RESPIRATORY METABOLISM OF THE ANTARCTIC TICK, IXODES URIAE

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Abstract—1. The respiratory metabolism of the Antarctic tick, Ixodes uriae White (Acari: Ixodidae) was investigated at Palmer Station, Anvers Island (64°46'S, 64°03'W) during the austral summer, January 1981.

2. At 20°C the metabolic rate of females was 303 nl/mg live w/hr, approximately three times that of males and engorged nymphs.

3. Laboratory acclimation of females, males and nymphs to 0°C and 10°C for 2 wk had no effect on respiration rates, suggesting that I. uriae lacks the ability for compensatory acclimation of respiration rate.

4. Metabolic rates of temperature ixodids are similar to those for females of I. uriae, which suggests that metabolic cold adaptation is absent in this species.

INTRODUCTION

The ixodid tick, Ixodes uriae White, is a widely distributed circumpolar species in both the northern and southern hemispheres (Wilson, 1964). This tick has been associated with or found to parasitize 48 seabird hosts (Wilson, 1970). I. uriae is the predominant tick on sub-Antarctic islands.

I. uriae is a 3-host tick, larvae and nymphs fall to the ground and molt after each engorgement (Murray & Vestjens, 1967; Balashov, 1972). This species requires 4-5 yr to complete its life cycle (Flint & Kostyrko, 1967; Eveleigh & Threlfall, 1974). Typically, eggs, engorged larvae and engorged nymphs overwinter; however, some individuals feed and molt in the same summer before overwintering (Eveleigh & Threlfall, 1974). This species appears to opportunistic with regard to the number of blood meals taken per year. On Macquarie Island where Royal penguins are in residence for 6 months of the year, I. uriae may complete its life cycle in 2 yr (Murray & Vestjens, 1967).

Metabolic cold adaptation refers to an elevation of the basal or standard metabolism in ectotherms. Originally, this concept arose from studies of polar marine ectotherms (Scholander et al., 1953), however, recently it has been extended to include Antarctic terrestrial mites (Block & Young, 1978). The respiratory metabolism of polar cryostigmatid and mesostigmatid mites was elevated 2-4 times over that of temperate species (Block & Young, 1978). On the Antarctic Peninsula I. uriae is the largest species of the Acari, and is free-living for more than 11 months each year. Therefore, it is of interest to determine whether I. uriae also exhibits metabolic cold adaptation.

This study provides data on the standard respiratory metabolism of females, males and nymphs of I. uriae. These results are interpreted with respect to the significance that metabolic cold adaptation and compensatory acclimation of respiration rate may play in the respiratory physiology of this species.

METHODS AND MATERIALS

During January 1981, specimens of I. uriae were collected on small islands adjacent to Palmer Station, Anvers Island, Antarctica (64°46'S, 64°03'W). All life stages (egg, larva, nymph and adult) were found beneath rocks in aggregations ranging in size from a few individuals to more than 1000. Invariably these aggregations were located in well-drained sites within 5 m of Adelie penguin rookeries. There was approximately one aggregation per 40 m of rookery perimeter.

During the first week of January, engorged adult females frequently were collected in capulo. At this time none were observed laying eggs. Engorged nymphs could be divided into two classes based on motility. Near the center of the aggregations nymphs were immobile and light grey in color as compared to active nymphs on the edges of the colony. During January the size of the aggregations gradually increased as new nymphs arrived, lost mobility and became a part of the aggregation. Females began ovipositing in late January.

Oxygen consumption was measured with constant pressure microrespirometers similar to those described by Engelmann (1963) and Conradi-Larsen (1974). Respirometers were prepared by sealing 10, 20 or 50 μl micropipette tips into the tip of a 1 or 3 cc plastic syringe tip. Respiratory metabolism of females and sometimes nymphs (see Fig. 5) were measured singly, while determinations for males and nymphs were based on 2-3 individuals per respirometer. The plunger was weighted with washers, inserted into the syringe barrel and set upright in a bath (±0.02°C) with the micropipette extending above the surface. A 10% KOH solution was introduced into the microvessel to serve as both an absorbent for carbon dioxide and a manometric indicating fluid. For each determination a respirometer without ticks served as a thermobarometer. One hour was allowed for equilibration with oxygen consumption measured for a following 2 hr.

Each respiration rate (± SEM) in Figs 1-3 is based on 6-8 respirometers per treatment. Water content is...
Fig. 1. Effect of temperature on metabolic rate of engorged females, males and engorged immobile nymphs of *I. ricinus* (mean ± SEM). See Table 1 for regression equations.

