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Parasites and showy males: malarial infection and color variation in fence lizards

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Summary. Hamilton and Zuk (1982) proposed that the quality of male showy traits reflects genetically-based resistance to parasites and can be used by females to select mates that are less prone to parasitic attack. The hypothesis requires that a particular state of a variable showy trait should be associated with parasite infection. We tested this idea with a population of western fence lizards, *Sceloporus occidentalis*, infected with the malarial parasite, *Plasmodium mexicanum*. Ventral color pattern is strongly dimorphic in fence lizards and varies greatly among males in this population. Malaria-infected males exhibited significantly more black and less pale on their ventral surface than did noninfected males of similar body size. This difference was not a function of differing ages of infected and noninfected animals of the same body size. However, logistic regression demonstrated that females using male ventral color as a gauge of infection status would only marginally improve their chance of choosing a noninfected lizard over random selection of mates.

Key words: Parasites – Malaria – Lizards – Sexual selection – Sexual dimorphism – Hamilton/Zuk hypothesis

Although some parasites cause obvious severe damage to their hosts, in many others the influence of the parasite on infected hosts appears slight. However, the consequences of parasitic infection that seem minimal at first consideration, such as minor alteration of a host's appearance or behavior, could well profoundly influence the biology of the host. For example, alteration of a host's appearance, although subtle, might conceivably decrease its status in social interactions. Hamilton and Zuk (1982) proposed an intriguing hypothesis that incorporates the effects of parasites on their hosts into sexual selection theory. They argued that sexually dimorphic traits, in which one sex (usually males) displays extravagant colors or structures, have evolved in part because they allow the other sex to evaluate the parasite load of potential mates. The dimorphic trait in infected males would appear scrofulous, or simply less extravagant, when parasitized. Discriminating females in such situations would select males with the showiest trait, equating that phenotype with a genotype that confers resistance to parasites.

To test this hypothesis Hamilton and Zuk (1982) and Read (1987) used a clever interspecific comparison to demonstrate that bird species with colorful males tend to be exploited by a greater variety of blood parasites than birds with blandly colored males. Although suggestive, interspecific comparisons are only indirect tests of the hypothesis. Despite considerable interest in Hamilton and Zuk's hypothesis (Hamilton 1982; Zuk 1984, 1987; Dawkins 1986; Borgia 1986; Kirkpatrick 1986; Partridge and Harvey 1986; Read 1987), and in the effect of parasites on social behavior of their hosts in general (Rau 1983; Schall and Dearing 1987), no examples of effects of parasites on sexually dimorphic morphological traits of their hosts have been described.

Here we examine the effects of a malarial parasite on the ventral color of the western fence lizard (*Sceloporus occidentalis*) of California, USA. This system is exceptionally useful for such a study because the parasite is known to cause severe physiological, hematological, reproductive, and behavioral pathology in its host (Schall et al. 1982; Schall 1983a; 1983b; Schall and Dearing 1987), and the lizard is strongly dimorphic in a trait important in intersexual communication in lizards (Carpenter and Ferguson 1977), its ventral color.

We ask three questions: First, does the parasite alter the ventral color of the fence lizard? This question was difficult to address because older lizards are more likely to be infected and ventral color changes as the lizard grows and ages. Therefore, we had to partition out the effect of the host's age to determine if infection alters its appearance. Second, can female lizards use the appearance of potential mates to determine its infection status? Third, do our results support the Hamilton and Zuk hypothesis? These results are the first examination of the effect of parasitic infection on the appearance of a sexually dimorphic trait of any reptile and one of the few tests of the much-discussed Hamilton and Zuk hypothesis.

Rationale for use of the study system

For a study system to be suitable for a test of the Hamilton-Zuk hypothesis, the following conditions must be met: (1) there must be a variable sexually dimorphic trait; (2) this trait must be important in courtship; (3) the animal must be frequently chronically infected with a parasite known to severely harm its host; (4) the parasite must alter physiological processes involved in formation of the sexually dimorphic trait in males. We document each of these in turn.

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Adult male *S. occidentalis* are territorial during the breeding season and perform a characteristic "signature display" (Carpenter and Ferguson 1977) of repetitive "push-ups" exposing their entire ventral surface. This behavior is directed toward rival males and females during courtship (Smith 1946; Schall and Sarni 1987; Schall and Dearing 1987). During bobbing behavior by males, the ventral color pattern is clearly visible to human observers from considerable distances. The male's body is often laterally compressed, starkly revealing the color pattern. This color pattern is highly variable among males (below).

