המאמרים بمטרת הדפסתם ויורדם על-פי הוק 2 ווית יוצרים הדפסת מאמרים על-פי ליצירת זכויות והוראה בלבד איין לעשה כל שימוש מחקרי במאמרים.
balance when feeding on diets containing low nutrient levels.

In conclusion, I believe Izhaki and Safriel have made a significant contribution to our understanding of avian frugivory by providing estimates of the AM of nitrogen for a number of fruits. Nevertheless, I believe their suggestion that secondary compounds are responsible for the negative AM values they observed is premature. Their data can be explained by the simpler hypothesis that the low nitrogen levels contained in experimental fruits, possibly combined with low biological value of crude protein, prevented birds from ingesting sufficient protein to balance endogenous losses. I believe this hypothesis should be critically examined before invoking secondary compounds to explain their results.

Acknowledgements – An earlier draft of the manuscript benefited from comments by R.G. White.

References


Weight losses due to exclusive fruit diet – interpretation and evolutionary implications: a reply to Mack and Sedinger

Ido Izahki and Uriel N. Safriel, Dept of Zoology, Hebrew Univ. of Jerusalem, Jerusalem 91904, Israel (present address of H. Oranim, Univ. of Haifa, P.O. Kiryat Tivon, 36910 Israel)

Two major questions were raised by Mack (1989) and Sedinger (1989) when criticizing our paper (Izhaki and Safriel 1989). First, should secondary compounds be invoked for explaining the nitrogen deficiency of birds maintained on an exclusive fruit diet? Second, is exclusive frugivory indeed rare in nature, as a result of the adaptive significance we attributed to secondary compounds in ripe fruits? Let us reiterate our major findings and interpretations with respect to the first issue. In our experiment birds ate huge amounts of fruits, yet they lost weight. We estimated that the birds had consumed more protein than they required, and proposed that the loss in body mass was due to poor nitrogen assimilation (poor apparent digestibility, following Robbins (1983) terminology, as also used by Buchsbaum et al. 1986 for example), resulting in relatively large amounts of nitrogen in their feces. We hypothesized that secondary compounds were involved in the apparent poor nitrogen assimilation just as secondary compounds of leaves.
impair nitrogen assimilation by mammals, see references in Robbins et al. (1987).

We did not analyse our fruits for secondary compounds, but since our paper has been written Jordano (1980) reported on tannins and alkaloids, some of which known as potential digestive inhibitors, in ripe fruits of several species of the Spanish scrubland. Four of these species are congeneric of the species we used in our experiments. One can only hypothesize how digestive inhibitors in ripe fruits have evolved, and what their adaptive significance might be. We suggested that our birds lost weight because such secondary compounds interfered with protein digestion, and proposed an adaptive interpretation to such possible interference.

Mack and Siedinger, on the other hand, suggest that we underestimated our birds' protein requirements; the birds lost weight simply because their diet was too poor in nitrogen to satisfy the true, higher than what we estimated, requirement. As stated in our paper, we estimated protein requirement using Robbins' (1981) equation, which is derived from available data on all studied species. As stated in our Discussion, much of these data come from values of granivorous birds including domestic chicken. Mack and Siedinger may be correct that based on granivores' data, weight loss in our birds is to be expected. But frugivores need not behave as granivores. Data on nutritional requirements of frugivorous birds is scanty, but the only available pertinent data support a relatively low estimate of frugivores' protein requirement: The frugivore garden warblers Sylvia borin fed on low protein (2.4% of wet weight) artificial diet, lost weight initially, but later maintained a constant weight (Bairlein 1987: Fig. 1, p. 340). Our birds (including Sylvia species), fed on wild fruits with similar or higher protein contents than in Bairlein's experiment, could not maintain their weight. Bairlein (1987) concluded that "the Garden warbler required much less protein than supposed... it is suggested that fruit eating in this species is less restricted by the protein contents of these vegetables than assumed." Note that Bairlein maintained his frugivorous birds on a low-protein non-fruit diet, and that we could not maintain our birds when provided with a similar, and even higher, amount of protein in wild fruit. Thus, both Bairlein's and our diet contained enough protein. Either the fruits were deficient in some amino acids present in Bairlein's diet, as indeed suggested by Mack and Siedinger and not pointed out in our paper, or, the fruits contained something which prevented the birds from fully assimilating the available protein, something which did not occur in Bairlein's artificial diet.

If we stick to Robbins' (1981) estimate of mean protein requirement, then as pointed out rightly by Siedinger, our average individual did not ingest significantly more nitrogen than required, given the 95% confidence interval on the above estimate. By the same token, our birds did not ingest significantly less nitrogen than required, hence their dramatic weight loss requires explanation. We agree with Siedinger that some of it may be attributed to a possible low level of essential amino acids and a possible high level of non-digestible nitrogen such as in secondary compounds. Our knowledge of the contents of amino acids, non-digestible proteins and secondary compounds in ripe fruits is still very meagre to allow distinction between the alternative hypotheses explaining our experimental results.

