

Landscape features associated with infection by a malaria parasite (*Plasmodium mexicanum*) and the importance of multiple scale studies

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SUMMARY

In a 3-year study, we examined landscape features (aspect, slope, sun exposure, canopy cover, type of ground cover, and nearest water source) that were potentially related to prevalence of infection with *Plasmodium mexicanum* in fence lizards (*Sceloporus occidentalis*) within a 4.5 ha study area in northern California, USA. Logistic regression analysis showed that ground cover type was the primary mediator of the probability of *P. mexicanum* infection. Infected lizards were captured more often in rock and/or leaf litter locations than in grassy ones. In another experiment, the study area was divided into 9 sites (0.07–0.33 ha), and infection prevalence was calculated for each. Three sites with high (> 30%) infection prevalence had significantly more rocky outcrops and leaf litter than those with low (< 20%) or moderate (20–30%) infection prevalence ($N = 3$ sites each). We conclude that lizard site selection may influence the probability of exposure to infected vectors and thus the likelihood of *P. mexicanum* infection. We also demonstrate that studies at different spatial scales may be required to understand fully the relationship between landscape features and parasite distribution.

Key words: *Plasmodium*, malaria, landscape features, spatial scale.

INTRODUCTION

A central theme in ecology is to gain an understanding of the distribution and abundance of organisms. Because of their potential importance to human health and economics, much attention has been given to describing the distribution and abundance of parasites infecting humans and livestock (Schmidt & Roberts, 1989). Far less attention has been paid to parasites infecting wildlife species, despite their potential significance for conservation biology (Grenfell & Dobson, 1995). In general, models of parasite abundance within host populations (infection prevalence) for parasites with complex life-cycles have focused on the abundance of infected and susceptible hosts, abundance of vectors and vector activity (MacDonald, 1957; Aaron & May, 1982; Anderson & May, 1992). Several studies have demonstrated that such parameters, as well as host site selection, are often associated with landscape features (Audrey, 1958; Pavlovsky, 1966; Esch & Fernandez, 1993; Sapp & Esch, 1994; Beck *et al.* 1994; Jokela & Lively, 1995; Kitron, 1998; Frank, Fish & Moy, 1998; Tälleklint-Eisen & Eisen, 1999; Zelmer, Wetzal & Esch, 1999). Understanding the relationship between landscape

features and prevalence of infection is critical to designing effective control programmes for parasites of humans, livestock and wildlife (Pavlovsky, 1966; Anderson & May, 1992).

Plasmodium mexicanum, a malaria parasite of fence lizards (*Sceloporus occidentalis*), is a useful model system for studying such associations. The parasite is transmitted through the bite of infected sandflies (*Lutzomyia vexator* and *L. stewarti* (Ayala, 1977)). It then undergoes the typical *Plasmodium* life-cycle in which asexual replication occurs within the red blood cells of the vertebrate host and sexual recombination takes place during the brief period in the vector. Most commonly, *P. mexicanum* infections grow rapidly to reach a peak parasitaemia and remain at a stable level throughout the warm season. Once infected, lizards typically remain infected throughout life, and thus blood smears provide an accurate estimate of *P. mexicanum* infection status (Garnham, 1966; Bromwich & Schall, 1986; Perkins, Osgood & Schall, 1998; Eisen, 2000). In contrast, avian, rodent and primate malaria infections generally have a period of exponential increase followed by a period of decline and clearing from the host's blood, making infections difficult to detect on blood smears (Garnham, 1966). The second advantage of this study system is that fence lizards have small home ranges (Davis & Ford, 1983) with most lizards captured repeatedly on the same perch site (R. J. Eisen, personal observation). This strong site

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fidelity, especially among adults, reduces the dispersal of lizards among local populations. Therefore, point capture data provide better estimates of infection prevalence for a given area than in many other malaria systems.

Plasmodium parasites of lizards, which account for about half of all described *Plasmodium* species, have been described on all warm continents except Europe (Telford, 1994; Schall, 1996). However, the geographical distribution of these parasites is generally uneven. For example, lizards are commonly parasitized by *Plasmodium* in wet tropical forests, forested areas and grasslands, but not in deserts (Ayala, 1977). Patchy distributions are also seen at finer spatial scales. For example, a long-term study of *P. mexicanum* in northern California, found 15-fold differences in infection prevalence among sites only 150 metres apart (Schall & Marghoob, 1995).

