# Human host selection by anophelines: no evidence for preferential selection of malaria or microfilariae-infected individuals in a hyperendemic area

T. R. BURKOT*, A. NARARA, R. PARU, PATRICIA M. GRAVES* *and* P. GARNER†

*Papua New Guinea Institute of Medical Research, P.O. Box 378, Madang, Papua New Guinea*

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SUMMARY

Host selection among humans by *Anopheles punctulatus* was studied in an area of Papua New Guinea endemic for malaria and filariasis. Blood films were made from the stomach contents of freshly engorged mosquitoes found resting on the walls of houses in which the parasite status of the occupants was known. Engorgement rates on humans were non-random but could not be consistently related to the parasite status of individuals in the houses for either malaria or filaria. In some households, anophelines preferentially fed on parasitaemic individuals while in other households aparasitaemic individuals were significantly more often selected. This finding is believed to reflect the fact that malaria and filarial infections in this endemic area are predominantly asymptomatic. There were no significant differences in axillary temperatures between malaria or microfilariae positive or negative individuals.

Key words: *Anopheles punctulatus*, host selection, malaria, filariasis.

## INTRODUCTION

Host selection by mosquitoes is dependent on a variety of cultural factors (bednet usage, house construction, animal husbandry practices, etc.) and intrinsic mosquito preferences (zoophilic versus anthropophilic, adults or children, etc.) (Burkot, 1988). Models predict that non-homogeneous selection among available humans by mosquitoes will increase the reproductive rate of mosquito-borne human diseases; should the preferred group contain infected individuals, the disease prevalence will increase (Dye & Hasibeder, 1986). Easier maintenance of a high stable infection equilibrium is predicted by models assuming an increasing preference for more heavily infected individuals (Kingsolver, 1987).

Recent laboratory investigations provide evidence for parasite-induced behaviour changes that result in preferential selection of parasitized hosts by mosquitoes. Preferential selection of infected animals may be expressed at three levels in the feeding process: attraction and penetration, probing and blood location, and engorgement (Edman, Day & Walker, 1985). Arboviral infections in chickens and lambs as well as malaria infections in mice were shown to increase the mosquito engorgement success rates on infected individuals (Mahon & Gibbs, 1982; Day & Edman, 1983; Day, Ebert & Edman, 1983; Turrell, Bailey & Rossi, 1984). For Rift Valley fever virus-infected lambs, the frequency of mosquito bites was positively correlated with body temperature (Turrell *et al.* 1984). Similarly, malaria-infected rodents suffering symptomatic parasitaemias exhibit a reduction in defensive behaviour resulting in an increased rate of mosquito feeding success (Day *et al.* 1983; Day & Edman, 1983). The reduced haematocrit associated with heavy rodent malaria or arboviral infections also facilitates a more rapid rate of mosquito engorgement (Rossignol *et al.* 1985).

The ability of malaria parasites to induce similar behaviour changes in humans which affect the mosquito engorgement success rate has yet to be confirmed by studies in endemic areas. Described below are a set of experiments designed to elicit whether malaria and/or filaria-infected humans in an endemic area are preferentially fed upon by their natural vectors.

## MATERIALS AND METHODS

The study was conducted in Butelgut and Buksak villages in Madang Province, Papua New Guinea. The area is hyperendemic for malaria with *Plasmodium falciparum*, *P. vivax*, *P. malariae* and *P. ovale* present (Cattani *et al.* 1986). In addition *Wuchereria bancrofti* is endemic in Buksak village. The primary vector of human malaria and filariasis in these two villages is *Anopheles punctulatus* (Burkot *et al.* 1988*b*). The rationale behind the study and the methods to be used were explained to the residents of both villages. Those consenting were entered into the study.

* Present address: Queensland Institute of Medical Research, Bramston Terrace, Herston, Brisbane 4006, Australia.
† Present address: London School of Hygiene and Tropical Medicine, Keppel St., London WC1E 7HT.

Between 17.00 and 22.00 h, residents of Butelgut had fingerprick blood slides made and immediately thereafter 10–20 laboratory reared *Anopheles farauti* were allowed to engorge on each individual. *A. farauti*, a member of the *An. punctulatus* complex, is easily maintained in a laboratory colony whereas *An. punctulatus* is difficult to establish in a colony. Immediately following feeding, mosquitoes were stored on ice while being transported to the laboratory. The stomach contents of the engorged mosquitoes were then dissected in 3 $\mu$l of phosphate-buffered saline on a glass slide and thick and thin films made from the stomach contents. Blood films from both fingerpricks and mosquito stomach contents were air-dried for 2 days. Thin films were then fixed with methanol and films stained in 4% Giemsa for 30 min. Thick blood films were examined at 1000 × for malaria parasites as described previously (Burkot *et al.* 1987).

