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## STOMACH NEMATODES (*MASTOPHORUS MURIS*) IN RATS (*RATTUS RATTUS*) ARE ASSOCIATED WITH COCONUT (*COCOS NUCIFERA*) HABITAT AT PALMYRA ATOLL

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**ABSTRACT:** Black rats (*Rattus rattus*) and their stomach nematodes (*Mastophorus muris*) were historically introduced to islets at Palmyra Atoll in the central Pacific Line Islands. To investigate patterns of parasitism, we trapped rats and quantified nematodes on 13 islets of various sizes and habitat types. Most rats were parasitized (59%) with an average of 12 worms per infected rat. Islet size did not greatly influence parasite population biology. Nematodes also did not appear to affect rat condition (weight to skull length). The only strong and consistent factor associated with the mean abundance of nematodes in rats was habitat (dominant cover and locally dominant plant species). Thus, nematodes were much more abundant in rats from sites dominated by coconut trees (*Cocos nucifera*). Coconut trees may also be an introduced species at Palmyra Atoll.

In the course of studying terrestrial fauna on Palmyra Atoll (Fig. 1), we found nematodes were common in the stomachs of non-native European black rats (*Rattus rattus*). Palmyra Atoll is a small United States protectorate in the Line Islands, near the equator in the central Pacific. Its islets, most of which have rats, range in size from a few square m to about 1 km<sup>2</sup>, forming a chain around central lagoons (Fig. 1). Distances vary between the islets, but their circular distribution and proximity reduces variation in colonization potential for rats. Individual rats probably do not commute regularly from islet to islet. Of the 40+ rats that have been radio collared and followed on Cooper, Home, Whippoorwill, and Fern islets, none ever left the island from which they were tagged within the 2- to 4-wk study period (Howald et al., 2004; Buckelew et al., 2005). However, experimental rat removals have indicated that recolonization can occur within 9 mo (Buckelew et al., 2005). Therefore, islets probably do not differ in the genetic makeup of their rat populations, as has been demonstrated in similar situations elsewhere (Abdelkrim et al., 2009). There is no evidence that Polynesians inhabited Palmyra Atoll, and it lacks native terrestrial mammals. Black rats (*Rattus rattus*) could have been part of the fauna as early as the 1800s, as Streets (1877) reports that his collection of bird eggs from Palmyra was destroyed by rats on board his ship; subsequent publications in the early 1900s did not indicate they were present. Rats were certainly present after military occupation during World War II, and the Atoll continues to receive occasional visits from vessels.

The coconut palm (*Cocos nucifera*) presently comprises about half the forest canopy of Palmyra Atoll (Fig. 1, Table 1). *Cocos nucifera* were intentionally planted at Palmyra Atoll for copra production until at least 1957, and it is possible that Polynesian explorers introduced them as well; however, the status of *C. nucifera* as native or introduced is unclear (Streets, 1877; Rock,

1916, 1929; Dawson, 1959; Harries, 1978). Other major vegetation types at Palmyra Atoll include coastal strand forest, with native shrub-like *Scaevola sericea* and *Tournefortia argentea* trees, and the native *Pisonia grandis* forest (Herbst, 1992). Less extensive native vegetation types include *Pandanus fischerianus* monoculture, the fern *Phymatosaurus grossus*, and the endemic *Lepturus repens* var. *palmyrensis* grassland. Potentially introduced *Hibiscus tileaceus* and *Terminalia catappa* also occur in large patches.

Black rats on Palmyra Atoll regularly move between the tree canopy and ground (Howald et al., 2004). Black rats are omnivorous (Townsend et al., 2006). Studies elsewhere indicate they eat various items present at Palmyra Atoll, including green coconuts in the trees as well as fallen coconuts (Marshall, 1955), the leaves and fruits of native vegetation such as *Scaevola* and *Tournefortia*, and they can forage on intertidal crustaceans (Fall et al., 1971). We have observed rats at Palmyra Atoll eating various native and non-native fruits, seeds, and nuts as well as attacking the hermit crabs (e.g., *Coenobita perlatus*), fiddler crabs (*Uca tetragonon*), and land crabs (*Cardisoma* spp.) whose carapace pieces are common items at rat husking stations.

