternal mean fruit diameters to estimate heritability (h^2). Because pollen donors were unknown, the slope of the single parent-offspring regression equation was multiplied by 2 to calculate h^2 (Falconer 1989). Note that this method potentially overestimates h^2 for several reasons. First, it overlooks possible maternal genetic effects (e.g., cytoplasmic genes; long-term effects caused by maternal provisioning of the seed are less likely). Second, it assumes that F₁ trees grown from seeds taken from the same parent tree were half-sibs, when their relatedness may actually be greater if they shared the same pollen donor. Another potential problem is that fruits produced by F₁ trees may have resulted from mating between siblings in the experimental plots. In spite of these potential confounding factors, a strong parent-offspring resemblance in fruit traits almost cer-

tainly would indicate an appreciable genetic basis to phenotypic variation. Regressions and other statistical analyses were performed on Statview (Abacus 1988) on a Macintosh computer. Unless noted otherwise, descriptive statistics are presented as $\bar{x} (\pm 1 \text{ SD})$.

Results

Variation in fruit diameter

Within the natural *O. tenera* population, there was wide variability in fruit size. The smallest fruits (1.41 cm in diameter) were only 60% the size of the largest (2.37 cm; $\bar{x} = 1.82 \pm 0.14$ cm, coefficient of variation [CV] = 7.7%, N = 674 fruits). Although none of the fruits was too small to be eaten profitably by the major seed dispersers of *O. tenera*, the bigger fruits were too broad to be swallowed by bellbirds and perhaps toucans (Wheelwright 1985a).

Fruit diameter was positively correlated with other traits, including fruit length, fruit mass, seed diameter, seed length, and seed mass (linear regression; $r^2 = 0.21, 0.72, 0.77, 0.21,$ and $0.60,$ respectively; $P < 0.001$). From the perspective of fruit profitability (Herrera 1981), fruit diameter was positively correlated with pulp mass (fruit mass - seed mass) ($r^2 = 0.56$; N = 415 fruits; $P < 0.001$) (Fig. 2), although it was a relatively

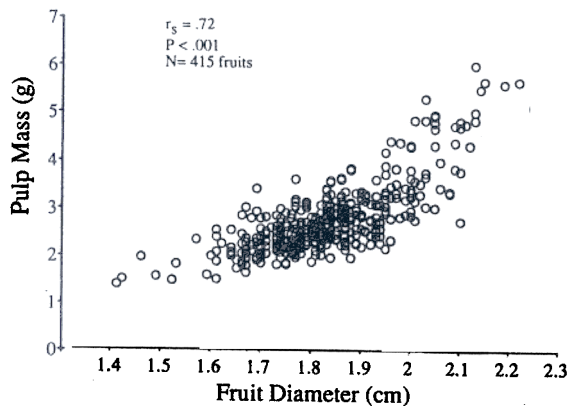


Fig. 2. Relationship between fruit diameter and pulp mass (fresh fruit mass - seed mass) in *Ocotea tenera*.

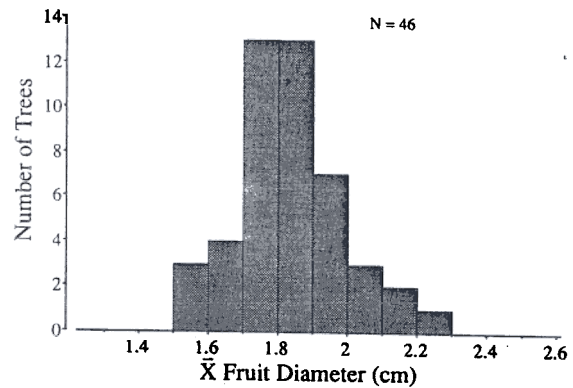


Fig. 3. Frequency distribution of the mean fruit diameters for 46 *Ocotea tenera* trees.

poor predictor of seed mass/fruit mass ($r^2 = 0.01$; $P < 0.05$). A relatively small increase in diameter was associated with a relatively large gain in edible pulp. For example, a 6% difference in fruit diameter (e.g., 1.8 cm to 1.9 cm in diameter) meant an 18% increase in pulp mass (2.61 to 3.08 g).

