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HOST SELECTION AND GONOTROPHIC CYCLE LENGTH OF *ANOPHELES PUNCTIMACULA* IN SOUTHERN MEXICO

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ABSTRACT. The host preference, survival rates, and length of the gonotrophic cycle of *Anopheles punctimacula* was investigated in southern México. Mosquitoes were collected in 15-day separate experiments during the rainy and dry seasons. Daily changes in the parous–nulliparous ratio were recorded and the gonotrophic cycle length was estimated by a time series analysis. *Anopheles punctimacula* was most abundant during the dry season and preferred animals to humans. The daily survival rate in mosquitoes collected in animal traps was 0.96 (parity rate = 0.86; gonotrophic cycle = 4 days). The length of gonotrophic cycle of 4 days was estimated on the base of a high correlation coefficient value appearing every 4 days. The minimum time estimated for developing mature eggs after blood feeding was 72 h. The proportion of mosquitoes living enough to transmit *Plasmodium vivax* malaria during the dry season was 0.35.

KEY WORDS *Anopheles punctimacula*, host selection, gonotrophic cycle

INTRODUCTION

Anopheles (Anopheles) punctimacula Dyar and Knab is distributed at low elevations from northern South America (Colombia and Venezuela), through Central America and the Yucatan Peninsula, to the states of Sinaloa, San Luis Potosí, Veracruz and Chiapas in México (Gabaldon and Cova-Garcia 1946, Vargas and Martinez-Palacios 1955, Diaz Najera 1966, Wilkerson and Strickman 1990).

Anopheles punctimacula is a presumed vector of malaria in Central and northern South America. Man-to-mosquito transmission of *Plasmodium vivax* (Grassi and Feletti) and *P. falciparum* (Welch) was demonstrated in the laboratory by Simmons (1937). Malaria-infected *An. punctimacula* have been collected in Panama (Simmons 1936, Rozeboom 1938), and circumstantial evidence led other researchers to suggest that malaria in Costa Rica (Kumm & Ruiz 1939) and Colombia (Pinzón 1945, Ronnefeldt 1957) was transmitted by this mosquito species. However, it was only recently that *An. punctimacula* and *An. malefactor* was separated from synonymy, casting doubts on the identity of the specimens collected in areas where both species coexist (Wilkerson 1990).

Malaria transmission persists in the Lacandon Forest and the Pacific Ocean coastal plains of Chiapas, Southern Mexico (Tellaeche 1998). In these areas, *An. punctimacula* coexists with the confirmed malaria vectors *An. albimanus* and *An. vestitipennis* (Fleming 1986, Loyola et al. 1991, Arredondo-Jiménez 1995, Ulloa 2001), indicating the possibility that *An. punctimacula* could play a role, although secondary, in the persistence of malaria transmission. Nevertheless, no studies on the bionomics of this mosquito have been conducted to assess its potential capacity as a vector in the region. The present study was carried out in a village on the Tapachula Coastal Plain to estimate the host selection, gonotrophic cycle, and daily survival rates of this species.

MATERIALS AND METHODS

Study area: The study was conducted in Nueva Independencia (14°37′30″N, 92°16′14″W, elevation 50 m), a village on the Pacific Ocean Coastal Plain of Chiapas, Mexico, with 112 inhabitants living in 23 households. In general, houses in this village are made of split bamboo or palm pole walls and palm thatch roofs. The climate in the area is hot subhumid (Garcia, 1973), with a rainy season extending from May through October, and the intervening dry season. Mean annual rainfall in the area is 2,100 mm, average monthly temperature is 27°C, and relative humidity ranges from 61 to 100% (Arredondo-Jiménez 1990).

Host selection experiments: Two experiments each were conducted during 1 rainy and 1 dry season. Mosquitoes were collected with the use of 2 modified Magoon traps (Service 1993) placed 5 m apart from each other, approximately 30 m away from the nearest house of the village, and 150 m from the nearest larval breeding site; no domestic animals were detected nearby.