With the exception of elevation, which is known to be associated with *P. mexicanum* distribution on a large spatial scale in northern California, factors controlling the abundance and distribution of this parasite remain elusive. In a 3-year study, we determined which habitat features (aspect, slope, sun exposure, canopy cover, type of ground cover, and nearest water source) were related to prevalence of infection with *P. mexicanum* in fence lizards.

MATERIALS AND METHODS

Study site and detection of parasites

Fence lizards were collected from June to August 1996, April to September 1997, and April to August 1999 at the University of California Hopland Research and Extension Center (HREC), located in southeastern Mendocino County, California. The study was conducted in a 4.5 ha oak savannah woodland area on a predominantly south-facing slope, with numerous rocky outcrops and logs, and dominated by oak (*Quercus* sp.), California bay (*Umbellularia californica*), and California buckeye (*Aesculus californica*) trees. The climate at HREC is Mediterranean with hot, dry summers and cool, wet winters. Lizards can be active at this location from March to October (Ayala, 1970; Bromwich & Schall, 1986).

Lizards were captured by hand or slip noose between 08.00 and 14.00 h. Upon collection, each lizard was marked with a number using liquid paper® on its dorsal surface, and by a unique toe-clip combination. The exact sites of capture were recorded and flagged with surveyor's tape to assure release at the point of capture.

All animals were transported in cloth bags to a field laboratory where sex and snout-vent length (SVL) were recorded. A drop of blood was drawn from a toe clip of each lizard to produce thin blood smears that were later stained with Giemsa's stain

(pH = 7.0, 50 min). Each slide was examined at $\times 1000$ for 6 min or until a malaria parasite was detected. For each negative slide, approximately 10000 erythrocytes (RBCs) were examined. Infections with parasitemia $< 1/10000$ RBC, and thus not detected by this protocol, are rare at HREC (Perkins *et al.* 1998). Lizards were returned to the exact site of capture within 24 h. Associations between *P. mexicanum* infection and landscape features were examined at 2 scales: for individual lizards and for 9 populations of lizards within the 4.5 ha study area.

Infection status of individual lizards in relation to landscape features

To determine the relationship between infection status and landscape features, we recorded the following data upon capture of 178 lizards collected during 1999: aspect (north, south, east or west), slope (flat [0°], slight [5–10°], moderate [15–30°] or steep [$> 30^\circ$]), sun exposure (full sun or shade), perch type (rock, log or other), type of closest water source (drainage stream or vernal pool) and ground cover (grass, leaf litter or rock). Common grasses identified within the study area ranged in height from approximately 30 to 75 cm and included the following species: *Aira caryophylla*, *Avena barbata*, *Bromus hordeaceus*, *Cynosurus echinatus*, *Deschampsia elongata*, *Phalaris aquatica* and *Polypogon monspeliensis*. Leaf litter was patchy with an average depth ranging from approximately 4 to 10 cm. The dominant rock form was tertiary metamorphosed marine sediment of the Franciscan formation. If rocky ground cover was continuous for at least 1 m, the area was considered to be 'rocky'. All data were recorded based on the landscape features within a 10 m radius of the lizard. In situations where a lizard was captured on a rock, log or other substrate, the slope and aspect of the ground upon which the perch was situated was recorded. Seven ground cover types were encountered within the study area: grass, rock, leaf litter, grass and rock, grass and leaf litter, rock and leaf litter and grass, rock and leaf litter. Because ground cover categories of rock or leaf litter alone were rare, we combined these groups together with 'leaf and rock' in our analyses. For exploratory purposes, as well as to correct for multiple comparisons, we constructed and tested logistic regression models (Hosmer & Lemeshow, 1989). All of the parameters described above, as well as host sex and SVL, which is an indicator of host age (Schall, 1996), were used as independent variables in the models; infection status was the response variable. All data were treated as categorical with the exception of SVL. The model that fit the data best was selected among all possible models. Significance of the effects was estimated using likelihood ratio statistics (Hosmer & Lemeshow, 1989). Contingency

table analyses were then used to determine the relationships between infection status and habitat features. All statistical analyses were performed using JMP® (Cary, North Carolina) statistical package.

