3. For Lana, the background color of the symbol originally indicated word class. However, all of the words used in the above study were assigned a single background color to prevent confounding. For Sherman and Austin, background color never indicated word class.
4. Tools included scrub brush, shovel, screwdriver, juice squeezer, ball bearing, locking pin, spoon, saucepan, hammer, sink stopper, knife, scissors, cutting board, and can opener. Foods included ice cube, peanut, celery, peanut butter, jelly, raisins, cabbage, grapefruit, cucumber, chim crackers, turnips, white potatoes, lemon, and cheese.
5. Only Sherman and Austin were continued in this later phase, since Lana's inability to encode referential relationships symbolically implied that it would be fruitless to move from real objects to photographs, in her case.
6. Because the Yerkish symbols are arbitrarily assigned to all objects, it is not possible to decide, simply by looking at the symbol, whether it represents a food or a tool. Austin was given one more than Sherman because one of the test lexigrams was to be used with Sherman in another study.
7. It is possible to unintentionally cue chimpanzees by the way in which one holds objects, touches the chimpanzees, looks at the stimuli, and so forth. In order to make certain that such cuing was not occurring, we reran the final phase of the study with Austin and Sherman. During this retest (i) the experimenter did not know which lexigram the chimpanzee was viewing, and (ii) lexigram presentation was completely random; any lexigram could be followed by itself or by any other lexigram any number of times. No constraints were placed on the number of consecutive food and tool responses. Sherman was correct on 68 of 70 trials, and Austin was correct on 65 of 70 trials.
8. Individuals who are interested in seeing the work reported in this report may purchase a color video cassette from the authors.
9. For more detailed account of this study, see E. S. Savage-Rumbaugh, *Ann. N.Y. Acad. Sci.*, in press.
10. Supported by grants from the National Institute of Child Health and Human Development (HD-06016) and from the Division of Research Resources, National Institutes of Health (RR-00165).

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Nutmeg Dispersal by Tropical Birds

Abstract. *Frugivorous birds preferentially remove fruits from Panamanian* Virola *trees where the ratio of edible aril to indigestible seed is high. A negative correlation between the proportion of the crop removed and mean seed size explains 59 percent of the variance in removal, suggesting that birds minimize ingestion of useless bulk.*

Many tropical trees bear fruits that attract animals (*1*), and many tropical vertebrates consume fruit and either disperse or destroy seeds (*2*). Relationships between frugivores and plants are of general interest in tropical ecology because the mortality of seeds and seedlings under parent trees is density-dependent (*3*) and because dispersal by animals results in a more even distribution of adult trees than passive dissemination by gravity or wind (*4*). Factors promoting efficient seed removal by animals are poorly understood. Synthetic treatments have had to rely upon anecdotal accounts of animal visitation at plant species that vary widely in fruit structure, nutritional reward, and crop size (*2, 3, 5-7*). No one has shown that differences in fruit quality within a population influence seed removal. Here we report dramatic differences in the proportions of seeds removed from individual *Virola surinamensis* (Rol.) Warb. (Myristicaceae) trees that vary in mean aril (pulp) and seed weights. Frugivores preferentially remove fruits from trees producing small seeds; small seed size is generally associated with a high ratio of edible aril to indigestible seed. Partial correlation analysis uniquely distinguishes two attributes of fruits: dispersibility and seed size likely to influence seedling survival.

Virola surinamensis is a canopy tree of the mature wet forest of Barro Colorado Island, Panamá (*8*). Between 20 May and 7 September 1979, 17 trees produced 214 to 10,412 mature fruits (median 2,082) (*9*). Golf ball-sized capsules opened in early morning and midmorning to expose the unit of dispersal, a single seed 2 cm long surrounded by a brilliant red aril (Fig. 1). The hard seed tastes bitter; 15 percent of its 2.0 ± 0.4 g (dry weight) consists of tannins, which inhibit protein activity when ingested by animals (*10, 11*). In contrast, less than 3 percent of the 0.9 ± 0.1 g (dry weight) of the aril consists of tannins. The arils are among the most nutritious known (*12*); edible components include 9.2 ± 1.5 percent usable carbohydrate, 63.1 ± 14.0 percent fat, and 2.5 ± 0.7 percent proteins, leading to an overall energetic reward of 6.5 ± 0.9 kcal per aril (*10*). Six birds swallow the aril and seed and regurgitate the seed in viable condition; one monkey passes intact seeds through the digestive tract (Table 1) (*13*). With the exception of the tityra, a fruit thief that eats arils without ingesting seeds, all birds attempt to swallow all arillate seeds encountered. Selection by birds is of trees, not of fruits within trees. Monkeys actively smell and reject fruits within a tree crown, indicating that their choice is based on a chemical cue (*14*).