During courtship, female fence lizards often remain near a male as it displays, sometimes for over 1 h, and appear to be looking directly at the male (Schall and Houle unpubl.). Although the role of body color in *S. occidentalis* has not been defined experimentally, the closely related eastern fence lizard (*S. undulatus*) clearly uses ventral color as a signal during intersexual interactions (Noble 1934; Carpenter and Ferguson 1977; Cooper and Burns 1987).

Plasmodium mexicanum is a common parasite of the western fence lizard (Ayala 1970). Infection appears lifelong and parasite-induced pathology is substantial, affecting hematological, physiological, behavioral, and reproductive processes (Schall et al. 1982; Schall 1983a, b; Bromwich and Schall 1986; Schall and Sarni 1987; Schall and Dearing 1987). Ventral color of male fence lizards would be affected by malarial infection if the parasite alters melanophore physiology. Melanophore production in *S. occidentalis* is controlled by steroids secreted by the testes (Kimball and Erpino 1971). *Plasmodium* infection reduces testis mass in fence lizards (Schall 1983a, b) suggesting reduction of hormonal titers as well. Some melanophores contain a lipid component (Fox 1953) and infected lizards suffer disruption of lipid metabolism (Schall 1983a, b). Although this cause-effect sequence is based solely on circumstantial evidence, it is plausible that color formation in fence lizards could be sensitive to the effects of malarial infection.

Methods

We conducted the study at the Hopland Field Station of the University of California, located 160 km north of San Francisco (description in Bromwich and Schall 1986). During mid May to early September 1984 we collected fence lizards. Before disturbing a male lizard, we noted the presence of females, if any, that were near the animal. That evening, the ventral portion of each lizard was photographed under standardized conditions (Ressel 1988). The resultant photographic slides revealed color pattern with great detail and excellent color fidelity.

The photographic slides of lizard venters were projected onto a digitizing tablet of a ZIDAS image analysis system (Carl Zeiss, Inc.). *Sceloporus occidentalis* venters display a pattern of unpigmented (referred to here as "pale"), blue, black, and yellow scales (Stebbins 1966). Areas covered by these colors within a total belly area were traced and computed in square mm. The boundaries for total belly area were: anterior = gular fold, lateral = lateral-most boundary of blue patch on both sides of the belly, posterior = posterior boundary of axilla-groin region. The four color areas were later converted in the analysis to relative proportions by dividing each color area by total belly area.

Male lizards with very similar proportions of ventral colors could still differ both in the arrangement and intensity of colors. Preliminary observations demonstrated that the intensity of ventral colors also varied among males in *Sceloporus occidentalis*. One factor that alters intensity is the lizard's body temperature (Ressel 1988). Therefore, over a two week period, 100 lizards were cooled in a refrigerator until their body temperature stabilized at around 16° C, and a photograph made immediately upon removal. Each of the same lizards was later exposed to direct sunlight until it began to pant (body temperature at 38–44° C), and the ventral surface was photographed again. This procedure allowed us to document color intensity extremes over the entire range possible.

Photographic slides from lizards subjected to temperature extremes were scanned to select 35 distinct color classes that were unique in color pattern and intensity. Prints from these slides were grouped in a notebook that could be easily referenced in the field. During the last two weeks of May 1985, we returned with an assistant to test the possible correlation between color class and infection status. After capture, male lizards were quickly matched to a specific color class based on their color pattern and intensity. The coordinated efforts of three observers led to a judgment of color class within seconds of capture. Two kinds of analysis were done on these data. First, the 35 color classes were grouped into two intensity categories, bright and dull, for comparison between infected and noninfected lizards. Second, to allow adequate sample sizes in all elements in a contingency table analysis, the 35 classes were collapsed to seven pattern classes, based on the subjective judgement of three individuals. In summary, these analyses allowed us to address all three kinds of variation in male ventral color in terms of infection status: color proportion, intensity, and arrangement.

Each lizard was permanently marked with a unique sequence of toe clips and released at the point of capture. Some marked animals were later recaptured for determination of growth rate of malarious and noninfected lizards. Body size was measured from tip of snout to vent (SVL) to the nearest mm. During toe clipping, a drop of blood was drawn to make a blood smear. Smears were stained with Giemsa, a standard blood stain, and later viewed to detect infection with *Plasmodium* (methods in Bromwich and Schall 1986). Past studies have shown that low malarial parasitemia can induce levels of pathology comparable to high parasite loads (Schall 1983a, b), so parasitemia levels were not considered in our analysis and smears were scored as either infected or noninfected. Unfortunately, the length of malarial infection cannot be determined by these techniques.

Results

Nature of variation in ventral colors

A total of 827 male *Sceloporus occidentalis* were caught and examined in 1984. Of these, 119 males (14.4%) were infected with *Plasmodium mexicanum*. Fence lizards we collected were strongly sexually dimorphic in their ventral pigmentation. Both sexes share a basic pattern of elongated blue patches on either side of the belly, edged medially with black. There is a blue throat patch, and yellow areas are sometimes found on the underside of forelimbs and thighs. Males, however, are distinctly colored, while females

Table 1. A comparison of ventral color proportions and corresponding variation for male and female *Sceloporus occidentalis*. Males = 708, females = 100. An arcsine transformation of data was performed on proportions to normalize data for statistical test of homogeneity of coefficient of variation (Lewontin 1966)

		Proportion of belly surface area					p
		Mean	S.D.	S.E.	Min	Max	
Pale	Male	0.245	0.236	0.008	0.000	0.772	<0.05
	Female	0.638	0.092	0.009	0.405	0.831	
Black	Male	0.349	0.182	0.007	0.006	0.683	<0.05
	Female	0.072	0.064	0.006	0.000	0.231	
Blue	Male	0.365	0.071	0.003	0.150	0.647	<0.05
	Female	0.286	0.047	0.005	0.109	0.393	
Yellow	Male	0.040	0.059	0.002	0.000	0.542	<0.05
	Female	0.004	0.013	0.001	0.000	0.084	

exhibit only light blue markings with the black borders either faint or absent. Juveniles of both sexes show no throat patch and faint belly markings. Therefore, sexual dimorphism in color results from differential accumulation of pigment over time in male and female lizards (Kimball and Erpino 1971).

Male *S. occidentalis* varied greatly in the proportion of their ventral surface covered with the four colors (Table 1). Compared to females, males were much more variable in their ventral colors (Table 1). Even males with very similar proportions of each color on their ventral surface could differ considerably in the pattern formed by the colors. For example, black scales on the chest and midventral area may form either large patches, or be widely scattered. Intensity of the ventral colors was found to change within seconds, this was partly associated with body temperature changes. The ventral colors of cool males were lighter compared to those of males warmed to their normal activity temperature. For example, deep black markings faded to pale gray when animals were cooled. However, the proportion of different colors did not change as color intensity changed (Wilcoxon-Signed rank tests, $P > 0.05$; $N = 100$ males). In summary, variation in ventral pigmentation is of three kinds, long-lasting pigmentation differences in proportion and pattern, and short-term color intensity changes.

Malarial parasitism and ventral colors

Figure 1 presents a comparison of regression lines for infected ($N = 119$) and noninfected ($N = 708$) male *S. occidentalis* for ventral color proportion over a range of body sizes. Figure 1 demonstrates that lizards change color pattern as they grow and unpigmented (pale) scales turn black, blue, or yellow (discussed in detail in Ressel [1988]); therefore, body size must be held constant when comparing the color pattern of infected and noninfected fence lizards. Analysis of covariance found a significant difference in regression lines for ventral pale (residual variance and slopes, $P > 0.05$; elevations, $P \leqslant 0.05$) and ventral black (residual variance, $P \geqslant 0.05$; slopes, $P \leqslant 0.05$). Infected males exhibit less ventral pale and more ventral black than noninfected males at any given body size. No significant difference was found for ventral blue. As ventral yellow is not tightly correlated with body size (Ressel 1988), we tested the null hypothesis of random deviation of means for infected males in either direction of means for noninfected males. A binomial test failed to reject this null hypothesis ($P = 1.0$, $P > 0.05$).

The infected group contained males ranging from just recently infected to males infected throughout their adult life. Thus, the correlation between size and ventral color should be weaker for the infected sample, compared to the noninfected group. Infected males did have significantly weaker correlations between color proportion and SVL (Fisher's z transformation [Zar 1984]; pale $z = 2.06$, $P < 0.05$; black $z = 3.24$, $P < 0.001$). This further supports the conclusion that infection with malaria alters the course of deposition of dark ventral color.

Infected and noninfected lizards clearly differed in their proportion of ventral black. We next sought to determine if the intensity of the colors differed. In May 1985 500 additional lizards (425 noninfected and 75 infected) were scored for ventral color intensity and pattern using 35 ventral color classes. Malarial infection was not related to ventral color intensity (bright vs. dull) among sexually mature males (homogeneity of groups; $P < 0.05$, $N = 321$), a not surprising finding because activity body temperature of infected and noninfected lizards do not differ (Schall unpubl.). The color class scores of the 500 lizards were also used to determine if the pattern, or arrangement, of colors differed between infected and noninfected males. The seven pattern classes represented vastly different color patterns in that ventral color proportions were similar between some pattern classes but differed in the arrangement of ventral colors (Table 2). The distribution of body size groups for noninfected males among the color classes supports previously discussed data; males become less pale as they grow (homogeneity of groups; $P \leqslant 0.05$, $N = 425$). Among sexually mature males (SVL > 60 mm), Fig. 2 shows those infected were overrepresented in the darkest color class (homogeneity of groups; $P < 0.05$, noninfected $N = 225$, infected $N = 75$). Although no smooth trend appears when moving across color classes (perhaps variation caused by the length of infection), infected males dominated color class 7, which is characterized by 63% black and 4.6% pale. Curiously, color class 6, which has similar color proportions but dissimilar arrangement of colors, contained few infected lizards. These results reaffirm that malarious males differed from noninfected males in their ventral color pattern, namely having more black.

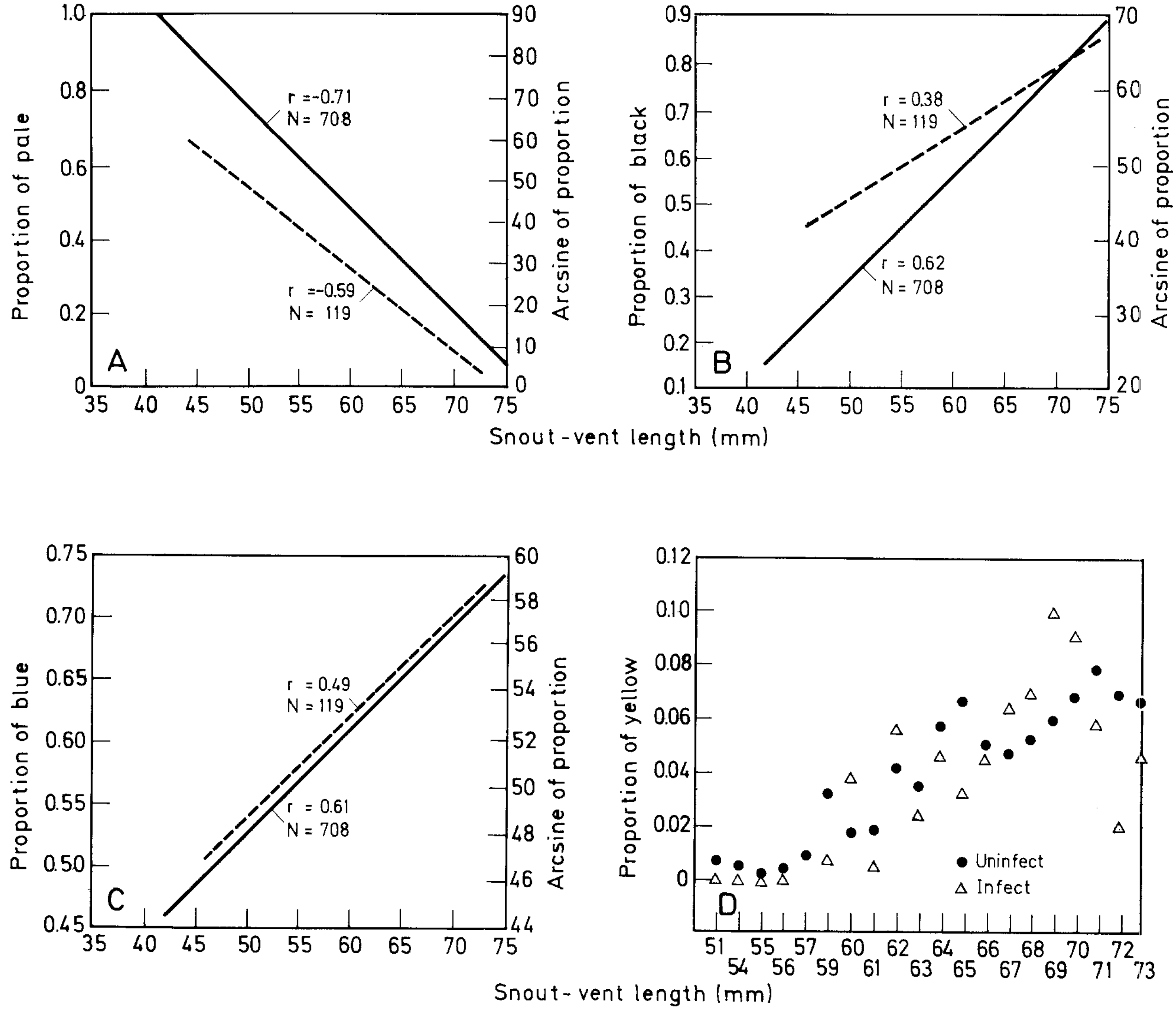

Fig. 1A–D. Comparison of ventral colors of male western fence lizards (*Sceloporus occidentalis*) infected with the malarial parasite, *Plasmodium mexicanum*, or not infected, over a range of lizard body sizes. *Solid regression lines* = noninfected lizards; *dashed regression lines* = infected animals. All correlations significant at $P < 0.05$. Proportion yellow is not strongly correlated with body size, so mean proportion of yellow for each body size class is shown. Infected animals exhibit significantly less pale and more black across most body sizes than do noninfected male fence lizards

Table 2. A description and corresponding ventral color proportions for seven color pattern classes observed in western fence lizards

Class	Characteristics	Pale	Black	Blue	Yellow
1	two distinct blue areas, edged by very thin black bands; pale medial band and chest	0.572	0.159	0.259	0.009
2	two distinct blue areas; yellow chest with black freckles; thin pale to yellow medial band	0.087	0.401	0.326	0.185
3	two distinct blue areas, edged by moderate width black bands; gray and yellow mottled chest	0.074	0.441	0.324	0.161
4	two distinct blue areas, edged by thin black bands; pale medial band with black freckles; pale chest with black and yellow freckles	0.149	0.470	0.353	0.111
5	two distinct blue areas, edged by thick black bands joined at midpoint; pale medial band; black, pale, and yellow mottled chest	0.086	0.551	0.331	0.032
6	two distinct blue areas separated by gray and black medial band; gray, black, and yellow mottled chest	0.027	0.605	0.351	0.016
7	two distinct blue areas separated by mostly black to black medial band; black chest with a few yellow freckles	0.046	0.634	0.301	0.018

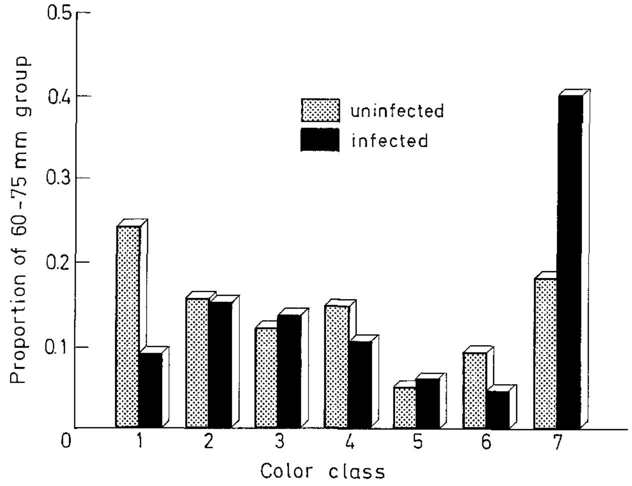

Fig. 2. Distribution of sexually mature male lizards (snoutvent length >59 mm) among seven color pattern classes (see Table 2) base on infection status

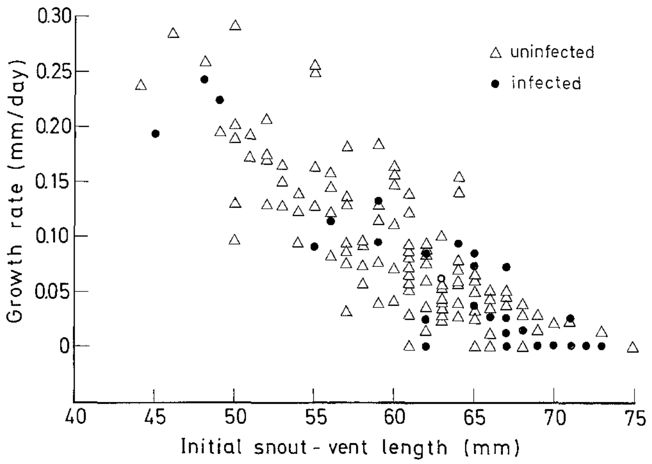

Fig. 3. Comparison of growth rates for male fence lizards infected with malaria ($N=38$), and not infected ($N=176$), based on animals marked and recaptured during the warm season of 1984

Age difference between infected and noninfected lizards

If infected fence lizards tend to be older than noninfected animals, this could seriously bias comparisons of color between infected and noninfected males. The preceding analysis of color by body size of infected and noninfected lizards was a required, but insufficient, control for such a bias. For example, infected animals of any size class could be darker simply because they are older, and older animals would have had a greater chance of exposure to the parasite. This situation could arise if the parasite reduces growth rate of its lizard host. However, markrecapture analysis demonstrated that infection does not reduce the lizards' growth rate. Growth rate is a function of size in these lizards, declining as they mature (Schall 1983a). Although plotting growth rate against body size does not provide instantaneous growth rate points, such plots are useful in intraspecific comparisons (Andrews 1982). Figure 3 presents a plot comparing growth rates of infected and noninfected males, using mark-recapture data to calculate growth rate. No significant difference was detected in growth rate between the two groups (analysis of covariance), agreeing with Schall (1983a) that infection with malaria does not significantly alter normal growth rate in fence lizards.

A second kind of analysis also discounted the possibility that infected lizards are darker simply because they are older. Malaria at our study site has a patchy distribution in fence lizards, probably due to a patchy distribution of its insect vector. We collected a sample of adult (62–70 mm SVL) male fence lizards from a site where malaria has not been detected over the previous 12 years. This site appears identical in habitat structure and is adjacent to areas where malaria is common. None of the lizards in the sample ($N=24$) fell above color pattern class 4 and the mean proportion of black (37.3%) was lower than any adjacent malarious location (X for those sites=43.5%, $N=371$). As there is no reason to suspect that lizards at the site lacking malaria were younger, grew at a different rate, or experienced different hormonal states than lizards at other nearby locations, these results argue that malarial infection alters the color of fence lizards.

Reliability of color pattern as predictor of infection

Although infected lizards tended to be darker on their venters than noninfected animals, could this trend be used by female lizards to aid in choosing mates? To gain insight into this issue, we use logistic regression. The goal of this analysis is to assess the accuracy of male ventral color as an indicator of infection. Logistic regression, seldom used in ecological studies, uses independent variables of choice to classify individuals into discrete groups or classes (Afifi and Clark 1984). A preliminary multivariate categorical analysis of variables, led us to chose only proportion of ventral black as the variable to classify adult males (SVL= 60–75 mm) into either the category of infected or noninfected. That is, once the male lizards reach adult size, only a minimal amount of color variation can be accounted for by body size (entering body size into the logistic equation did not improve the efficiency of classification). The resulting logistic equation included a constant and the estimate of proportion of ventral black:

$$\Pr\{\text{male not being infected}\} = \frac{1}{1+e^{-[2.710+2.597\,(\%\,\text{black})]}}$$

A probability of being infected was obtained for all 633 adult males from the data by incorporating their proportion of ventral black into this equation. This probability was used to classify the individuals as infected or not infected by noting where the calculated probability fell relative to a cutoff point (Afifi & Clark 1984). If an individual's calculated probability of being noninfected was greater than or equal to this cutoff point, it was classified as noninfected. The cutoff point here is the percentage of noninfected adult males that a female would inappropriately reject as being infected. The cutoff point that would best minimize both kinds of errors of misclassification (infected as noninfected, and noninfected as infected) is 0.725, and produced a misclassification rate of 16.9% for both groups. Therefore, any female using proportion of ventral black of an adult male to judge its malarial infection status would be only marginally more efficient than selecting males at random (17.2%

of adult males were infected). To increase her efficiency in rejecting infected males (i.e. to be more conservative in mate choice), to a misclassification rate of 7.0%, the female would also reject 85% of noninfected males.

