THE USE OF THE FORAGE RATIO TECHNIQUE IN MOSQUITO HOST PREFERENCE STUDIES [1]

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A knowledge of mosquito-host relationships is important to understand the epidemiology of many diseases of man and animals for which these insects serve as vectors. Mosquito host preference studies have received a major emphasis during recent years from the studies of Tempelis, Reeves, and associates (1–4). Their use of chickens for production of antisera and refinement of the capillary precipitin technique for determining the source of blood meals has expanded greatly our knowledge of mosquito host feeding patterns (5, 6).

Some mosquitoes, such as *Culiseta inornata* and species of *Aedes* and *Anopheles,* appear to have "fixed" host preference patterns and feed primarily on mammals; others, such as *Culiseta melanura* and several species of *Culex* feed primarily on birds; a third group, which includes *Culex tarsalis* and members of the *C. pipiens quinquefasciatus* complex, exhibit a variable feeding pattern with regard to birds and mammals. Epidemiologically it is important to know the relative extent to which the feeding patterns of this latter group are influenced by availability or host preference; furthermore, it is desirable to know the conditions of host availability under which species with fixed feeding patterns may deviate from their normal host. The present paper makes application of the forage ratio technique (7–9) to answer these questions. The technique was originally used to study the food habits of fishes and similar techniques have been applied to other animals, such as waterfowl (10). The procedure simply compares the percent of use with the percent of abundance. Applied to blood-sucking mosquitoes, this is 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 forage ratio of one (or near one) indicates neither preference nor avoidance of the indicated host animal; forage ratios significantly greater than one indicate selective preference; and values less than one indicate avoidance in favor of other hosts.

The field and laboratory techniques used in these studies have been described previously (1–3, 11) and will not be repeated here.

DESCRIPTION OF STUDY AREAS. Studies of mosquito host preferences on the island of Oahu, Hawaii, provided a good situation for application of the forage ratio technique. Three study areas were selected for this purpose, Mokapu Point, Kawainui Swamp and Vause Dairy.

Mokapu Point is a volcanic promontory on the windward side of Oahu beyond the Kaneohe Marine Corps Air Station. It is covered with a dense growth of 8′ to 10′ shrubs (mostly *Leucena glauca*) in which large populations of pelagic birds nest and roost. These birds are mostly of a single species, the red-footed booby *(Sula sula).* Populations of this species range from about 800 in the non-nesting season in the fall and early winter to 1,500 birds at the peak of the nesting season in April and May. Mammals are relatively scarce in the area and consist almost

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entirely of mongooses, with an occasional feral cat or stray dog. Thus, birds were estimated to comprise at least 97 percent of the vertebrate hosts available to blood-feeding mosquitoes on Mokapu Point.

Kawainui Swamp is an area on the main shore of Oahu a few miles south of Mokapu Point. It is covered mostly with swamp grass and patches of other wetland vegetation, trees and shrubs. An "auto graveyard" occupies one edge of the swamp. There are three houses in the study area with seven human occupants and a variety of domestic animals (dogs, cats, cows, and chickens). Several species of wild birds also are present (house sparrows, doves, mynah birds, cardinals, etc.). It is estimated that bird and mammal hosts are about equally available in this study area.

Vause Dairy is on Highway 72 southwest of Kawainui Swamp near Waimanalo. In addition to over a hundred head of cows, it has an abundance of other domestic animals, including horses, dogs, chickens, pigeons, ducks and geese. Thus, it provides a good site to study comparative attractiveness of man and domestic animals for mosquitoes.

Two species of mosquitoes were involved in these studies, *Culex quinquefasciatus* and *Aedes albopictus*. General observations indicate that the Hawaii strain of *C. quinquefasciatus* exhibits a variable feeding pattern for birds and mammals, whereas *A. albopictus* has a fixed preference for mammals typical of many species of *Aedes*.

RESULTS. Data obtained from the Mokapu Point and Kawainui Swamp study areas during 1966 are presented in Table 1. If we looked only at the results of precipitin tests for *C. quinquefasciatus* and *A. albopictus* collected from Mokapu Point without reference to host availability, we might conclude that both species feed predominantly on birds. When we look at the forage ratios, however, we obtain an entirely different picture. It is then apparent that the 99 percent feeding of *C. quinquefasciatus* on birds was in line with their relative availability and that mammals had a low forage ratio due primarily to the absence of feeding on mongooses. In contrast, *A. albopictus* showed a mammal forage ratio over 10 times that for birds, and apparently fed upon birds only as a "last resort" because of the unavailability of mammals. Results of the precipitin tests showed that it fed on the few mongooses present, on man (possibly one of the observers), and upon a stray dog.

TABLE 1.—Forage ratios for *Culex quinquefasciatus* and *Aedes albopictus* collected from two study areas on Oahu, Hawaii, 1966. Numbers in parentheses indicate numbers of engorged specimens for which the source of blood meal was identified.

