

PRELIMINARY OBSERVATIONS OF ALPINE GRASSHOPPERS IN A HABITAT MODIFIED BY DEER AND CHAMOIS

C. L. BACHELER

Forest Research Institute, Wellington

INTRODUCTION

A study of deer and chamois was begun in Cupola Basin, 60 miles south-west of Nelson, in 1960. Once this project had settled into a routine (Christie 1967 describes some aspects of techniques), opportunity arose for a study of the role played by alpine grasshoppers in the same general area. This seemed desirable because fairly large numbers of grasshoppers observed close to scree-vegetation ecotones—which in many places are eroding rapidly—suggested they might have a significant effect on this critical vegetation.

Casual observations showing that both juveniles and adults appeared to overwinter and were present throughout the snow-free season influenced the study to a considerable extent because they indicated an unusually flexible life cycle. In turn, this suggested the prospect of an interesting study of adaptation of the New Zealand alpine species.

Four brachypterous Acrididae, *Paprides nitidus* Hutton, *Brachaspis collinus* Hutton, *B. nivalis* Hutton and *Sigauss villosus* Salmon occur in alpine habitats of Cupola Basin (Dr. R. Bigelow, pers. comm.). *Paprides* is common in the vicinity of timber-line scrub where soil is exposed, though it is most abundant in grasslands near the timber-line which contain a large proportion of *Poa colensoi* and *Festuca matthewsii*. *Sigauss* has been collected only above 6,000 ft. *B. collinus* is ubiquitous in grass and fell-field communities from timber-line to about 6,500 ft. and is most numerous in the vicinity of scree and bare soil and the most abundant grasshopper in the area. *B. nivalis* has been identified in only one area of Cupola Basin, at 5,700–6,000 ft., in December 1966.

BIONOMICS

From January 1965 to April 1966 1,903 specimens of *Brachaspis* and 511 of *Paprides* were collected. Several measurements, detailed below, were made of this material. Preliminary analysis showed that these provided evidence of population structure, growth rate, mortality attributable to

summer snow-storms, overwintering biology, population turn-over and oviposition cycles. Only the data for *Brachaspis* have subsequently been examined in detail, and discussion on bionomics is accordingly restricted to that species.

Collections were made—usually by two collectors—with fine mesh nets along transects about 100 yards wide on Hut Face and Dry Face (Fig. 1).

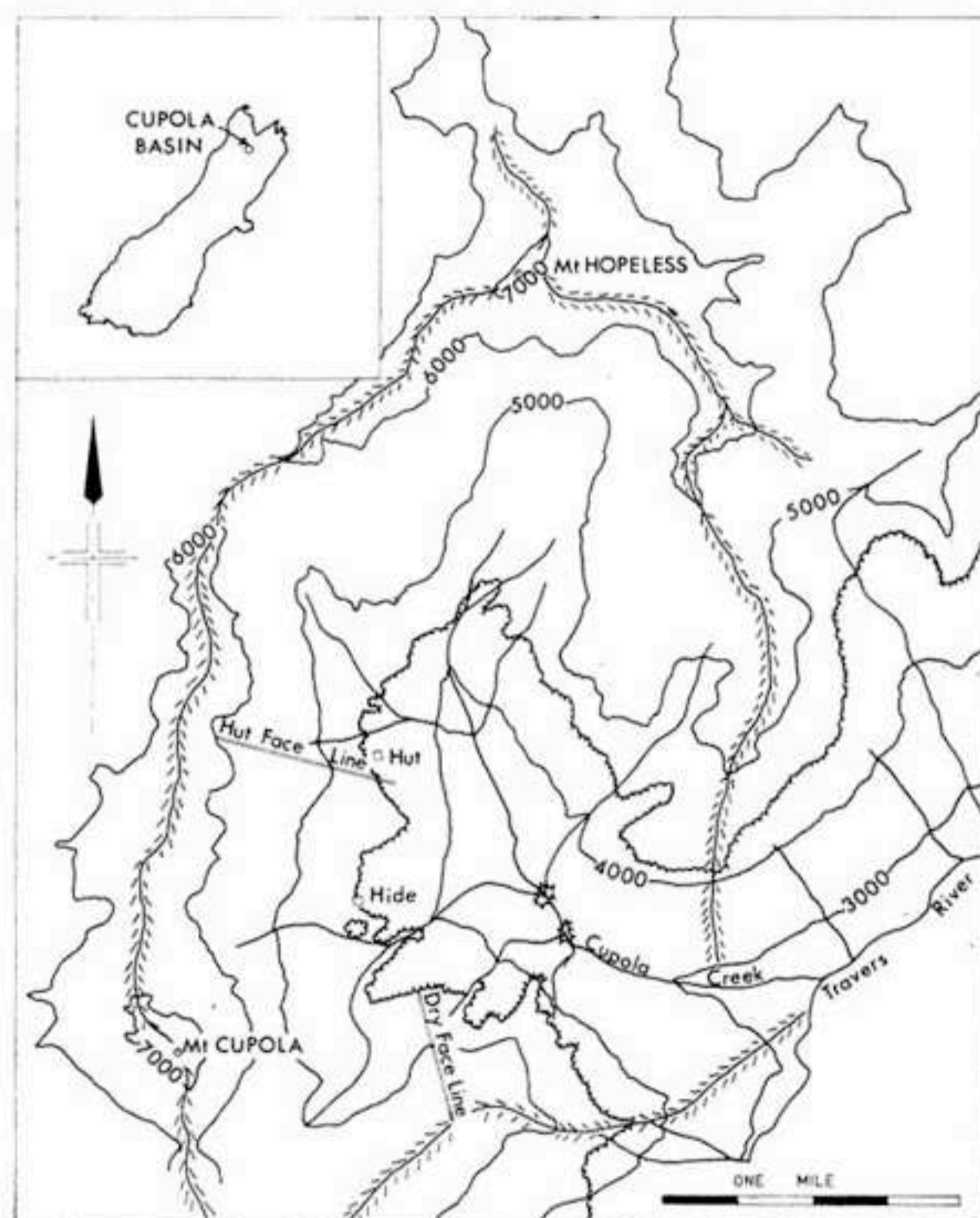


FIGURE 1. Location map of Cupola Basin, South Island, New Zealand.

