Frequency-dependent host selection by parasitic mites: a model and a case study

Abstract Previous studies on frequency-dependent food selection (changing food preferences in response to changes in relative food abundance) have focused on predators and parasitoids. These organisms utilize several victims during their lifetime. We introduce the case of parasites which, having accepted a host, do not change it. We propose two alternative models to explain the biased occurrence of parasites on different host types: (1) through the option of rejecting less-preferred hosts prior to accepting one of them; (2) by differential parasite survival on different host types. These models predict that host rejection, but not differential survival, can create frequency-dependent parasitism (FDP). Unlike previously described factors responsible for frequency dependence of food selection, which act through changing the foraging behaviour of individual predators or parasitoids, FDP involves no adjustment of parasite foraging strategy according to previous feeding experience. The mite *Hemisarcoptes coccophagus* is an obligate parasite of armoured scale insects (Homoptera: Diaspididae). Our field data show that *H. coccophagus* is found more frequently on ovi-posting than on young host females. Our model, combining the effects of host rejection and differential survival, is used to estimate the relative contribution of these factors to parasite biased occurrence on different hosts. Our model, combining the effects of host rejection and differential survival, is used to estimate the relative contribution of these factors to parasite biased occurrence on different hosts. The contribution of differential survival was dominant in *H. coccophagus*, and overrode any effect of host rejection. Nevertheless, our prediction that FDP may be found in parasites is supported by literature data about a parasitic water mite.

Key words Differential survival · Frequency-dependent parasitism · Host rejection · Host preference Switching

Introduction

A predator's preference for a certain prey may be expressed in terms of the deviation of the proportion of that prey attacked from the proportion available in the environment (Hassell 1978; Begon et al. 1990). Of the various methods proposed for preference estimation (Chesson 1978, 1983; Cock 1978; Manly et al. 1972; Manly 1974), the most widely accepted measure of preference (*V*) relates the ratio of the numbers of two prey types in the environment to their ratio in the predator's diet:

\[
e_i/e_2 = V(A_1/A_2)
\]

Eq. 1

where \(A_1\) and \(A_2\) represent the available numbers of the two prey types, and \(e_1\) and \(e_2\) are the numbers of the two prey types actually consumed. If \(V > 1\) then prey type 1 is preferred; when \(V = 1\) no preference exists for either prey; \(0 < V < 1\) indicates a preference for prey type 2. Re-arranging Eq. 1 expresses the relationships between the proportion of prey type 1 available (A) and the proportion of that prey actually consumed as:

\[
e = VA/(1 - A + VA)
\]

Eq. 2

where: \(e = e_i/(e_i + e_2)\) and \(A = A_1/(A_1 + A_2)\). Equation 2 predicts that \(e\) as a function of \(A\) is a non-linear curve, which becomes linear with a slope = 1 when no preference is expressed (Murdoch and Oaten 1975).

If preference changes as relative prey abundance (\(A\)) changes, then predation is said to be frequency-dependent (Ayala and Campbell 1974). The cases in which a predator eats disproportionately more of the more abundant prey have been termed “switching” in ecological parlance (Murdoch 1969) and “apostatic selection” in population genetics (Clarke 1962). Elton and Greenwood (1970) incorporated the measure of frequency-dependent predation (\(b\)) into Eq. 1:

\[
e_i/e_2 = (VA_1/A_2)^b
\]

Eq. 3

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The departure of $b$ from unity indicates switching. This model is not based on predator behaviour but is, rather, a descriptive statistic (Manly 1973). For example, Elton and Greenwood (1970) assumed that $V$ is a constant for any given prey-predator system, and frequency dependent predation is therefore measured by $b$. An equally valid equation might be produced by assuming $V$ to be a variable which measures changes in frequency dependence. Under this condition $b$ is redundant. We show below that under certain conditions, $V$ represents an expression constructed of a set of variables that describe the behaviour of the exploiter (here, parasitic mite). To make the distinction between these two separate assumptions, we shall denote the latter by $V'$.