	Mokapu Point (150)		Kawainui Swamp (1,447)	
C. quinquefasciatus	Mammals	Birds	Mammals	Birds*
A. Percent blood meals	0.7	99	51	49
B. Percent in population	3.0	97	47	53
Forage ratios (A/B)	0.2	1.0	1.1	0.9
	Mokapu Point (41)		Kawainui Swamp (14)	
A. albopictus	Mammals	Birds	Mammals	Birds*
A. Percent blood meals	27	73	93	7
B. Percent in population	3.0	97	47	53
Forage ratios (A/B)	9	0.8	2	0.1

* A few wild birds not included in counts.

In the Kawainui Swamp area blood meal sources for *C. quinquefasciatus* were about equally distributed between birds and mammals, and the forage ratios indicate that this was in line with their relative abundance. The results for *A. albopictus* collected from Kawainui Swamp again show the high feeding preference of this species for mammals. The total number of blood meals identified was only 14, but only one of these was avian (chicken).

The Vause Dairy provided an opportunity to determine whether *C. quinquefasciatus* exhibited feeding selectivity between different kinds of domestic animal hosts. Results for the 1966 season are presented in Table 2. For the domestic species present at Vause Dairy, *C. quinquefasciatus* showed a three to one preference for birds over mammals. This was due primarily to the high forage ratio for chickens (3.5) and the low forage ratio for cows (0.3). This difference is even more impressive when we consider the much greater size of the cattle and the fact that they comprised almost 50 percent of the total available domestic animal hosts. Among the mammals, however, dogs had an even higher forage ratio (3.7) than chickens. None of the almost 500 engorged mosquitoes tested had fed on man. A possible explanation is that the nine resident humans were usually inside the screened house during the night and thus were unavailable to the night-biting *C. quinquefasciatus*.

TABLE 2.—*Culex quinquefasciatus* forage ratios for domestic animals, Vause Dairy, Oahu, Hawaii, 1966.

	A. Percent Blood Meals	B. Percent in Population	Forage Ratio (A/B)
Dog	10	2.7	3.7
Horse	3.1	2.3	1.3
Cow	16	49	0.3
Human	0	3.5	0
Mammal Subtotals	29.1	57.5	0.5
Chicken	67	19	3.5
Pigeon	0.7	8.5	0.1
Duck	0.9	11	0.1
Geese	2.4	3.9	0.6
Bird Subtotals	71.0	42.4	1.7

There was also a marked difference in the host preferences for different avian species at Vause Dairy; for example, the forage ratio for chickens was 35 times that for ducks, even though these two species are comparable in size.

DISCUSSION. It is obvious from these studies that one cannot make valid interpretations of mosquito blood-feeding patterns in terms of host preference unless data also are available on the relative numbers of the different kinds of hosts which are present in the study area. The forage ratio technique provides a convenient method for converting such data to indices of host preference. It readily distinguishes species which have "fixed" feeding preferences for birds or mammals from those which exhibit a variable or "opportunistic" feeding pattern influenced primarily by host availability. Even for the latter type, it is apparent from the Hawaii studies that the bird-mammal host preference pattern may vary from area to area, depending upon the overall composition of available host species. Studies in other areas have shown that there may also be seasonal variations in host preference for some mosquitoes (2, 3, 11).

The studies at Vause Dairy show that there may be marked differences in preferences between host species within the same class, such as chickens and ducks, which from casual observation would appear to be equally suitable sources of blood meals. Such data would be most useful for determining the relative values of different domestic animals in providing zooprophylaxis against mosquito-borne diseases (deviation of blood-sucking mosquitoes from man to other hosts). For example, at Vause Dairy it is apparent

that chickens and dogs would be the most effective species for zooprophylaxis against *C. quinquefasciatus*. Such data on specific host preferences also are useful for evaluating the ecologic potential of different vertebrates as reservoir hosts of arboviruses or other vector-borne zoonoses.

Epidemiologically, it is also important to know the conditions under which a mosquito with a fixed feeding pattern may be deviated from its preferred hosts, as was *A. albopictus* in the Mokapu Point study area. Here again, the forage ratio technique provides a method for determining the degree to which host-specific feeding patterns are actually obligate.

One of the problems in the use of the forage ratio technique is the difficulty usually encountered in obtaining accurate population estimates for the available vertebrate hosts. Even when the results are based on rough population estimates, however, they are much more meaningful than they would be without any information on host availability.

SUMMARY. Microprecipitin techniques were used to determine the blood meal source for engorged *Culex quinquefasciatus* and *Aedes albopictus* mosquitoes collected from three study areas on the island of Oahu, Hawaii during 1966. It was shown that a valid interpretation of the data in terms of host preference could not be made without information on the relative availability of vertebrate hosts in the study areas. The forage ratio technique provided a convenient method for converting the data to indices of host preference. These indices increase greatly the usefulness of mosquito host feeding data for ecological and epidemiological investigations.

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