Each collector wandered back and forth across the slope, sweeping the ground and vegetation with the net, while gradually moving uphill. The grasshoppers were killed in an atmosphere of ethyl acetate, sorted into three groups according to altitude: 4,650 ft. (timber-line)–5,000 ft., 5,000–

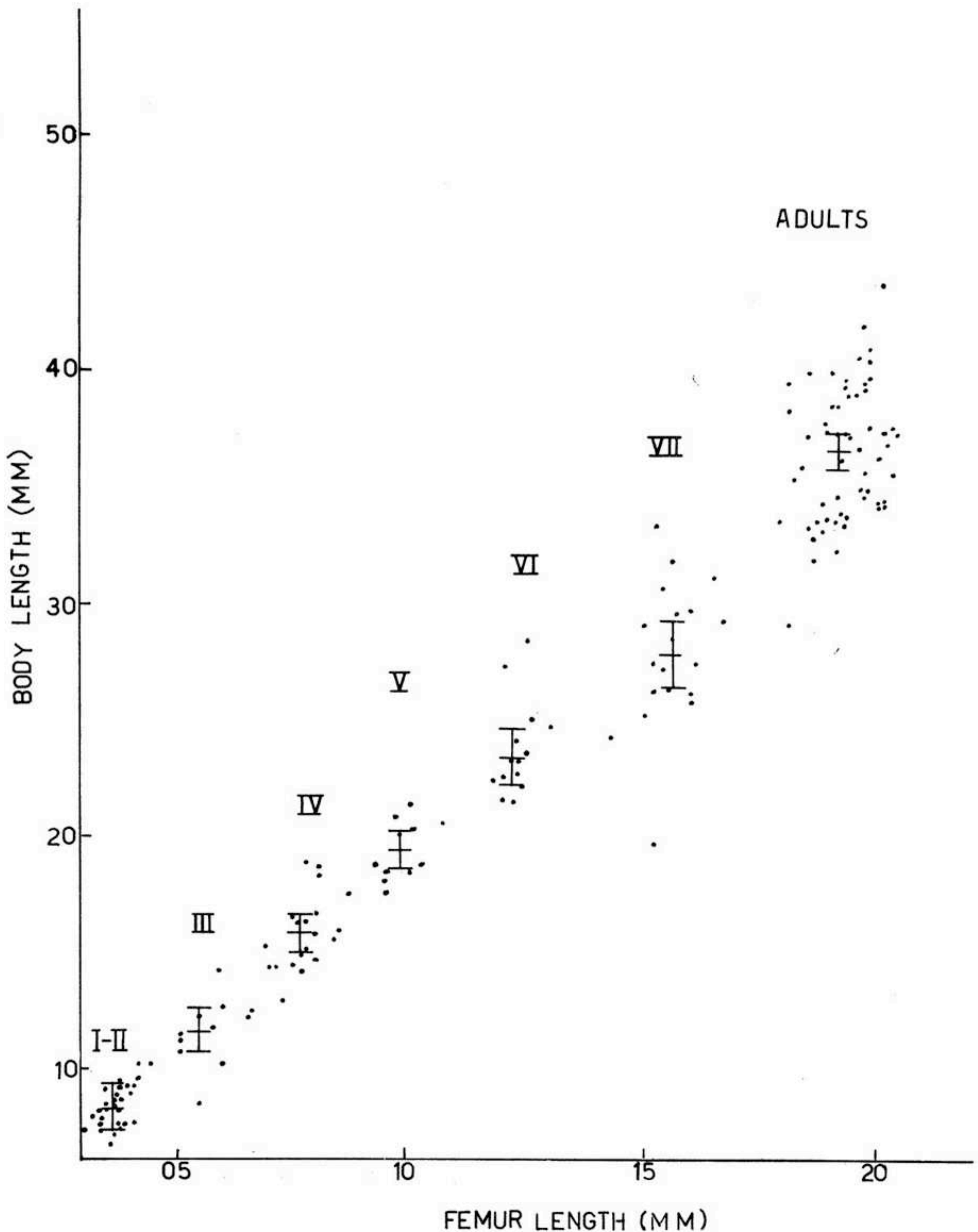


FIGURE 2. Scattergram of measurements of body and femur length, *Brachaspis* females. Two standard error limits of each instar (identified by femur length) show that body length serves to identify stadium within \pm one instar.

5,500 ft. and 5,500–6,000 ft.,* and, after measuring, were transferred to preservative. Samples were collected from the Hut Face transect in January, February, March, October, November and December 1965; February, March and April 1966, and from Dry Face in January 1965, March and April 1966.

The measurements of specimens include: Body length from frons to tip of abdominal appendages (all 2,414 specimens); body length and weight of 286 specimens; body length and femur length of 172 juveniles and 105 adults; body length and length of egg mass (along the mid-dorsal line) of 160 *Brachaspis* females.

Instars

The length-frequency dispersion in February, November and December 1965 and February and April 1966 (Fig. 3) indicated that all stages were well represented, so these samples were examined to determine the number, characteristic size and weight of each instar. The third left femur and the body from frons to the tip of abdomen (males) or genitalia (females) of 172 juvenile *Brachaspis* and 105 adults were measured.

A scattergram of the data for females indicates six instars (Fig. 2). Since making this interpretation, Miss L. Hudson, University of Canterbury, has examined in detail the characters of vestigial wings, genitalia, and femur length of my specimens. She considers (pers. comm.) that two instars occur in the group which I had identified as 1st instar, thus giving a total of seven instars of females. She has similarly identified six instars of males.

Figure 2 shows that the length of bodies of specimens within each instar overlap by about one quarter of the range of both previous and subsequent instars. On the other hand, length of femur facilitates sorting into instars I–II, III, IV, V, VI, VII and adult. This measurement is therefore a better indicator of the stadium than total body length. Although the possibility of this result was overlooked in deciding which measurements should be taken, the two S.E. limits of mean body length of each instar (identified by femur length) do not overlap (Fig. 2). About 95% of each sample within a specified length will therefore be of a stated instar, and the extreme error should not be more than \pm one instar.

I have been unable to place males within instars with equal certainty. For this reason, and because the bionomics appeared to be clearly indicated by the data for females alone, further study of males has been deferred.

Growth and overwintering of females

The length distributions of unsexed (instars I and II) and all known females taken in monthly catches were drawn as a composite length-frequency diagram for the three altitude zones. This diagram indicated rate of growth, the main features of overwintering stages and susceptibility to summer snow storms. The following concerns the catch taken between 4,650–5,000 ft. (Fig. 3).

