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Prevalence of a malarial parasite over time and space: *Plasmodium mexicanum* in its vertebrate host, the western fence lizard *Sceloporus occidentalis*

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Summary

1. We studied patterns of abundance of the malarial parasite *Plasmodium mexicanum* in its vertebrate host, the western fence lizard *Sceloporus occidentalis*, over a 13-year period at 51 study sites in northern California, USA. Abundance of the vectors, sandflies in the genus *Lutzomyia*, was also studied among sites during a single warm season, and among nights at one site during two seasons.

2. The parasite differed in prevalence (per cent of lizards infected) in males and females; males were more often infected. Prevalence increased with body size (= older lizards were more often infected).

3. Malaria prevalence varied among sites: 0–50% of lizards were infected. Topography explains part of this variation because malaria was rare or absent at sites > 500 m elevation. However, sites at lower elevations, even when within short distances of one another, varied in malaria prevalence.

4. Abundance of vectors was not related to prevalence of malaria at a site; sandflies were found at some sites where malaria was rare or absent, including those at high elevations. Wind speed, relative humidity and sky brightness did not affect numbers of sandflies active, but vectors were active only when air temperature was > 16 °C.

5. Parasite prevalence varied among years. Environmental conditions (temperature, rainfall and plant biomass produced at the study region) were not correlated with parasite prevalence. The changes in prevalence over time resembled a cycle of long duration (10 years).

6. Classical models developed for study of malaria in humans suggest explanations for variation in prevalence of *P. mexicanum* among sites, and a more recent theory suggests an explanation for the possible long-duration cycle observed in this study.

Key-words: lizards, malaria, parasite prevalence.

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Introduction

Understanding the distribution and abundance of organisms is a core issue in ecology. Vector-borne parasites with complex life cycles present particularly vexing problems for population ecologists who attempt to understand the parasite's abundance patterns. For example, malarial parasites (genus *Plasmodium*) exploit vertebrate hosts for asexual replication, then produce sexual cells (gametocytes) that are passed to a blood-feeding insect (mosquito or sandfly). The parasite then undergoes both sexual and asexual replication in the vector and travels to the

insect's mouthparts to be transmitted during a subsequent blood feeding. Clearly the parasite's geographical distribution and abundance among sites or over time could depend on the population size of both hosts, percentage of vertebrates that are immune to malarial attack, the life span of the vector, biting behaviour of the insect, and many other details of the natural history of both hosts.

Ross (1911) recognized that an understanding of malaria population ecology demanded mathematical models that were realistic enough to capture the complex web of life history and behavioural traits of both hosts and the parasite, but simple enough to be both general and tractable. His models were developed in greater detail by Macdonald (1957) and more recently

by Aron & May (reviews in Aron & May 1982 and Anderson & May 1991). These models conclude that the prevalence of malaria can be driven by only a few characteristics of the system, most importantly the biting behaviour of the vector. In humans, malaria has a notoriously patchy distribution within the geographic range that is apparently suitable for the parasite (Clyde 1967; Bruce-Chwatt 1985). Likewise, the dynamics of prevalence of the parasite also varies among locations. Macdonald (1957) argued that the parasite's abundance in a malarious region shows one of three patterns: absent at a site, stable at fairly high prevalence levels, or unstable in which prevalence is typically fairly low but shows periodic sudden epidemic outbreaks. The basic Macdonald model demonstrates that the number of blood meals taken by the vector during its lifetime determines if malaria is absent (few bites), unstable (more bites) or stable (many bites) (Aron & May 1982).

Although the Macdonald model has been useful in the design of malaria control programmes, it does not explain all the patterns seen in malaria abundance. In some places, prevalence of the parasite in humans has followed a very long cycle, lasting more than a century; in the Punjab there are periodic epidemics spaced about 8 years apart (Pampana 1969), and in the early 20th century a 7-year cycle may have existed in Mississippi, USA (Faust 1949). Perhaps casting light on these kinds of patterns, more recent theory (May 1985; Nowak & May 1994; Gupta, Swinton, & Anderson 1995) has shown that some simple, but realistic, parasite-host population models show complex dynamics including long-term oscillations and even chaotic patterns.

Theoretical and empirical studies on the prevalence of malaria have significance beyond issues of human public health. Only four of the approximately 179 described species of *Plasmodium* infect humans; the others are parasites of a variety of mammals, birds, and especially lizards (Schall 1990a). The findings of studies on human malaria can be of value in understanding the prevalence and distribution of the other 175 malaria species. The complex, indirect life cycle of malaria also can serve as a prime model in understanding the population ecology of other vector-borne parasites. Unfortunately, rather few long-term studies have been done on the abundance of malaria over time, and almost all of these have been done on the species infecting humans. Studies on human malaria often are also confounded by on-going efforts to eradicate the parasite or by mass population movement which would alter the natural abundance of the parasite.