Trees differed substantially in the size of the fruits they produced. Some trees had characteristically small fruits ($\bar{x} = 1.64$ cm in diameter) whereas others produced large fruits ($\bar{x} = 2.22$ cm; \bar{x} of tree means = 1.88 ± 0.15 cm; one-way ANOVA comparing trees: $P < 0.001$) (Fig. 3). Fruit diameter within trees varied significantly among years; the magnitude of year-to-year differences varied between trees (two-way ANOVA: among years: $P = 0.004$; among trees: $P < 0.001$; year-by-tree interaction: $P = 0.002$). Nonetheless, absolute average fruit size difference within trees between years were slight (Fig. 4), and a tree's

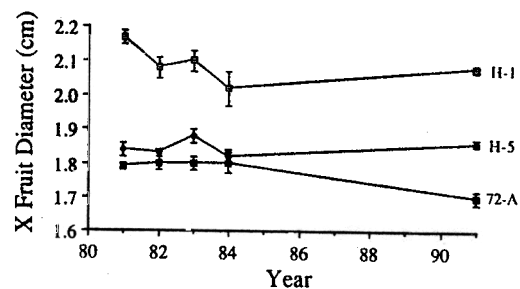


Fig. 4. Mean fruit diameter in three *Ocotea tenera* trees whose fruits were measured in at least five years between 1981 and 1991. Error bars represent $\pm 1 \text{ SE}$.

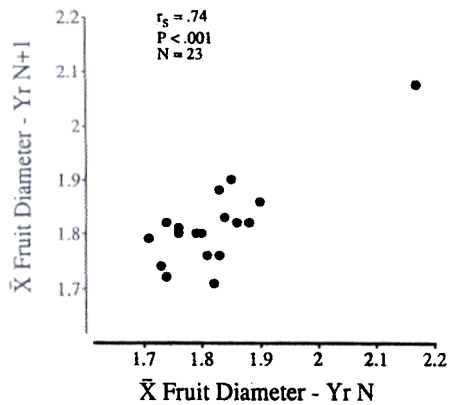


Fig. 5. Relationship between mean fruit diameter in a given year and mean diameter in subsequent years for eight trees whose fruits were measured in at least four years.

mean fruit diameter in a given year was a good predictor of its fruit diameter in subsequent years (Fig. 5).

There was also appreciable variation in fruit diameter within individual trees. In trees 72a and H-1, for example, the largest fruits had diameters 22–29% broader than the smallest fruits (range = 1.55–2.00 and 1.95–2.37 cm; $\bar{x} = 1.79 \pm 0.08$ and 2.11 ± 0.10 cm; CV = 4.5 and 4.7%, respectively). Thus, if fruit size influenced birds' choices of fruits, their preferences could be expressed at the level of trees or individual fruits within trees.

Fruit diameter and removal

Ocotea tenera fruits ripened over a 5-month period from late December into May, with 60.7% of fruits ripening during a 4-week period. Counting all marked fruits, only 46.2% were removed by avian seed dispersers, as judged by empty receptacles and no evidence of damage, predation, or dropped fruits. About an equal proportion of the remaining fruits was damaged by herbivores or fungi, or stayed uneaten on the plant until they desiccated or were aborted.

The proportion of a tree's fruit crop that was removed and presumably dispersed by birds varied from 0 to 100% (Fig. 6). Overall, fruits that were removed were slightly larger in diameter than

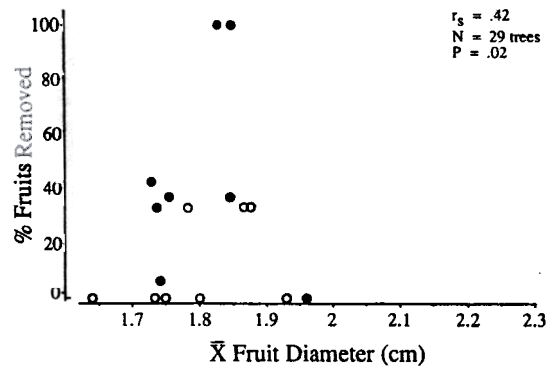


Fig. 6. Relationship between mean fruit diameter and the proportion of the fruit crop removed by avian seed dispersers within individual trees. Open circles represent trees with crop sizes less than the median for the population (30 fruits); closed circles represent trees with crop sizes exceeding the median.