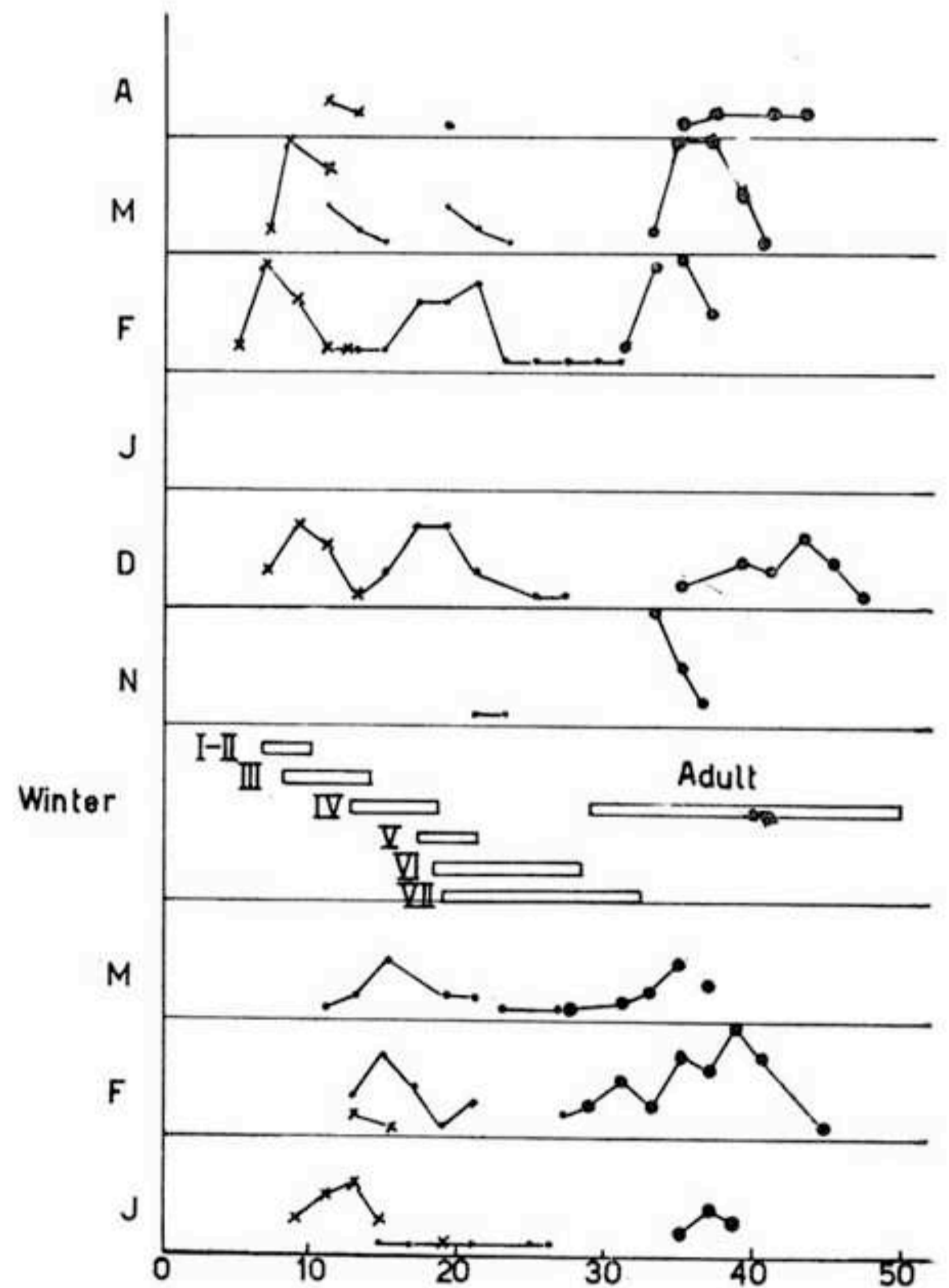


FIGURE 3. Length frequency diagram of female *Brachaspis* caught from timber-line to 5,000 ft. on Hut Face, Cupola Basin, between Jan. 1965–April 1966. (Small cross = unsexed instar I and II nymphs; small dot = sexed nymphs (female), large dot = adult females.)

* Figures given throughout this paper are based on the Lands and Survey provisional compilation 162 on S33 of the one mile series, which shows the timber line at the origin of the Hut Face line to be 4,650 ft. Four aneroid altimeters have been used to check this figure during the walk from John Tait Hut. They all indicated timber line to be 4,450 ft. Figures given may therefore err by being about 200 ft. too high.

The samples contained a modal group which had an average length of 9 mm. in February, 11 mm. in March and 12 mm. in April 1966 (upper left, Fig. 3). These comprise a generation, which are presumed to have hatched in January, and which had advanced to instar III by April. Similar evidence — a clear mode in the length distribution — indicates a generation hatched in October–early November 1965. By December these averaged 9 mm. length (instar II).

The probable fate of that generation is of interest. As shown in the figure, only a few specimens between 10 and 14 mm. were collected in February 1966. Yet to judge from apparent growth of the generation hatched in January, the spring generation should have grown to about 13 mm. by February. The observation therefore suggests that considerable mortality occurred within this group between December and February and is suspected to have been caused by a snow-storm which occurred on 26–27 December 1965. This interpretation is reinforced by the occurrence of corresponding gaps in the length dispersion of males caught on Hut Face and in the dispersion of both sexes caught on Dry Face during February and March 1966 (unpubl. data).

Growth of an earlier generation is traceable in Figure 3 over the whole of the two summers. It was hatched about November–December 1964 (bottom left, Fig. 3). By March 1965 the average length was about 15 mm, and, though no samples were collected in April, they would probably have been about 17 mm. long by the onset of winter. Following this, the snow-pack of winter 1965 began to break in early October and soon after, a few juveniles around seven mm., 15 mm., and adults between 33–35 mm. were collected. Those 13–27 mm. long in December were about the same size as those observed in March (Fig. 3). This indicates that individuals had overwintered in instars III, IV, V, VI and VII. The bulk of these, having hibernated in instar IV, are clearly samples of the generation hatched the previous spring.

Occurrence of active adults within hours or a few days of emergence of tussocks from the snow-pack in spring provides certain evidence that they can hibernate at this stage. From that time, the distribution of lengths in the adult population changes in a complex manner which suggests onset of distinct breeding and oviposition seasons and the succession of generations.

For instance, adult females caught in January 1965 measured 35–41 mm. A month later, some up to 45 mm. long were caught. In March, how-

ever, the largest specimen caught was only 37 mm. A similar increase and decline in length was found in the summer of 1965–66. Very large individuals — up to 47 mm. — were recorded in December 1965, whereas the greatest length observed in February 1966 was 37 mm. Again, modal length and extreme length increased during March and April 1966.

These large *Brachaspis* females indicate that peaks of ovipositing activity occurred about February and December 1965, and about April 1966. This suggestion was tested by measuring the egg mass in all 160 females collected on Hut Face below 5,000 ft. and it was found that egg masses were larger in these three samples, particularly in the largest specimens and that the eggs themselves were also larger (Fig. 4).

Specimens caught in January, February and March 1965 were, unfortunately, stored in 10% formalin after live measurements had been made and it was subsequently found that they became too brittle for safe handling. Specimens collected later were therefore stored in 2% formalin–30% alcohol. In this, they remained soft, and natural colours were better retained, but when the significance of changes of length in respect of breeding biology was recognised, it was realised that specimens in formalcohol had distended in storage (cf. Figs. 3 and 4). Measurements of those stored in formalcohol are therefore not applicable to living gravid animals. However, as shown in Figure 4 the positive correlation between length of the egg mass and length of body is not unduly obscured by this complication and supports the deductions concerning oviposition seasons based on Figure 3.

With this evidence, interpretation of other facets of the life cycle is simple. Adults sampled in January and February 1965 (Fig. 3) consist of at least two generations, one of which laid eggs and died, whereas the younger entered diapause. Distinct bimodality in distribution of egg and body size of these adult females (Fig. 4) bears this out. Development recommenced in October 1965, and the adults which survived winter laid eggs about December and died. This leads to the deduction that adults caught between February and April 1966 were of the same generation which had measured 25–32 mm. in spring and which had overwintered in instars VI and VII.