We report on a long-term (13-year) study on the abundance of the malarial parasite *Plasmodium mexicanum* Thompson and Huff in its lizard host, the western fence lizard *Sceloporus occidentalis* Baird & Girard (Iguanidae), in northern California, USA. The variation in abundance of the parasite was also com-

pared among sites scattered over the study region. These sites serve as analogues to the human villages often compared in studies of malaria in people. The lizard has a short life span (mark-recapture studies show most lizards live <2 years; J. J. Schall, unpublished data) and remains in a small home range throughout the year (Bromwich & Schall 1986; Schall & Houle 1992). The vectors of this malarial parasite are two species of phlebotomine sandfly, *Lutzomyia vexator* (Coquillett) and *L. stewarti* (Mangabeira & Galindo), but the parasite overwinters only in the lizard host. Thus, changes in parasite prevalence from year to year would indicate real changes in transmission and percentage of the vertebrate host that is infected. Reviews on previous studies on this parasite-host system can be found in Schall (1983, 1990a,c). Our goals were to determine the variation in prevalence of *P. mexicanum* at different sites and among years and to evaluate the importance of two factors that might influence this variation: weather (for among years) and vector presence, abundance and activity (comparing among sites). The results were then compared with patterns predicted by current models of malaria population biology.

Materials and methods

STUDY SITES

Lizard malaria was studied from 1978 to 1991 at the 2169-ha University of California Hopland Field Station in southern Mendocino county, approximately 160 km north of San Francisco. The habitat is hilly oak savannah in lower elevations and chaparral above 610 m. The climate is Mediterranean with cool wet winters and warm dry summers. Rainfall averages 889 mm year⁻¹, with almost all falling during the winter wet season between November and May. Mean temperature during the warm season is 21 °C, with the warmest month being July when daytime temperature can reach 40 °C. Fifty-one study sites were chosen in all habitat types; these ranged from 244 m to 854 m in elevation (Fig. 1). Not all study sites were visited each of the 13 years; therefore, some analyses must limit the number of sites used (discussed in the Results).

LIZARDS AND PARASITES

Western fence lizards are small [adults range from 58 to 84 mm snout to vent length (SVL)], diurnal, insectivorous animals that are extremely abundant at the Hopland Field Station. They spend daylight hours perching on logs, rocks, tree trunks and fences, while defending a territory, courting mates or watching for insect prey. Lizards were collected with a slip noose on the end of a fishing pole, kept in cloth sacks until evening, when they were measured, sexed and a tiny drop of blood drawn from a toe clip. A blood smear

