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nomical predators, because they eventually kill their victims" (Wheeler 1923). This quotation refers to what are now called parasitoids which kill evolutionary individuals. The words predation, predacious and predatory, from which predator is derived, are much older and refer to plunder and pillage.

Eating modules or other plant parts may be ecologically interesting but is of little evolutionary significance. Moreover, as shown by Paige and Whitham (1987), plant-eating can scarcely be regarded as plunder if the subsequent fitness and hence evolutionary prospects of the eaten plant are enhanced. Using the word predator to describe plant-eating by animals immediately suggests the action is detrimental, an unnecessary suggestion and one which could bias subsequent interpretation of observations.

Tightening up the language

Fig. 1 shows an "unexpected" result of browsing but it is unexpected only because of the language used to investigate, describe and interpret the effects of herbivores on plants. It could be said that in stating my case I have relied too heavily on the results of this one investigation. However, I consider it likely that such an experiment has not been done before because of indoctrination with the all-pervasive attack and defence approach. There is always the chance that investigators find what they are looking for and miss what they are not looking for. It could also be said that my argument is a semantic one and that it does not matter what language is used, but I see no value in emotive and inaccurate words and phrases when there are more precise ways for describing and interpreting plant/herbivore relationships.

It is easy to imagine how the language of attack and defence has been developed for, after all, it has probably been used ever since the beginnings of agriculture 10,000 years ago when people first noticed that animals ate their crops. But the problem now is to sort out the extent and the nature of reciprocal adaptive radiation between plants and herbivores: tightening up the language should help in the solution of this problem.

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Is frugivory limited by secondary compounds in fruits?

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Izhaki and Safriel (1989) (hereafter I & S) pose the question "why are there so few exclusively frugivorous birds?" This question has been posed before and is usually answered by what they call the "nutritional deficiency hypothesis" which suggests that fruits alone do not provide a sufficiently balanced diet for the maintenance of total frugivory. I & S propose that fruits do contain adequate quantities of nutrients for a balanced, totally frugivorous diet but that plants invest in secondary compounds which reduce the ability of frugivores to digest fruit nutrients, particularly proteins. This forces frugivores to range more widely, seeking insects for protein, and thus more effectively disperse the plant's seeds. I will call this the "secondary compound hypothesis." First, I will discuss why I believe their data do not support the secondary compound hypothesis and then I will discuss alternative, non-exclusive hypotheses, to explain the apparent rarity of total frugivory.

Support for the secondary compound hypothesis

The data I & S present come from feeding six species of birds on pure diets of one of six fruit species and measuring nutrient intake, nutrients in excreta and weight loss of the birds. However, they were unable to feed all bird species all plant species. As a result, statements they make such as "··· carbohydrates were digested most efficiently in madder and least efficiently in gardrobe" are suspect since madder was only tested with a single individual bird. Likewise, their finding that birds fed on joint pine lost weight is suspect because joint pine was only fed to two individuals of one species. The values I & S cite for known dietary protein requirements of birds are 7%, 8% and 20%. Of the six plant species they used, joint pine had 10.7% protein, pistachio had 7.1% protein, and the other four species had less than 6.5%. From this alone it is not surprising that the birds demonstrated weight and nitrogen loss.

The primary evidence I & S provide for the proposed secondary compounds which interfere with protein uptake is that birds fed a *single species* of fruit increased fruit consumption, lost weight and voided more nitrogen. I & S state that "the digestion of proteins is more rapid than that of carbohydrates (Parra 1978)." Therefore, they expect the increased consumption of fruits to lead to greater absorption of protein cf. carbohydrate. However, Parra (1978) refers to the complex structural carbohydrates cellulose and hemicellulose. The carbohydrate rewards found in fruit pulp are simple mono- and di-saccarides which are as digestible or more digestible than proteins (Karasov et al. 1986, Diamond et al. 1986). Hence, increased consumption of fruit will not necessarily produce increased absorption of proteins relative to carbohydrates.

Nitrogen absorption is a function of digestibility, nitrogen concentration in the gut, and gut retention time. I & S claim that the excretion of more nitrogen when fruit intake increased is evidence of some secondary compound inhibiting nitrogen uptake. However, if the rate of gut passage increased with the increase in total consumption (a reasonable assumption), we might expect to observe decreased efficiency in nitrogen absorption as a function of reduced retention in the gut. The actual amount of nitrogen absorbed can increase while apparent efficiency decreases. Their statement that the birds "ate so many fruits that the amounts of protein they ingested should be enough to meet their needs" assumes a fixed ability to absorb protein. Possibly, protein in the fruit was not digested due to faster gut transit, not due to a hypothetical secondary compound retarding nitrogen absorption.