A total of 32 individuals in 7 households in Buksak village participated in the second part of the study. Bednet usage in the households was determined through interviews and examination of the houses. Individuals in these households had fingerprick blood films made between 17.00 and 18.00 h on the two consecutive days of the study for later examination for malaria parasites. Axillary body temperatures were taken and recorded at this time as well as at a previous malariometric/filariasis survey, in which *Wuchereria bancrofti* microfilariaemic-infected individuals in the village were identified by filtration of 2 ml blood samples collected by venepuncture between 22.00 and 01.00 h.

Prior to commencement of the study, residents of the 7 households were instructed to exclude domestic animals from the households for the duration of the study. As a check, a sample of blood-engorged mosquitoes collected from the houses before and after the study were analysed by ELISA (Burkot *et al.* 1988*a*) for host blood meal source using rabbit antiserum against sera of human, dog, pig, cat and chicken, the most common domestic hosts in the area.

At 23.00, 01.00, 03.00 and 05.00 h on 2 consecutive nights, a relative of the household entered the house and searched the walls of the house for 15–20 min for blood-engorged resting anophelines. Engorged anophelines were dissected immediately as described above and thick and thin films made with the stomach contents. Blood films were dried, fixed, stained and examined for malaria parasites as described above. In addition, the entire thick film was examined for microfilariae at 100 × magnification.

## RESULTS

A total of 503 laboratory reared *An. farauti* successfully fed on 87 Butelgut residents who participated in the first study. It was found that 208 *An. farauti* fed on the 33 malaria-positive individuals with 117 mosquitoes having detectable malaria parasites in their stomachs. None of the 83 mosquitoes that fed on 11 of the malaria-positive individuals ingested detectable densities of malaria parasites. The weighted average proportion of mosquitoes with detectable malaria parasites in their stomachs following engorgement on a malaria positive individual was 0·562.

Of 90 engorged *An. punctulatus* captured in the 7 Buksak households during the study and tested by ELISA for host blood meal source identification, all were positive for human blood. Residents of households 1050, 2030, 2070, 2120 and 2131 slept without bednets. The occupants of house 1030 shared 2 bednets with 3 and 4 occupants/bednet. As house 2040 had a single bednet with only 2 of the 3 individuals sleeping inside it, results from 2040 were excluded from the overall analysis as the individual outside the bednet would be more susceptible to mosquito attack than the others. The other 6 households were analysed separately and together for the effect of parasite status on host selection by *An. punctulatus*. Demographic and parasitological information on the participants in the study is given in Table 1.

Summaries of the proportions of humans and wild-caught mosquitoes in Buksak with detectable malaria and microfilariae infections are given in Table 2. Although individual parasite species identifications were recorded, for the purposes of this analysis, malaria parasites were treated as a group. The expected probability of a mosquito having detectable malaria parasites ($P_{em}$), assuming random host selection within a house, was calculated as the proportion of malaria-positive individuals in that house multiplied by the predicted proportion of mosquitoes which would have detectable malaria parasites in their stomach after having fed on a known malaria-infected individual (0·562 as calculated from the Butelgut study). Buksak house 2040 gave an independent verification of this analysis as 52·2% of engorged mosquitoes captured in this house (all 3 occupants being malaria positive) had malaria parasites compared to the predicted 56·2% ($\chi^2 = 0{\cdot}2$, D.F. = 1, $P > 0{\cdot}5$).

The expected probability of an anopheline taking up microfilariae after having fed on a microfilaraemic individual was calculated by the formula: $P_{ei} = 1 - e^{-u}$ where $u$ = average number of microfilariae ingested/mosquito. This value was based on the assumption of random microfilariae distribution in the blood as estimated by the density of microfilariae found by venepuncture and an average anopheline blood meal of 1·5 $\mu$l (as determined by weighing 33 engorged laboratory reared *An. farauti* and comparing their weight to the average weight of mosquitoes from the same colony). The sum of the