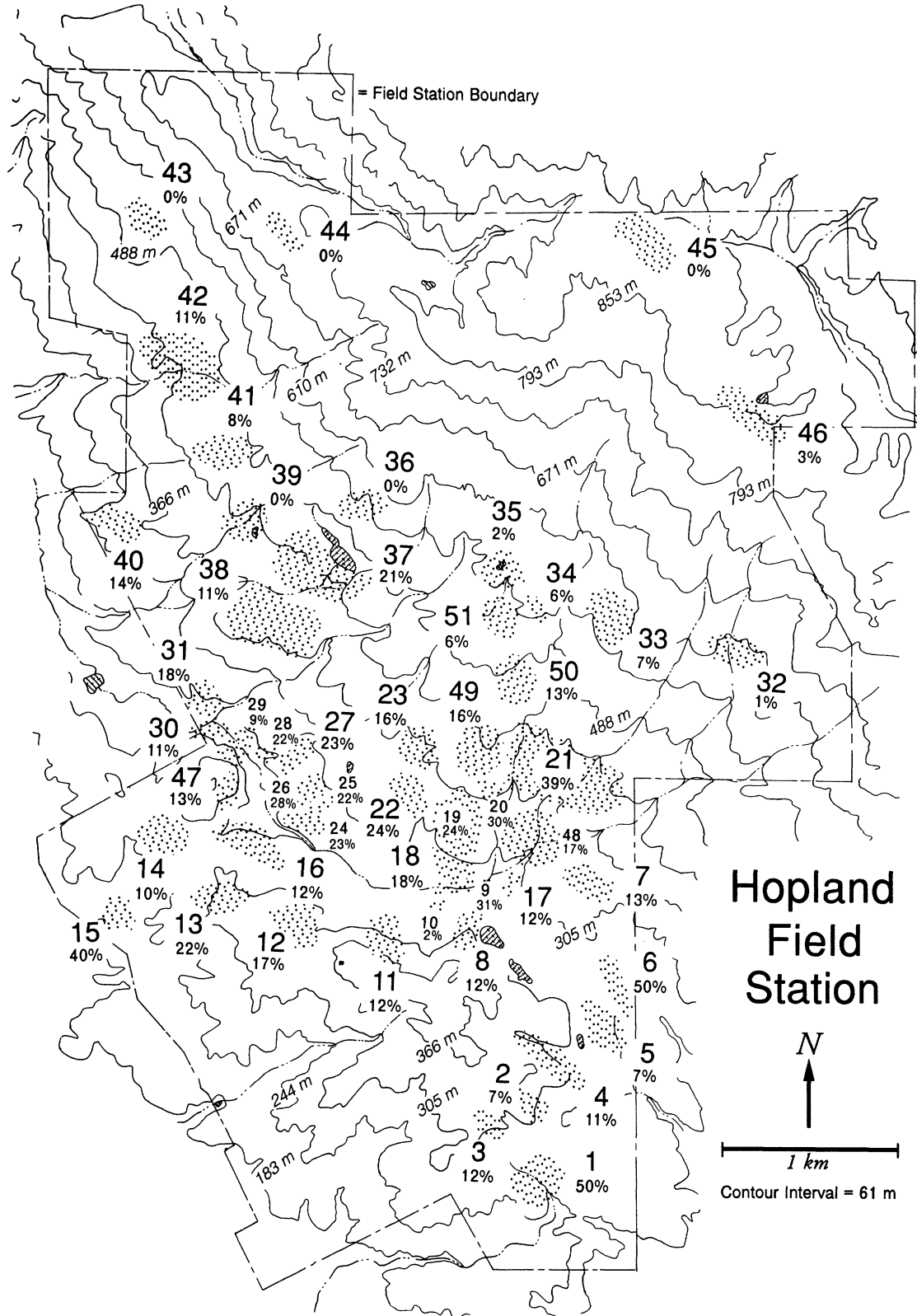


Fig. 1. Map of study sites at the Hopland Field Station. Area of study sites indicated by stippling. Below each site's identification number is the percentage of all lizards infected there over the 13-year study. Contour intervals are not rounded values because the only available map of the Station uses the English system of measures.

was made, fixed in absolute methanol, and stained at pH 7.0 for 50 min in 1:10 Giemsa stain. Most lizards were returned to their point of capture the next day. Smears were examined at 900 \times to detect infections.

False positives in scoring blood smears in this study were certainly very rare or absent; however, some false negatives must have occurred when very weak infections were scored as uninfected. The results on

parasite prevalence could be compromised if the number of these infections varied among years or sites. In studies on mammal and bird malaria, non-patent infections are abundant because most infections experience a period of exponential growth, then drop to very low chronic states when the immune system becomes activated against the infection (Clyde 1967; Atkinson & Van Riper 1991). Macdonald (1926) long ago demonstrated that only 60% of infections of humans were detected by inspecting a single blood smear. We believe false negatives from very low density infections are rare in our study because *P. mexicanum* typically reaches a stable, and often high, density without a drop-off driven by the immune system (Bromwich & Schall 1986). Also, in hundreds of natural infections of *P. mexicanum* followed over time, no infection was ever observed to decline to undetectable levels (Bromwich & Schall 1986; J. J. Schall, unpublished data). The slow and low-grade immune attack by the reptilian immune system against malarial attack thus makes lizard malaria a tractable system to use in studying variation in malarial prevalence over time and space.

ENVIRONMENTAL CONDITIONS AND SANDFLY ABUNDANCE

A weather station at 244 m at the Hopland Field Station provided data each year to calculate mean hourly temperature from May through to August (both monthly mean and total warm season mean) and total precipitation from November to May inclusive. Temperature and rainfall vary among the study sites, but are correlated over years (unpublished Hopland Field Station data). Herbaceous plant biomass produced each year served as a bioassay of overall habitat conditions. Each year field station personnel hand clip to the ground all vegetation in three 30 × 30 cm plots within each of 36 2 × 2 m fenced patches scattered over the entire field station, but below 500 m elevation. The clippings are dried to constant mass, weighed and reported as kg herbage ha⁻¹. The amount of this annual plant material produced during the warm season most probably depends on rainfall over the rainy season, distribution of the rain by time, and warm season temperature and cloud cover. Winter rainfall was correlated with herbage production (Spearman rank correlation, $r_s = 0.76$, $P = 0.008$, $n = 13$ years).

