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Adaptations of insects at high altitudes of Chimborazo, Ecuador

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Abstract. Carabid beetles (Coleoptera: Carabidae) were collected from an altitudinal gradient at Chimborazo, Ecuador, in March 1994. *Bembidion andinum* Bates was the dominant species at 4,800 m, *Pelmatellus andium* Bates at 4,500 m and *Agraphoderus integer* Bates at 4,250 m. During daytime, the beetles were sheltering under rocks, but were caught in pitfall traps on open ground during the night. At 0.5 cm depth, soil temperatures from –4 to 41°C were recorded at 4,800 m and from –3 to 52°C at 4,500 m, but fluctuations were greatly buffered at 2 and 5 cm depths. All three species had mean supercooling points of –5 to –6°C. Rates of water loss at 18°C and 5% RH were 4.4, 1.2 and 1.1% of fresh weight per hour, respectively. Apparently, the carabid beetles are poorly adapted to low temperatures and aridity. To survive the harsh climatic conditions at high altitudes on Chimborazo, they depend on sheltered microhabitats under rocks or below vegetation. Surface activity is restricted to certain periods during the night when conditions are more favorable. In comparison, lower rates of water loss were found in an unidentified species of Dermaptera and a curculionid beetle.

INTRODUCTION

At high altitudes in equatorial mountains, high daytime temperatures alternate with freezing night temperatures (Troll, 1968; Azocar & Monasterio, 1980; Sarmiento, 1986). Diel cycles are more pronounced during the dry season, and minimum temperatures decrease with increasing altitude. Due to the thin and clear air at high altitudes, insolation is strong during daytime. Similarly, radiation during the night is greater than in the lowlands, resulting in ground surface temperatures several degrees centigrade below freezing.

Humidity is another abiotic factor of great ecological importance. In general, relative humidity decreases with increasing altitude (Franz, 1979; Mani & Giddings, 1980), although there are great local variations. An arid atmosphere is more typical of large continental mountain systems than of isolated peaks and coastal mountains. The reduced water vapour tension of the air is a result of the reduced atmospheric pressure at high altitudes, and the vapour pressure is further lowered with decreasing temperatures. As a result, the terrestrial environment becomes increasingly arid with increasing elevation.

To insects and other terrestrial arthropods, the fluctuating climatic conditions at high altitudes present special problems of adaptation (Mani, 1968; Sømme, 1989). To survive in exposed habitats, many species have to tolerate freezing temperatures during the night and be able to avoid desiccation during daytime. Unlike species from temperate areas, tropical alpine insects have no time for physiological preparation before the onset of low temperatures. Actively feeding animals are particularly vulnerable to freezing due to the presence of ice nucleating agents in their guts. High ground surface temperatures and low relative humidities of the air during daytime represent other critical factors for many species.

As pointed out by Sømme (1989), most tropical alpine terrestrial arthropods do not possess a sufficient degree of cold hardiness to survive exposure to the ambient night temperatures. In many species, the degree of resistance to desiccation is also limited. Another strategy, or manner of adaptation found in such species, is to escape from the temperature extremes by hiding under rocks or seeking sheltered microhabitats within the leaves of plants. In plants with dense layers of leaves, such as *Espeletia* spp. (Asteraceae) of the Andean paramos, ambient temperature fluctuations are greatly buffered (Sømme, 1986). Temperatures within the senescent leaves remain constantly low, restricting the activity and rate of development of insects and other terrestrial arthropods. Other tropical alpine species are active in the open during favourable periods and seek protected microhabitats only to avoid extreme cold and drought.

At Mount Kenya in Africa, Sømme & Zachariassen (1981) recorded both freeze tolerant and freeze avoiding insect species. Above 4,000 m, however, most species apparently avoided exposure to low night temperatures by seeking shelter under rocks and in the vegetation. Behavioural avoidance of extreme temperature conditions was also observed by Edwards (1986) and Sømme (1986) in the Venezuelan Andes. According to Sømme (1986), the acridid grasshopper *Meridacris subaptera* is freeze tolerant and able to survive ground surface temperatures at 4,200 m. Duman & Montgomery (1991) found that *Agrotis* sp. (Noctuidae) larvae at 4,200 m from the summit of Mauna Kea, Hawaii were freeze tolerant, while the lygaeid bug *Nysius wekiuicola* and a wolf spider (*Lycosa* sp.) depended on supercooling for low temperature survival.

The present study was conducted to obtain more information on the adaptations of tropical alpine insects. Due to its high altitude (6,200 m) and position close to the equator, the volcanic peak of Chimborazo in Ecuador was chosen as the site of the present studies. The insect fauna of the mountain is partly known since the collections by E. Whymper (Bates, 1891). Considerable diel temperature fluctuations are expected in this region, in which the frostline on the average is around 3,000 m (Troll, 1968). Although rain and clouds at high altitudes occur all year round, insects in the open highlands may be exposed to desiccation during periods of strong insolation.

MATERIAL AND METHODS

Sites of collection

During a visit to Chimborazo in March 1994, live beetles were collected underneath rocks, particularly below those that were partly covered by vegetation. In addition, several specimens were caught in pitfall traps. The following sites at four different altitudes were chosen for sampling on the SW side of Chimborazo (approximately 01°27′S, 78°53′W).

