Resource selection by tropical frugivorous birds: integrating multiple interactions

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Summary. Resource selection is a function of interactions of organisms (competition, predation) as well as characteristics of the resource and organisms. I provide a quantitative model that integrates these factors. I use the model to predict profitability of fruits to tropical birds, but the model and its predictions are applicable to a wider array of systems and organisms. Profitability of a fruit is determined by rewards provided by the pericarp (mass and caloric yields) relative to costs (metabolic requirements, handling time, search time, behavioral interference, predator avoidance) associated with finding and eating that fruit (Fig. 1). Fruits increase in profitability with increases in fruit size until increases in handling time offset increases in pericarp mass. The fruit size at which increases in handling time offset increases in pericarp mass varies among bird species due to differences in bill and body size. Decreases in feeding rate due to decreasing numbers of fruits and increasing search time causes reduced profitability and this effect becomes more severe with decreasing fruit size and/or increasing frugivore size. Consequently, as fruit size decreases relative to frugivore size, fruit abundance becomes increasingly important to fruit selection by frugivores. However, while profitability of resources is a function of characteristics of the resources and the organisms, biological interactions can change profitability rankings; resources that may be more profitable in the absence of behavioral interference, exploitation competition, or predation risk can become less profitable in the face of these interactions. The proposed model integrates these interactions to provide predictions of resource selection and these predictions are supported by published studies.

Co-occurrence of species is often thought to depend on partitioning of available food types, space, or habitat (see Schoener 1974; Moermond 1979). Tropical fruit trees represent an interesting case where many avian frugivore species select the same individual resource patch (fruit tree) containing the same single food type (i.e., Land 1963; Howe and Primack 1975; Howe 1977, 1980, 1981; Greenberg 1981, Martin 1982; and others). Many studies of tropical birds and fruits have focused on trying to predict the numbers and kinds of avian species selecting particular fruit species based on characteristics of the fruits (e.g. Howe and Primack 1975; Howe 1977, 1980, 1981; Howe and Vande Kerckhove 1979, 1981; Cruz 1981). However, resource selection must also be influenced by organismal characteristics (energy demands, mouth size) and biological interactions (exploitation competition, behavioral interference, and predation risk). Understanding the way these factors and interactions are integrated provides a means for understanding resource selection and for predicting the numbers and kinds of species that select the same resource (food type, patch, habitat, or larger system).

Resources are potentially selected based on profitability (i.e., Werner et al. 1983 a, b), where profitability is a function of energy gained per unit time (see Schoener 1971; Pyke et al. 1977). Herrera (1981a, 1982a) suggested fruit profitability could be indexed by relative yield (pericarp dry mass relative to pericarp and seed mass) times pericarp nutrition. I will show that a much broader range of factors influences profitability of fruits and other resources.

Single factor approaches to understanding ecological patterns can be misleading (Martin 1981 a, b; Connell 1983; Quinn and Dunham 1983). Yet, estimates of resource profitability generally do not include effects of interactions among organisms. Instead, organisms are thought to avoid resources that are considered most profitable due to biological interactions such as predation risk (Milinski and Heller 1978; Mittlebach 1981; Werner et al. 1983 a, b), behavioral interference (Willis 1966, 1967, 1972; Shields and Bildstein 1979; Wrobel et al. 1980; Peters and Grubb 1983), or exploitation competition (Inouye 1978; Werner and Hall 1979). Rather than concluding that species do not follow profitability predictions because of such biological interactions, these interactions need to be incorporated in estimates of profitability.