In each season, 1 experiment was conducted with the use of 1 trap baited with 2 men and the other trap with 1 horse. In a 2nd experiment, 1 trap was also baited with 2 men and the other with 1 cow. Traps were baited with the use of equivalent surface areas for humans and animals: 2 human volunteers, per 1 horse or 1 cow). The body surface area (BSA) of the baits was

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calculated by the formula BSA (m^2) = ([height (cm) × weight)]/b3600)$^{1/2}$ (Mosteller 1987). The 2 human volunteers weighted 72 and 79 kg and had heights of 170 and 172 cm, respectively; resulting surface areas were 1.85 and 1.94 m^2, totaling 3.79 m^2. The cow, with a height to the cross of 142 cm and 363 kg of weight: resulted in 3.78 m^2 BSA.

Mosquito collections were conducted for 6-h periods (1800–2400 h) during 20 consecutive nights carried out during the rainy season. But during the dry season the 1st experiment was conducted for 10 consecutive nights and 2nd for 15 nights. In traps baited with humans, mosquitoes landing on the human volunteers or resting on the inner surface of the trap during the first 45 min of each hour were collected with the use of mouth aspirators and placed in individual containers (World Health Organization 1975, Bown et al. 1987). In animal-baited traps, mosquitoes that accumulated during the same time period and were resting on the inner surface of the traps were collected during the remaining 15 min of each hour. This collection design diminished the chances of mosquito biting on human volunteers, and as mosquitoes entering the traps tend to fly at higher altitude within the trap, the number of specimens that escape is negligible; the times of collection in each trap are comparable. Host selection was assessed by recording the number of mosquitoes collected in each trap. Mosquitoes were identified by the key of Wilkerson and Strickman (1990).

Blood meal identification: Collection of mosquitoes resting indoors and on the peridomicile was conducted during the dry season. Engorged mosquito abdomens were squashed on Whatman filter paper and after drying at room temperature, samples were stored at −20°C until processed. An indirect ELISA modified by Loyola et al. (1990) was used to identify the blood meal smeared on filter papers. Briefly, the samples were eluted overnight at 4°C with 200 µl of a phosphate buffer saline solution (PBS, pH 7.2). Five milliliters of each eluted sample were placed with 50 µl of coating buffer (sodium bicarbonate 35 mM, pH 9.6) in 6 wells of a polystyrene microtiter plate (Dynatech Laboratories, Inc., Alexandria, VA) and incubated for 2 h at room temperature. After blocking unreacted sites with 5% dry skimmed milk in 7.2 pH PBS for 1 h, the wells were treated with rabbit IgG antihuman, horse, pig, and cow (Sigma Chemical Co., St. Louis, MO) diluted 1:10,000 in 2.5% dry skimmed milk and 0.05% Tween 20 in 7.2 pH PBS for 1 h. The wells were washed with PBS and treated with horseradish peroxidase-conjugated goat serum antirabbit IgG. Color was developed using 2,2′-azino-bis (3-ethylbenz-thiazoline-6-sulfonic acid) (ABTS) (Kirkegaard and Perry Laboratories Inc., Gaithersburg, MD) as a substrate. Blood samples of the same host species were dried on filter paper and used as positive controls for homologous sera detection and as negative controls for heterologous sera. A test was positive when its absorbance value was higher than 2 times the mean of the negative controls. The negative control for each antiserum corresponded to wells reacting with heterologous blood species.

Dynamics of parous–nulliparous ratios and survival: One separate experiment was conducted to determine the length of the gonotrophic cycle and survival rate during the dry season. One modified Magoon trap (Service 1993) baited with 1 cow was placed 150 m from the nearest house of the village and the nearest larval breeding sites. Female *An. punctimacula* were collected resting on the inner surface of the trap during the last 15 min of each hour during a 6-h period (1800–2400) for 15 consecutive nights. A sample of females was dissected the same night of collection to determine parity rates (Detinova 1962), and the daily changes in the parous–nulliparous ratio were recorded. Mosquitoes were identified by the key of Wilkerson and Strickman (1990).

A time-series analysis of the 16-day sampling period was conducted. The length of the gonotrophic cycle was estimated with the use of a cross-correlation analysis (Birley and Rajagopalan 1981) with the formula: $M_t = P_u T_{(t-u)}$, where M is the number of parous individuals captured on day t; P the survival rate per gonotrophic cycle, calculated from the slope in a regression model, $T_{(t-u)}$ is the total number of females (nulliparous and parous) captured on day $(t - u)$, and u is the length of the gonotrophic cycle. The r coefficient for day 0 represents the correlation between P_t and T_t data pair from mosquitoes captured the same day (15 data pairs). The r coefficient for day 1 was obtained by pairing daily P_t data with the corresponding T_t data of 1 day before. The day 2 coefficient was calculated by pairing daily P_t data with corresponding T_t data of 2 days before, and so on. It was assumed that a significant cross-correlation coefficient (r) between the time-series express a time delay (u) equivalent to the gonotrophic cycle. The highest significant cross-correlation coefficient (r) obtained after day 0 ($u = 0$) indicates the number of days per gonotrophic cycle, with descending peaks occurring at multiples of this interval. To eliminate spurious cross-correlations, data were filtered with the use of an autoregressive process with a lag of 1 day with the formula: $Z_t = X_t - \beta(X_{t-1})$, where Z_t is the time series to be filtered, X_t is the time series to be filtered and β is the estimated autoregressive parameter (Holmes and Birley 1987). A significant correlation between 2 filtered time series M_t and $X_{(t-u)}$ was assumed, and the correlation r corresponds to a lag u equivalent to the

gonotrophic cycle, with regular peaks at the start of each cycle.

Daily survival rates (p) were calculated with the use of the parity rates using the formula $p = (PR)^{1/CG}$, where PR is the parity rate and CG is the duration of the gonotrophic cycle (Davidson 1954). The percentage of the population expected to live long enough to become infective (p^n) and the subsequent life expectancy of the infective population ($p^n/-\ln p$) was calculated with 9 days (at 26.2°C) used as the time (n) for *Plasmodium vivax* extrinsic cycle (Macdonald 1957, Villarreal-Treviño et al. 1998).

Vitellogenesis: The duration of Christopher's stages of ovarian development were determined in a sample of *An. punctimacula*, on the base of the appearance of ovarian follicles (Clements 2000). Mosquitoes were collected in a horse-baited trap during the dry season (temperature = 24.75 ± 2.60°C and HR = 85 ± 13.31%). A subsample of 10 unfed females (without traces of blood) was dissected to determine their status of ovarian maturation; the remaining females, held in small cages, were blood fed on a tethered calf (unfed mosquitoes without traces of blood were discarded) and immediately transported to the Center for Malaria Research (CIP) in Tapachula. Adults were supplied with cotton pads soaked with a 10% sucrose solution and maintained in a temperature-controlled room at 29 ± 1°C during the day and 24 ± 1°C at night and a 12-h light:12-h dark photoperiod with 70–100% of relative humidity. Beginning at 12 h after blood feeding and continuing every 6 h up to 78 h, groups of 10 mosquitoes were dissected to determine their Christopher's stages.

Data analysis: Differences between collections of mosquitoes in each experiment were analyzed using Mann–Whitney U-test.

RESULTS

Mosquito collections

Overall, in the 2-experiment series, *An. vestitipennis* Dyar and Knab was the predominant anopheline caught in the rainy season (56%, n = 23,142), followed by *An. albimanus* Wiedemann (40%) and *An. punctimacula* (4%), whereas more *An. punctimacula* mosquitoes were collected in the dry season (70%, n = 2,784), followed by *An. vestitipennis* (23%) and *An. albimanus* (7%).

Host selection

Of 194 *An. punctimacula* female mosquitoes collected in the 1st experiment conducted during the rainy season, 153 and 41 selected horse and human baits, respectively, making a horse to human mosquito collection ratio of 3.73:1 (U = −3.368, P = 0.0008). In the 2nd experiment conducted during this season, 680 and 133 *An. punctimacula* females were collected in cow and human baits, respectively; resulting in a cow to human mosquito collection ratio of 5.11:1 (U = −4.074, P = <0.0001). More mosquitoes were attracted to the cow bait that to the horse bait (U = −3.470, P = 0.0005).

During the dry season, a total of 403 and 90 *An. punctimacula* females were collected in horse and human baited traps, respectively, corresponding to a horse to human mosquito collection ratio of 4.47:1 (U = −3.402; P = 0.0007). In the 2nd experiment conducted in the same season, 1,349 and 111 specimens were collected in cow and human traps, respectively, corresponding to a cow to human ratio of 12.15:1 (U = −3.028, P = 0.0025), but not significant differences occurred between the number of mosquitoes collected in horse- and cow-baited traps (U = −1.831, P = 0.0672) during this season.

After pooling, more mosquitoes were collected in animal-baited traps than in human-baited traps, 833 and 174, respectively (ratio of 4.78:1, U = −5.364, P = <0.0001), during the rainy season; and 1,752 and 201, respectively (ratio of 8.71:1, U = −4.443, P = <0.0001) during the dry season (Table 1).

Blood meal identification

A total of 37 blood engorged females of *An. punctimacula* were collected indoors and outdoors. Horse blood was detected in 81% (30/37) by ELISA, human blood was detected in the others 19% (7/37).

Parity rate

Of 884 *An. punctimacula* females collected during 15 consecutive nights in the cow baited trap, 496 were dissected to assess parity; of these 318 mosquitoes were parous (64 ± 5.84%; range 13–97% among collecting nights). The number of specimens that were dissected varied according to the number of mosquitoes collected; this was particularly low during the 6th night of collection,

Table 1. Host selection of *Anopheles punctimacula*.

Host	Rainy season	P	Dry season	P
Humans	41		90	
		0.0008		0.0007
Horse	153		403	
Humans	133		111	
		<0.0001		0.0025
Cow	680		1,349	
Humans	174		201	
		<0.0001		<0.0001
Animals	833		1,752	

Table 2. Correlation indexes (r) in parity rates of *An. punctimacula* collected in animals using cross-correlation analysis in a time series (data of the 1st 10 days of collection).

Day	r	p
0	0.711	0.003
1	0.078	0.7915
2	0.031	0.919
3	0.337	0.283
4	0.547[1]	0.081
5	0.273	0.445
6	0.480	0.191
7	0.493	0.214
8	0.651[1]	0.112
9	0.131	0.804
10	0.659	0.226

[1] High correlation index at intervals of each 4 days ($P > 0.05$).

when only 6 were dissected out of 11 collected specimens.

Dynamics of parous–nulliparous ratios and survival

No significant correlation was observed on daily changes of parity rates over 15 days when data obtained from cow-collected mosquitoes during the dry season were analyzed. However, r values were highest every 4th day, suggesting a 4-d gonotrophic cycle (Table 2). The daily survival rate was 0.89 (parity rate = 0.64; gonotrophic cycle = 4 days). The percentage of the population expected to live long enough to become infective (p^n) was 0.35 (0.89^9), whereas the corresponding duration of infective life was 3.0 days ($p^n = 0.3503/-\log_n p = 0.1165$).

Vitellogenesis

All unfed females dissected at the beginning of the experiment were at Christopher's stage II. The females completed oogenesis at 72 h post-feeding, and all ($n = 120$) completed egg development (Table 3).

Table 3. Vitellogenesis of *Anopheles punctimacula* populations collected in animal host.

Hours post-feeding	No. dissected	Christopher's stage[1] I	II	III	IV	V
0	10	10	90			
12	10		90	10		
18	10			90	10	
24	10			30	70	
30	10				100	
36	10				100	
42	10				100	
48	10			10	90	
54	10				100	
60	10			10	90	
66	10				100	
72*	10					100
78	10					100

* Minimum time required to develop mature eggs (Christopher's stage V).

[1] Stages I and II = previtellogenic phase, III = initiation phase, IV = trophic phase, V = posttrophic phase (Clements 2000).

DISCUSSION

The feeding preference of *An. punctimacula* for animals over humans on the Ocean Pacific Coast of Southern Mexico was similar to previous observations reported in the area, as well as in Costa Rica, Peru, Ecuador (Garrett-Jones 1964) and Colombia (Levi-Castillo 1949, Elliot 1971, Fleming 1986, Loyola et al. 1991, Arredondo-Jiménez 1995, Ulloa 2001).

The low numbers of specimens collected during the rainy season did not permit estimation of the length of the gonotrophic cycle. Raw and filtered data on parity rates obtained from females collected in the dry season could not be adjusted to the criterion of Birley and Rajagopalan (1981) and Mutero and Birley (1987), but high correlation coefficients every 4th day suggest a gonotrophic cycle length of 4 days (Bockarie et al. 1995). The temporal progression to complete oogenesis occurred around 72 h after engorgement, and adding 24 h to account for the time required for location of an oviposition site and egg lay before searching for a blood meal (Mekuria et al. 1991) indicates a gonotrophic cycle of 4 days, which is in agreement with the length suggested by the recurrent peak in the correlation. Based on this assumed gonotrophic cycle length, a daily survival rate of 0.89 was calculated. Nevertheless, the accuracy of this calculation should be taken with caution because of the short sampling period and because the various conditions that could limit the precision of this estimate were not assessed, among them a possible sampling bias due to possible differences in the collections of nulliparous and parous females, as well as a constant recruitment rate and constant survival rate during the sampling period (Lord and Baylis, 1999).

Previous studies documenting the participation of *An. punctimacula* as a vector in Central and South America are inconclusive because of its mistaken synonymy with *An. malefactor* (Wilkerson 1990). Thus the identity of laboratory *Plasmodium*-infected Panamanian (Simmons 1937) and naturally infected specimens collected in Central America (Simmons 1936, Rozeboom 1938), where both species coexist, is in doubt. Also, malaria-infected specimens previously classifies as *An. punctimacula* collected on the Andean Pacific Ocean coast (Calderon et al. 1974, Levi-Castillo 1949) were proven to be *An. calderoni*

(Wilkerson 1991). However, the abundance of *An. punctimacula* in these areas is still an argument for its consideration as a potential malaria vector.

On the Pacific Ocean coast of Southern Mexico, the number of *An. punctimacula* in relation to the number of *An. vestitipennis* and *An. albimanus* was very low during the rainy season, but it represented the most abundant anopheline during the dry season. *Anopheles albimanus* daily survivorship, estimated by parity rates, is 0.67–0.69 (Rodriguez et al. 1992), whereas *An. vestitipennis* survival rate is 0.93 and 0.88 in zoophilic and anthropophilic female mosquito populations, respectively (Arredondo-Jiménez et al. 1998), which is similar to the survival rate calculated here for *An. punctimacula* (0.89). A proportion of both *An. albimanus* and *An. vestitipennis* present pregravidity determining a higher number of blood feeds, and may contribute to the role of the former as one of the most important malaria vectors (Bown et al. 1991), and of *An. vestitipennis* as a secondary vector (Loyola et al. 1991, Padilla et al. 1992) in the region. Nevertheless, malaria transmission by *An. albimanus* occurs mainly during the rainy season, when its highest abundance occurs (Levi-Castillo 1949, Bown et al. 1991). We show here that during the dry season, when other anopheline populations are abated, *An. punctimacula* population peaks and could survive long enough to transmit *P. vivax*, the main agent of malaria in the region, but further studies are necessary to implicate this mosquito as a malaria vector in the region.

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