The nematode common in the stomach of rats at Palmyra Atoll is *Mastophorus muris* (Gemelin, 1790). Female worms are large (up to 70 mm); males lack copulatory bursae, have prominent caudal alae, and the right spicule is long and blunt whereas the left is shorter and pointed (Wertheim, 1962). Infection with stomach nematodes does not generally appear to compromise survival or reproduction (Spratt, 1990). The larvae of *M. muris* require insects as intermediate hosts (Kisielewska, 1970), although some stomach nematodes (*Physaloptera* sp.) of rats can use geckos as paratenic hosts (Goldberg and Bursley, 2002). Larval nematodes in intermediate and paratenic hosts are more likely to affect host fitness (Kuris, 2003). *Mastophorus muris* adults occur in rats and mice around the world and across latitudes (Vukicevic-Radic et al., 2007) and have been commonly reported from Pacific islands (Morrison, 1954; Marshall, 1955; Fall et al., 1971), though not previously from Palmyra Atoll. Prevalence varies, but can exceed 50% (e.g., Miller and Miller, 1995). For instance, 10 yr after nuclear testing on Eniwetok Atoll, prevalence on islets ranged from 0 to 70% (Fall et al., 1971). In New Zealand, infection in black rats can vary with season and sex, with worms being more abundant in male hosts and during their fall–winter (Charleston and Innes, 1980). For Polynesian rats in New Zealand, infection is higher in mature than in immature rats and in forested habitats relative to grassland habitats (Roberts et al., 1992).

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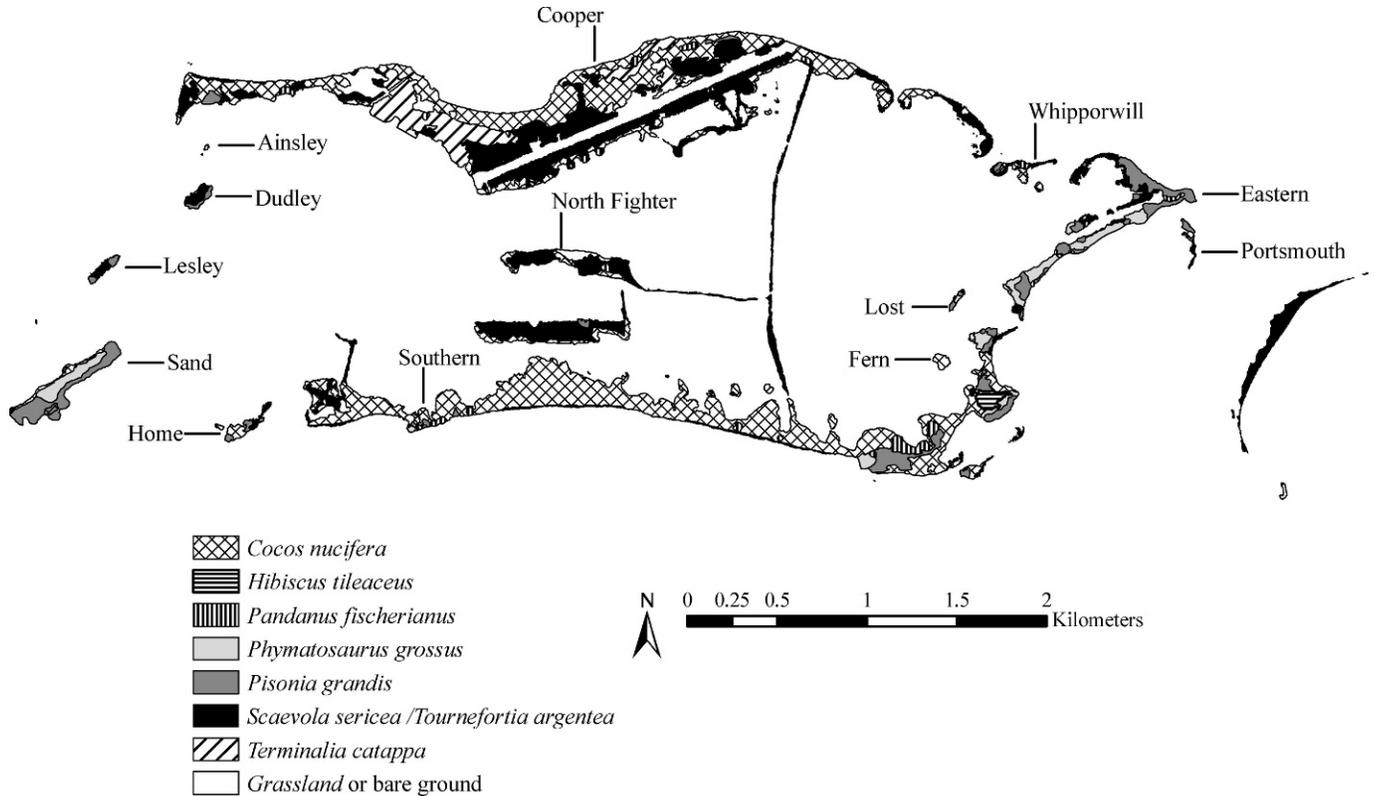