Sandflies, the vectors of *P. mexicanum*, spend most of their time in burrows of ground squirrels *Spermophilus beecheyi* (Richardson 1929) this is the only place where they oviposit eggs because the larvae feed on the squirrel faeces. They emerge from burrows at night to seek out mates, nectar for food and, in the case of females, lizards and other ectothermal vertebrates for a blood meal (Chaniotis & Anderson 1968; J. J. Schall, personal observation). Knowledge of the movement and host-seeking behaviour of *L.*

vexator and *L. stewarti* is nil. However, some estimate of the number of sandflies present at a site can be obtained from abundance of the entrances to ground squirrel burrows and from number of flies emerging from these burrows. To determine abundance of the vectors, we first sought evidence of ground squirrel burrows at each site. For some sites, with varying prevalence levels of malaria, we placed funnel traps over burrows during the hours when the sandflies emerge (18.00–01.00 hours) to determine if the sandflies were present. Each of these sites was surveyed for at least three nights.

Because we suspected that weather conditions might regulate the abundance and activity of the sandflies, and thus the frequency of transmission of malaria to the lizards, we sampled 75 traps set over the entrances to a ground squirrel burrow system in a meadow each evening from May through to August for 42 nights in 1989 and 57 nights in 1990 (site 5 on Fig. 1). Traps were set at approximately 16.00 h, and flies removed and counted between 22.00 and 01.00 h. Recorded at 23.00 h were temperature at 1.5 m above ground, relative humidity with an electronic hygrometer (Hanna Instruments Co., Jackson, MS, USA) at 1.5 m above ground, wind-speed with a hand-held electronic anemometer (Davis Instrument Co., San Leandro, CA, USA), and sky brightness ranked by eye from 10 (full moon and no clouds) to 0 (no moon and cloudy sky). Previous studies over four seasons showed that at least 90% of the sandflies emerging from rodent burrows are *L. vexator* (J.J. Schall, unpublished data).

Results

PREVALENCE BY BODY SIZE AND GENDER

Over the 13-year study period 10 546 lizards were sampled; however, not all of these could be used for each analysis. Figure 2 shows percentage of lizards infected by body size for lizards collected from sites where malaria was present. Males were more likely to be infected (*G*-test, $G = 53.2$, $P > 0.01$), and prevalence of malaria increased with body size (comparing animals <60 mm with those ≥60 mm: *G*-test for males, $G = 96.5$, $P < 0.01$, and for females $G = 81.7$, $P < 0.01$). Overall, 22.4% of males and 16.3% of females were infected (7.8% of small females vs. 19.1% of adult females; 12.6% of small males vs. 25.6% of adult males). In subsequent analyses, only animals ≥60 mm SVL length were used and results for males and females are usually reported separately.

PREVALENCE OVER YEARS

Figure 3 shows prevalence patterns over time for malaria in adult fence lizards. Only sites that were sampled most years and where malaria was always present in the lizards were used in this analysis. The

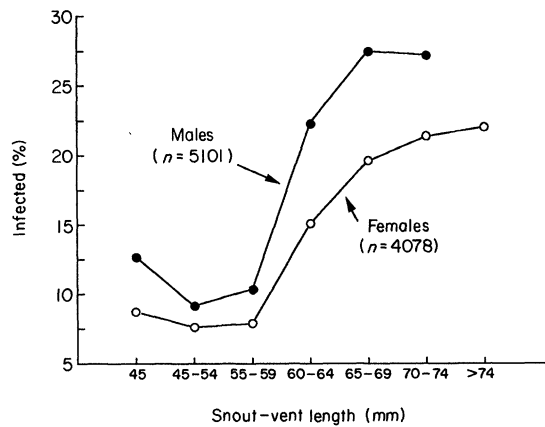


Fig. 2. Percentage of western fence lizards infected with the malarial parasite *P. mexicanum* at sites where the parasite is present in the lizards, with data divided by lizard gender and body size. Sample sizes for each point range from 63 to 1730.

1983 sample was too small to use. Prevalence ranged from 17.2% to 39.4% for males and 10.0% to 29.7% for females; prevalence differed significantly among years (χ^2 -test, $2 = 43.8$, $P < 0.001$ for males, and $\chi^2 = 42.9$, $P < 0.001$ for females). Prevalence of malaria varied in similar ways over time for males and females (Spearman correlation for percentage infected males vs. females, $r_s = 0.71$, $P = 0.014$).