Unless fruit thieves intervene (*15*), specialized frugivores should consistently remove fruits with highly nutritious rewards (*2, 5, 16*). The predominance of a small set of highly frugivorous birds meets the first expectation, and the mean level of seed removal of 62 percent (± 19 percent) meets the prediction of efficient dispersal of nutritious fruits. However, proportions of seeds removed from individual trees range from 13 to 91 percent (*9*). Such variation could occur (i) because the quantity of fruit produced influences removal success (*5, 16*), (ii) because nutritional quality of the arils varies from tree to tree, or (iii) because plants offer different expectations of edible reward and indigestible bulk to birds that must swallow fruits (*17*). Large-seeded fruits burden birds with excess weight, and reduce feeding efficiency by filling the crops of the birds with useless bulk (*18*).

The first hypothesis was tested by regressing the proportion of the seeds removed against crop size. Neither linear nor second-order polynomial fits were significant ($P > .25$). Rewards are apparently sufficient to ensure that birds visit small trees and deplete fruits at large ones; variance in crop depletion must be attributable to factors other than crop size.

The second hypothesis presumes that

Fig. 1. A *Virola surinamensis* fruit as presented to birds. The unit of dispersal is a single inedible seed surrounded by an edible aril of brilliant red coloration. Seeds average 20 mm in length by 16 mm in width; arils are 1 mm thick.

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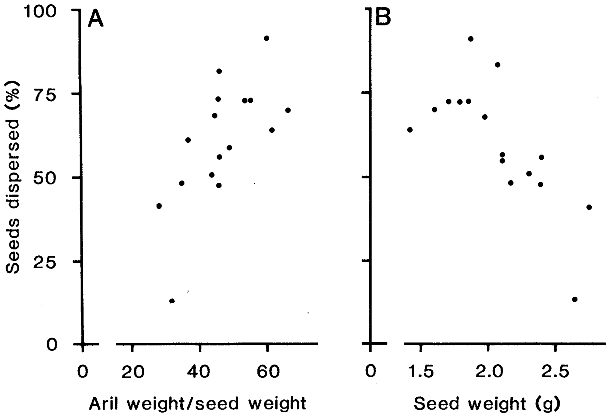

Fig. 2. Crop depletion and fruit attributes of individual *Virola* trees. (A) Proportion of seeds removed plotted against the ratio of aril to seed dry weight ($r = 0.72$, $P < .001$). (B) Proportion removed against seed dry weight ($r = -0.77$, $P < .0002$). [See (*22*).]

frugivores detect differences in the quality of arils produced by different trees. Partial correlations that control for seed weight give no evidence that differences among trees in the amounts of protein, carbohydrate, or fat in the aril influence crop depletion ($P > .15$; $N = 15$) (*19*). Phenolics in the aril may restrict the disperser assemblage by excluding wasteful mammalian frugivores (*16, 20*), but differences in phenolic content are not associated with differences in crop depletion. If the nutritional quality of the aril influences seed removal, its effects are subtle.

The third hypothesis derives from arguments by Snow (*21*) and McKey (*2*) that frugivores should prefer species of plants that offer a high reward for the amount of indigestible bulk consumed. The principle of a cost-benefit analysis is more easily applied to intraspecific comparisons than to comparisons between species of plants that differ in fruit morphology and content. A dramatic positive correlation between the proportion of seeds dispersed and the ratio of aril to seed weight indicates that frugivores tend to prefer trees offering a high reward for the amount of ballast consumed (Fig. 2A) (*22*). Partial correlation of dispersal success and the ratio of aril to seed, controlling for aril weight, shows that aril weight itself has little influence on the relationship ($r_{\text{part}} = .18$; $P = .25$; $N = 17$, for all analyses). A simple negative correlation between dispersal success and seed weight explains a remarkable 59 percent of the variance in dispersal success (Fig. 2B). The critical point is that foragers tend to prefer trees with a large ratio of reward to seed, but the key factor is seed size. There is no simple correlation between dispersal success and aril weight alone ($r = .28$; $P > .1$).