Mack proposes that the low nitrogen assimilation we observed was not due to inhibitory effect of secondary compounds, but to a low efficiency of nitrogen absorption due to the rapid gut passage which we reported. Indeed, when retention time is short, low digestion efficiency is expected. But the critical issue is what brought about the observed low retention time, not what the consequences of this rapid passage were. If our experimental diet was low on protein, the birds should have increased rather than decreased digestion efficiency of protein (as long as this does not cause deficiencies in other nutrients). This should have resulted in a longer retention time and a lower nitrogen deficiency than we observed. On the other hand, suppose that together with protein the birds ingest digestive inhibitors, due to which only a small portion of each ingested protein unit can be assimilated irrespective of retention time. Then it is advantageous to consume as many protein units as possible, which can be achieved (given a sufficient supply of fruits) by an acceleration of passage time. To conclude, our secondary compounds hypothesis is at least as plausible as others, is supported by some circumstantial evidence which our experimental results provide, and should indeed be critically examined by further, carefully designed experiments.

With regard to the second issue, we hypothesized that plants improve seed dispersal by forcing birds to break frugivory by bouts of inactivity, and that the impairment of protein assimilation by secondary compounds in ripe fruits prevents birds from being exclusive frugivores. Mack challenges our question "Why are there so few exclusively frugivorous birds?" and suggests that exclusive frugivory is more common than can be implied from our question. Indeed, Foster (1978) evaluated data on protein requirements of nestlings, parents' feeding rates and protein contents of fruits, and concluded that tropical nestlings could fledge successfully if maintained on an exclusive fruit diet. These findings point at a potential, but when Wheelwright (1983) looked at what birds actually did he found that half of the food items brought to nest by a typical tropic frugivore such as resplendent quetzals ( Pharomachrus mocinno) were insects and lizards. Mack cites Wheelwright as implying that there are birds which "can and do survive on nearly-pure fruit diet", whereas what Wheelwright concludes is that "Quetzals in Costa Rica eat at least 41 species of fruits and an uncertain (though minor) amount of animal prey" (Wheelwright 1983). However, even if conclusive evidence for birds that are maintained on exclusive fruit diet existed, this could point at the
evolution of detoxifying mechanisms (e.g., Eriksson and Nummi 1982), rather than at the absence of protein-inhibition compounds in wild fruits.

Mack rightly suggests that exclusive frugivory should not be expected in temperate regions, where fruit availability is restricted by season. But the crucial point is that even when fruits are available (in the Mediterranean region this is mainly not during breeding season) and insects are very scarce (in Israel the peak availability of fruits is in the driest part of the year, when insects are rarest, compared with all other seasons), frugivorous birds take then also lots of insects (Izhaki 1986).

Finally, Mack raises the issue of the adaptive significance of the proposed phenomenon. Freeland and Janzen (1974) suggested that a herbivore tolerates a small amount of a secondary compound which protects a given plant species. After consuming this amount, it moves to another species, where it consumes an additional small amount of a different compound. Mack suggests that if secondary compounds operate also in ripe fruits, a bird could move from one fruit species to another to avoid intolerable damage, rather than abandon fruits and switch to insects. Only if all fruit species have the same compound, switching to insects rather than moving to another fruit species would be advantageous. Mack rightly points at the difficulty of invoking an independent and concurrent evolution of the same compound in many unrelated plant taxa, given the diversity of secondary compounds produced by plants.

Indeed, if each plant species produced only one secondary compound, and each secondary compound imparted a unique and different function of the bird, birds could switch between different species of fruits rather than always alternate between fruits and insects. But our hypothesis does not require that impairment of protein assimilation, for example, is executed by a single, universally distributed compound. Different secondary compounds may have the same effect (Robinson 1979, Ryan 1979). Just as fleshy fruits advertise themselves using different methods, they could be able to interfere with the birds' protein assimilation and thus achieve better seed dispersal, using different secondary compounds. Thus, we propose that many fruit species have secondary compounds of a similar function, rather than different species differ in their secondary compounds, such that each plant affects a different physiological function.

To conclude, our answer to Mack's question "why invest a reward (pulp) and then reduce the value of the reward by further investing in secondary compounds?" is that if an individual plant invested only in pulp, a bird would forage on it until it consumed all edible fruits, by which time most of the seeds would be deposited under the parent plant. If it invested only in secondary compounds in its ripe fruits birds would not be attracted to them. Thus, to maximize seed dispersal plants should invest both in pulp and in secondary compounds.

References


Izhaki, I. 1986. Seed dispersal by birds in an eastern Mediterranean scrub. - Ph.D. Diss., The Hebrew Univ. of Jerusalem.


Seelinger, J.S. 1990. Are plant secondary compounds responsible for negative apparent metabolizability of fruits by passerine birds? A comment on Izhaki and Safriel. - Oikos 57: 140.