Temperature during June through to August did not vary much over the 13 year period. Mean of daily low temperatures ranged from 9.9°C to 11.7°C. Malarial prevalence each year was not correlated with either that year's mean low temperature or mean low temperature of the previous year (Spearman rank correlations, $P > 0.05$). In contrast to temperature, rainfall varied substantially among years (range = 570–1699 mm). Percentage of lizards infected was not correlated with rainfall of that year's rainy season, nor rainfall the previous year (Fig. 4a). Malaria prevalence was not correlated with herbage (Fig. 4b), nor with herbage of the previous year. Thus, no climate or

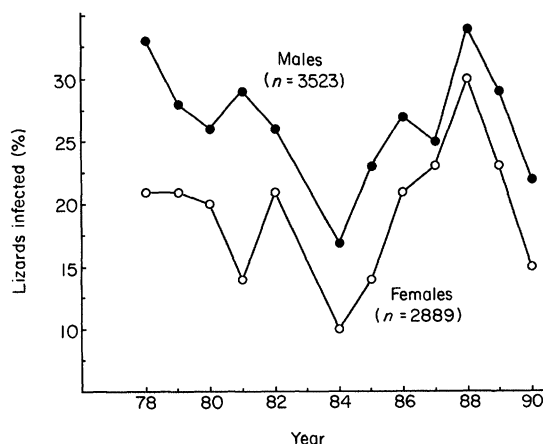


Fig. 3. Prevalence of *P. mexicanum* in adult (≥ 60 mm SVL) fence lizards over the 13-year period. Data are from sites sampled most years. Sample sizes for each point range from 91 to 523.

environmental measure accounted for the variation among years in percentage of lizards infected with malaria.

VARIATION IN PREVALENCE AMONG SITES

Combining all data (all years, both sexes, all body sizes) shows substantial variation among sites in percentage of lizards infected (Fig. 1; range = 0–50% infected). Some of this variation can be explained by elevation (Fig. 5; percentage infected vs. elevation, $r_s = 0.53$, $P = 0.0007$). Figure 1 shows that sites in the south and west of the study region were always malarious, but that the parasite was rare or absent at sites above 500 m elevation in the northeast part of the field station. A transect, 975 m long, from site 20 to site 35 confirmed this pattern. The transect showed approximately 30% prevalence at site 20 (355 m elevation), dropping to 16% at site 51 (396 m), 13% at site 52 (460 m), 6% at site 53 (540 m) and finally 3% at site 35 (549 m).

Below 500 m, however, prevalence varied greatly (Figs 1 and 5). Even some sites that were nearby one another differed (Fig. 1). For example, sites 8, 9 and 10 were within 150 m of one another, yet prevalence was only 7% at site 10, 13% at site 8, and 31% at site 9. Site 10 was always low in malaria among the

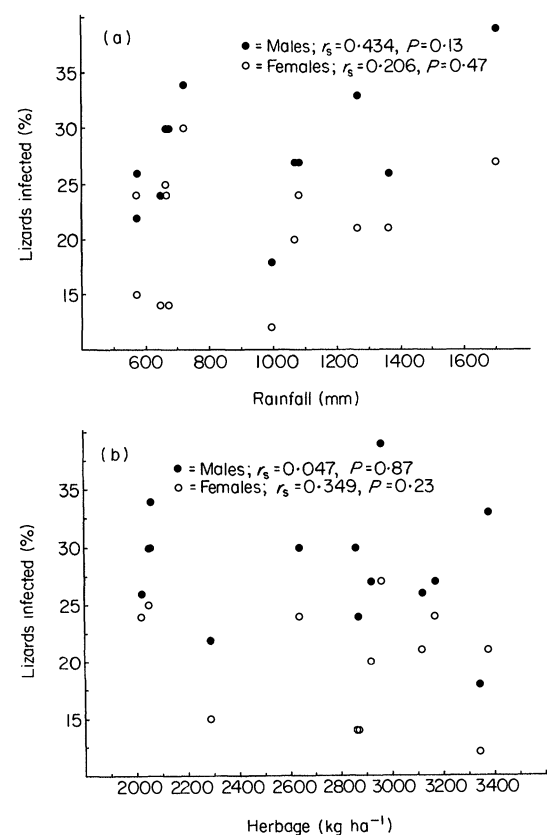


Fig. 4. Prevalence of malaria in western fence lizards among years compared with environmental measures. (a) Rainfall the previous wet season; (b) plant biomass (herbage) in open fields in kg ha^{-1} .

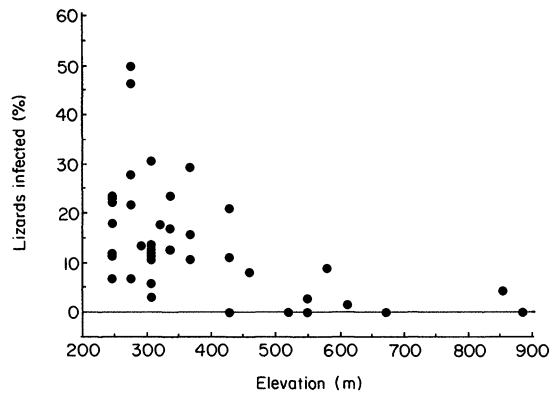


Fig. 5. Percentage of fence lizards infected with malaria at sites that varied in elevation. Sample size is 41 sites; 10 sites were not used in this figure because they were sampled in only 1 year.