Assuming this, the generation hatched in October–November 1965 is derived from eggs laid about February, i.e., after winter diapause. Simi-

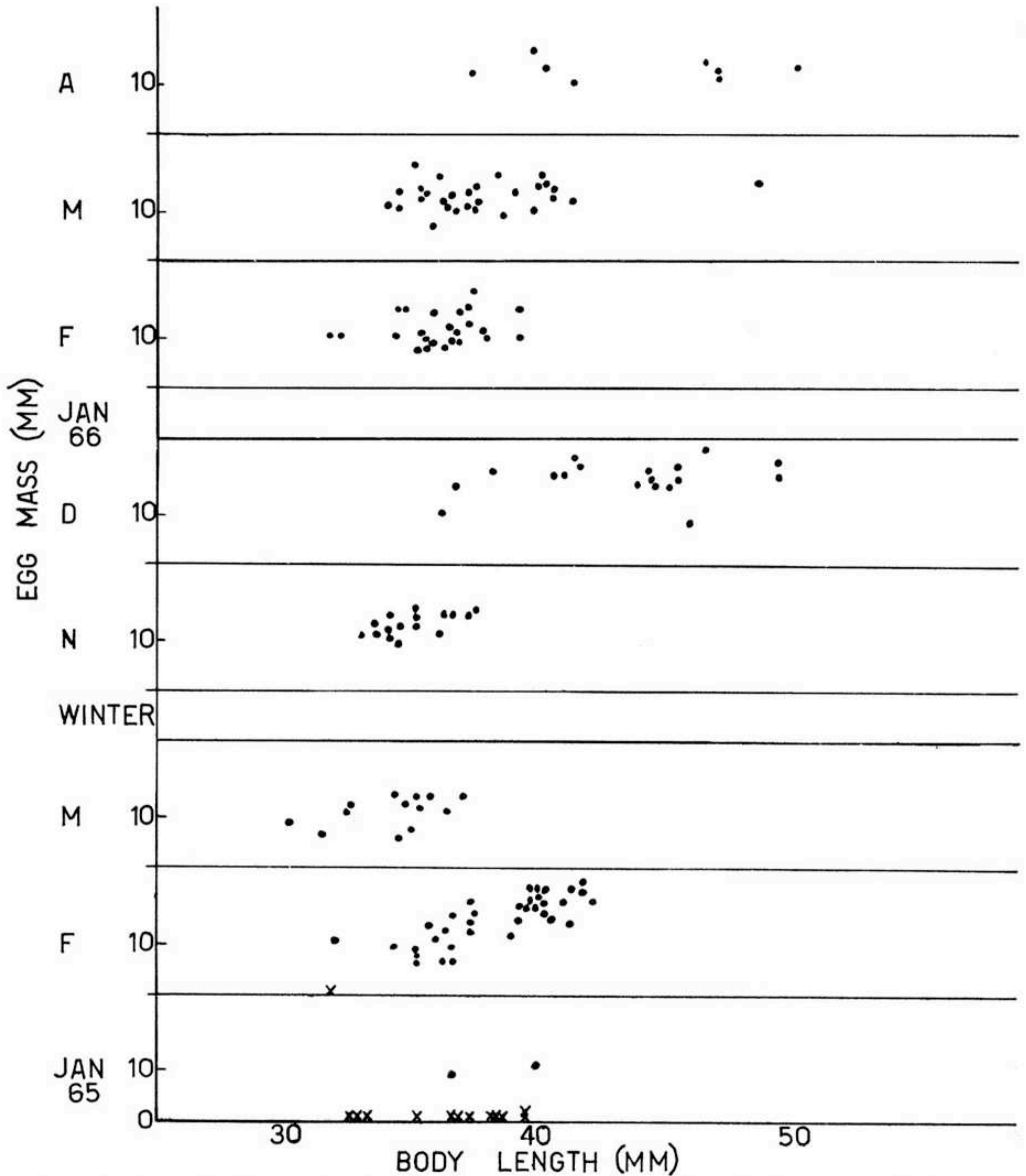


FIGURE 4. Correlation diagram showing bodylength (abscissae) and length of egg mass (ordinates) within specimens of adult *Brachaspis* females caught from timber-line to 5,000 ft. on Hut Face, Cupola Basin, between Jan. 1965–April 1966. Height of dot above abscissa shows length of egg mass. Cross denotes no eggs observed.

larly, the generation of first instar juveniles of January–February 1966 is attributable to the peak of egg-laying in December.

Two observations suggest females mate and lay once only, then die: (1) The wings of a substantial number of females over about 38 mm. length, i.e., gravid females, were damaged to some extent, often leaving a stump only 2–3 mm. long (probably caused by mites which shelter beneath the wings, see p. 24) whereas this injury was not observed among smaller specimens. Presumably, if females breed more than once, the wings of some smaller individuals would be damaged. (2) Catches of adults taken soon after greatest body lengths were recorded usually contained about a 2:1 preponderance of males. At other times, females were usually more numerous (p. 22). Both observations suggest the same cause, death of females after oviposition.

To summarise these deductions: A considerable degree of synchrony occurs in growth, mating, egg-laying and hatching of subsequent generations. Eggs may overwinter or juveniles hatch without a winter diapause if females mature and lay early in the summer. Juveniles are vulnerable to summer snow until about the third instar; instars IV–VII, and perhaps instar III, and adults, can withstand summer snow and overwinter successfully.

It follows that a generation hatched in spring may typically develop as follows:

- a) attain instar III, usually IV or perhaps V by autumn and hibernate for the first winter;
- b) develop to instar VI or VII by the second autumn;
- c) mature during the third summer.

Corresponding records of specimens caught at 5,000–6,000 ft. indicate rather slower growth at higher altitudes. Only one generation that hatched early in spring on warmer slopes appeared to develop sufficiently to hibernate in the winter of 1965. Most are thought to have attained instar V by the second winter, instar VII by the third winter, and to have matured in the fourth summer after hatching. However, samples were few in some of these high altitude catches and the interpretation is open to much doubt.

GRASSHOPPER BIOMASS ON SOME ALPINE SITES

METHOD

Live weight (lb./acre) of grasshoppers has been estimated for 7 plots on Hut Face in March 1965, and 18 plots in March 1966. The technique used

incurred estimation of mean weight per animal for each class which could be recognised with reasonable confidence in the field, and multiplication of weight per individual by the number counted in sample areas of about 100 sq. ft.

Mean weight per grasshopper

Two hundred and eighty-six grasshoppers from samples collected in May and December 1965 and February and April 1966 were weighed and measured within a few hours of death. Linear, second, and third order regression curves of weight on length were fitted by least squares. Second degree curves left least residual squares when applied to three of the four samples and a third degree curve gave a significant improvement to only one of the regressions. All data were therefore combined and the second order curve calculated to describe the general regression of weight in grams (y) on body length in millimetres (x): Its value is $y = 0.0956 - 0.0200x + 0.0015x^2$ (Fig. 5).