The study revealed only weak observational evidence that females actually chose males based on color pattern. Males with females seen nearby their perching location tended to have a higher proportion of ventral blue (Mann-Whitney test; $P < 0.05$; $N = 514$), but the median difference was only about 3%.

Discussion

When Darwin (1871) proposed that some exaggerated sexually dimorphic features act as charming signals between males and females during courtship, he did not attempt an explanation for the origin of female preference for a particular trait. Hamilton and Zuk (1982) suggested that the quality of showy sexually dimorphic traits may reflect the overall health of a male, determined in part by infection with parasites. Whatever the merits of the specific features of their hypothesis, Hamilton and Zuk's arguments rightfully called to attention the possible role of parasites in the social behavior of their hosts. Parasites can alter the outcome of male-male competition for mates in hosts (Freeland 1976; Schall and Dearing 1987), but whether females choose mates based on their parasite loads is an intriguing, but unexplored, possibility.

Here we documented that malarial infection alters the ventral colors of the western fence lizard, causing infected animals to deposit additional dark pigment on their ventral surface. Curiously, the likely physiological effect of the parasite (decreased testis size and presumed hormonal titers) suggests less black should be deposited over time, rather than more. Although we avoided injecting human bias of what a female lizard considers showy into the analysis, to our eye a male *Sceloporus occidentalis* venter accented with copious black is the most impressive color pattern. Noninfected male fence lizards add black pigment as they age; thus, infected males would appear older than they actually are, and perhaps would be more desirable to courting females. In the only other study similar to this one, Schall (1986) found a similar result in the Aruba island whiptail lizard, *Cnemidophorus arubensis*; bright blue males were more likely to be infected with a haemogregarine than dull blue or brown males. The biological significance of such findings ultimately depends on how a female lizard perceives phenotypic differences among males. Only manipulative experiments can resolve this perplexing issue. However, if additional studies on other systems frequently demonstrate that more showy males are more often infected with parasites, this might suggest a quite different evolutionary scenario from the one proposed by Hamilton and Zuk, perhaps one resembling the handicap principle of Zahavi (1975).

The logistic regression analysis revealed that ventral color provides a risky gauge of infection status. Thus, in order to improve their chances of finding a noninfected male compared to random mate choice, females would have to reject a large majority of noninfected courting males. We have observed female fence lizards interacting with a courting male over a period of hours before accepting or rejecting him. The mental processes of a female fence lizard cannot be similar to the high speed computation of logistic regression analysis on a large data set while she appraises a male's ventral colors. However, our study lasted only two years, and the ability of female fence lizards to choose the best available male has presumably been fine-tuned over at least a million generations by natural selection. Even if an assessment of male color gives females only minimal information that is useful in judging the quality of males, this would still be an important advantage and should be favored by natural selection.

Considering the risky nature of the information to be gleaned from ventral color, do female *S. occidentalis* actually use the differences in color between malarious and nonparasitized male lizards to choose a mate? Ventral color is but a single component of complex intersexual signals in *Sceloporus*; perhaps other kinds of signals are far more important during courtship rituals. For example, Carpenter (1962) described a complex of behaviors exhibited by a female during her rejection of courting males in *S. undulatus*, and Duvall (1979) demonstrated the importance of glandular secretions of male *S. occidentalis* in eliciting species-typical displays by both males and females. Thus, while choosing a mate, female *S. occidentalis* may observe the outcome of male-male interactions, the movement patterns of courting males, and male odors, as well as the male's color display. Malarial infection hinders male courtship behavior (Schall and Sarni 1987; Schall and Dearing 1988), and might well alter odorous glandular secretions produced by male fence lizards. The relative importance of each of these components of male-female interaction is unknown, but it appears possible that each is affected in turn by the malarial parasite.