13 years (for most years prevalence at this site was 0%), whereas the parasite was common at site 9 even during periods of overall decline in malaria at the Hopland Field Station. These sites were very different in structure: site 10 included a house and cleared land for human activities, site 8 was a rocky slope adjacent to a pond, and site 9 was a stream-bed that went through a wooded area. Sandflies seeking a host for a blood meal may avoid areas where their home sites (rodent burrows) are rare (such as human habitations), or could congregate in stream-beds if they use them as corridors to travel moderately long distances. Other discrepancies among nearby sites suggest no ready explanation; for example, sites 1 and 6 were always among the most malaria-prone places at the field station, but were surrounded by very similar habitat where malaria was always much less common (site 5, only about 100 m from site 6, averaged only 7% infected lizards).

Table 1 scores sites by relative number of rodent burrow entrances seen and prevalence of malaria in the lizards. Malaria was ranked as low (0–5% lizards infected), moderately abundant (6–15% infected) or high (16–50% infected). Table 1 shows that there was no association of number of rodent burrows present and prevalence of malaria in the lizards, nor were sandflies more abundant at sites with more malaria. Many of our sites were close to other study plots (Fig. 1). Sandflies can travel at least 1 or 2 km (Killick-Kendrick *et al.* 1986), so we determined the distance to the nearest known rodent burrow system for each of the 13 sites that had no burrows but did have malaria at $\pm 6\%$ of lizards infected. Mean distance to known rodent burrows was 457 m (range = 244–762 m). This was certainly an overestimate because we did not search for rodent burrows over every ha of the study region. However, these results do show that prevalence of malaria at a site was not related to the likely very local abundance of the vector.

Prevalence of malaria may depend not just on the number of vectors present, but also the average num-

Table 1. Number of sites where malaria prevalence in fence lizards was low, medium or high (criteria given in text) grouped by abundance of ground squirrel burrows seen. Also given are data for sandfly presence at 19 sites where their presence was surveyed. The sandflies (genus *Lutzomyia*) are the vectors of lizard malaria and use the rodent burrows as home sites and for ovipositing eggs on rodent faeces

	Malaria prevalence		
	High	Moderate	Low
No burrows	7	6	3
Uncommon burrows	5	4	2
Many burrows	5	5	3
Sandflies present	6	5	3
No sandflies	3	2	0

ber of blood meals each takes. This could vary by site or over time if environmental conditions significantly affect the vector's activity level. Figure 6 shows that the number of sandflies leaving rodent burrows varied substantially among nights. Relative humidity varied among nights (21.3–55.3%), as did temperature (12.2–23.9°C) and sky brightness (on 46% of nights the sky was bright and on 30% overcast or no moon). Wind speed varied much less (on only 14% of nights wind speed was $> 0.4 \text{ m s}^{-1}$; range 0–2.6 m s^{-1}). Sandflies increase in abundance over the warm season probably because there are several generations produced during this period (J. Schall & J. Bliss, unpublished data). Therefore, to determine the role of environmental conditions on sandfly activity, the effects of date must be held constant via a step-wise regression. Using nightly data on number of sandflies emerging from burrows, and temperature, relative humidity, wind speed and sky brightness taken at the same site during the warm seasons of 1989 and 1990, it can be seen that only temperature explains variation in sandfly numbers (R^2 for 1989 = 0.410 and for 1990 $R^2 = 0.487$; $P < 0.001$). Examining each month's data for both years shows few sandflies were active when air temperature was $< 16^\circ\text{C}$.

Discussion

After over a century of intense investigation, information on the biology of malarial parasites is enormous. Yet knowledge of these parasites is scanty in a sense because only a few of the species of *Plasmodium* have been studied in the laboratory, and even fewer in the field. The Macdonald models describing the abundance and dynamics of malaria have proven very influential in human malariology (Bruce-Chwatt 1969), but have never been applied to a malarial parasite of non-humans in nature. We therefore organize our discussion of some of the patterns seen in this study of lizard malaria (spatial and temporal variation in prevalence) by referencing conclusions emerging

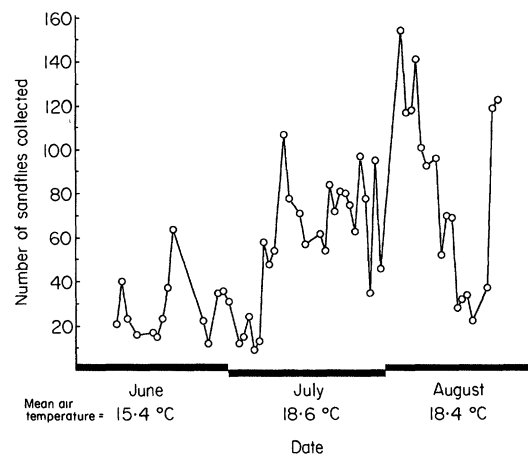


Fig. 6. Number of sandflies collected in 75 traps set each night at site 5 at 274 m elevation during the warm season of 1990. Similar results were seen at the same site during 1989. Mean air temperature for each month at the site is also given. The 75 burrow entrances sampled were a small fraction of the many hundreds of burrow holes at the site. Numbers of sandflies collected combines two species: *L. vexator* (90% of sandflies) and *L. stewarti*, both of which are vectors of *P. mexicanum*.

from the Macdonald models as well as results from recent modifications of these models. Because the Macdonald models emphasize the importance of the abundance and behaviour of the vector, we centre our discussion on *Lutzomyia* spp., the vectors of lizard malaria in California.

Our results on the prevalence of *P. mexicanum* in its lizard host show significant variation of three kinds: by gender and size of host, among study sites, and among years. Male fence lizards were more often infected at Hopland. A similar result was found for other lizard malaria systems [*P. azurophilum* and *P. floridense* in *Anolis gundlachi* in Puerto Rico (Schall & Vogt 1993), but no gender-based differences in prevalence were observed in *P. giganteum* and *P. agamae* in *Agama agama* in west Africa (Schall & Bromwich 1994) or *P. azurophilum* in *A. sabaenus* on Saba island in the eastern Caribbean (C. Staats, unpublished data)]. It is possible that the nocturnal resting places of male fence lizards at Hopland differ from those of females and make them more prone to bites by the vector. More probably, the elevated testosterone level of males could reduce the efficiency of their immune system (Dunlap & Schall 1995).

Prevalence of malaria at Hopland increased with lizard body size. Larger animals are assumed to be older and the increase in prevalence with body size probably represents a greater cumulative chance of an animal becoming infected as it ages. A similar trend has been seen in other lizard malaria systems (Schall 1990b; Schall & Vogt 1993; Schall & Bromwich 1994). This pattern is strikingly different from that seen in some human populations in areas with endemic malaria; in those cases the proportion of humans infected declines sharply with age because of the

action of the immune system (Macdonald 1951). Our results suggest that lizards do not develop immunity to malaria, but instead may harbour the infection for life. Laboratory data support this conclusion (Schall 1990c; Schall & Bromwich 1994). The shape of the prevalence-size curve in Fig. 2 is curious: the younger (smaller) lizards maintained low infection levels until they reached maturity, and at maximum only about a quarter of the lizards at malarious sites at Hopland were infected. Even a site-by-site (Fig. 1) examination shows that prevalence levels were usually <50%. These results could be explained if the malaria transmission rate is low at Hopland and if mortality in infected younger lizards is high. However, demographic data relating size with precise age of the lizards as well as mortality curves for infected and non-infected hosts are not available, preventing the kind of age-specific analysis possible for human malaria systems.

Environmental temperature appears to play an important role in determining the distribution and abundance of lizard malaria, just as it does for human malaria. Jordan (1964) surveyed many sites along the southeast coastal region of the USA and found no malaria in lizards north of 32° latitude. At Hopland the more common sandfly species, *L. vexator*, may be an inefficient vector of *P. mexicanum* because its normal preferred body temperature is close to the minimum needed by the parasite to finish its development in the insect before the sandfly takes its next blood meal (Fialho & Schall 1995). Thus, even small differences in temperature available to the sandfly could have serious consequences for transmission success of the parasite. Our data also indicate that temperature is the only environmental variable having a significant effect on activity levels of the vector. Night-time air temperature below 16°C will restrict sandfly activity. For example, at site 45 (885 m elevation) only one fly was collected from 40 traps set on a night when air temperature was 7°C, yet on another night 164 flies were taken from those same traps when air temperature was 18°C. In contrast, environmental temperature variation should have a minimal effect on *P. mexicanum* in its vertebrate host; laboratory experiments show the parasite in the lizard host has the ability to buffer changes over a broad range of temperatures (Schall 1990c).