4,800 m. Open, rocky habitat on a slope with scattered moss and phanerogamous polster plants approximately 200 m below the border of permanent snow and ice. The brown volcanic soil had an irregular surface structure, apparently formed from frequent freezing and thawing events.

4,700 m. Plain area covered with rocks and gravel and with sparse and scattered polster plants.

4,500 m. Rocky field between two moraines; scattered vegetation of which some plants were taller and more bush-like compared with those at higher altitudes. The surface of the ground was covered by dry sand and gravel, but the soil was moist below 2–3 cm depth.

4,250 m. Plain habitat covered by dry sand and gravel; scattered low vegetation of polster plants with open areas in between. High densities of beetles and several specimens of Dermaptera were found in vegetation around a pile of rocks.

Hourly recordings of microclimate temperatures were performed with two Grant Squirrel 1,200 data loggers for 6 and 4 days, respectively, at 4,800 and 4,500 m. At both sites, probes were placed in the soil at 0.5, 2 and 5 cm depths below the surface, close to the vegetation. One probe at each site, shaded by rocks, was used to measure air temperatures approximately 15 cm above the ground.

In order to record surface activity of insects outside the vegetation, pitfall traps, made from plastic cups 9.5 cm high and 6.5 cm in diameter, were placed in the soil in between the scattered vegetation. The traps were shaded by small flat rocks raised above the ground by pebbles. To keep the trapped beetles alive, no preservative liquid was used in the traps.

For laboratory experiments, live beetles were brought to the University of Oslo. During transportation they were kept on moist filter paper in perforated plastic vials inside a Thermos flask cooled with ice.

Identification of carabid beetles

For the most part, Andean insects remain poorly known and largely unrevised. Identification is often difficult. Fortunately, most species at high altitude are endemic to a single mountain range, making identification a little easier in unrevised groups where species have been described stochastically. Thanks to the pioneer collections of E. Whymper, many of the high altitude insects of Chimborazo were described early on, including many Carabidae described by Bates (1891). Thus many of the species can be identified.

This study was based primarily on three species of carabid beetles. A small species (3–4 mm) from 4,700–4,800 m belongs to the genus *Bembidion* (Tribe Bembidiini). Bates (1891) described two species from Chimborazo. The specimens match most closely the description of *Bembidion andinum* Bates, taken at similar high altitudes, and they are almost certainly this species. The brief description of *Bembidion fulvocinctum* Bates, described from lower altitudes on Chimborazo and from several other mountains, does not allow it to be excluded entirely without recourse to the type specimens. A medium-sized species (7–8 mm) from 4,500 m and 4,250 m is certainly *Pelmatellus andium* Bates (Tribe Harpalini). A larger species (8–11 mm) from 4,250 m is undoubtedly *Agraphoderus integer* (Bates) (Tribe Pterostichini), at least for the most part. Straneo (1991) described the similar *Agraphoderus liodes planoculis* from the same area. Examination of the holotype and paratype of the latter species and specimens determined by Straneo of the former species suggests they are all a single variable species.

Cold tolerance

Supercooling points of the beetles were measured with copper-constantan thermocouples at a cooling rate of approximately 1°C min^{-1} (e.g. Sømme, 1986). The beetles were removed from the cooling apparatus after the freezing exotherm at a temperature corresponding to the supercooling point. Their survival was evaluated after 30 min. Beetles unable to walk were considered as moribond, and only those showing normal movements as alive.

Rates of water loss

Rates of water loss were measured at 18°C and 5% relative humidity above activated silica gel. The specimens were kept in separate open vials inside a 3 litre desiccation chamber until they died after various time intervals. Body weights were determined on a Sauter RE1614 balance (± 0.05 mg) before and at intervals during the experimental period. Total water content was found by drying the insects to constant weight at 70°C at the end of the experiment.

RESULTS AND DISCUSSION

Microclimate

As expected, considerable diel temperature fluctuations were recorded at 4,800 and 4,500 m. Maximum and minimum temperatures, as well as the mean, for the periods of 6 and 4 days, respectively, are presented in Table 1. Greatest fluctuations were found at 0.5 cm, while temperatures at 2 and 5 cm below the surface were more buffered. Frost usually occurred in the early hours of the morning. Lowest temperatures occurred on clear nights while radiation was reduced by cloud cover. Similarly, highest temperatures were recorded on clear days when insolation was most intense. Mean temperatures during the recording periods were lower at 4,800 m compared with 4,500 m, and higher at the surface of the soil compared with 2 and 5 cm depth (Table 1).

TABLE 1. Maximum, minimum and mean temperatures (°C) in the soil during 6 days at 4,800 m and 4 days at 4,500 m on Chimborazo, Ecuador during 22–28 March 1994.

	4,800 m			4,500 m		
Site of probe	min	max	mean	min	max	mean
Soil 0.5 cm	–0.4	40.8	5.4	–2.7	52.2	10.4
Soil 2 cm	0	15.6	4.2	2.4	17.6	8.9
Soil 5 cm	0.4	12.0	3.9	1.1	18.2	7.5
Air[1]	–2.8	13.6	2.5	–2.3	21.7	5.3

[1] Between rocks, 15 cm above ground.

