The Probable Basis of the Relationship between Growth Rate and Winter Mortality in the Lizard *Amphibolurus ornatus* (Agamidae)

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**Summary.** At Bakers Hill, differential winter mortality of juvenile slow-growing *Amphibolurus ornatus* is correlated with the incidence of frosts (Bradshaw, 1971). The present study shows that the probability an individual will spend the night in a refuge that is safe from the lethal effect of a frost is directly related to the individual's size. Thus should frosts occur during any particular winter, juvenile slow-growers, will suffer a higher mortality than juvenile fast-growers. At Tuttanning, animals do not segregate according to size, and consequently juvenile slow-growers do not suffer increased mortality during frosty winters.

**Introduction**

*Amphibolurus ornatus* is an agamid lizard restricted to granite outcrops in the south west of Western Australia. Eggs are laid in December and juveniles hatch in February and March with a snout-vent length (SVL) of 35 mm. Females are mature at an SVL of 69 mm and males at 75 mm (Bradshaw, 1971).

A remarkable feature of a population of *A. ornatus* at Bakers Hill, 80 km east of Perth, is the marked variation in growth rates of young. By December of their first year, juveniles vary in size from 55 to 75 mm SVL in females, and 58 to 85 mm SVL in males (Bradshaw, 1971).

In order to analyse the variation in growth rate more fully, individuals were classified as either fast-growers or slow-growers according to whether or not they reached mature size (69 mm SVL in females and 75 mm SVL in males) by December 31st of their first year. Analysis of the comparative survival of fast and slow-growers revealed that fast-growers had a higher mortality than slow-growers during summer drought, while slow-growers had a higher mortality than fast-growers during frosty winters, but only in their first year.

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Following a frost-free winter, mortality of juvenile fast and slow-growers did not differ (Bradshaw, 1971). Subsequent studies have revealed the basis of the relationship between severe drought and high mortality of fast-growers (Bradshaw, 1970; Baverstock, 1975; Baverstock and Bradshaw, 1975). During droughts, sodium levels in the ants upon which *A. ornatus* feeds become elevated. Consequently sodium levels in *A. ornatus* also become elevated. Slow-growers are able to tolerate the hypernatraemia but fast-growers respond by increasing urinary and evaporative water-loss, leading ultimately to weight-loss and death.

The present paper addresses the problem of differential mortality of fast- and slow-growers during frosty winters.

**Materials and Methods**

Field studies were conducted at Bakers Hill from 1969 to 1972, and at Tuttanning, 150 km southeast of Perth, from 1971 to 1972. Tuttanning was chosen because it is within one of the most frostsusceptible areas of Western Australia, and experiences 16 to 26 frosts per year.

*A. ornatus* is a diurnal lizard that emerges when ambient temperature reaches 20°C (Bradshaw and Main, 1965) and at night seeks refuge under rocks and in crevices on the rock outcrop. Thus a proportion of the population can be captured at night by lifting all of "loose" rocks on the outcrops, a "fixed" rock being defined as one that is attached to the outcrop or is too heavy to lift (Bradshaw, 1971). The populations at Bakers Hill and Tuttanning were sampled at approximately 2–6 week intervals. Immediately upon capture an animal was individually marked by toe-clipping and SVL measured to the nearest mm with a pair of vernier calipers.

**Results**

Because frosts cause high mortality of slow-growers only in their first year, it seemed likely that frost susceptibility was a function of size per se rather than growth rate. It was therefore postulated that larger animals (i.e. adult fast- and slow-growers and juvenile fast-growers) might exclude smaller individuals (juvenile slow-growers) from the more favourable microhabitats. To test this hypothesis, one could compare the microhabitat distribution of animals in favourable and unfavourable habitats at night. It seemed likely, however, that the most favourable microhabitat on a frosty night would be that beneath a large (i.e. "fixed") rock, where temperatures on a frosty night do not fall below 7°C, whereas those under the slabs of granite follow ambient (Bradshaw, 1965), and this hypothesis could be tested directly only by destruction of the habitat. An alternative indirect test was therefore devised.

The test I devised has been misunderstood frequently, and so I will present an example in some detail. Between September 1969 and February 1970, 12 trips were made to Bakers Hill. A total of 77 different individuals of the 1969 cohort (Born in February March, 1969) were captured on these trips. (There may well have been more individuals belonging to the 1969 cohort present on the outcrop at that time, and not caught, but this fact does not interfere with the analysis.) Of these 77 individuals, 51 (or 66%) were fast-growers and