Table 1. Demographic and parasitological information on the Buksak participants in the study

| House | Age (years) | Sex | *Wuchereria bancrofti* microfilariae/cm³ | Malaria density* (parasites/mm³) Day 1 Total† | Day 1 Sexual‡ | Day 2 Total | Day 2 Sexual | Temperature Day 1 (°C) | Day 2 (°C) |
|---|---|---|---|---|---|---|---|---|---|
| 1030 | 4 | Male A§ | 0 | 1440 | 0 | 1880 | 80 | 36·2 | 37·4 |
| | 32 | Female A | 0 | 0 | 0 | 80 | 20 | 36·5 | 36·7 |
| | 8 | Female B | 200 | 40 | 20 | 0 | 0 | 36·7 | 37·0 |
| | 9 | Female B | 0 | 0 | 0 | 0 | 0 | 36·8 | 36·7 |
| | 5 | Female B | 0 | 520 | 60 | 1240 | 0 | 37·4 | 36·9 |
| | 5 | Female A | 392 | 440 | 0 | 40 | 0 | 37·7 | 37·0 |
| | 4 | Male A | 0 | 480 | 80 | 960 | 120 | 37·6 | 36·7 |
| 1050 | 50 | Male | 6391 | 80 | 0 | 1040 | 0 | 36·6 | 36·4 |
| | 13 | Female | 0 | 0 | 0 | 0 | 0 | 37·2 | 37·5 |
| | 9 | Male | 0 | 10960 | 0 | 0 | 0 | 36·4 | 37·5 |
| | 6 | Female | 1 | 3360 | 0 | 1440 | 0 | 37·0 | 36·4 |
| | 4 | Female | 0 | 200 | 60 | 1280 | 60 | 37·3 | 36·7 |
| 2030 | 48 | Female | 0 | 0 | 0 | 0 | 0 | 36·6 | 36·2 |
| | 15 | Female | 0 | 0 | 0 | 0 | 0 | 37·4 | 37·1 |
| | 8 | Female | 1950 | 440 | 160 | 2140 | 160 | 37·0 | 38·3 |
| | 5 | Male | 0 | 640 | 180 | 1320 | 100 | 36·7 | 35·9 |
| 2040 | 37 | Female C | 2692 | 320 | 0 | 760 | 80 | 36·0 | 36·7 |
| | 14 | Female | 0 | 5320 | 0 | 680 | 0 | 36·0 | 36·1 |
| | 7 | Male C | 0 | 3760 | 60 | 1000 | 0 | 36·4 | 36·8 |
| 2070 | 39 | Female | 640 | 0 | 0 | 0 | 0 | 36·5 | 36·9 |
| | 11 | Male | 1 | 280 | 0 | 200 | 0 | 36·2 | 36·8 |
| | 23 | Female | 150 | 80 | 0 | 80 | 40 | 37·1 | 37·2 |
| | 4 | Male | 0 | 120 | 0 | 240 | 20 | 36·2 | 35·9 |
| | 8 | Female | 220 | 0 | 0 | 0 | 0 | 37·1 | 37·6 |
| 2120 | 55 | Male | 1678 | 0 | 0 | 0 | 0 | 36·3 | 38·7 |
| | 45 | Female | 4246 | 0 | 0 | 0 | 0 | 36·3 | 36·9 |
| | 8 | Female | 0 | 640 | 0 | 120 | 0 | 37·0 | 37·4 |
| | 13 | Female | 5650 | 0 | 0 | 160 | 20 | 36·2 | 36·4 |
| | 3 | Female | 0 | 760 | 60 | 4840 | 20 | 36·4 | 35·3 |
| 2131 | 26 | Female | 0 | 0 | 0 | 0 | 0 | 36·8 | 36·9 |
| | 7 | Male | 900 | 1120 | 40 | 1000 | 20 | 36·5 | 37·2 |
| | 5 | Female | 0 | 0 | 0 | 40 | 0 | 36·2 | 36·3 |

* All parasite species combined.
† Total asexuals and gametocytes.
‡ Total gametocytes.
§ Sex followed by the same letter shared a bednet; all others slept outside a bednet.

$P_{ei}$ divided by the total number of individuals in a household gave $P_{ef}$, the probability of a mosquito collected in a house having ingested microfilariae assuming random host choice.

When data from the 6 houses were analysed together, human host selection by *An. punctulatus* was not found to be random with respect to the malaria parasite status of the occupants ($\chi^2 = 4{\cdot}19$, D.F. = 1, $P < 0{\cdot}05$). Significant divergence from the hypothesis of random feeding with respect to malaria status was seen in houses 1030 and 2030. Captured engorged *An. punctulatus* in these two houses were found to have selected non-malarious hosts significantly more often. Feeding patterns with respect to filarial infections were not significantly different from the hypothesis of random selection of hosts regardless of microfilarial infections ($\chi^2 = 1{\cdot}28$, D.F. = 1, $P > 0{\cdot}25$). In 4 houses, host selection was not significantly different from the hypothesis of random selection. However, in house 2070, mosquitoes preferentially fed on microfilaraemic individuals, whereas in house 1050, amicrofilariaemic individuals were preferred.