Results

**Metabolic rate and temperature**

The respiration-temperature (R-T) curve of engorged females increased steadily from 0 to 30°C reaching a maximum of 418 ± 15 nL/mg live wt/hr (Fig. 1). For immobile engorged nymphs the respiration rate reached a peak at 15°C (90 ± 7 nL/mg live wt/hr), while males, non-feeding as adults, reached a maximum of 110 ± 6 nL/mg live wt/hr at 20°C before falling to lower levels at 25°C (Fig. 1). At 20°C the metabolic rate of females was approximately three times greater than corresponding values for males and engorged nymphs. Linear regression equations of metabolic rate vs temperature for each life stage are summarized in Table 1.

**Compensatory acclimation of metabolic rate**

Prosser (1975) defines compensatory acclimation as changes in the rate of metabolic processes which occur after long-term exposure to altered environmental conditions. One method of assessing an organism's capacity for compensatory acclimation of metabolic rate is to maintain two groups of animals at differing temperatures for a period of time, usually on the order of days or weeks, and then compare respiration rates (Precht et al., 1973). Females, males and nymphs were laboratory acclimated at 0 and 10°C for 2 wk. Figures 2 and 3 summarize the data of these experiments. The temperature of laboratory acclimation produced no differential effect on metabolic rate within any life stage. Precht (1958) classified this lack of compensatory response Type 4 (no acclimation).

An examination of Figures 1 and 2 reveals that the break in the R-T curve for females in Fig. 1 occurs at 30°C vs 15°C in Fig. 2. This difference might be a result of laboratory acclimation, however, it is likely a result of metabolic changes associated with oviposition. The metabolic rate of females in Fig. 1 was measured on 2 January 1981. At this time no females were observed ovipositing in the field. The females of Fig. 2 were held in the laboratory from 8 January until assayed on 22 January. By the third week of January females were commonly observed ovipositing in the field. Changes in respiratory metabolism have been commonly associated with the onset of oviposition in ixodid ticks (Belozero, 1966; Sweatman & Koussa, 1968; Aboul-Nasr & Bassal, 1971).

**Metabolic rate and live weight**

The respiration rate of individual engorged females and immobile engorged nymphs was measured in order to determine the relationship between respiratory metabolism and live weight. Respiration rates for

<table>
<thead>
<tr>
<th>Stage</th>
<th>Individual weight (mg)</th>
<th>Temperature range (°C)</th>
<th>Regression line ( y = b + mx )</th>
<th>Correlation coefficient ( r )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>113 ± 3.6</td>
<td>0-30</td>
<td>13.63 ± 4.55 ( P &lt; 0.001 )</td>
<td>+0.99</td>
</tr>
<tr>
<td>Male</td>
<td>74 ± 3.0</td>
<td>0-20</td>
<td>4.16 ± 0.64 ( P &lt; 0.01 )</td>
<td>+0.93</td>
</tr>
<tr>
<td>Nymph</td>
<td>11.1 ± 0.6</td>
<td>0-20</td>
<td>4.40 ± 0.47 ( P &lt; 0.001 )</td>
<td>+0.96</td>
</tr>
</tbody>
</table>
Respiratory metabolism of an Antarctic tick

Fig. 3. Effect of temperature on metabolic rate of males and engorged immobile nymphs of *I. uriae* laboratory acclimated at 0 or 10°C for 14 days.

females were variable with no significant correlation between live weight and respiratory metabolism (Fig. 4). Similar results were obtained for nymphs (Fig. 5). The coefficient of determination (r²) accounted for only 16%, of the variability in metabolic rate in relation to live weight.

**DISCUSSION**

**Metabolic rate vs temperature**

The most striking feature of the R-T curve for females in Fig. 1 is the fact that it is linear over a 30 range, breaking downward at 30°C. The downward break in the R-T curve is commonly interpreted to represent heat stress to the organism and may be taken as one measure of the upper lethal temperature limit (Precht et al., 1973; Keister & Buck, 1974). The supercooling point represents the temperature at which spontaneous freezing occurs, and for freezing intolerant organisms it represents the lower lethal temperature limit. Females of *I. uriae* are freezing intolerant and supercool to −13.8 ± 1.1°C (Lee & Baust, unpublished data). The overall viable temperature range for this species extends from the supercooling point to at least the break point in the R-T curve. The skin temperature of Adelie penguins ranges between 36 and 39°C (D. Murrish, personal communication). Thus, the upper limit of the naturally experienced temperature range extends to near 40°C, at least during that portion of the year when they are on the host.