FIGURE 1. Map of Palmyra Atoll indicating approximate distribution of the dominant vegetation types (modified from Wegmann, 2005).

## MATERIALS AND METHODS

### Sampling

Rats were captured using Haguruma-brand live traps baited with fresh coconut coated with peanut butter. Before use, traps were seasoned with rancid cooking oil by quickly dipping the traps in a bucket of oil and then letting it drain off before being brought to the sampling site. Traps were spaced approximately 10 m apart, and most were set on inverted 19-L buckets to prevent traps from being tripped or destroyed by land crabs (*Coenobita* spp., *Birgus latro*, and *Cardisoma* spp.). On a few islets where coconut crabs repeatedly destroyed traps, we attempted to capture rats by nailing traps to trees (primarily *C. nucifera*) with entries facing downwards. Tree traps were also approximately 10 m apart. Traps were checked daily in the mornings and re-baited, and the condition of each trap, i.e., rats captured, trap closed, trap destroyed, was recorded. To evaluate associations between trap success and habitat type, we recorded the locally dominant plant species at the location of each trap (on most islets) and calculated the percent cover of the dominant vegetation types per islet using an available map (Wegmann, 2005).

We generally stopped trapping once we had obtained at least 10 rats per islet. Due to variation in trap success from islet to islet, variability occurred across sites in the number of traps set; in the number of nights traps were open; and the number of traps tripped with no captures, or destroyed, or damaged by crabs on a given night. To estimate trap success standardized by effort, we only used the average number of trap stations open for each site per night, i.e., discounting traps that were tripped or destroyed.

All rats ( $n = 165$ ) were killed within 3 hr after removal from a trap, then weighed, measured for total length, and sexed. Skull and hindfoot length were measured on a subset of rats, but these measurements showed little variation among individuals. Stomachs were excised and carefully opened with scissors. A squirt bottle and forceps were used to separate food in the stomach from worms and the worms from each other. Worms were set on a clean tray with a black background and counted (the count combined male, female, and immature worms). Nematodes were easily identified according to morphological characteristics (Wertheim, 1962). We note that for some

initial samples, the full array of variables, e.g., habitat and rat size, were not quantified. For this reason, sample size varied among the analyses. Although they had few fat stores, rats appeared to be in good health.

