APPLICATION OF THE "FEEDING INDEX" CONCEPT TO STUDIES OF MOSQUITO HOST-FEEDING PATTERNS

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ABSTRACT. The Feeding Index concept, introduced for analysis of host-feeding patterns of mosquitoes, may be defined as "the observed proportion of feeds on 1 host with respect to another divided by the expected comparative proportion of feeds on these 2 hosts, based on factors affecting feeding." The advantages of the Feeding Index are that (1) it departs from the inference that feeding patterns are attributable to host preference; (2) it does not require a full animal census which is often impracticable or even impossible; and (3) it draws attention to, and allows assessment of, some of the multiple factors that influence feeding patterns.

INTRODUCTION

The study of host-feeding patterns is an essential part of understanding the epidemiology of diseases transmitted by arthropods. Although the techniques for determining the host sources of arthropod blood meals are well established, interpretation of the results can be complex and potentially misleading. Recent studies have highlighted the problems involving unbiased sampling of blood-engorged insects, difficulties of identifying closely related species and multiple feeds, and analysis of the data (Boreham 1975, Tempelis 1975). Some progress has recently been made in detecting multiple blood meals (Boreham and Lenahan 1976) and in the development of a new test, the latex agglutination test, which will allow identification of blood meals under field conditions (Boorman et al. 1977). However, in many reports of feeding patterns little information is given on the numbers and distribution of available hosts, and it is often assumed that blood-meal results reflect host preferences, which may well not be true (Boreham and Garrett-Jones 1973).

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Data from blood-meal analyses are commonly presented in crude form or as percentages. For anopheline mosquitoes the concept of Human Blood Index (HBI) was conceived (Garrett-Jones 1964). HBI may be defined as "the proportion of freshly fed *Anopheles* found to contain human blood." Because of the problems of obtaining a representative sample for this index, Garrett-Jones (loc cit) suggested that the best estimate could be obtained by taking the unweighted mean of samples collected from human dwellings and other habitats.

The forage ratio was originally used to study the food preferences of herring (Savage 1931) and was later introduced to separate preferential from opportunistic feeding patterns of mosquitoes (Hess et al. 1968). It may be defined as: "the percent of engorged mosquitoes which have fed upon a given vertebrate host divided by the percent which it comprises of the total population of hosts available in the mosquito's habitat." A ratio considerably greater than 1, supposedly indicates selective preference and values less than 1 indicate avoidance. Values of, or close to, 1 suggest opportunistic feeding. This method has been used to investigate possible seasonal shifts in feeding-patterns (Hayes et al. 1973).

The deficiencies of the forage ratio concept are detailed by Edman (1971). These include neglecting ecological and behavioral differences among hosts and mosquitoes and host availability and accessibility to the mosquito. It also requires a complete numerical census of the animal population which may often be difficult or even impossible. Edman concludes that "each situation must be evaluated separately and on the basis of the prevailing circumstances present." There is however a need to devise a quantitative method of analyzing blood meal identification results. In this paper we present a method which aims to depart from the idea of measuring host preference, eliminates the need for a complete animal census, and which allows for the weighting of additional factors influencing feeding patterns.

THE FEEDING INDEX. We propose the introduction of the term "Feeding Index" which may be defined as "the proportion of feeds on one host with respect to another divided by the expected comparative proportion of feeds on those 2 hosts based on factors affecting feeding." These factors include abundance and size of hosts, their temporal and spatial concurrence with the mosquito and its feeding success. It may be expressed mathematically as $FI = \frac{Ne/Ne'}{Ef/Ef'}$

where FI = Feeding Index
Ne = Number of feeds on host I
Ne′ = Number of feeds on host II
Ef = Expected proportion of feeds on host I
Ef′ = Expected proportion of feeds on host II

Thus an index of 1.0 indicates equal feeding on the two hosts being compared while figures less than one and greater than one indicate a decrease or increase in feeding on the first host relative to the second. From the Feeding Index, seasonal shifts in feeding can readily be examined.