In other Antarctic terrestrial arthropods the tolerated temperature range is considerably less. Larvae of *Belgica antarctica* are freezing tolerant to −15°C (Baust & Edwards, 1979), but die after only two days exposure to +20°C (Baust & Lee, unpublished data). The break point in the R-T curve for an arctic midge larvae occurs at 20°C (Scholander et al., 1953). Heat stress in two species of Antarctic collembola is evident after short-term exposure to 20°C (Janetschek, 1967; Burn, 1981). Fitzsimons (1971) reports that the temperature range for normal activity of *Stereotusus mollis* is 0–23°C. The Antarctic collembolan, *Isotoma klarstadi*, survives a maximum of 6 hr at 22°C (Strong et al., 1970). The acclimation of *Alaskozetes antarcticus* to 15°C stressed this mite species causing a break in the R-T curve at 10°C (Young, 1979a). The wide range of temperature tolerance in *I. uriae* is the result of an extension of the upper limit associated with the ectoparasitic portion of its life cycle.

**Compensatory acclimation of metabolic rate**

All available data indicate that the capacity for compensatory acclimation of respiration rate is lacking in Antarctic terrestrial arthropods. Young (1979b) concluded that compensatory acclimation of respiration is absent in the mite, *Alaskozetes antarcticus*. Similar results were obtained for the larval chironomid, *Belgica antarctica* (Lee & Baust, unpublished data).

Fig. 4. Relationship between live weight of engorged females of *I. uriae* and respiration rate.

Fig. 5. Relationship between live weight of engorged immobile nymphs of *I. uriae* and respiration rate.
data). In the present study, laboratory acclimation of females, males and engorged nymphs to 0 and 10 C revealed no compensatory changes in respiratory metabolism (Figs 2 and 3).

Ectothermic animals from constant environments generally lack the capacity for compensatory acclimation, while animals from variable habitats may possess considerable acclimatory potential (Somero et al. 1968; Hazel & Prosser, 1974; Feder, 1978). In the Palmer Station area, the substrate temperature at 1-cm depth may be markedly constant, remaining between 0 and −2 C for over 300 days of the year (Baust, 1980; Baust & Lee, 1981). The aggregations of *I. uriae* were commonly located beneath large, flat rocks, 5 or more cm thick. Some individuals were recovered in rock crevices as much as 20 cm beneath the underside of the covering rock. Thus, the subarctic microhabitat of *I. uriae* during most of the year affords a substantial buffer against environmental temperatures. The observed lack of compensatory acclimation of respiratory metabolism in this species is consistent with its stenothermic microhabitat and suggests a lack of seasonal changes in its respiratory metabolism.

**Metabolic cold adaptation**

The hypothesis of metabolic cold adaptation in polar aquatic ectotherms has been the subject of considerable debate during the last 30 yr. Scholander et al. (1953) reported that the basal metabolic rates of arctic fish, molluscs and crustaceans were elevated in comparison with tropical species. Clarke (1980) cites a number of subsequent studies whose data support this hypothesis. Holeton (1974) challenged this view by suggesting that the previous reports of elevated metabolism in polar fish were an artefact of the experimental technique and did not accurately measure basal metabolism. Recent review articles by Everson (1977) and Clarke (1980) have concluded that polar marine fish and invertebrates lack metabolic cold adaptation. Rather, polar ectotherms are characterized by slow growth rates, a reduction in annual reproductive output and low basal metabolic rates.

Block & Young (1978) have recently extended the hypothesis of metabolic cold adaptation to include Antarctic terrestrial arthropods. They found that the respiratory metabolism of Antarctic cryptostigmatid and mesostigmatid mites is elevated 2-4 times relative to that of temperate species. However, the arctic terrestrial invertebrates studied by Scholander et al. (1953) revealed no elevation of metabolic rate. Likewise, the respiratory metabolism of *Belgica antarctica* was similar to those of temperate species (Lee & Baust, unpublished data).

In order to evaluate the possible significance that metabolic cold adaptation may play in the respiratory physiology of *I. uriae* we examined previous studies on ixodid ticks from temperate regions. Unfortunately little work has been done in this area with the exception of investigations on engorged, gravid females. The most comparable data from these studies are summarized together with that obtained for *I. uriae* in Table 2. Rates were converted to nL/mg live wt/hr to facilitate interspecific comparison. Respiration rates for *I. uriae* are similar to those reported from temper-
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