These selection patterns also cannot be explained by the ages of the hosts alone. Although the 3 oldest individuals in house 2120 were microfilaraemic, there was no significant preference for these individuals. Anophelines engorging in house 2030 preferentially selected malaria-negative individuals (the two adults) significantly more often than expected from a random feeding hypothesis. These results confirm the earlier findings of large variations in the attractiveness of individuals in which some children were preferred by anophelines over their mothers, but in other cases the mother was preferred over the child (Burkot *et al.* 1988*a*).

There were no significant differences in average axillary body temperatures among malaria-negative

Table 2. Anopheline selection for parasite infected individuals by house

| | Malaria | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Mosquito | | Humans | | | | | |
| House | Pos.* | Total | Pos.† | Total | $P_{em}$‡ | $P_0$ | $\chi^2$ | $P$ |
| 1030 | 22 | 103 | 5 | 7 | 0·401 | 0·214 | 9·02 | < 0·005 |
| 1050 | 37 | 69 | 3·5 | 5 | 0·393 | 0·536 | 3·62 | N.S. |
| 2030 | 4 | 75 | 2 | 4 | 0·281 | 0·053 | 13·86 | < 0·001 |
| 2040 | 36 | 69 | 3 | 3 | 0·562 | 0·522 | 0·20 | N.S. |
| 2070 | 33 | 97 | 3 | 5 | 0·337 | 0·340 | < 0·01 | N.S. |
| 2120 | 9 | 48 | 2·5 | 5 | 0·281 | 0·188 | 1·50 | N.S. |
| 2131 | 36 | 114 | 1·5 | 3 | 0·281 | 0·316 | 0·50 | N.S. |
| Overall§ | 141 | 506 | 17·5 | 29 | 0·331 | 0·279 | 4·19 | < 0·05 |
| | Filaria | | | | | | | |
| | Mosquito | | Humans | | | | | |
| House | Pos.* | Total | Pos.† | Total | $P_{ef}$‖ | $P_0$ | $\chi^2$ | $P$ |
| 1030 | 7 | 105 | 2 | 7 | 0·100 | 0·067 | 1·17 | N.S. |
| 1050 | 2 | 71 | 2 | 5 | 0·200 | 0·028 | 10·48 | < 0·005 |
| 2030 | 12 | 77 | 1 | 4 | 0·236 | 0·156 | 2·10 | N.S. |
| 2040 | 2 | 77 | 1 | 3 | 0·327 | 0·026 | 21·34 | < 0·0005 |
| 2070 | 53 | 100 | 4 | 5 | 0·220 | 0·530 | 43·68 | < 0·0005 |
| 2120 | 34 | 50 | 3 | 5 | 0·583 | 0·680 | 0·81 | N.S. |
| 2131 | 28 | 119 | 1 | 3 | 0·247 | 0·235 | 0·07 | N.S. |
| Overall§ | 136 | 522 | 13 | 29 | 0·237 | 0·261 | 1·28 | N.S. |

* Number of mosquitoes in which malaria parasites were found in the blood meal.
† Average number of people in a household parasitaemic for malaria or microfilariae.
‡ The expected probability of a mosquito feeding on a malaria-infected individual and ingesting a detectable density of parasites assuming random host choice.
§ $\chi^2$ value for house 2040 was excluded from the overall analysis as not all occupants were equally accessible to mosquitoes.
‖ The expected probability of a mosquito ingesting microfilariae assuming random host choice, a random distribution of microfilariae in the blood of microfilariaemic individuals and an average blood meal of 1·5 $\mu$l.

individuals ($n = 64$, temperature (T) = 36·7 °C) compared to individuals with light parasite densities ($\leqslant 600$ parasites/mm$^3$; $n = 54$, T = 36·7 °C) or heavier parasite densities ($> 600$ parasites/mm$^3$; $n = 44$, T = 36·7 °C) (ANOVA, $F = 0{\cdot}20$, D.F. = 2,159, $P > 0{\cdot}1$). Similarly, there were no significant differences in mean axillary body temperatures among individuals who were microfilariae negative (T = 36·6 °C, $n = 86$) compared to individuals with light infections (< 500/ml blood; T = 36·7 °C, $n = 23$) or individuals with heavier infections (> 500/ml blood; T = 36·6 °C, $n = 25$) (ANOVA: $F = 0{\cdot}16$, D.F. = 2, 131, $P > 0{\cdot}1$).