Integration of these interactions into a model predicting resource selection is rare. Rosenzweig (1979, 1981) and Pimm and Rosenzweig (1981) used isocline analyses and tied energy gain with population density to examine competition in determining habitat selection. However, the models do not consider predation risk nor examine organismal or resource characteristics that influence energy/time. I examine effects of forager (energy needs, mouth size) and resource (mass, size, density, nutritional quality) characteristics, exploitation competition, behavioral interference and predation risk on resource selection. I integrate this com-
plex array of factors and interactions (Fig. 1) in a general model that provides testable predictions of resource selection. This model could be applied to a variety of biological systems (i.e., birds-nectar, birds-seeds, fish-invertebrates, etc.) and at several levels depending on the definition of a resource (i.e., food type, patch, habitat). For example, the model and its predictions fit well with patterns described by Pimm and Pimm (1982) for tropical nectarivores. I draw on patterns from a diversity of terrestrial and aquatic systems to show the broad applicability of aspects of the model. However, here, I apply the model to fruit selection by tropical birds to address fruit profitability from a much broader perspective than previously attempted and to provide testable predictions and potential explanations of reported patterns of fruit use and general resource selection.

Justification of a profitability approach

Maximization of energy/time is a plausible criterion for fruit choice by frugivorous birds because they need energy for growth, survival, and reproduction (Snow 1962a, b, c; Morton 1973; Foster 1978). Also some frugivores may be time minimizers (sensu Schoener 1971) in their feeding because of the time needed for the elaborate courtship displays associated with their polygamous mating habits (i.e., D. Snow 1962a, b, c, 1971, 1980; B. Snow 1970, 1972, 1973, 1977; Foster 1977a; Snow and Snow 1979; Beehler 1983).

Experimental (Cowie 1977; Krebs et al. 1977, 1978; Erichsen et al. 1980; Houston et al. 1980; Lima 1983) and observational (Gill and Wolf 1975a; Wolf et al. 1975; Davies 1977; Goss-Custard 1977, 1979; Hainsworth 1978; Connors et al. 1981) studies have demonstrated that birds are able to assess and respond to resource profitability. Frugivores prefer fruits with higher pericarp to seed weight ratios (Howe and Vande Kerckhove 1980; Herrera 1981b; Moermond and Denslow 1983), showing that they also can assess and respond to some aspects of fruit profitability in the field. My purpose is not to argue that frugivores always forage optimally. Rather, I use optimization theory to provide a framework for understanding and predicting patterns (Charnov 1976a; Maynard Smith 1978) of fruit use by tropical birds.

Chemical factors

Fruits vary in their composition of minerals (White 1974) and amino acids (Foster 1978). Energy content may not necessarily reflect the profitability of a fruit source due to nutrient constraints (Pulliam 1975). However, since data on specific biochemical needs of frugivorous birds are rare and because energy is always needed, I will focus on energy gained per unit time as a starting point. Resources that do not follow predictions of the energy/time model can then be identified as possible cases of nutrient constraints for more specific future tests.

Retention time

Large fruits that have large seeds provide more bulk and occupy a greater gut volume per seed, but it is not clear that these negative effects increase proportionally with fruit size, as assumed by the relative yield index of Herrera (1981a). Frequency of regurgitation is positively associated with seed size relative to body size (Johnson et al. 1985); seeds that are large relative to body size are frequently regurgitated, whereas small seeds tend to be defecated. Seed retention time is shorter for regurgitation than for defecation (Herrera 1981a; Johnson et al. 1985). Consequently, birds eating small-seeded fruits carry the bulk and lose the intestinal volume to seeds for longer periods than if they consumed a large-seeded fruit whose seed could be regurgitated. Thus, volume of gut and time occupied (i.e., gut volume-hours) do not necessarily increase with seed size because differences in seed volume may be compensated by differences in retention time. Rather than include an arbitrary adjustment for this effect in the following model, I simply note that more work is needed on the ecological effects of retention time and seed size.

Energy yield of fruits

Energy yield of a fruit is provided by pericarp mass \( F_{mn} \) and nutritional quality \( F_r \) of the fruit. I use the term "pericarp" to mean the digestible portion of a fruit (whether it is arrilate or pulpy) and the term "fruit" to mean the digestible portion plus seed. Nutritional quality is the usable...