fruits that were ignored or preyed upon (1.85 ± 0.14 cm vs. 1.81 ± 0.14 cm; $N = 213$ vs. 311; ANOVA: $P < 0.001$). Much of this was due to differences in removal rates between plants differing in mean fruit diameter, and did not necessarily indicate selectivity by birds within a canopy. Thus, there was a positive correlation between mean fruit diameter and the proportion of the fruit crop that was removed (Fig. 6). Nonetheless, in some of the trees, birds preferentially took larger fruits (ANOVA: $P < 0.05$).

For all fruits that were eventually removed, there was no correlation between diameter and the number of days between ripening and removal ($r_s = 0.07$; $N = 210$ fruits; $P = 0.31$). Nor was mean fruit diameter within a tree related to the mean duration of fruits on the tree ($r_s = -0.08$; $N = 29$ trees; $P = 0.72$) (Fig. 7).

The fact that there was a positive correlation between fruit diameter and the probability of removal, but there was no correlation between fruit diameter and the duration of ripe fruits on plants, indicates that other factors influence removal by birds and points out the necessity of analyzing several variables simultaneously. Therefore I performed a multiple regression with the proportion of the fruit crop removed as the dependent variable and each tree's mean fruit diameter, mean pulp mass, mean seed mass/fruit mass, crop size, and mean ripening date as independent variables.

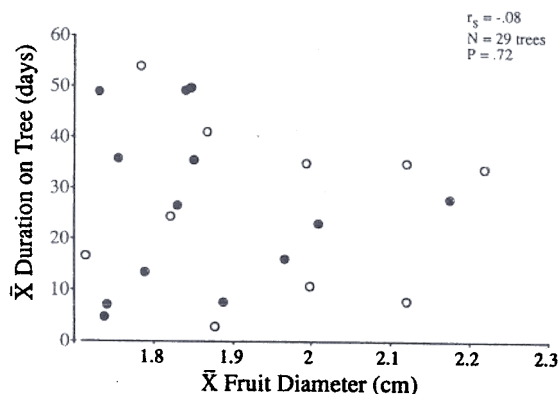


Fig. 7. Relationship between mean fruit diameter and the mean number of days between ripening and removal within individual trees. Open and closed circles as in Fig. 6.

Controlling for other variables, mean diameter continued to be positively correlated with the proportion of fruits removed ($P = 0.018$). The only other variable that had a statistically significant effect on the proportion of fruits removed was ripening date ($P = 0.005$): trees whose fruit crops ripened early in the season had a greater proportion of their fruits removed than those whose fruits ripened relatively late, regardless of crop size (Fig. 8). Overall, the multiple regression model including all independent variables was statistically significant ($P = 0.005$).

When a multiple regression was performed with the same independent variables and mean dura-

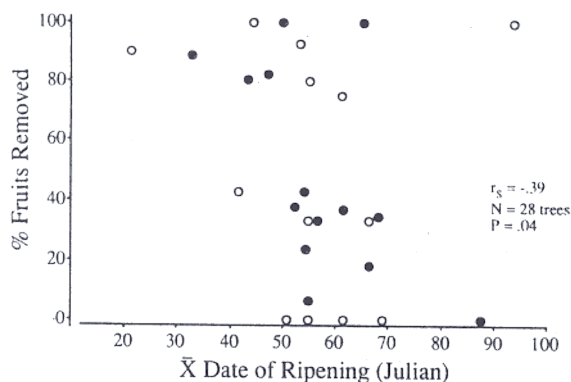


Fig. 8. Relationship between mean date of ripening and the proportion of the fruit crop removed by avian seed dispersers within individual trees. Open and closed circles as in Fig. 6.