It is conceivable that subtle differences in temperature experienced by the sandflies at different sites at Hopland could alter parasite development time or the number of nights the insects were active, and thus the average number of blood meals each *Lutzomyia* would take over its lifetime. The number of bites taken by each vector plays a leading role in determining presence or absence of the parasite according to the Macdonald model (Aron & May 1982). We conclude that this is a likely explanation for the rarity or absence of malaria above 500 m in elevation where it is cooler. However, our subjective judgement is that tem-

perature among sites at lower elevations does not vary over just a few hundred metres compass distance, the distance separating some malarious vs. non-malarious locations. This situation is reminiscent of the fairly fine-scale variation in prevalence of specific serotypes of human malaria observed by Forsyth *et al.* (1989) in New Guinea villages despite no clear differences in habitat quality among sites.

At Hopland, malaria can be common hundreds of metres from the vector's resting and reproductive sites (ground squirrel burrows), suggesting the sandflies can travel over fairly long distances. Over all, malaria prevalence was not related to the apparent abundance of the vectors and knowledge of the local abundance of the vector was useless in explaining malaria prevalence for this system. These results suggest to us that only knowledge of the complexities of sandfly flight, host seeking and feeding behaviour will allow an understanding of the number of blood meals taken by a sandfly during its lifetime and consequently the distribution of *P. mexicanum* among sites. However, recent theory devised to suggest control strategies for human malaria argues that vector abundance is not a prime predictor of malaria prevalence because the immune resistance to malarial infection develops very slowly, resulting in children having a high risk of infection even when vector bites are uncommon (Gupta *et al.* 1994). Information on the action of the reptilian immune system to malaria is lacking, so the relevance of these important models for lizard malaria is unknown.

The variation in abundance of *P. mexicanum* over time is even more perplexing. Individual fence lizards at Hopland typically remain for the entire warm season at one location and have a short life span, perhaps only 1–2 years (Schall & Sarni 1987; Schall & Houle 1992; our unpublished observations), so variation among years in abundance of detected infections must represent changes in the parasite's transmission and maintenance in the host population. Again, if vector abundance or feeding behaviour is critical in determining the parasite's prevalence, then environmental forces such as rainfall or temperature should be correlated with percentage of lizards infected each year. The warm season environment at Hopland did vary greatly from year to year; in fact, we have been struck by the changes in appearance among years at the site. In some years the vegetation appears lush and remains green well into the dry summer season, and insect abundance (grasshoppers, for example) is obviously high. In other years the area looks dusty, with far fewer insects and standing herbs. Prevalence of malaria, however, was not correlated with any environmental measure, including temperature, rainfall and a biological assay of environmental quality, herbage produced per ha.

After the first 3 years of this study, Schall (1983) suggested that lizard malaria at Hopland was a stable system because percentage of lizards did not vary

much over that period despite great changes in rainfall. The rainy season prior to the summer of 1978 produced heavy precipitation (1263 mm) after a 60-year severe drought, but rainfall dropped again the next year to only 665 mm, and then rebounded prior to 1980 to 1080 mm. Examination of Fig. 3 reveals, though, that there was actually a 7-year gradual decline in prevalence of malaria at Hopland from 1978 to 1984 that was not detectable during the first 3 years of the study. This observation demonstrates the importance of long-term studies before making an assessment of the stability of any parasite–host system.

The shape of the prevalence distributions over time presented in Fig. 3 suggests that the pattern is not random, but instead is a cycle of very long duration. Peak-to-peak of this cycle appears to take about 10 years. The only other long-term study of malaria in a natural non-human host is one by Jordan (1971) who examined *P. floridense* in the small iguanid lizard *Anolis carolinensis* in Georgia, USA during a 13-year period. Her results were strikingly similar to the those seen in Fig. 3. Prevalence of *P. floridense* in *Anolis* was ~50% in 1958, but dropped steadily to ~10% in 1964, then began to rise again to ~50% by 1970. Again, this suggests a cycle of about 10 years. Such cycles have been reported for human malaria at some sites (Faust 1949; Pampana 1969; Forsyth *et al.* 1989) but are not predicted by the standard Macdonald model [despite Macdonald's own claim that his model predicts cycles (Macdonald 1957)]. Molineaux (1988) notes that the typical period of human malaria cycles is about 10 years and suggests the cycles are driven by changes in vector abundance caused by cyclic variation in climatic factors. However, entering changes in vector abundance into the Macdonald model does not lead to long-term cycles (Gupta *et al.* 1995; Nowak & May 1994). This recent theory instead shows that cycles can appear if two parasite strains wax and wane as they interact with the host population's immune defences. This kind of change in abundance of a specific malaria strain over time has been observed by Forsyth *et al.* (1989). Thus, cycles in malaria can be driven, not by environmental variation, but instead by factors intrinsic to the parasite and host. Whether lizard malaria also exists in strains that vary in their cross-immunity, or if lizards in fact mount any immune response to malarial infection, is unknown.

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