Prevalence of infection in lizard populations in relation to landscape features

The 4.5 ha study area was divided into 9 sites (0.07–0.33 ha) based on natural breaks in the landscape, such as large grassy patches in which lizards were not captured. The boundaries of the entire study area, as well as those of the 9 sites were recorded with a Trimble® GPS unit and mapped using ArcView® software. The area of each site was calculated using ArcView® software.

Infection prevalence was calculated for each of the 9 sites using data collected over all 3 years. The percentage of canopy cover for each site was quantified by overlaying the site boundaries from a geographical information system (GIS) coverage on a georeferenced aerial photograph of the study site. Association between canopy cover and infection prevalence and abundance of leaf litter was examined using Spearman correlation analyses. In addition, abundances of leaf litter, rocky ground cover and grass were estimated for each site based on the presence or absence of each substrate, measured at 2 m intervals within 4 randomly selected 30 m transects for each site. To increase the sample size within each category, sites were grouped by infection prevalence into 3 categories: low (< 20%), moderate (20–30%) and high infection prevalence (> 30%). No statistically significant differences were detected among sites within each category (contingency table analysis: $\chi^2 < 0.909$, $P > 0.05$). Contingency table analyses were used to determine if infection prevalence (low, moderate or high) was related to the presence or absence of leaf litter, rocky ground cover and grass; ANOVA was used to determine if infection prevalence was related to abundance of each ground cover type.

To determine if host density was associated with infection prevalence in the 9 sites, a Spearman correlation analysis was used. We estimated lizard density as the number of lizards captured per site divided by the area of each site (measured in ha).

RESULTS

Infection status of individual lizards in relation to landscape features

Logistic regression models suggested that the type of ground cover was the primary mediator of the probability of *P. mexicanum* infection (Likelihood ratio; $\chi^2 = 19.45$, $P = 0.0006$). Based on odds ratio

statistics, lizards captured in rock and/or leaf habitats are more likely to be infected than those captured in grass alone (95% confidence interval: 0.519–2.56). Inclusion of other covariates in the model did not significantly improve the model. The infection status of 72% of lizards were correctly classified by our model. During 1999, malaria infections were significantly more common in rock and/or leaf litter locations than in grassy ones ($\chi^2 = 18.95$, $P = 0.0008$) (Fig. 1). Comparisons of infection status by presence or absence of grass, and presence or absence of leaf litter showed that malaria infections were significantly less common in areas where grass was present, as compared to absent ($\chi^2 = 13.086$, $P = 0.0003$), and more common in areas where leaf litter was present, as compared to absent ($\chi^2 = 5.817$, $P = 0.0159$).

Overall, for lizards collected in 1999, infection status was not related to the sex of the lizard ($\chi^2 = 1.42$, $P = 0.23$), SVL ($\chi^2 = 3.04$, $P = 0.08$; $r^2 = 0.02$), perch type ($\chi^2 = 3.761$, $P = 0.15$), type of closest water source ($\chi^2 = 3.466$, $P = 0.08$), slope ($\chi^2 = 7.483$, $P = 0.06$), aspect ($\chi^2 = 2.236$, $P = 0.69$), or presence of rocky ground cover ($\chi^2 = 3.355$, $P = 0.0670$).

Prevalence of infection in lizard populations in relation to landscape features

A total of 691 fence lizards were captured during the 3-year study. Infection prevalence was similar among years (range: 20.3–26.4%; $\chi^2 = 0.540$, $P = 0.7635$), and was similar within each site among years for 8 of 9 sites ($\chi^2 < 5.40$, $P > 0.05$). Among sites, infection prevalence ranged from 11 to 33%, and was not significantly associated with lizard density ($r_s = -0.228$, $P = 0.555$).

Sites with the lowest infection prevalence were found along the eastern border of the area whereas sites with moderate or high infection prevalence were grouped in the northwestern corner and around a large rocky outcrop in the centre of the study area, respectively. Sites that grouped together based on infection prevalence were not always those closest to each other (Fig. 2).