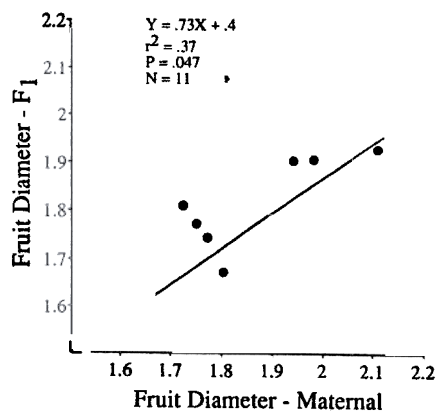


Fig. 9. Regression of mean maternal fruit diameter against mean offspring fruit diameter (averaged across siblings). $N = 11$ maternal lineages. Twice the slope in single-parent-offspring regressions provides an estimate of h^2 (c. 1.0).

tion of fruits as the dependent variable, only ripening date was related to mean duration ($P = 0.04$), and overall the model was not statistically significant ($P = 0.31$).

Heritability of fruit diameter

Upon reaching reproductive maturity, trees grown from seeds of known maternity produced fruits that closely resembled their mothers' fruits in diameter. Regression of the mean fruit diameters of maternal trees against those of their offspring yielded a significant positive correlation with a slope of $0.73 (\pm 0.32; N = 11$ maternal lineages; $r^2 = 0.30; P = 0.047$) (Fig. 9). Twice the slope gives an estimate for h^2 that exceeds 1.0, indicating that a large proportion of the variation in fruit diameter in *O. tenera* is genetic. In general fruit and seed dimensions in this species show high resemblance between female parents and their offspring ($h^2 = 0.61 \rightarrow 1.0$; Wheelwright unpubl. data), as do non-reproductive traits such as leaf shape (Wheelwright *et al.* unpubl.).

Discussion

To the extent that a fruit's characteristics affect its detection by potential seed dispersers, influences

its probability of being eaten or the time between ripening and removal, or determines how it is handled externally or processed internally, such traits may be the target of natural selection. The implications of such a conclusion are that the day-to-day interactions between fruit-eating animals and fruiting plants that biologists commonly document can have evolutionary significance. Moreover, much of the richness of reproductive features among animal-dispersed plants may legitimately be considered 'adaptations,' shaped by generations of interactions with animals acting as seed vectors. This requires, of course, that fruit traits have a genetic basis. Research in the field of seed dispersal and plant-animal interactions has explicitly or implicitly assumed that fruit characters influence the probability of dispersal, and that much of the phenotypic variation in those characters is heritable, but the longevity of most trees and the brevity of most studies have prevented a full assessment of such assumptions.

This study demonstrates that in at least one tree dispersed by birds, a fundamental fruit character, diameter, shows wide variation between and within individuals, in contrast to earlier studies which emphasized the constancy of seed (and by implication, fruit) size within species (Harper *et al.* 1970). Other species in the Lauraceae are equally variable in fruit morphology (Mazer & Wheelwright, 1993). Faced with a hierarchy of choices between trees that have distinct fruit traits, and within trees that produce fruits of varying sizes, avian seed dispersers appear to be discriminating foragers. Birds favored fruits of larger-than-average diameter, presumably because such fruits offered more pulp per fruit (although not necessarily a more profitable pulp:seed ratio) (Herrera 1981; Howe and Vande Kerckhove 1981; Piper 1986; Levey 1987; Murray *et al.* 1992). Birds' fruit-size preferences mean that plants with less-favored fruits disperse few or no seeds, and that, within canopies, some fruits are ignored and exposed for longer periods to pulp- or seed-damaging herbivores. If birds' preferences are relatively stable, they should have a compounding effect on a plant's seed dispersal success year after year, because mean fruit diam-

eter changes little throughout the course of a tree's life, at least in *O. tenera*.

Mean fruit diameter also changes little between generations within a lineage; in other words, it is highly heritable in *O. tenera*. Heritability expresses the percentage of phenotypic variation of a trait that is attributable to genotype (the additive genetic variance). Although my estimate of h^2 may be biased upward because of maternal effects and the assumption that F_1 trees were only half-sibs (see Methods), the results clearly show a strong genetic basis to fruit morphology. The significance of demonstrating that fruit diameter in *O. tenera* is heritable is that relatively small selective pressures can quickly drive evolutionary change in such traits. Selection on traits that are genetically correlated with fruit diameter could have effects similar to direct selection on fruit diameter (Prymack 1987). Traits that are most closely related to fitness, as fruit diameter might be expected to be, are ordinarily expected to have relatively low h^2 because most of the additive genetic variance has already been fixed by natural selection (Falconer 1989), but sufficient variability may be introduced by mutation or maintained by fluctuating selection to result in high heritabilities of traits such as fruit diameter.