Our results point to matters of general interest. Seed-eating finches select food on the basis of handling cost as well as energy intake per seed (*17*); our study suggests that free-ranging frugivores also attempt to minimize the consumption of indigestible bulk by preferentially visiting trees that produce small seeds. That such a choice only covaries with a favorable ratio of reward to bulk emphasizes that food selection is based on imperfect information; seeds are at least twice as large as arils and presumably are easier for birds to assess than arils. Sources of selection on trees are complex. An obvious advantage accrues to a tree that achieves a higher dispersal success per offspring than a neighbor (*3, 5*), but it is not immediately clear why some individuals produce energetically "expensive" fruits that are inefficient dispersal organs. We suggest that disruptive selection may act on dispersal attributes of fruits and on those characteristics, such as seed size, that influence seedling survival after dispersal (*23*). We hypothesize that the dispersal efficiency of plants producing small seeds is offset, under unusual conditions of low disperser abundance or efficiency, by enhanced seedling survival for parent trees that invest more in endosperm. Under controlled conditions, seedlings from large seeds fare better in competition for light and nutrients than those from small seeds (*24*), and a similar result is likely in dense forest understory (*2, 21, 25*). Alternating selection for dispersibility and competitive seedling reserves probably maintains variation in the investment in reward and seed, thereby accounting for the otherwise anomalous lack of correlation between aril and seed weight.

Table 1. Relative importance of eight frugivores observed eating *Virola* fruits on Barro Colorado Island (*13*).

Common name and binomial	Seeds eaten (%)
Crested guan *Penelope purpurascens*	10
Slaty-tailed trogon *Trogon massena*	11
Rufous motmot *Baryphthengus martii*	17
Chestnut-mandibled toucan *Ramphastos swainsonii*	42
Keel-billed toucan *Ramphastos sulfuratus*	11*
Collared aracari *Pteroglossus torquatus*	1
Masked tityra *Tityra semifasciata*	0†
Spider monkey *Ateles geoffroyi*	7*

*Dropped or knocked down more seeds than it consumed. †Fruit thief that ate arils without consuming seeds.

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9. Fruits were sampled with weekly checks of traps (1 m^2) of plastic tubing and nylon mesh that were placed in a randomized design covering 6 to 15 percent of the area under the tree crowns. The number of seeds removed is estimated by subtracting seeds in traps from capsules in traps. Procedures have been described [H. F. Howe, *Ecology* **61**, 944 (1980)].
10. Means of 15 seeds and arils per tree are accompanied by their standard deviations. Commercial analyses were performed on freeze-dried material at Colorado State University. Techniques were derived from: S. E. Allen, *Chemical Analysis of Ecological Materials* (Wiley, New York, 1974); P. H. Heinze and A. E. Murneck, *Mo. Agr. Exp. Stn. Res. Bull.* **314**, 1 (1940); D. Smith, G. N. Paulsen, C. A. Raguse, *Plant Physiol.* **39**, 390 (1964).
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13. Foraging was observed for 40 hours at each of eight trees, with observation from 0600 to 1100 hours. Most (90 percent) visitation was before 1000 hours. Relative dispersal roles were determined from the combined observations of the number of fruit eaten and dropped per visit and the total visits recorded (H. F. Howe and G. A. Vande Kerckhove, in preparation). Similar procedures were used by Howe (*9*).
14. To avoid sampling bias, nutritional analyses were performed on intact arillate seeds not handled by animals.
15. H. F. Howe, *Ecology* **58**, 539 (1977).
16. In a *Casearia* population in which oily arils are produced in limited supply, 90.6 percent of the available seeds are taken by birds [H. F. Howe and G. A. Vande Kerckhove, *Ecology* **60**, 180 (1979)]. In a *Tetragastris* system characterized by sugary fruit with little protein or fat, 28 percent of the crop is carried away.
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18. A fourth hypothesis, that birds avoid trees frequented by predators (*6*), does not apply where important dispersers are "fearless frugivores" of large size. The only attempted predation seen during 320 hours of observation and 3960 census checks was of a tityra by a forest falcon (*Micrastur*). The tityra is smaller than other visitors, and has been identified as a "fearful frugivore" (*15*).
19. Total content = nutrient proportion × mean aril weight.
20. All arils are bitter; those from some trees are edible to humans, those from others are not. Tannins account for 1.2 to 3.3 percent (2.4 ± 0.6

percent) of the dry weight of arils. Mammals common at nearby *Tetragastris* trees (*9*), which produce sugary fruits sweet to the taste, avoided *Virola* day and night. Spider monkeys smelled and rejected as many arils as they consumed; this fruit was not an important part of their diet; see A. Hladik and C. M. Hladik, *Terre Vie* **23**, 25 (1969).
21. D. Snow, *Ibis* **113**, 194 (1971).
22. An alternative but less intuitive procedure shows that dispersal success is negatively correlated with the weight of the arillate seed ($r = -0.66$, $P = .002$). Partial correlation controlling for aril weight shows little influence ($r_{part} = -0.78$, $P < .001$); partial correlation controlling for seed weight shows decisive influence ($r_{part} = 0.32$, $P > .1$). There is no correlation between aril and seed weight ($r = -0.10$, $P > .3$). The percentage of seeds dispersed similarly shows a strong correlation with the difference between aril and seed weights.
23. Neither aril weight, seed weight, nor their ratio correlate with fecundity ($P > .1$).
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22 January 1980; revised 5 August 1980

Nerve Terminals Are as Metabolically Different as the Muscle Fibers They Innervate

Abstract. *The rate at which glucose enters nerve terminals in muscle was estimated indirectly by measuring changes in miniature end-plate potential frequency.* D-*Glucose entered nerve terminals in muscles with a fast twitch more rapidly than it entered those with a slow twitch. This suggests that nerve terminals in fast- and slow-twitch muscles differ in their rate of metabolism.*

A motor unit is composed of a motor neuron and the muscle fibers that it innervates. Motor units can be divided into those that contract rapidly, type F, and those that contract slowly, type S. These units differ in their physiological properties, such as rate of firing, and in the histochemical properties of their muscle fibers (*1*, *2*). Differences in neuronal metabolism would also be expected. This report presents evidence that glucose enters type F nerve terminals more rapidly than it enters type S terminals.

Experiments were performed on nerve-muscle preparations from Sprague-Dawley rats (100 to 200 g). Conventional methods for intracellular recording were used. The bathing solution contained 160 m*M* NaCl, 5 m*M* KCl, 2 m*M* $CaCl_2$, 1 m*M* Na-Hepes, and 11 m*M* D-glucose (*p*H 7.0 to 7.4; temperature, 32° ± 0.5 C°). Hyperosmotic neurosecretion (*3*, *4*) was used to estimate glucose entry into single nerve terminals (*5*). Miniature end-plate potential (MEPP) frequency (f) was recorded by inserting a microelectrode into a muscle fiber near the nerve ending. Measurements were made 5 to 8 minutes (f_5) and 17 to 20 minutes (f_{20}) after sucrose was added to the solution to make it hyperosmotic. The recorded frequencies were then compared to the resting MEPP frequency (f_0). Figure 1 shows that there is a linear relation between log (f_5/f_0) or log (f_{20}/f_0) and the osmotic gradient across the nerve terminal membrane. These results are similar to those reported by Hubbard *et al.* (*6*).