Sites with high infection prevalence had significantly more rocky outcrops than moderate or low infection prevalence sites (55, 26 and 19% of transect points with rocky outcrops present, respectively; $\chi^2 = 40.82$, $P < 0.001$, $N = 576$) (Fig. 3). Similarly, sites with high infection prevalence had significantly more leaf litter than areas with moderate or low infection prevalence (low = 24% leaf litter, moderate = 30% leaf litter, high = 46% leaf litter; $\chi^2 = 53.32$, $P < 0.001$, $N = 576$). Abundance of grass in each site was not significantly different among those with high, moderate or low infection prevalence ($\chi^2 = 4.44$, $P = 0.11$, $N = 576$). For the 9 sites, pro-

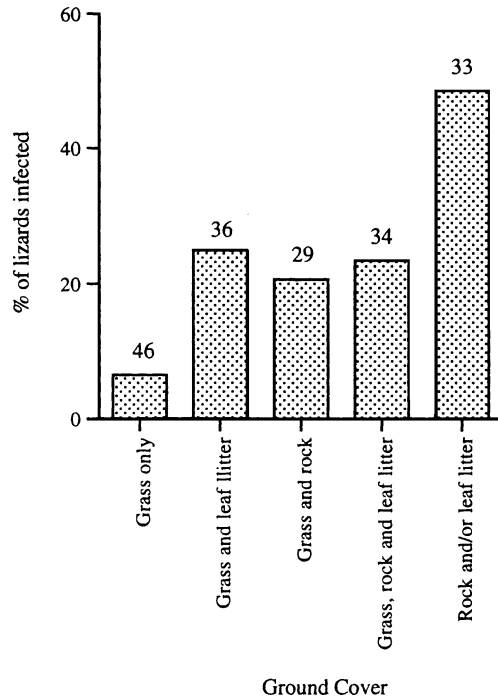


Fig. 1. Infection status of individual lizards and its relationship to type of ground cover. Grass and leaf litter, grass and rock, and grass, rock and leaf litter do not differ significantly from one another. All other pairwise comparisons were statistically significant. Numbers on the figure indicate sample sizes within each ground cover category.

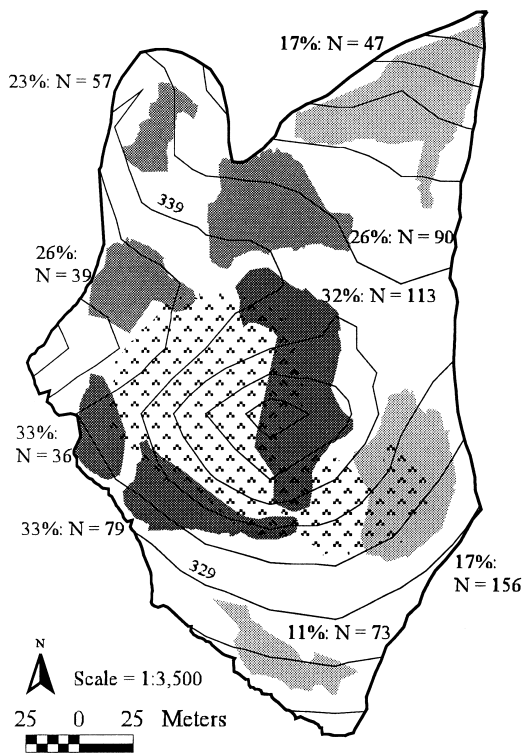


Fig. 2. Map of 4.5 ha study area. Sites with high (> 30%), moderate (20–30%) and low (< 20%) infection prevalence of *Plasmodium mexicanum* are shaded as black, dark grey and light grey, respectively.

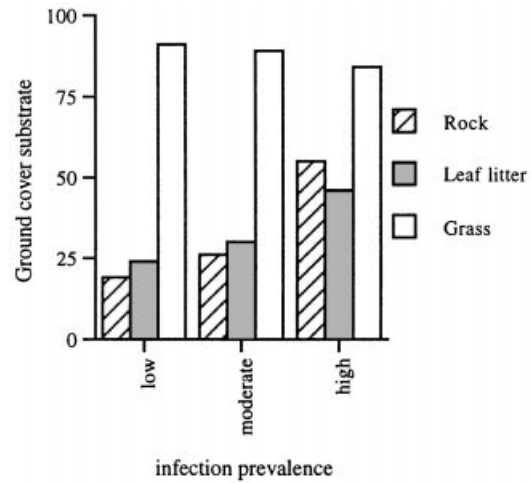


Fig. 3. *Plasmodium mexicanum* infection prevalence in relation to ground cover type. The proportion of leaf litter and rock differed significantly among infection prevalence groups ($\chi^2 > 40.82$, $P < 0.05$). The proportion of grass was similar among transects in areas with low, moderate and high infection prevalence ($P > 0.05$).

portion of canopy cover was not correlated with either infection prevalence ($r_s = 0.30$, $P = 0.43$; Spearman correlation) or percentage leaf litter per site ($r_s = 0.25$, $P = 0.51$; Spearman correlation).

Finally, to determine the relative importance of fine-scale (within a 10 m radius of each capture site) and course-scale (within the 9 sites) habitat features, the logistic regression analysis was repeated with the addition of 3 course-scale attributes (percentage of transect points with leaf, percentage with rock and percentage with grass). Again, fine-scale ground cover type was the best predictor of infection status (Wald $\chi^2 = 11.80$, $P = 0.02$). The following course-scale attributes were of less significance: percentage of leaf litter per site (Wald $\chi^2 = 4.47$, $P = 0.03$), percentage of grass per site (Wald $\chi^2 = 3.40$, $P = 0.07$), and percentage of rocky substrate per site (Wald $\chi^2 = 1.68$, $P = 0.19$).

DISCUSSION

Infection prevalence differed significantly among 9 sites within the 4.5 ha study area (range 11–33%), and these differences were associated with landscape features. For example, lizards captured in areas with leaf litter or rocky ground cover were more likely to be infected than lizards captured in areas lacking these types of ground cover. Other traits (e.g. type of closest water source and slope) were of borderline significance, and ranked as less important than ground cover type. Because of the small home range of fence lizards (upper limit of approximately 80 m², Davis & Ford, 1983), infections likely were acquired

close to the area the lizard was captured. The positive association between presence of infection and abundance of leaf litter and the negative association between presence of infection and grassy ground cover were replicated at 2 scales; for individual lizards and for lizard populations within the 9 sites. However, previous studies have demonstrated that exclusion of spatial correlations in linear and logistic regression models can exaggerate the impression of significance of regression relationships (Kitron *et al.* 1996; Thomson *et al.* 1999). Individual home-ranges were not mapped in this study, and thus analyses of spatial autocorrelation were not conducted. A follow-up study in which lizard home-ranges are mapped is thus necessary to verify that ground-cover type is the primary mediator in predicting lizard infection status.

Although studies focusing on the association between landscape features and the presence of parasites are scant relative to those of free-living organisms, previous studies have demonstrated, across broad taxonomic classifications, that such relationships are not unusual. This association is presumably the result of overlapping habitat preferences of all hosts involved in a life-cycle (MacLeod, 1935; Sousa & Grosholz, 1991; Sapp & Esch, 1994). For example, *Plasmodium* infections in birds and lizards are limited to low elevation sites within the vertebrate host's distribution that are more conducive to vector survival and activity (van Riper *et al.* 1986; Schall & Marghoob, 1995). Similarly, trematode infections in snails are often associated with shallow water where definitive hosts are common (Sapp & Esch, 1994; Jokela & Lively, 1995; Zelmer, Wetzel & Esch, 1999). Finally, infestations by *Ixodes pacificus* ticks on fence lizards are more common in woodland areas where the risk of desiccation may be lower relative to open grassland (Tälleklint-Eisen & Eisen, 1999).