Determination of numbers

An unsuccessful attempt was made to determine abundance of grasshoppers by a mark-recapture technique. Seven plots, 66 ft. \times 20 ft. (long axis uphill) were delineated with light string and boundary pegs on 8 January 1965. All adults found in the plots were marked with nail varnish. Four of the seven plots were revisited on 9, 10, 17 and 18 January and on each occasion, all grasshoppers within the plot boundaries were counted and unmarked specimens marked. By 9 January marked animals were observed outside the plots, and continuation of markings did not result in a corresponding rise of recaptures. The experiment was therefore abandoned.

The only practicable alternative was to estimate the minimum number by careful counts over convenient sample areas. Earlier observations indicated grasshoppers were basking or feeding and most easily seen in sunny and calm conditions, so counts were made when air temperature exceeded 55°F. at the screen (4,650 ft. a.s.l.). Areas were chosen subjectively to sample populations in habitats ranging from dense snowgrass swards to unstable, bare scree and the plots were marked by small stone cairns.

The counting procedure involved two observers who approached the plot with care to avoid disturbance. A 10 ft. tape was kept taut to mark the base line of each plot, and all grasshoppers seen

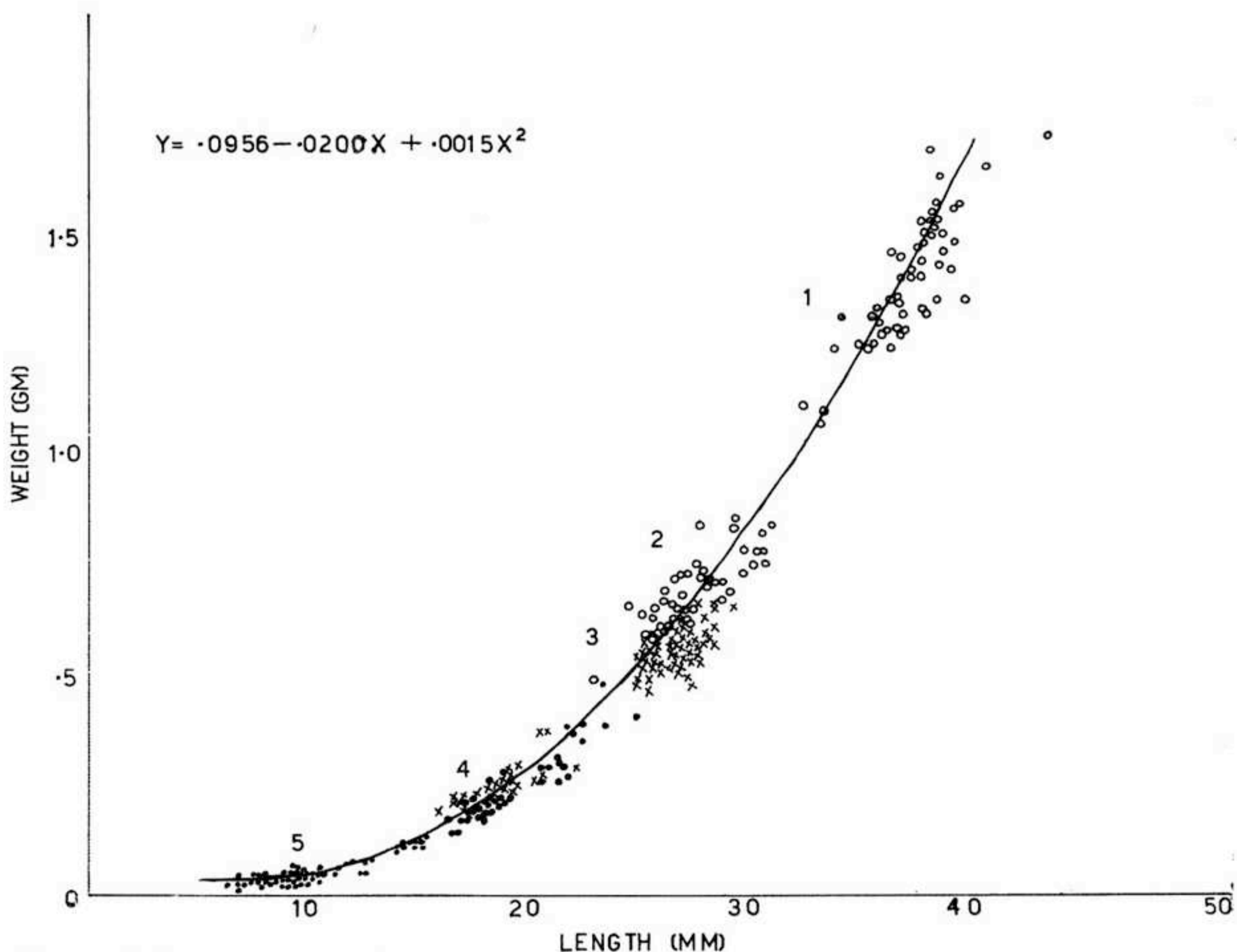


FIGURE 5. Regression of weight on length of 286 grasshoppers caught at Cupola Basin. (Open circles = adult females; crosses = adult males; dots = juvenile of both species (5). 1 and 3 *Brachaspis collinus*; 2 and 4 *Paprides nitidus*).

were recorded by classes. Each count ended when the area examined was judged to be about 10 ft. \times 10 ft., then the plot was measured accurately.

The mean length of each class, e.g., adult *Brachaspis* females, was calculated from the length-frequency of samples collected in the monthly catch along the Hut Face transect. Mean length per animal in each class was then transformed to mean weight from the regression equation and the total for all classes counted on the 10 ft. \times 10 ft. plots was calculated in lb./acre.

RESULTS

Seven estimates made for March 1965, and 18 for March 1966 with corresponding numbers per acre are summarised in Table 1. Less than 1 lb./

acre was recorded for the two dense snowgrass (*Chionochloa pallens*) sites. On other sites, which represent a gradient from dense grass to scree (Fig. 6), estimates ranged to a maximum of 22.8 lb. per acre in 1965 and 28.7 lb. in 1966.

The estimates of biomass for March 1966 on plots up to 5,000 ft. warrant comment. While at these sites, the observers noticed that adult male *Brachaspis* outnumbered females by about three to one, whereas the ratio observed most commonly in the sweep samples was about 100 males:120 females. This suggested biomass calculated directly from these counts would be low compared with the previous year especially since average weight per female is about twice that of a male.

TABLE 1. Summary of biomass and census estimates, March 1965 and 1966.