Since previous microclimate temperature recordings from this location are not available, it is not known if the present data are representative for these altitudes. During the present study, the weather was relatively cloudy. Longer periods of clear skies, resulting in still lower temperatures during the night, will probably occur at other times of the year. In comparison, Sømme & Zachariassen (1981) reported air temperatures of –7°C almost every night at 4,200 m at Mt. Kenya in Africa.

Cold hardiness

Mean supercooling points (± SD) of *Bembidion andinum*, *Pelmatellus andium* and *Agraphoderus integer* were –5.6 ± 2.3 (n = 10), –6.2 ± 2.0 (n = 12) and –5.3 ± 2.3 (n = 8), respectively. Most beetles were killed by freezing, although a few specimens survived when freezing took place at –3 and –4°C. High supercooling points are characteristic of summer-acclimated insects (Zachariassen, 1985). Based on the present results, the carabid beetles from Chimborazo cannot be considered as particularly cold hardy.

Rates of water loss

Rates of water loss in *P. andium* and *A. integer* were slightly higher than 1% $fw.h^{-1}$ (Table 2). At this rate, the beetles only survived for 24–48 h at 18°C and 5% RH. In *B. andinum*, the rate of water loss was four times higher, and these beetles were killed within 4–6 h under the present experimental conditions.

The rates of water loss correspond very closely to those of other carabid beetles from high altitudes (Sømme, 1995), but are generally higher than those of carabids from arid habitats in East Africa (Zachariassen et al., 1988). In this respect, it appears that the species from Chimborazo have a low tolerance of desiccation. According to Zachariassen et al. (1988), Tenebrionidae and Curculionidae are better adapted to arid environments than Carabidae. In accordance with this, an unidentified species of Curculionidae from Chimborazo had a much lower rate of water loss than the carabid species, and even lower values were found in the wingless dermapteran (Table 2).

TABLE 2. The effect of desiccation (mean ± SD) at 18°C and 5% RH on insect from Chimborazo, Ecuador.

Species	n	Fresh weight (fw) mg	Max survival hours	Max weight loss % fw	Rate of water loss, % fw.h^{-1}	Percent initial water content
Bembidion andinum	10	2.45 ± 0.25	5.5 ± 2.0	26 ± 6	4.40 ± 1.49	61.9 ± 3.4
Pelmatellus andinum	10	21.8 ± 2.1	< 22	< 25	1.23 ± 0.20	59.5 ± 2.5
Agraphoderus integer	9	37.5 ± 4.3	24 ± 4	25 ± 4	1.09 ± 0.27	55.6 ± 3.3
Dermaptera indet.	5	54.9 ± 2.7	> 96	—	0.39 ± 0.26	70.4 ± 3.1
Curculionidae indet.	6	19.4 ± 5.3	> 48	32 ± 3	0.69 ± 0.17	62.1 ± 2.1

Diel activity of carabid beetles

Carabid beetles were never observed on the ground surface during daytime, but could be found in moist soil by turning over rocks partly covered by vegetation. The beetles are apparently not active during the day but seek shelter from aridity and excessive insolation. In contrast, carabid beetles were frequently caught overnight in pitfall traps (Table 3). It is not exactly known at which time of the night these catches took place, but it is reasonable to assume that the beetles are active soon after sunset and before temperatures become too low. Since the pitfall traps were placed away from rocks and vegetation where the beetles were found during daytime, they apparently leave their shelters and move across the surrounding open ground at night. The function of their nightly activity may be to hunt, reproduce and disperse.

TABLE 3. Catches of carabid beetles in pitfall traps at four altitudes on Chimborazo, Ecuador.

Species	Altitude (m)	No. of traps	Days	No. of beetles
Bembidion andinum	4,800	6	2	12
	4,700	6	7	28
Pelmatellus andinum	4,500	10	2	16
Agraphoderus integer	4,250	9	1	3

CONCLUSIONS

Since the supercooling capacity of all three species of carabid beetles is very poor, some specimens would have been killed at temperatures corresponding to the lowest surface temperatures recorded during the present study. The risk of freezing will increase considerably if the temperature drops even lower, as it presumably does on clear nights and less cloudy periods of the year.

As with cold hardiness, the tolerance of desiccation is low in all species. None of the species are adapted to an active life oon the surface during periods of high temperatures and insolation.

In conclusion, although the carabid beetles of Chimborazo inhabit an environment which may be both dry and cold during diel climatic fluctuations, they are not physiologically adapted to low temperatures and aridity. Only through their behaviour are they able to survive the harsh conditions at high altitudes on Chimborazo. Apparently, the beetles seek shelter to avoid extremely high and low temperatures as well as drought, and are only active on the ground surface when conditions are more favourable during the night.

The results demonstrate the importance of behavioural adaptations, as pointed out by Cloudsley-Thompson (1991) for desert arthropods and by Sømme (1995) with regard to insects in hot and cold arid environments.

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