Alternative hypotheses

The nutritional deficiency hypothesis

The usual explanation for the apparent rarity of total frugivory is that fruits alone cannot meet the metabolic needs of a total frugivore (Morton 1973, Foster 1978, Thomas 1984). The deficiency can be expressed in terms of quantity or quality. A quantitative deficiency means that there simply is not enough of a nutrient in fruits. Plants need invest only the minimum required to attract dispersers. Plants may allocate low levels of proteins to fruits because nitrogen is often limiting and thus allocated to other permanent, critical plant tissues (Harper 1977, Abrahamson and Caswell 1982). The proteins are so dilute in the watery, carbohydrate-rich pulp that frugivores might not be able to process enough fruits to obtain the minimum required protein. Instead, birds obtain a quick and easy source of energy, carbohydrates, from fruit and forage for insects to obtain protein.

The qualitative deficiency implies fruits contain enough of the basic nutrients but that these might not be in the proper form to meet metabolic requirements. A fruit diet which apparently has adequate amounts of protein might not have sufficient amounts of some essential amino acids. Consequently, the imbalance in protein consumption and excretion reported by I & S could be due to the birds' efforts to obtain adequate amounts of some amino acids while excreting substantial quantities of other, unneeded amino acids. Juncos fed a lysine-deficient diet consumed more food, lost weight, had less efficient energy utilization and had a negative nitrogen balance compared with juncos fed the same diet with a lysine supplement (Parrish and Martin 1977). These results, similar to those of I & S, were a function of an amino acid imbalance, not secondary compounds. Herbst (1986) examined fruit consumption by frugivorous bats and found that fruit species which appeared to provide a sufficient amount of protein (assuming bat physiology is similar to rat physiology) in fact did not provide a proper balance of amino acids. Bats appeared to compensate for amino acid deficiencies by consuming a mixed diet of fruits – an option unavailable to the birds used by I & S.

The temporal patchiness hypothesis

I & S expect foraging for fruits to be easier than foraging for seeds, and thus expect total frugivory to be more common than total granivory. Such expectations commonly arise when we see abundant, conspicuous fruiting plants in the field and ask "Why are so few birds feeding at this abundant, undefended resource?" However, virtually all phenological studies throughout the world reveal there are periods of severe fruit scarcity (Baker et al. 1983, Terborgh 1986). The potential to evolve total frugivory and the capacity for a site to support total frugivores are constrained by the periods of lowest fruit availability. Even a short period where fruit is unavailable could be lethal to a total frugivore, particularly a small passerine such as studied by I & S. Therefore, periods of fruit scarcity may create selection against total frugivory and favor frugivores that are adept in harvesting some alternative resource (e.g. insects). Fruit scarcity does not imply seed unavailability because fruits rot quickly but seeds may remain edible for long periods. Consequently, it is not necessary to expect total frugivory to be as common as total granivory.

The defense of immature fruits hypothesis

If secondary compounds are found in fruit pulp, it is not necessary to hypothesize that their presence somehow serves to enhance seed dispersal through the "manipulation" of frugivore foraging behavior. A wide array of secondary compounds have been implicated in the defense of plant tissues from herbivores (Rosenthal and Janzen 1979). Likewise, developing fruits need to be defended from herbivores. Secondary compounds in mature fruits may be leftover from defense of the developing fruit or defense of the ripe fruit from non-dispersing frugivores (Herrera 1982). It may be energetically inefficient or impossible to tear-down existing secondary compounds when a fruit matures. I believe, however, that the secondary compounds found in ripe fruits may indirectly serve a purpose similar to that proposed by I & S. That is, these compounds may incidentally promote movements by frugivores just as they do with foraging herbivores. Generalist herbivores often elude chemical defenses by foraging on a wide array of plant species, thereby never consuming dangerous levels of any one kind of secondary compound (Freeland and Janzen 1974). A foraging frugivore may deal with secondary compounds in the same manner; never consuming too much of any one fruit species. In fact, studies of specialized frugivores indicate they consume a diversity of fruits within a relatively short period of foraging (e.g. Wheelwright 1983, Stocker and Irvine 1983).

Such a plant "strategy" differs significantly from what I & S propose. The secondary compounds they envision in most fruit species must act on the frugivore similarly – to inhibit their ability to assimilate nitrogen and force them to eat non-fruit resources, i.e. insects. What is probably more likely is that secondary compounds in fruits act in a variety of ways; the total frugivore must merely avoid consuming too much of any one toxin. They could do this by foraging on fruits with other toxins or by switching to alternative food sources, either way they are moving more widely and possibly dispersing seeds more effectively. This effect may largely be a by-product of selection generated by herbivores for defence of immature fruits, not selection to enhance seed dispersal. Jordano (1988) found a variety of secondary compounds in the fruits of Mediterranean scrubland plants. Jordano's study included four congeners of fruits studied by I & S. In these he found a wide variety of secondary compounds which act as toxins as well as some digestibility inhibitors.

The chick provisioning hypothesis.

Because fruits may be inadequate protein sources or too rich in calories cf. proteins for developing chicks (Morton 1973, Foster 1978), parent birds must forage efficiently for insects when feeding young even through the fruits could be adequate to meet their own protein requirements. The need to forage intensively for insects during the breeding season may constrain the evolution of total frugivory in birds. Would a bird which has fed exclusively on fruits for eight months forage for insects as effectively as a bird which daily forages for insects? Birds which forage regularly for insects may have a higher fitness (e.g. be able to fledge larger broods) than total frugivores for this reason. Likewise, the annual need to supply insects to chicks could produce selection away from a specialized frugivore phenotype (e.g. maintain a narrow gape which limits maximum consumable fruit size) or physiology (Herrera 1984). Partial insectivory in "frugivorous" birds may result from the need to provide protein-rich insects to developing chicks, not as a consequence of the secondary compound hypothesis.

The myth of scarcity of total frugivory hypothesis

Perhaps the apparent scarcity of total frugivores stems not from some special aspect of frugivory, but rather our expectation that there should be more total frugivores. Most animals will consume a nutritious, digestible food item if available regardless of what food class the food item falls into. The degree of specialization of an animal on any food type depends on how restricted the animal is by its behavioral, morphological, and physiological adaptions to that food type. For example, carnivorous raptors cannot probe flowers for nectar but "insectivorous" wood warblers can probe flowers and at certain times of year some warbler species consume significant quantities of nectar. Frugivory may not demand many specializations which exclude other food sources, for example, insects (Herrera 1984).

I & S do not present any data to support the contention that total frugivory is rare, or that it is rarer than any other total "   – ivory." They state frugivory is rarer than granivory, reflecting perhaps a temperate bias. In tropical forests frugivory is more common than granivory (e.g. Terborgh 1986). Also, seeds may be richer in nutrients and more reliable temporally than fruits (see above); hence there would be no further explanation required for why there are more granivores than frugivores.

What proportion of an an animal's diet must be non-fruit before we consider it a non-total frugivore? Certainly many birds can and do survive on nearly-pure fruit diets (Foster 1978, Wheelwright 1983). If the secondary compound hypothesis is true, how do these near-total frugivores survive? Likewise, there are large numbers of frugivorous bats which subsist well on diets of fruit (Thomas 1984). I & S state that their hypothesis would be invalidated if birds were found to survive on diets of mixed fruit; such birds (and bats) do exist.

In summary, I & S provide a hypothesis for the apparent scarcity of total frugivory. Their hypothesis differs from the nutrient-deficient fruit hypothesis by stating that fruits are nutritionally adequate for total frugivory but that plants invest in secondary compounds which reduce the digestibility of the fruit pulp. The presumed selective advantage of investing in these secondary compounds comes when the frugivore moves off in search of insects and more effectively disperses the plant's seeds. This presumes fruit resources are so abundant and nutritious that frugivores could remain in one fruiting plant and obtain adequate nutrition. If, however, one were to accept their hypothesis, it begs the question: Why invest in a reward (pulp) and then reduce the value of the reward by further investing in secondary compounds? It would seem more parsimonious to just produce a fruit which requires a protein supplement.

If we speculate that such a secondary compound does exist, it is difficult to perceive how it could have evolved. As I & S allude, all plants would have to share the compound, otherwise frugivores would merely avoid those plants which have the compound and feed on those plants without it. How could such a compound arise independently and concurrently in many unrelated plant taxa? Given the diversity of secondary compounds plants produce and the diversity of plants which produce fleshy fruits, it seems unlikely that plants, in general, could "opt" for a common tactic which collectively manipulates the foraging behavior of seed dispersers.

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Are plant secondary compounds responsible for negative apparent metabolizability of fruits by passerine birds? A comment on Izhaki and Safriel

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Izhaki and Safriel (1989) showed that several species of passerine birds were in negative nitrogen balance and could not maintain body mass when fed pure diets of a number of fruit species ranging in crude protein content from 2.7% to 10.7% of dry mass. They attributed the negative apparent metabolizability to secondary compounds present in the fruits. Their data