PLOT	NO.	DATE	NO./AC.	LB./AC.	DESCRIPTION OF SITE
2 (5000 ft.)	1	March 1965	13712	14.71	loose scree 2"-8" stones
	2		9680	11.47	70% cover
	3		4536	5.38	stable scree
	4		19800	22.83	Apex of stable scree by Cp.
		Mean		13.60	
5 (5200 ft.)	1	March 1965	792	.65	Dense Cp.
	2		396	.22	Mod. dense Cp. and stones
	3		4356	8.36	50 rock and stones, 50 <i>Celmisia</i> spp. <i>Poa</i>
1 (approx. 4800 ft.)	1	March 1966	436	.49 (.49)	Dense Cp. E. aspect
	2		11761	3.28 (3.28)	3% turf, 95% cover, Ca, Du, C ps.
	3		9223	12.97 (12.97)	Coarse scree at edge tall Cp.
	4		12672	10.55 (17.07)	Coarse scree at edge tall Cp.
	5		15246	8.95 (14.92)	Scree edge into low Cp.
	Mean (scree)		(14.99)		
2 (5000 ft.)	1	March 1966	8865	7.15 (13.37)	Loose scree 2"-8" stones
	2		16333	10.66 (28.69)	70% cover, prostrate <i>Du</i> , <i>Cps</i> , <i>Ca</i> .
	3		10970	7.32 (11.30)	Open Cp ½ plot and stable scree ½ plot
	4		16723	5.98 (14.93)	Apex of stable scree by Cp.
		Mean		7.77 (17.07)	
3 (5600 ft.)	1	March 1966	4355	2.49 NA	40 soil runnel carpet grass scree, 40Ca, 20Cp.
	2		3485	.93 ..	90 Ca, 5 Du, 5 stones
	3		2660	1.84 ..	80 Ca, 15 Cp, 5 stones no soil
	4		2837	0.54 ..	80 Ca, 10 Soil, 5 Cp, 5C. spec/C. disc.
	5		2813	0.07 ..	70 Ca, 10 Soil, 10 scree, 10 <i>Celmisia/Gaultheria</i>
	Mean		1.17		
4 (approx. 5900 ft.)	1	March 1966	2127	2.54	80 rocks and soil 20 Cp.
	2		3168	1.16	100 scree with soil fines
	3		871	0.58	80 Ca, 20 scree and soil, trace Cp.
	4		1307	2.33	70 Cp, 10 Du/ <i>Drapetes</i> /C. spec, 20 rubble
		Mean		1.65	

NB.: C p *Chionochloa pallens*; Ca. *C. australis*; Du *Dracophyllum uniflorum*; C ps *Copnosma pseudocuneata*; C spec *Celmisia uniflorum*; C disc *C. discolor*.

Site 2 was therefore revisited three times in an effort to establish whether females were for some reason tending to emerge and feed at some other time of day or night. Visits were made late in the afternoon of 19 March 1966 (1506-1600 hours), during the night (2000-2152 hours), and again at sunrise on 20 March 1966 (0653-0754 hours). Only two adult males and three females were seen on the scree surface in the afternoon. At night when air temperature 12 inches above ground was 52-53°F., 101 *Brachaspis* were observed about 2-3 inches below the crest of the scree pavement, and two were observed in adjacent grassland. Seventy-six of these were adults: 52 male and 24 female, a ratio of 2:1. Of these adults, 8 pairs were copulating. At dawn, on a small area, grasshoppers appeared on the scree within a minute of sunrise (air temperature 53°F.). During the next hour five males, one female (copulating), and one juvenile were seen.

These data reinforce the suggestion that many females had disappeared. Whether the disparate ratio reflects death of females after laying — as

might be attributed to the egg laying peak in December 1965 (Fig. 3), or early diapause of females following mating, which could be inferred from the high incidence of mating observed between 2000-2200 hours on 19 March — is not clear. In either case, biomass estimated directly from the data would underestimate the population before disappearance of the females. A ratio of 1 male:1.2 females was therefore assumed, and biomass of adult females was calculated from mean weight per female (determined from the weight-length regression and the March net sample length records), multiplied by 1.2 times the number of males observed. Estimates obtained in this manner are shown in parentheses in Table 1.

No corresponding adjustments of estimates appear to be necessary for samples about 5,000 ft. because examination of the records of the netted samples and of the counts recorded on the higher altitude plots showed females were present in about usual proportions.

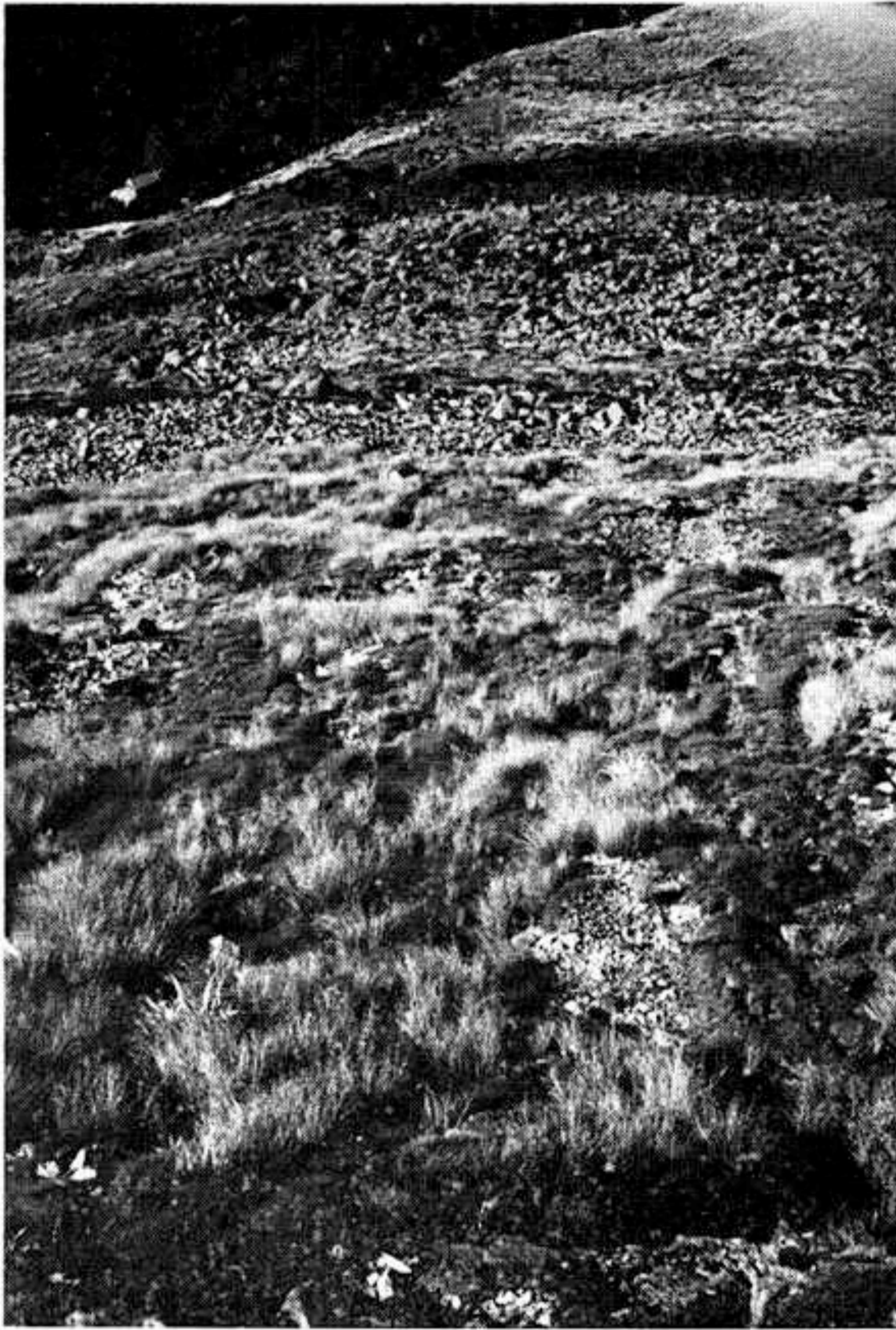


FIGURE 6. Lower half of Hut Face grasshopper sampling transect (see Fig. 1). Estimates of 25 lb./acre biomass were obtained near the scree-grass ecotone across the upper middle of the photograph. This is typical *B. collinus* habitat. The timber-line is about 4,500 ft. a.s.l.