In this limited sample of body temperatures on consecutive days, changes in axillary body temperatures did not significantly differ among individuals whose malaria parasite density increased, decreased or stayed the same (ANOVA: $F = 0{\cdot}90$, D.F. = 2, 29, $P > 0{\cdot}1$). Increasing parasitaemia, defined by a change in parasite status from negative to positive or from a light to a heavy parasite density as defined above, was accompanied by an average 0·03 increase in temperature ($n = 9$). A decreasing parasitaemia (from parasite positive to negative or from a heavy to a light parasite density) was accompanied by an average rise in temperature of 0·6 °C ($n = 3$) while individuals without a change in parasite status (negative, light or heavy on both days) differed in body temperature on consecutive days by an average of 0·1 °C ($n = 20$).

## DISCUSSION

Laboratory based experiments described parasite-mediated behaviour changes which result in preferential selection of malaria infected rodents (Day *et al.* 1983; Day & Edman, 1983). Using the results from these experiments as a theoretical basis, a series of malaria models was developed and compared assuming either random host choice, a consistent preference for infected hosts, an increasing preference with increasing infection or a switching behaviour in which the mosquito preference switches from uninfected to infected hosts as the level of infection increases (Kingsolver, 1987). All models predicted either a stable uninfected state or a stable parasite prevalence. However, models assuming increasing selection for infected hosts or switching

behaviour predicted either easier maintenance of a high stable parasite prevalence or the uninfected state, the outcome being determined by the initial infection levels in hosts and vectors.

No evidence was found for preferential feeding by *An. punctulatus*, the vector of human malaria and filariasis in Buksak village, on either malaria or filaria-infected individuals. Statistical analysis revealed that human host selection by *An. punctulatus* was not random with regard to the malaria parasite status of the human hosts. In none of the households were malaria-infected individuals preferentially fed upon. Despite 2 of the 4 occupants of house 2030 being positive for both malaria asexuals and gametocytes, the 2 uninfected individuals were significantly more often selected by the natural vector. There was no consistent host choice observed for *An. punctulatus* for microfilaraemic positive or negative individuals. In one household, wild anophelines preferentially selected microfilaraemic individuals but in another house amicrofilaraemic individuals were significantly more often selected.

Numerous previous studies have emphasized the importance to transmission in malaria endemic areas of asymptomatic malaria parasitaemias which have been estimated as being between 4 and 12 times more common than symptomatic infections (Covell, 1960). In this hyperendemic area, no correlation was found between parasite status for either malaria or filaria and fever. Although a positive correlation between temperature and *P. falciparum* infections was reported in a holoendemic area of Africa, it was not a strong correlation and temperature was judged to be an insensitive indicator of parasitaemia (Molineaux & Gramiccia, 1980).

In endemic areas, the association between malaria and fevers is strongest with high parasitaemias. In the hyperendemic Madang area, only 3·3% of *P. falciparum* infections have parasitaemias exceeding 0·4% (Graves *et al.* 1988). Moreover over 82% of gametocytaemic individuals have gametocytaemias under 0·0016%. In contrast, the rodent malarias, *P. berghei*, *P. chabaudi* and *P. yoelii*, used to demonstrate selection for parasitaemic hosts at times of peak gametocytaemia, had peak parasitaemias of 45, 72 and 9%, respectively (Day *et al.* 1983; Day & Edman, 1983). These heavy infections exert a much more profound effect on the host's body temperature and behaviour (Day & Edman, 1984). Mean rectal temperatures of mice and hamsters infected with *P. berghei* dropped by 7·4 and 6·8 °C, respectively, compared to uninfected hosts. *P. chabaudi*-infected mice experienced a 6·0 °C average drop in temperature. Significant decreases in activity patterns of rodents infected with either *P. berghei* or *P. chabaudi* corresponded with increases in the success with which mosquitoes successfully fed on these hosts. Although *P. yoelii*-infected mice did not undergo a significant change in mean body temperature, significant changes in activity patterns were associated with parasitaemia and increased mosquito feeding success. All three rodent malarias induced discernible reductions in defensiveness which corresponded with increased mosquito feeding success. As such, these symptomatic rodent malarias probably are not very appropriate models for malaria in humans living in endemic areas in which low-density asymptomatic parasitaemias predominate (Covell, 1960). These results do not necessarily preclude the possibility of using rodent malarias as a model for mosquito host selection during a malaria epidemic among non-immune humans. In such an epidemiological situation, symptomatic parasitaemias would be more common and the associated changes in human behaviour might render such individuals more susceptible to mosquito attack.

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