If *Ocotea tenera* is representative of other species in the Lauraceae, which have fruits of similar size and form, share the same avian seed dispersers, and are an important component of neotropical forests (Wheelwright *et al.* 1984), there may be the potential for evolutionary responses on the part of those plants to birds' fruit-size preferences. Whether other plant taxa show equivalent variation in reproductive traits, interact with their seed dispersers in comparable ways, and exhibit high heritabilities in such traits is still unknown, but it is not unreasonable to expect qualitatively similar patterns (cf. Mazer & Wheelwright 1993).

The results of this study should not be construed to imply that directional selection on fruit size or any other reproductive character is likely to be strong or constant. Depending upon whether one views the amount of variation in fruit size found in this study as wide or narrow, the high

heritability of fruit traits could be interpreted as reflecting stabilizing selection (Gorchov, pers. comm.). In any case, the maintenance of extensive phenotypic variation in fruit size within the *O. tenera* population appears to be inconsistent with strong directional selection, and it may be explained by a variety of factors. First, this study has not answered a crucial question: does speedy fruit removal in fact result in measurably improved plant fitness? If it does not, directional selection on fruit diameter would be weak, despite apparent fruit size preferences by birds. Second, there is clearly ample phenotypic variation in fruit form in *O. tenera*, and regressions of maternal traits against that of their daughters established that the variation is heritable, but to what extent is variation within fruit crops caused by differences in pollen donors, and what is the genetic basis of those effects? A recent study using molecular techniques to examine population genetic structure and investigate paternity and maternity in seedlings and saplings in *O. tenera* may be able to fill in many important details about the relationship between fruit removal by birds and plant fitness, and shed light on the paternal effects on fruit form (Gibson and Wheelwright, unpubl.). Third, even though this study shows that fruit diameter hardly fluctuates between years, and other studies suggest that interactions with seed dispersers, or at least assemblages of dispersers, remain quite constant in the face of wide annual variation (Howe 1983), other parameters change extensively, such as a plant's fecundity (Wheelwright 1986b, unpubl.) and, perhaps more importantly, the fecundity of its neighbors (Howe 1983; Sargent 1990). Fourth, for many reasons plants may be constrained in their evolutionary response to selection by avian seed dispersers. Among these are fluctuating selection in space and time, opposing selection, asymmetries in generation lengths of animals and the plants whose seeds they disperse, and genetically correlated characters (Wheelwright & Orrians 1982; Herrera 1985; Wheelwright 1988b; Mazer & Wheelwright 1993). Slight preferences on the part of birds for a trait such as fruit size, for example, may be overshadowed by their response to differences in fecundity

between plants (Howe 1983; Murray 1987; Jordano 1987a).

General rather than specific adaptation of plants to their seed dispersers is the more likely outcome of evolutionary interactions, and may explain both diversity and convergence in fruit traits within habitats and between taxonomically distinct plant communities. The general premises of models of coevolution between mutualists look more credible in light of this study because, in at least one neotropical tree species, reproductive traits are highly variable, they matter to birds, and they have a genetic basis.

Acknowledgements

I thank Monteverde residents, especially D. Lee, S. Perly, the Hoges, Hollanders, Stuckeys and Trostles, for permitting me to study on their land; F. Joyce, Jr., S. Sargent, J. Wolfe, and W. Zuchowski for helping to establish and monitor the experimental plots; D. Gorchov, T. Fleming and A. Estrada for helpful comments on an earlier draft; V. Sork for illuminating discussions about maternal genetic effects; and the Organization for Tropical Studies, the Douroucouli Foundation, the National Science Foundation, the Council for International Exchange of Scholars, and Bowdoin College for support of my research.

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