In order to illustrate the use of the Feeding Index, data are presented from studies undertaken between 1974 and 1976 of the host-feeding patterns of *Culex annulirostris* at Kowanyama, an Aboriginal township 26 km inland from the Gulf of Carpentaria, Cape York peninsula, North Queensland (15°28′S, 141°41′E) (Kay et al. 1977). These studies included bloodmeal identification of hosts by using the precipitin test (Boreham 1975), host preference studies *per se* employing closely spaced stable traps which also gave information on mosquito feeding success, and quantitative studies on man-mosquito contact indoors and outdoors. Full details of these studies will be published elsewhere.

Within the village, counts were made of humans and domestic animals. Approximately 800 Caucasians and Aboriginals were resident in the village. During the early hours of darkness when *Cx. annulirostris* is most active (Standfast 1967, Standfast and Kay unpubl. data), approximately half of the human population was indoors.

Mongrel dogs (15–25 kg) number 100 from dog registration records but this was probably an underestimate. Dogs wandered the streets freely and slept outdoors, indoors, under houses or on verandahs. Approximately 90% were outdoors when mosquitoes were biting. These dogs often intermingled with Aboriginals who often sat outdoors in social groups.

There were 80 domestic fowl kept outdoors in several yards until the 1975 dry season when 35 from one yard were slaughtered. In the following transitional period, the yard was restocked with 20 chickens which were almost adult by the following wet season.

It was not possible to make an accurate census of a herd of 5–50 cattle which occasionally entered the village at night until mid-1975 when new fences and grids were constructed. Swarms of fruit bats, *Pteropus* spp. (Megachiroptera) fed on mangoes at night during the late dry season in October-November.

In the surrounding area, an accurate census of the animals was impracticable for a number of reasons.

(1) Limited manpower and expertise permitted only rough estimates.

(2) Many animals such as kangaroos, wallabies, feral pigs, cattle and birds visited the study area at will.

(3) The census should be done at night when mosquitoes are active.

(4) In the wet season roads are closed even to light traffic and dense grass and reeds in excess of 2 m tall made animals difficult to see.

In this example dog-fowl, dog-human and human-fowl host-feeding patterns of *Cx. annnulirostris* were compared using the Feeding Index (Table 1).

The expected rate can be, most simply, calculated from the relative abundance of the 2 hosts. For example, if feeding occurred equally on dogs (population 100) and fowl (population 80 until 1975 dry season) the expected ratio in precipitin tests would be 1:0.8 or 1.25. This figure changed to 2.22 and 1.54 on later trips because of fluctuations in fowl numbers. The observed proportion (Ne/Ne[1]) of feeding from blood-meal analyses in the 1974 dry season was $\frac{35}{8}$ or 4.38 giving a Feeding Index of $\frac{4.38}{1.25} = 3.5$. This result therefore indicates greater feeding on dogs relative to fowl at that time.

The accuracy of the expected comparative rate can be improved by the addition of 3 other factors.

1) Temporal and spatial concurrence of hosts and mosquitoes. This was calculated from observations of host movements and from a study of mosquito feeding indoors and outdoors. For *Cx. annulirostris*, the mean outdoors catch was 169.8 per night whereas a mean of only 15.0 per night was collected indoors. This means that *Cx. annulirostris* was 11.3 times more common biting outdoors than indoors or 8.1% of the biting occurred indoors and 91.9% occurred outside. *Cx. annulirostris* would therefore have a greater opportunity to feed on hosts outdoors and this could seriously affect the results if one of the hosts under study was found predominantly indoors.

Host-mosquito concurrence for dogs and fowl can be calculated from the relative numbers of host and mosquito available for contact indoors and outdoors:

		Outdoors	Indoors
Host:	Dogs	0.9	0.1
	Fowl	1.0	0
Mosquito:			
	Cx. annulirostris	0.92	0.08

Concurrence for dogs relative to fowls

$$= \frac{(0.9 \times 0.92) + (0.1 \times 0.08)}{(1.0 \times 0.92)}$$

$$= 0.91$$

Hence *Cx. annulirostris* was more likely to encounter fowl than dogs based on these criteria.

2) Mosquito feeding success. In the animal-baited stable trap experiments 96% of the *Cx. annulirostris* successfully engorged on dog and 83% on fowl. The figures do not allow for those eaten by the bait animals. Hence, the adjustment for feeding success would be $\frac{96}{83}$ (1.16) for dogs relative to fowl.

3) Size of host. At present we know no satisfactory method of evaluating the effect of size. The relative sizes of the hosts could possibly be incorporated into the calculation of the expected value.

Table 1. Numbers of *Culex annulirostris* feeding on fowl, dogs and humans at Kowanyama village and the calculated feeding index, based on abundance.

Season	Number of Feeds			Feeding Index*		
	Fowl	Dogs	Humans	Dogs:Fowl	Dogs:Humans	Fowl:Humans
Dry 1974	8	35	12	3.5	23.3	6.7
Wet 1975	8	26	2	2.6	104.0	40.0
Dry 1975	0	23	5	10.4**	36.8	3.6
Transitional 1975	6	36	6	3.9	48.0	12.3
Wet 1976	2	51	6	16.6	68.0	4.1

* See text p. 69 for details of calculation and host abundance.

** Zero collections scored as 1 for calculation purposes.

The expected proportion ($^{Ef}/Ef'$), if we assume the average size of a dog is 5 times that of a fowl, would become [relative numbers x size x host-mosquito concurrence x feeding success].

Thus for the samples collected in the 1974 dry season, the expected comparative feeding rate would be for dogs with respect to fowl

$$1.25 \times 5.0 \times 0.91 \times 1.16 = 6.59$$

$$\text{and the Feeding Index} = \frac{4.38}{6.59} = 0.66$$

DISCUSSION

Little is known of the underlying genetic mechanisms affecting feeding but the multiplicity of environmental factors that influence it are becoming abundantly clear. Edman (1971) has previously discussed mosquito-host proximity, varied flight patterns of different mosquitoes, inaccessibility of hosts, intolerance to mosquito attack and the concurrence of host and mosquito activity. Tempelis (1975) stated that temperature, photoperiod, wind and animal densities were recognized feeding variables. He amplified some aspects of mosquito behavior and host receptivity, and he reviewed the relationship of mosquito density to host selection first introduced by Reeves (1971) and documented by Edman et al. (1972).

Many of these factors are applicable to the study of feeding patterns at Kowanyama. Exophagic mosquitoes with catholic feeding patterns, e.g. *Cx. annulirostris*, would possibly feed on a less attractive host if it were encountered first or available outdoors. The zooprophylactic effect of dogs in diverting *Cx. annulirostris* from less-preferred humans (Kay et al. 1976), especially Aboriginals sitting in social groups, is another factor which could influence feeding patterns.

The purpose of this paper is to present a concept rather than the method; there are questions regarding the estimation of supplementary factors that are not entirely resolved. Host-mosquito concurrence estimates are probably applicable only to exophagous species as endophagous species, e.g. *Cx. quinquefasciatus* (= *Cx. fatigans*) will feed readily outdoors. Blood engorgement determined inside cages or stable traps may not always simulate what happens in natural conditions but we think the results are generally valid as long as the test animals have some freedom of movement and several individuals are tested.

The addition of animal size with abundance in the calculation at least illustrates that host-feeding patterns are influenced by the relative biomasses of animal species. However when size was introduced into these calculations the Feeding Index was reversed from 3.5 in the simplest form to 0.66. This implied decreased feeding on dogs relative to fowls which was contrary to previous data and expectations. If a size component is omitted, it is important that the average weight and breed of animal be listed to prevent erroneous comparisons, e.g. Great Danes from one locality with Dachshunds from another.

The main advantages of the Feeding Index are that it departs from the inference that feeding patterns are attributable to innate host preference though they, at times, may well be. It draws attention to the fact that multiple influences do operate, and it does not require a full animal census.

The difficulties in doing a census at Kowanyama have already been discussed. Perhaps another advantage of the Feeding Index concept is that it is flexible and allows the field worker to decide, in his own situation, whether he should undertake the extra studies necessary to determine these supplementary factors.

This method will be particularly suited for the analysis of a limited number of hosts as is intended for the latex agglutination test which has been developed for field use (Boorman et al. 1977).

The factors that determine host selection are so complex that perhaps it is unwise to attempt to quantify data from such studies, especially as the precision of some of the measurements is not sufficient to allow detailed statistical analysis. On the other hand, we do feel that this concept will provide a framework on which a better understanding of mosquito (and other blood-sucking arthropods) host-feeding patterns might be built.

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