### Statistical analysis

For analyses with islet as the unit of replication, we considered nematode prevalence (proportion of rats infected) or mean abundance (worms per rat sampled) of nematodes as the dependent variable. Islet area, capture success, host sex ratio, habitat (% *C. nucifera* estimated by canopy cover), and season were independent factors in the analysis. For analyses with individual rats as the unit of replication, we considered the number of worms per rat as the dependent variable. Here, we used rat sex, habitat (local dominant plant species, *C. nucifera* vs. other), rat weight, rat length, and season as potential independent variables.

We used 3 analytical approaches as follows. We met normality assumptions for general linear models of mean worm abundance and prevalence among islets. For analyses of worms in individual rats, residuals of analyses were non-normally distributed and could not be adequately transformed; therefore, we used generalized linear models (with Poisson distribution and log-link function) to analyze worm abundance and a nominal logistic regression of the presence or absence of worms in each rat. We entered all first-order interaction into our initial models. Non-significant interactions and main effects were excluded if they did not otherwise contribute to the explanatory power of the model as assessed by Akaike information criterion. Islets where 0 rats or 1 rat were trapped (Sand and Ainsley Islets) were excluded from the analysis. We ran the analyses using JMP 8.0 (2009, SAS Institute Inc., Cary, North Carolina).

## RESULTS

Capture rate (rats/trap night, discounting tripped and damaged traps) was relatively low in locations locally dominated by *Pandanus* sp. (19%) and *Pisonia* sp. (16%) compared to *C. nucifera* (34%) and *Scaevola* sp.–*Tournefortia* sp. (36%). With respect to parasitism and

TABLE I. Data summarized by islet. The large trap effort on Portsmouth, Home, and Whippoorwill resulted from a parallel project on bait efficacy. Capture is a measure of trap success standardized by trap effort. The column % *Cocos* indicates percent of islet covered by *Cocos*, and the column *Rats* indicates the number of rats caught and dissected. If a subsample was dissected, this is shown in parentheses.

Islet	Trap nights	Area (ha)	% <i>Cocos</i>	Capture	Rats	Worms/rat
Ainsley	7	0.1	100	0	0	0.00
Cooper	48	110.8	30	28	19	7.74
Dudley	8	1.2	0	0	0	0.00
Eastern	51	12.7	1	25	17	2.12
Fern	17	0.5	100	37	10	16.60
Home	421	7.1	43	5	23 (20)	11.25
Leslie	24	1.7	0	27	9	0.11
Lost	16	1	0	36	9	0.00
North Fighter	33	0.3	8	41	24	0.88
Portsmouth	193	61.4	9	14	31 (18)	0.06
Sand	92	0.8	13	1	1	0.00
Southern	75	8.2	75	18	17	24.35
Whippoorwill	443	1.9	38	17	92 (21)	7.19

habitat, a least-square means assessment of differences among local habitats suggested that none of the non-*C. nucifera*-dominated habitat classifications differed significantly in the mean abundance of worms per rat. For this reason, we pooled non-*C. nucifera* habitat together, resulting in a greatly simplified assessment of the dominant plant species near a trap, i.e., *C. nucifera* versus non-*C. nucifera*.

The overall prevalence of stomach nematodes at Palmyra Atoll was 59% (n = 165). The mean abundance of worms per rat was 7.0 (SE = 0.9) and the mean intensity (worms per infected rat) was 11.9 (SE = 1.2). Although a mass of worms can occupy more than half the volume of the stomach of a rat, no lesions were associated with parasitism, as it appeared the worms directly consume the food in the stomach. We saw no ectoparasites and only a few unidentified tapeworms, suggesting the parasite community of black rats on Palmyra is depauperate compared to mainland populations.

A nominal logistic regression of whether a rat was parasitized or not found a significant effect of islet ( $\chi^2 = 129$ , df = 11,  $P < 0.0001$ ), justifying a geographical approach. A generalized linear model of worm abundance in rats showed an even stronger result ( $\chi^2 = 1370$ , df = 11,  $P < 0.0001$ ). We then conducted an analysis at the islet level (Tables I, II).