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References

Afifi AA, Clark V (1984) Computer-Aided Multivariate Analysis. Wadsworth, Belmont, CA

Andrews R (1982) Patterns of growth in reptiles. In: Gans C, Pough H (eds) Biology of the Reptilia, vol 13. Academic Press, New York, pp 273–320

Ayala SC (1970) Lizard malaria in California; description of a strain of *Plasmodium mexicanum*, and biogeography of lizard malaria in western North America. J Parasitol 56:417–425

Borgia G (1986) Satin bowerbird parasites: a test of the bright male hypothesis. Behav Ecol Sociobiol 19:355–358

Bromwich CR, Schall JJ (1986) Infection dynamics of *Plasmodium mexicanum*, a malarial parasite of lizards. Ecology, 67:1227–1235

Carpenter CC (1962) Patterns of behavior in two Oklahoma lizards. Am Midl Nat 67:132–151

Carpenter CC, Ferguson B (1977) Variation and evolution of stereotyped behavior in reptiles. In: Gans C (ed) Biology of the Reptilia, Vol 7. Academic Press, New York, pp 335–554

Cooper WE, Burns N (1987) Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*. Anim Behav 35:526–532

Darwin CR (1871) The Decent of Man and Selection in Relation to Sex. Murray, London

Dawkins R (1986) The Blind Watchmaker. W.W. Norton, New York

Duvall D (1979) Western fence lizard, *Sceloporus occidentalis*, chemical signals. 1. Conspecific discriminations and release of a species-typical visual display. J Exp Zool 210:321–326

Fox D (1953) Animal Biochromes and Structural Colors. Cambridge University Press, Cambridge

Freeland WJ (1976) Pathogens and the evolution of primate sociality. Biotropica 8:12–24

Hamilton WD (1982) Pathogens as causes of genetic diversity in their host populations. In: Anderson RM, May RM (eds) Population Biology of Infectious Diseases. Springer, Berlin Heidelberg New York, pp 269–296

Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? Science 218:384–387

Kimball FA, Erpino M (1971) Hormonal control of pigmentary sexual dimorphism in *Sceloporus occidentalis*. Gen Comp Endocrinol 16:375–384

Kirkpatrick M (1986) Sexual selection and cycling parasites: a simulation study of Hamilton's hypothesis. J Theor Biol 119:263–271

Lewontin RC (1966) On the measurement of relative variability. System Zool 15:141–142

Noble GK (1934) Experimenting with the courtship of lizards. Nat Hist 34:3–15

Partridge L, Harvey P (1986) Contentious issues in sexual selection. Nature 323:580–581

Rau ME (1983) Establishment and maintenance of behavioural dominance in male mice infected with *Trichinella spiralis*. Parasitology 86:319–322

Read AF (1987) Comparative evidence supports the Hamilton and Zuk hypothesis on parasites and sexual selection. Nature 328:68–70

Ressel S (1988) Sexual color dimorphism, sexual selection, and malarial parasitism in the western fence lizard, *Sceloporus occidentalis*. Thesis, University of Vermont, p 59

Schall JJ (1983a) Lizard malaria: parasite-host ecology. In: Huey RB, Schoener TW, Pianka ER (eds) Lizard Ecology: Studies on a Model Organism. Cambridge: Harvard University Press, Cambridge, pp 84–100

Schall JJ (1983b) Lizard malaria: cost to vertebrate host's reproductive success. Parasitology 87:1–6

Schall JJ (1986) Prevalance and virulence of a haemogregarine parasite of the Aruban whiptail lizard, *Cnemidophorus arubensis*. J Herpetol 20:318–324

Schall JJ, Dearing MD (1987) Malarial parasitism and male competition for mates in the western fence lizard, *Sceloporus occidentalis*. Oecologia 73:389–392

Schall JJ, Sarni GA (1987) Malarial parasitism and the behavior of the lizard, *Sceloporus occidentalis*. Copeia 1987:84–93

Schall JJ, Bennett AF, Putnam RW (1982) Lizards infected with malaria: physiological and behavioral consequences. Science, 217, 1057–1059

Smith HM (1946) Handbook of Lizards. Cornell University Press, Ithaca

Stebbins RC (1966) A Field Guide to Western Reptiles and Amphibians. Houghton Mifflin, Boston

Zahavi A (1975) Mate selection – a selection for a handicap. J Theor Biol 53:205–214

Zar JH (1984) Biostatistical analysis, 2nd Edition. Prentice-Hall, Englewood Cliffs

Zuk M (1984) A charming resistance to parasites. Nat Hist 93:28–34

Zuk M (1987) The effects of gregarine parasites, body size, and time of day on spermatophore production and sexual selection in field crickets. Behav Ecol Sociobiol 21:65–72

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