Distribution of feeding pressure

Large numbers of *Brachaspis* may be observed on scree, especially when basking, sometimes 50 yards or more from the nearest tussock vegetation. But they are seldom seen feeding while on the scree, even on the meagre quantity of lichen and moss growing on the rocks. Usually, they are concentrated in a fringe near the vegetation-scrub ecotone.

At dawn, grasshoppers bask near the scree edges soon after sunlight begins warming the stones. They soon begin moving towards vegetation bordering the scree, then begin feeding on such plants as *C. pallens*, *Poa colensoi*, *Dracophyllum uni-*

florum, *Coprosma pseudocuneata*, *Anisotome aromatica*, *A. filifolia*, and flowers of *Gentiana patula*. After feeding for as long as two hours they begin drifting back on to the scree, moving and orienting themselves to present an optimum body surface to the sun (see Key and Day 1954 for description of orientation to the source of heat energy in *Kosciuscola tristis*). This pattern of movement indicates that the bulk of the population near a scree edge takes its food from a quite limited strip. Consequently, estimates of biomass, such as recorded in Table 1, probably give a figure well short of the biomass of grasshoppers actually being sustained by the vegetation of favoured sites.

Comparison of grasshopper and ungulate biomass

The main studies by Forest Service in Cupola Basin are concerned with red deer and chamois. Data from these studies have been extracted to determine the average biomass (lb. per acre) of the ungulates during the 12-month period May 1965–April 1966, within each 6.2 ac. grid square. Estimates covering the 3½-year period of observation, a discussion of sources of error, and a description of the technique are being compiled for a later report.

Three points from that analysis are pertinent: Biomass of deer and chamois near the timber-line is about 10 lb./acre in favoured areas of the Hide Basin (predominantly deer), and near the timber-line of Rib Face (predominantly chamois). Above timber-line, biomass decreases such that above 5,000 ft. less than 0.5 lb./acre was recorded in all except two localities of Cupola Basin.

GENERAL DATA AND DISCUSSION

Biomass of grasshoppers

The inference of the above comparison is that biomass of grasshoppers is much greater than that of deer and chamois in the greater part of the alpine grassland above about 5,000 ft. Although this suggests they may be considered the most important herbivore of this zone, a number of problems must be raised which qualify or jeopardise this conclusion.

The difference of scale of measurement upon which the comparison is based is very important. As indicated, values for the ungulates are averages based on grid squares of 6.2 acres, which is 2,700 times the plot area used for estimation of grasshopper biomass. Grazing of ungulates would need therefore to be confined to only 1/50–1/100 of each grid square, in the vicinity of scree ecotones,

for their biomass to equate effectively with the grasshoppers. At this stage of the study such a finding seems unlikely: observations of cover composition at sites within which the ungulates have been observed grazing indicate they prefer rather better vegetated ground than is occupied by large populations of grasshoppers.

The second difficulty is absence of direct data concerning energy dynamics of this alpine grasshopper population. A provisional calculation of energy required to achieve the growth attained by the population in February–March 1966 is therefore given, based on results published by other authors. The data and assumptions are:

1. Production of leaf material in a fully established carpet grass (*C. australis*) sward at 4,500 ft. is about 2,390 lb. dry weight/acre/annum (Wraight 1965). This order of production is assumed to apply to Cupola Basin and to be 1,000 lb./acre/annum or less at 5,500 ft., decreasing to zero at about 6,500 ft.
2. A production/ingestion ratio of about 13% (Weigert 1965) — as found for a lowland population of Acrididae in Michigan, U.S.A. — is applicable to *Brachaspis* and *Paprides*.
3. The calorific values of leaf material of 57 plant species and of the desert locust *Schistocerca* (4,429 cal./gm. and 5,363 cal./gm. respectively) (Golley 1961), are applicable to Wraight's production figures and to dry weight biomass of *Brachaspis* and *Paprides*.
4. The oven-dry weight of *Brachaspis* and *Paprides* is 23% of the live weight (Batcheler, unpubl. data).

The total gain of biomass from mid-February to mid-March (33% of that in February) was calculated from the increase of modal length of the generations shown in Figure 3. Assuming a similar rate applies throughout the snow-free season (about six months) a population of 15 lb. live weight requires 1.28×10^8 calories/acre/annum. Production of a fully established sward (using Wraight's data) totals 4.58×10^9 calories at 4,500 ft. and about 1.92×10^9 calories at 5,500 ft. so that minimum requirements of the grasshoppers are 3–6% of production at these altitudes when the sward is closed. Since biomass of grasshoppers is about 0.5–2 lb./acre in fully-vegetated swards, the proportion of leaf matter ingested appears to be negligible.

Production is doubtless lower, however, in scree-grass communities than in fully established swards. Assuming it to decline in direct proportion to vegetation cover, ingestion values become critically high in scree habitats. Thirty per cent of total leaf matter produced was calculated with the stated assumptions to be ingested at 4,500 ft. where 6% cover occurs, and at 5,500 ft. where 22% cover occurs. Such habitats are typically occupied by large populations of *Brachaspis* (Table 1 and Fig. 6), and, as will be shown in a later paper, are commonplace in Cupola Basin. This suggests *Brachaspis* may be a critically-important herbivore associated with much of the eroded ground and as passing comment, perhaps the same suggestion may be made of *Sigaus* above 6,000 ft.

This conclusion has far-reaching ecological implications because these are native grasshoppers. Therefore, an hypothesis which suggests they are critically important must imply modification of regulating mechanisms which formerly held numbers to a level consistent with a stable vegetation. A change of microclimate resulting from grazing by ungulates, or change of regional climate, or a combination of these, are possible causes which have been considered.

Bionomics

Perhaps the most significant observation in respect of this hypothesis is occurrence of one egg-laying cycle during summer 1964–65, and two in the year 1965–66; summers which were relatively cool and wet, and warm and dry respectively.