The only significant predictor of worm prevalence on a given islet was the *C. nucifera* canopy cover (Table II). The portion of the islet comprised of *C. nucifera* (% *C. nucifera*) was positively associated with the average abundance of worms in the rat population (Fig. 2). This analysis also found a significant interaction between season and percent *C. nucifera* (Table III). Rat sex ratio was a near-significant effect in this among-islet model of mean worm abundance (suggesting more worms per rat on islets where we caught a higher proportion of female rats).

We used a generalized linear model to evaluate whether gender, season, and local *C. nucifera* dominance affected parasitism at the level of individual rats. We removed non-significant variables such as host weight and length from the analysis. The dominance of *C. nucifera* at the trap site explained most of the variation in parasitism (Fig. 3). At trap sites dominated by *C. nucifera*, there

TABLE II. Among-islet general linear model of the prevalence of worms in rats.  $R$ -square = 0.69,  $F$ -ratio<sub>8,9</sub> = 17.8.

Main effect	Estimate	SE	$t$ -Ratio	$P$
Intercept	0.2435365	0.110163	2.21	0.0580
% <i>C. nucifera</i>	1.0409983	0.246553	4.22	0.0029

was a minor effect of host sex and season, such that male rats were more heavily infected than were female rats, and more worms occurred in summer than in fall (Table IV). A nominal logistic regression of the presence or absence of worms in a rat indicated that local *C. nucifera* dominance was the sole significant effect ( $\chi^2 = 39.4$ , df = 1,  $P < 0.0001$ ).

We explored variables associated with rat condition, expressed as body weight:skull length, for non-pregnant rats. Male rats were heavier for the same skull size, but there was no residual effect of worm abundance or habitat (plant species) on condition.

### DISCUSSION

The *C. nucifera* habitat (% cover per islet, or dominant plant species near trap) was the only consistent factor associated with the abundance of rat nematodes. *Mastophorus muris* requires an insect intermediate host, and *C. nucifera* might provide habitat for appropriate insect hosts, or suitable microclimate, for free-living stages of the nematode. Insects and rats might feed on the same coconut, opening opportunities for transmission. *Cocos nucifera* can occur in mixed vegetation type, so a categorical assessment of habitat was not always certain. For instance, cockroach carapace parts are frequently found at rat husking stations, and cockroaches are frequently found in palm crowns where we have observed rats also spend substantial time. For this reason, some rats caught at sites dominated by non-*C. nucifera* vegetation could have been infected while using nearby *C. nucifera* habitat. We do not know what factors associated with *C. nucifera* habitat drive

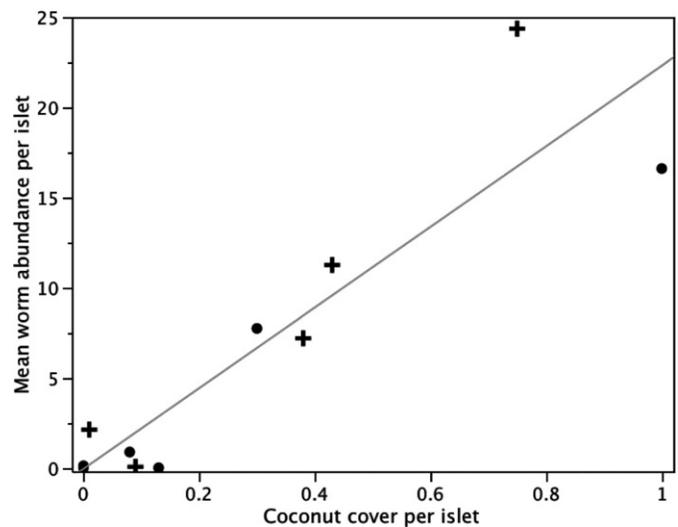


FIGURE 2. Mean abundance of the stomach nematode *Mastophorus muris* in the rats on an islet as a function of the percent of an islet consisting of *Cocos nucifera* habitat. Each point is an islet on Palmyra Atoll. Circles represent fall samples and pluses represent summer samples.