The reason for the association between *P. mexicanum* infection and leaf litter and/or rocky ground cover remains unclear. *S. occidentalis* generally prefer wooded areas to open grassland. Further, within woodlands they prefer rock and log perches to other forms, and their abundance is positively associated with cover of California black oak (Davis & Verbeek, 1972; Rose, 1976; Block & Morrison, 1998). The nocturnally active vectors of *P. mexicanum*, 2 species of sandfly, *Lutzomyia vexator* and *L. stewarti*, have been found in low abundance in burrows of the California ground squirrel, *Spermophilus beecheyi* (Chantiotis & Anderson, 1968; Fialho & Schall, 1995; Schall & Marghoob, 1995). In some locations, these burrows were associated with large rock outcrops (Chantiotis & Anderson, 1968). However, no association between proximity to burrows and infection prevalence was found at HREC (Schall & Marghoob, 1995). Because little is known about the sandfly vectors,

their role in the association between infected lizards and landscape features is speculative. To our knowledge, nothing is known about the movement or host-seeking behaviour of *L. vexator* and *L. stewarti*. We speculate that trees and rocks could provide a barrier to wind that might enable the small flies to fly on windy evenings, thus increasing the number of nights for transmission in areas with rocks and leaf litter. Additionally, leaf litter could provide a desirable high-humidity refuge for the sandflies.

Knowledge of habitat preferences of intermediate hosts, combined with remote-sensing techniques, has been useful in creating pathogen surveillance models covering large geographical areas (Beck *et al.* 1994; Dister *et al.* 1997; Kitron, 1998; Frank, 1998). However, as the application of such models increases in popularity, it is important to consider that as scale dimensions diminish, habitat features associated with infection status become more specific (Esch & Fernandez, 1993). These features could be undetectable by remote-sensing methods (Beck *et al.* 1994).

Our study, along with previously published data from the HREC, illustrates the utility of multiple-scale comparisons. A previous 13 year study on the infection prevalence of *P. mexicanum* at 51 sites (including the one described here) within the 2,169 ha HREC showed that the distribution of the parasite was patchy (Schall & Marghoob, 1995). Infection prevalence ranged from 0–50% among the 51 sites. Among-year variation in infection prevalence was observed and was independent of herbage, temperature and rainfall. Among sites, part of the variation was explained by elevation, such that malaria was absent at sites > 500 m. However, sites within 150 m of one another, and of similar elevation, showed up to 15-fold differences in infection prevalence (2–31%). The site with the lowest infection prevalence was a residential area with 'cleared land,' while the site with highest infection prevalence was a rocky slope located in a streambed that traversed a wooded area (Schall & Marghoob, 1995). Our results suggest that the variation in infection prevalence among sites observed by Schall & Marghoob (1995) could be explained by micro-habitat differences not examined in that study, such as the abundance of leaf litter. Models relying on elevation alone, or ground cover substrate on its own, would inaccurately estimate the abundance and distribution of malaria infections throughout the HREC. For example, some sites below 500 m are within the elevation range for infections to exist but are lacking malaria infection. Similarly, sites above 500 m have abundant leaf litter but lack malaria infections (Schall & Marghoob, 1995, R. J. Eisen, personal observation).

We conclude that infection prevalence of *P. mexicanum* is heterogeneous even at a fine spatial scale, and that part of the patchy distribution is related to landscape variation. Studies of the dis-

tribution of parasites within a host population, as well as the landscape features associated with such distributions, have important implications for the control of human, livestock and wildlife parasites. Understanding the relationship between parasitic infection and landscape features in other animal populations may be logistically more challenging than in this study in which infections were life-long and host mobility was limited. Nonetheless, several models of parasites with complex life-cycles have demonstrated that spatial heterogeneity leads to increased estimates of the basic reproductive rate of the parasite relative to estimates of a homogeneous population (Barbour, 1978; Dye & Hasibeder, 1986; Anderson & May, 1992). This discrepancy has serious implication for the design of immunization programmes, such that a larger proportion of a heterogeneous population must be vaccinated relative to a homogeneous one if vaccinations are prescribed under the assumption that the population is homogenous (Anderson & May, 1992). Understanding the landscape features associated with the distribution of parasites could therefore aid in disease surveillance programmes and improve parasite control strategies. However, in conjunction with the study presented by Schall & Marghoob (1995), we have demonstrated that studies at different spatial scales may be required to fully understand the relationship between landscape features and parasite distribution.

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