Snowbreak in spring 1964 occurred in November–December (November at timber-line), at least one month later than has been usual over the past 15 years. Much of the ground above 6,000 ft. was still blanketed in December. Light snowfalls were recorded each month of that summer, and rain fell during 58 of 94 days in which the Station was manned between 5 November and 11 March. It was also a relatively poor season in respect of onset and intensity of flowering in most angiosperms (C. M. H. Clarke, MS).

This poor season appeared to have marked effects on the grasshopper population. Though the generation which hatched in spring developed successfully (Fig. 3), no trace was found in March of a small number of instar I and II juveniles observed early in January. Adults were carrying an unusually obvious population of ectoparasitic mites (identified by Dr. G. R. Ramsay as larvae

of an undescribed species of *F. Erythreidae*, pers. comm.) by late January and the degree of infestation increased rapidly. By 8 March adult female *Brachaspis* carried, on average, 11.8 mites beneath the vestigial wings (unpubl. data): Adult female *Paprides* carried about six, and males of both species carried lesser numbers in approximate proportion to body size. In all respects, therefore, the season appeared to be unfavourable for grasshoppers.

Summer 1965–66 was much more pleasant. The spring thaw in 1965 occurred during September–October, the weather was generally drier throughout the summer and plants flowered more profusely. *Brachaspis* appeared in late September. Instars I and II appeared during October, some six weeks earlier than the previous year and peak infestation of mites occurred in February, a month earlier (but only six mites per adult female *Brachaspis* and correspondingly lower populations among other adults). Together, these observations amount to the suggestion that only one generation laid in the late wet season, whereas two laid in the drier, early season.

This is significant because, in a complementary study of climate patterns in the area, evidence has been gathered which indicates a considerable reduction in the extent and duration of winter snow during recent decades. Until the mid 1930's, the first heavy falls of snow could be expected during late April or May; they now usually occur in May or June, occasionally in July. In former years the winter snowpack remained until November–December; it now usually breaks during September–early November. Thus, generally, the alpine grassland appears usually to be free of snow from October through to May, about two months more than occurred in the first quarter of this century. This is consistent with the documented retreat of South Island glaciers during recent decades (Broderick 1891; Harrington 1952; Skinner 1958; J. D. Pascoe, pers. comm.) if downwasting of glaciers may be assumed to be caused by reduced quantity of snow. And it is interesting that this change of snow cover, like that of glacier ice (Harrington 1952), may have been proceeding for the past 200 years.

Thus the evidence linking longer summers with recruitment of two generations offers a plausible mechanism for suggesting *Brachaspis* populations have increased in recent decades.

Modification of the habitat because of grazing and trampling by the introduced ungulates is also believed to have favoured grasshoppers, particularly in more dense grasslands. Small juveniles have often been observed in the vicinity of soil which has been left denuded by the death of individual plants. Common examples of this include occurrence of instars I and II on soil exposed by the death of small patches of prostrate *Dracophyllum uniflorum* killed by deer; where individual broadleaved snowgrass tussocks (*C. flavescens*) in a matrix of the less palatable mid-ribbed snowgrass (*C. pallens*) have been killed; and in the runnels which have developed along animal trails in carpet grass (*C. australis*) associations.

Such commensal dependence of grasshoppers upon ungulates, though it may be envisaged as a mechanism which extends the range of *Brachaspis* into denser vegetation, cannot be invoked in explanation of any increase of populations adjacent to scree-fields and avalanche chutes. There, bare soil sites suitable for oviposition are doubtless normal. For this reason an amalgam of both hypotheses seems more reasonable; i.e., it is suggested that *Brachaspis* is a critically important herbivore because habitats have been modified by introduced ungulates and because climatic change has extended the snow-free season such that in one season two generations of adults may reproduce and two generations of juveniles may reach about instar IV, at which they can overwinter.

This calls attention to the very unusual degree of plasticity in the life cycle of *Brachaspis* compared with alpine Acrididae of other regions. Alexander (1951) notes that only one of all eleven resident alpine Acrididae in the Colorado Mountains does not overwinter solely in the egg state. *Aeropedellus clavatus*, the most abundant tundra species, overwinters by diapause of eggs extending through two winters (Alexander and Hilliard 1964). The exception, *Xanthippus corralipes altivolus*, overwinters solely as a juvenile, and matures in early summer (Alexander 1964).

Annual life histories in which winter diapause is confined to the egg-stage is also the rule among Orthoptera in the French Alps: Populations are composed entirely of juveniles in spring, mixed populations of juveniles and adults in mid-summer, and adults in autumn (Dreux 1961). On similar evidence, Dr. K. H. L. Key, C.S.I.R.O., Canberra

(pers. comm.), believes the same pattern holds good for alpine grasshoppers in Australia. In contrast, eggs, juvenile and adult *Brachaspis* hibernate, and eggs may hatch with or without a diapause.

The reasons for these adaptations indicate a profitable subject for study. The likelihood of snow in all summer months, the erratic nature and duration of the snow-pack, and relatively warm temperatures during winter (Morris 1965; Christie 1967) may be the root causes, for they would suggest considerable survival value in a flexible life history. But it is interesting that the mean summer temperature at the New Zealand timber-line, about 50°F., is about the same as at timber-line elsewhere, which suggests no basic reason for such a great difference of life span. It may be that since *Brachaspis* is a relatively large alpine grasshopper the difference is only of ultimate size, not of growth rate. But in turn, why is *Brachaspis* so large?

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SUMMARY

Four brachypterous grasshoppers, *Paprides nitidus*, *Brachaspis collinus*, *B. nivalis* and *Sigauss villosus*, occur above timber-line at Cupola Basin, a 3,000 acre tributary catchment of the Travers River, Nelson. Samples collected between January 1965 and April 1966 were measured to obtain information on population structure, overwintering and reproductive biology, and correlation between weight and length. Data for *Brachaspis* females are analysed and presented in this paper to illustrate the general bionomics. Population densities were calculated on plots of about 100 sq. ft. area. Biomass (lb./acre) was also estimated using the product of weight of each type of grasshopper recognisable in the field and their estimated numbers.

Brachaspis females appear to hibernate in instars III-VII, as adults, and as eggs in the soil. They mature

about three years after hatching. Adults mate and lay eggs at any period within the snow-free season, if weather is suitable. If laying occurs early in the season eggs hatch without a winter diapause. Such unusual longevity and flexibility of the life cycle are believed to reflect adaptation to the erratic nature of the New Zealand alpine climate: Snow may fall at any time of the year, the winter snow-pack may form between April and July and melt as early as September or as late as December. Winter temperatures are relatively mild.

Populations of *Brachaspis* weigh less than one lb./acre in dense grassland and up to 29 lb./acre where scree forms a high proportion of total cover. A population of 15 lb./acre is calculated to require over 30% of total leaf matter produced per annum on eroded sites, a result which suggests *Brachaspis* is a critically-important herbivore. The implications of this hypothesis are discussed. Modifications of the habitat by introduced ungulates, and recent changes in the pattern of snow-cover are considered as possible causes of the critical status of *Brachaspis* indicated by the calculations.

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