

brief communications

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Parasitic infection

Hunger tolerance and *Leishmania* in sandflies

The sandfly *Phlebotomus papatasi* transmits *Leishmania major*, the agent of cutaneous leishmaniasis, in desert and savannah regions of the Old World¹, where seasonal stress of dehydration and heat reduces the quantity of sugar in plant leaves². Without essential sugar, only a few flies that feed on leaves can survive for long enough to deposit eggs and transmit *Leishmania*^{3,4}. Accordingly, selection for hunger tolerance may also select for pathogen susceptibility in flies. Here we provide evidence of a link between these advantageous and costly^{5,6} properties by testing the susceptibility of flies selected by sugar deprivation and of flies from irrigated and arid habitats.

The experimental flies were obtained from a colony maintained on sucrose solution that was established in 1983 using flies from a desert habitat in the Jordan Valley. Susceptibility to infection with *L. major* promastigotes, the flagellated, parasitic form that inhabits sandflies, was evaluated sporadically using a standard procedure (Table 1)⁷. The previously high infection rate (338 of 394 flies, 85.7%) has declined in recent years to only 27.0% (48 of 178).

Experimental native plants *Atriplex halimus* (Chenopodiaceae) and *Malva nicaeensis* (Malvaceae), and the domestic *Bougainvillea glabra* (Nyctaginaceae), were chosen in a dry area. Sugar levels^{4,8} in the leaves of these plants were 3.6–13.8 times lower than in those of irrigated conspecifics. Groups of female *P. papatasi* were each fed exclusively on branches of one of the

plants⁴ and other groups were starved until about half of the flies died (4–6 days). The survivors and control groups, one previously maintained for 6 days on 30% sucrose solution and another of day-old flies, were then infected⁷. Significantly more infections, including greater numbers of parasites, were found in flies selected for hunger tolerance compared with control flies (Table 1).

As the increased susceptibility to parasitic infection could have resulted from pre-infection hunger rather than from being selected, we tested day-old progeny of hunger-selected females. The frequency of infection in the progeny series was 64.3% (9 of 14), 79.7% (59 of 74) and 65.6% (21 of 32) (parents fed on *B. glabra* or *M. nicaeensis* or starved, respectively), whereas only 25.4% (45 of 177) of control flies were infected. This difference is statistically as significant as that of the parent generation (Table 1). Similar differences in susceptibility were also seen after progeny of hunger-selected and unselected flies were infected with amastigotes, the mammalian parasite form of *L. major* (results not shown). Assuming that hunger resistance and host competence for *L. major* improve with size, we measured and found no difference between the experimental and control fly groups (results not shown).

We also tested the correlation between the abundance of plant sugar in an oasis (Neot-Hakikar, Israel) and its scarcity at an arid site (in the Jordan Valley), and the susceptibility of the local *P. papatasi* populations to *L. major*. We first tested trapped flies for the presence of sugar in the gut^{3,8} — most of the oasis flies (69 of 72, 95.8%), but only one-third of the arid-site flies (60 of 186, 32.3%), were positive. We then infected first-generation progeny of these populations with *L. major* promastigotes⁷. Only 24.8% (25 of 101) of the oasis progeny retained parasites (mean 5 s.e. per fly, 2435.71 promastigotes) compared with 82.5% (156 of 189) of the progeny of arid-site flies (mean 5 s.e. per fly, 3,412.5686 promastigotes). We conclude that the oasis-adapted population is less susceptible to *L. major* than are similar flies from an

arid area.

The cost of parasitic infection seems to be sufficient to elicit natural selection against competent hosts⁹. As far as we know, our findings represent the first evidence that this may be compensated for by linkage to endurance against environmental stress. Seasonal and incidental stress are prevalent in the life of insects¹⁰, including those that are vectors of disease, and selection may often favour lines of parasites that are adapted to stress-resistant vectors.

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correction

Ancient homes for hard-up hermit crabs

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It has been drawn to my attention that I inadvertently omitted to cite previous work relevant to my results — hermit crabs have also been found to use fossils in Bermuda^{1,2}, although in a different context. For some *Coenobita clypeatus*, namely those in Bermuda, the only shells available of appropriate size are fossils, and therefore little choice or active selection is being made by the resource users. The hermit crab *Coenobita rugosus* (in Madagascar), like most others elsewhere, is not able to excavate buried shells. Haas¹, however, has observed *C. clypeatus* digging up and clearing debris from partially buried shells in Bermuda, which was also seen by Kellogg³ in laboratory conditions.

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Table 1 Susceptibility of starvation-tolerant sandflies to *Leishmania major*

Pre-infection diet	Flies dead	No. of flies	Flies infected	Parasites per fly	
	(%)		(%)	Mean	s.e.
<i>Atriplex halimus</i>	56.7	18	61.1*	4,075	434
<i>Malva nicaeensis</i>	57.6	16	75.0*	588	113
Water only	53.6	33	78.8*	920	243
30% sucrose	0	78	12.8	211	136
None	0	177	25.4†	531	248

Experimental flies survived for 4–6 days when fed on low-sugar plant branches or starved (water alone). One control group received 30% sucrose for 6 days before artificial infection⁷; another was 1 day old when infected. Infective meals consisted of 1.2 × 10⁶ mi⁻¹ promastigotes (MHOM/IL/90/LRC-L585 and IPAP/IL/84/LRC-L465) in rabbit blood. Blood-fed flies were dissected and their parasites counted after 6 days of maintenance on 30% sucrose solution and water.

*Proportional data arcsine-transformed and significantly different from a standard control ($P < 0.001$; Fisher's exact test)¹¹.

†Combined results of nine series.