TABLE III. Among-islet general linear model of the mean abundance of worms per rat.  $R$ -square = 0.97,  $F$ -ratio<sub>4,6</sub> = 46.1.

Main effect	Estimate	SE	$t$ -Ratio	$P$
Intercept	-2.465547	1.081449	-2.28	0.0628
% <i>Cocos</i>	27.187394	2.267724	11.99	<0.0001
Season [fall]	-0.633804	0.650031	-0.98	0.3672
% Female	0.1567708	0.065047	2.41	0.0526
(% <i>C. nucifera</i> - 0.28818)*				
Season [ $F$ ]	-9.983403	2.268543	-4.40	0.0046

the association. A spurious correlation with rat density is a possibility, but density does not seem likely to explain all the variation in parasitism. Habitat is known to affect parasite distributions. For instance, habitat (grassland, forest, human structure) was the main explanatory variable for a community of helminths, including *M. muris*, in an island population of *Rattus exulans* in New Zealand (Roberts et al., 1992). Human alteration of habitat, such as the planting of coconut plantations at Palmyra Atoll, can also affect parasite distribution. For instance, rats on Martinique and Guadeloupe Islands only have fleas in areas with humans where domestic animals support flea populations (Pascal et al., 2004). Habitat type often varies with geography and, if it is not explicitly considered, could easily confound or mask interpretations of biogeographical studies of parasitism (or species distributions in general).

Finally, black rats, stomach nematodes, and perhaps *C. nucifera* are introduced species on Palmyra Atoll. Their relationships might not reflect coevolved patterns seen in native host-parasite assemblages. Future attempts to eradicate rats, and potentially *C. nucifera*, from Palmyra might eliminate nematodes. In a parallel study, we noted undescribed larval nematodes encysted in the stomach linings of native geckos and suspect the geckos could be serving as paratenic hosts for *M. muris*. Insects

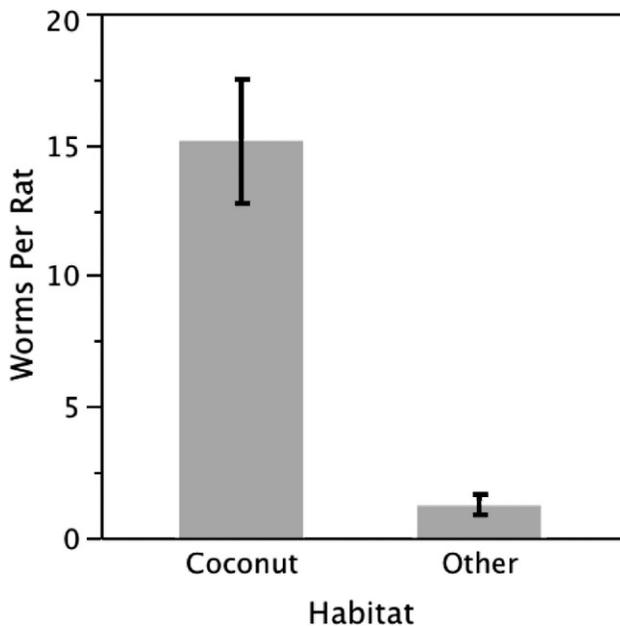


FIGURE 3. Mean abundance of worms in each rat with respect to whether the rat was trapped near coconut trees or near another vegetation type. Bars = SE.

TABLE IV. Generalized linear model of worm counts in individual rats. Df = 5,  $\chi^2$  = 909.0,  $P$  = <0.0001,  $R^2$ L = 0.6, overdispersion = 8.5 ( $P$  < 0.0001).

Main effect	df	$\chi^2$	$P$
Sex	1	0.25	0.618
Season	1	8.04	0.0046
Local <i>C. nucifera</i> dominance	1	76.4	<0.0001
Sex * season	1	0.58	0.4450
Sex * local <i>C. nucifera</i> dominance	1	0.96	0.326

that are intermediate hosts, and perhaps geckos that are potentially paratenic hosts, may indirectly benefit from rat removal.

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