A decrease in MEPP amplitude would cause small MEPP's to be lost in the amplifier noise and would therefore simulate a decrease in MEPP frequency. To avoid this complication I used small rats, for which the mean MEPP amplitude was 0.95 mV; data for cells in which the resting potential dropped by more than 10 percent were discarded. The concentrations of glucose and potassium in the bathing solution remained constant during the experiment, so the results do not reflect a change in the osmotic gradient across the nerve terminal membrane produced by the entry of glucose or potassium into the muscle fibers. An estimate of the osmotic gradient across the nerve terminal membrane at 5 and 20 minutes can be obtained from f_5/f_0 and f_{20}/f_0 (Fig. 1). The difference in the osmotic gradient at 5 and 20 minutes was used to estimate glucose entry into the nerve terminal during the last 15 minutes of the 20-minute exposure to 30 m*M* of the test sugar. Since MEPP frequency is determined solely by the presynaptic nerve terminal, this method can only measure a change in glucose concentration across the nerve terminal membrane.

The estimates of the rate of glucose entry are shown in Figure 2. The increase in MEPP frequency after 30 m*M* sucrose or 30 m*M* L-glucose was added to the bathing solution was sustained in all the muscles tested, suggesting that these sugars do not penetrate the nerve terminal and dissipate the osmotic gradient. On the other hand, adding 30 m*M* D-glucose or 3-*O*-methyl-D-glucose to the

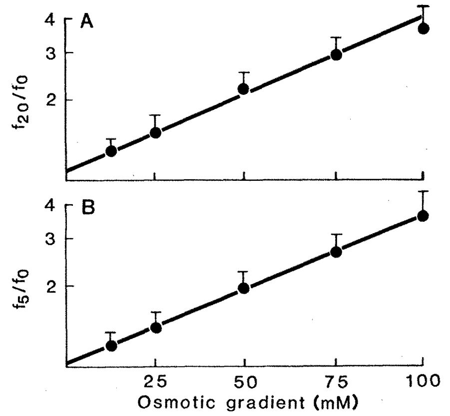

Fig. 1. (A and B) Increase in MEPP frequency as a function of osmotic gradient across the nerve terminal membrane. Each mean and standard deviation is based on ten cells. Ordinate: the ratio of mean MEPP frequency 5 to 8 minutes (f_5) and 17 to 20 minutes (f_{20}) after the osmotic gradient was increased with sucrose to the resting MEPP frequency (f_0), which was based on a 10-minute recording. Note logarithmic scale. Abscissa: the difference between test and control osmolarities The lines represent least-squares linear regressions. The results shown are from recordings made in the diaphragm; similar results were found in the extensor digitorum longus and soleus when osmotic gradients up to 30 m*M* were used.

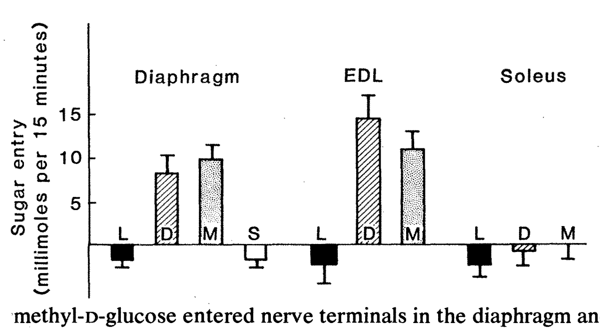

Fig. 2. Rates of entry of various sugars into presynaptic nerve terminals in the diaphragm, EDL, and soleus. Abbreviations: *L*, L-glucose; *D*, D-glucose; *M*, 3-*O*-methyl-D-glucose; and *S*, sucrose. Each mean and standard error is based on 15 cells. L-Glucose did not penetrate into nerve terminals in any of the muscles tested; D-glucose and 3-*O*-methyl-D-glucose entered nerve terminals in the diaphragm and EDL but not in the soleus. The statistical significance of these differences is evident even in the smallest difference [for transport of D-glucose in the diaphragm versus transport of 3-*O*-methyl-D-glucose in the soleus, $P < .01$ (Student's *t*-test)]. Whereas the rates at which D-glucose and 3-*O*-methyl-D-glucose enter nerve terminals in the diaphragm and EDL varied, no significant difference was detected by analysis of variance. Analysis of variance also failed to detect a significant difference in rate of entry among the other sugars. These results suggest that D-glucose and 3-*O*-methyl-D-glucose enter nerve terminals in the diaphragm and EDL more rapidly than they enter nerve terminals in the soleus.

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