Equation 3 describes a monotonic preference change which corresponds to changes in relative prey abundance. Furthermore, it describes preference reversal (a change from preference for one prey type to the other). However, sometimes one prey type is always preferred, although preference intensity changes as relative prey abundance changes (Greenwood 1984). Such cases are only partly described by Eq. 3 (e.g. Fig. 1c in Greenwood and Elton 1979).

This difficulty is resolved by a different type of model, using optimal foraging theory (Hubbard et al. 1982). This model offers solutions with respect to different preference strategies, so that fitness is maximized. It assumes that a preference change (including preference reversal) is expected whenever the foraging strategy changes. Hence it is a model that assumes adjustment of foraging behaviour by the predator, according to its previous feeding experience (handling time and fitness gain for each prey type). Our model is different in that it deals with parasites which cannot adjust their foraging strategy. This model shows that under certain conditions such adjustment is not necessary for the existence of frequency-dependent host selection.

Mites of the genus Hemisarcoptes are obligate parasites of armoured scale insects (Homoptera: Diaspididae) (Gerson et al. 1990). Mite eggs are deposited on the body of the host diaspidid, under the shield, and an ovipositing female will generally kill its host by its feeding. Offspring developing from the eggs leave the dead host and search for a healthy scale. Hence frequency-dependent parasitism (FDP), resulting from adjustment of the foraging behaviour of individual parasites according to their previous feeding experience (the commonly assumed mechanism of FDP), is technically impossible.

Mite preference for a host, expressed as a bias in their occurrence on different host types, may be a result of (1) enhanced long-distance attraction to some host types; (2) active rejection of certain hosts after mite arrival and physical probing; (3) differential parasite survival during penetration and/or feeding on different host types. For reasons explained in the Results, we postulate that the strength of the mite’s long-distance attraction to different host types is similar for all hosts. Consequently, we construct simple mathematical models to explore the effects of the other two factors that may result in bias in host parasitism rates: host rejection and differential parasite survival. We show that the first, but not the second, can result in FDP. Using field data on Hemisarcoptes coccophagus Meyer, we estimate the relative contribution of these two factors to the mite’s apparent preference.

The model

Host rejection

We assume that each parasite individual has a finite searching time. During that period the parasite is able to “evaluate” $n$ number of hosts encountered while scanning the area. This means that each parasite has $n$ chances of encountering the preferred host. If the host population consists of two host types, then the parasite will continue the search until it encounters the preferred host or the $n$th unpreferred host. Such foraging behaviour corresponds with the marginal value theorem (Charnov 1976), because the value of the less suitable host is always less than average, as long as search costs are insignificant. In the present model the parameter $n$ takes into account costs and constraints of searching. Assuming that for an individual parasite all preferred (or unpreferred) hosts are equally preferred (or unpreferred), the behaviour described above represents a rule-of-thumb process of food selection: the forager continues searching and sampling prey as long as the successive prey encountered are higher in quality (Real 1990).

If only one host individual may be examined (i.e. the parasite accepts the first encountered host, $n = 1$) then proportions of host type $1$ attacked ($e$) will equal the proportions of this type available ($A$). If $n = 2$ then

$$e = \frac{[\text{probability of encountering the preferred host during the first searching step (} \pm A\text{)] + [\text{probability of encountering the unpreferred host during the second searching step (} \pm A\text{)]}}{[\text{probability of encountering the preferred host during the first searching step (} \pm A\text{)] + [\text{probability of encountering the unpreferred host during the second searching step (} \pm A\text{)]}}$$

The general form of the proportion of preferred hosts attacked is given by

$$e = \sum_{i=1}^{n} A(1-A)^{i-1}, \quad i = 1, 2, \ldots, n \quad \text{Eq. 4}$$

Recognizing that $1-e = e/(e_1 + e_2) = 1 - \sum A(1-A)^{i-1} = (1-A)^n$ and that $1-A = A/(A_1 + A_2)$, Eq. 4 may be transformed to ratios as follows: