

COLOUR AND SIZE VARIATION WITHIN A POPULATION
OF BRACHASPIS COLLINUS (HUTTON)
(ORTHOPTERA : ACRIDIDAE)

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I. INTRODUCTION

There are at least two types of biological variation, i.e., "group, or geographical variation" referring to differences between populations and "individual variation" referring to differences among individuals in a single population. Variation among individuals has been of interest in descriptive zoology and especially to the taxonomist as a reaction to the 'type' species concept. Moreover, the occurrence of individual variation and its significance to the species is an important part of ecological and evolutionary study. A population can adapt itself to a varying environment either by producing phenotypes with a wide tolerance and plasticity, or by producing a wide variation of individuals, with certain individuals sacrificed to the advantage of the population.

Geographical and individual variation in size of animals is common, especially among insects. Widespread species which show similar adaptation to similar conditions are often considered in terms of "ecological rules". One of these is Bergmann's Rule concerning the size of individuals and temperature. Briefly, Bergmann's Rule predicts larger sized individuals in cooler parts of a species range. The validity of the rule has been shown for many birds and mammals but reports on its application to poikilotherms conflict. Bigelow (in press), recorded a significant clinal increase in size with increase in altitude within certain populations of two species of New Zealand Alpine Grasshoppers (Acrididae), viz:- Brachaspis nivalis (Hutton) and Sigaues australis (Hutton) but size

variation has not been investigated in populations of other New Zealand species of grasshoppers. Brachaspis collinus (Hutton), a fairly large brachypterous species, occurs above 3,000' in the mountains from N.W. Nelson to Arthur's Pass in the South Island. It was therefore of interest to determine the relationship of size and altitude in B. collinus to further test the applicability of Bergmann's Rule to New Zealand Grasshoppers.

The widespread occurrence of geographical variation among populations in colour and pattern has been noted by Mayr (1963) and by many others. This variation has been recorded for adult specimens of New Zealand grasshoppers by Bigelow (in press), who also notes a colour polymorphism in the adults of B. collinus in the more southern parts of its distribution. However, the extent of the variation of adults and the variation of juveniles in this species requires further study. This study has been concentrated on one population of B. collinus in an attempt to determine the extent and possible significance of the individual variation.

PRELIMINARY SURVEY

a. The Study Area.

Temple Basin is about 1,000' above the timber line near Arthur's Pass in the South Island. It is a three basin system of fragmentary patches of scree and alpine vegetation (Fig. 1). The general area can be divided conveniently into three habitat categories. Areas with less than 5% vegetation cover were defined as 'scree', those with greater than 80% cover as 'grassland', and all areas with intermediate proportions of grassland and scree as 'intermediate'. The latter were either patches of shingle interspersed with patches of grass, or scree extending down into grassland areas.

At lower levels, around 4,500', the habitat was generally grassland with the snow tussock Chionochoa pallens intermingled with Ch. crassiuscula and Ch. flavescens. Many other grassland plants were present, the commonest being Celmisia sp., Poa colensoi and Anistome aromatica. This grassland area extended to about 5,300', but was often broken by eroded areas of shingle, bare earth, rocks and creek gullies. In the Downhill Basin one side was covered predominantly by Ch. pallens and Ch. crassiuscula and to some extent by Poa novae-zealandiae and Poa colensoi, while the other side was largely scree. Above this, the Top Basin was mainly slopes of broken scree interspersed with small patches of vegetation composed of Ch. oreophila and Poa colensoi.

b. General distribution and abundance of B. collinus

A minimum count transect was carried out to estimate the

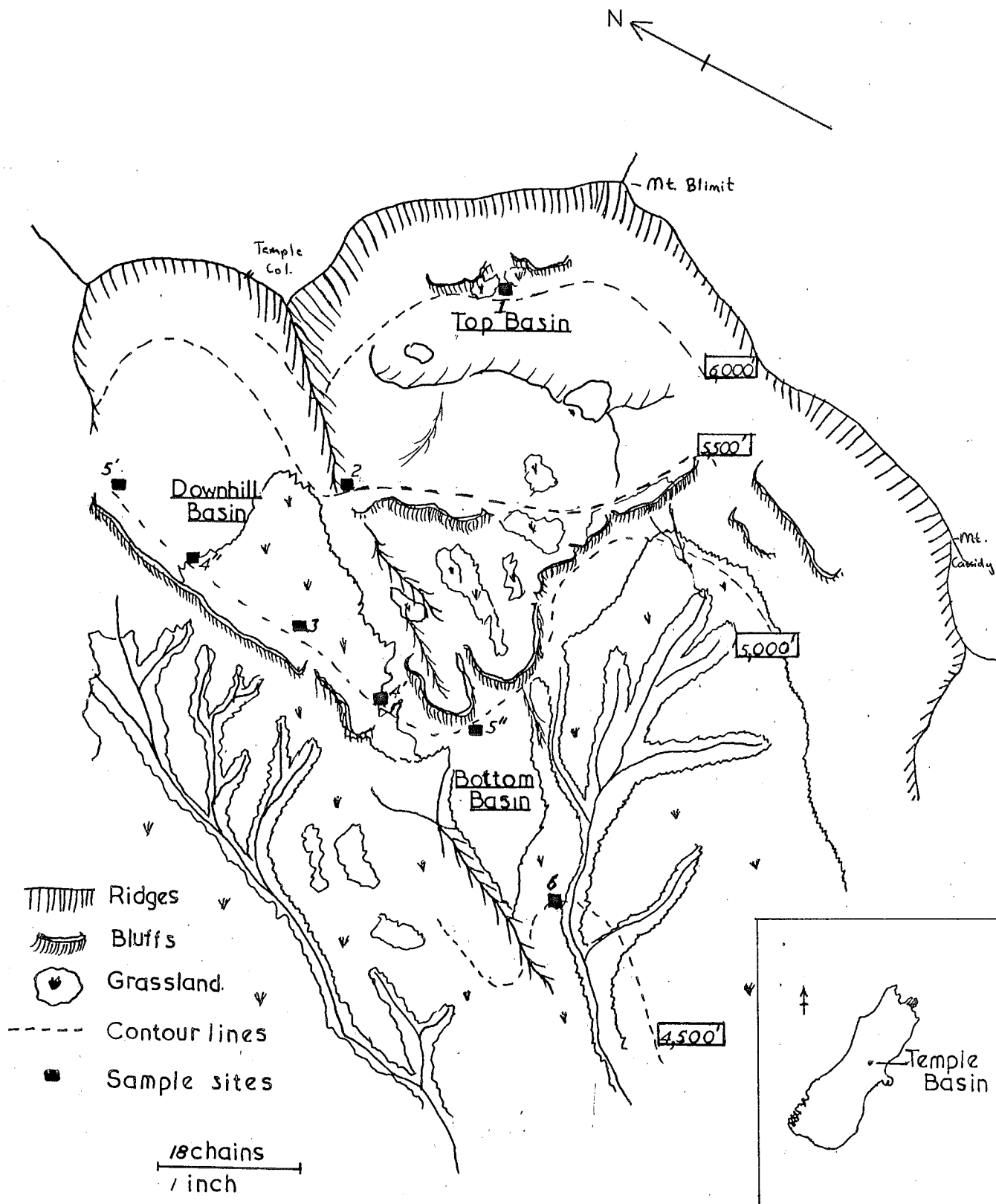


FIG.1 Sketch map of Temple Basin showing Sample Sites.

relative numbers and distribution of B. collinus. The transect line taken in February in fine, calm weather was from 4,500' to 6,700' directly upward from the Bottom Basin into the Top Basin. The altitudes of the habitats covered were recorded with an aneroid altimeter and each grasshopper observed within 1 yard of the line was classified as either adult female or otherwise. The presence or absence of stripes was noted wherever possible. The results showed that Paprides nitidus Hutton (Acrididae) was common at 4,500' but was replaced by B. collinus at 4,700'. From 4,700' to 6,700' B. collinus was very abundant on both scree and grassland but clumped in distribution. The greatest numbers occurred in the intermediate areas, especially in the grass-scrub ecotone. No adults were recorded on the bare scree areas where only moss and lichen existed, but a large increase in numbers was noted near isolated groups of plants. Generally, the numbers decreased with increasing altitude.

Many of the grasshoppers observed moved to the nearest vegetation for feeding and then ranged back onto the scree to bask, adjusting their position to the sun's direction.

The preliminary survey showed, firstly, that sampling would be most convenient at four altitudinal stations separated by 500' and secondly, that all habitats present could be sampled at 5,000'.

COLLECTION OF MATERIAL

Grasshoppers for the study of both size and colouration were collected in February and March of 1967. Six samples at four altitudes were taken as follows:-

<u>Altitude</u>		<u>Habitat</u>	
6,000'		Intermediate	
5,500'		Intermediate	
5,000'	Grassland	Intermediate	Scree
4,500'		Grassland	

This scheme enabled a direct comparison of similar habitats at different altitudes and a comparison of three habitats at the one altitude. Four of the samples were each taken from one site, the other two from two sites. Within each site, several plots were sampled over a period of several days. The description of the sites shown in Figure 1 are listed below:-

<u>Site No.</u>	<u>Location</u>	<u>Habitat</u>
1	Above hut in Top Basin at 6,000'.	Patchy intermediate area, Rocks and scree 70%, vegetation cover about 30%. Short grasses <u>Ch.oreophila</u> and <u>Poa colensoi</u> dominant.
2	On the ridge between Top and Downhill Basin 5500'.	Vegetation cover 60%, patches of shingle.
3	Near the bottom of Downhill Basin at 5000'. 150 yards from scree	<u>Grassland</u> - <u>Ch.crassiuscula</u> and <u>Ch.pallens</u> predominant, 20% of area bare ground and scattered rocks.

<u>Site No</u>	<u>Location</u>	<u>Habitat</u>
4'	To right of 3, Downhill Basin at 5,000'.	<u>Intermediate</u> - small scree tongue surrounded by grass.
4''	To left of 3, Downhill Basin at 5,000'.	<u>Intermediate</u> - Grass-scrree ecotone.
5'	Near middle of wide scree, Downhill Basin at 5,000'.	<u>Scree</u> - 2 isolated <u>Hebe haastii</u> plants
5''	Middle of scree Bottom Basin 5,000'.	<u>Scree</u> - Few small herbs and plants (e.g. <u>Epilobium</u> sp.)
6	Just below ski huts at 4,500'.	Vegetation cover about 80%, with snow tussock predominant, but with many other species present, particularly <u>Celmisia discolor</u> , <u>Gaultheria</u> sp. <u>Anistome aromatica</u> and <u>Poa colensoi</u> .

Within each site, sample plots of about 20 by 15 yards were marked out and grasshoppers were collected with a net for fifteen minutes. To reduce the bias towards larger individuals, each grasshopper seen was caught wherever possible. In densely populated areas the net was swept across the ground while moving gradually uphill. The grasshoppers from each plot were brought back alive to the laboratory for subsequent study.

II. SIZE VARIATION

Van Horn (1965) states that it is well known that grasshoppers become smaller with increasing latitude and altitude. In New Zealand, however, Bigelow (in press) has recorded a significant increase in size with increasing altitude in Brachaspis nivalis and Sigaus australis.

a. Method

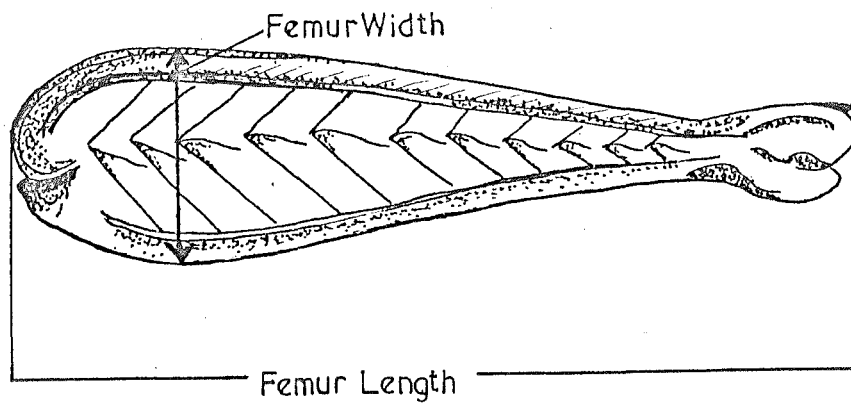
B. collinus collected in February and March from sites with similar aspect from 4,500' to 6,000', were stored in alcohol after colour analysis. The grasshoppers were subsequently sexed and classified into instar stages using the keys of Miss L. Hudson of Canterbury University (pers. comm.). These are based on morphological characters and distinguish 6 male and 7 female instars. Length-frequency data was also used as a check to identification.

As an indication of body size the length of hind femur (F.L.), the width of hind femur at the widest point (F.W.) and the median length of the pronotum (P.L.) (Fig.2) were measured using a micrometer eyepiece fitted to a binocular dissecting microscope. The mean length in mm. and the standard error were calculated for each group.

b. Results and Analysis

Appendix 1 gives the calculated means \pm standard errors for the three characters measured at each altitude. The mean FL, FW, and PL increased with increasing altitude in all instars. The adult means are shown in Figure 3. Student's t test was used to compare the samples of the adults taken at 5,000' and 6,000'. These results are listed below in table 1.

A.



B.

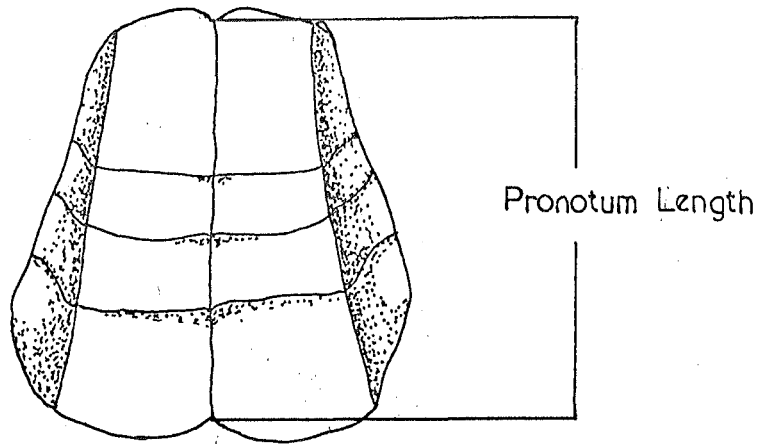


FIG 2 : Hind Femur and Pronotum showing points of Measurement

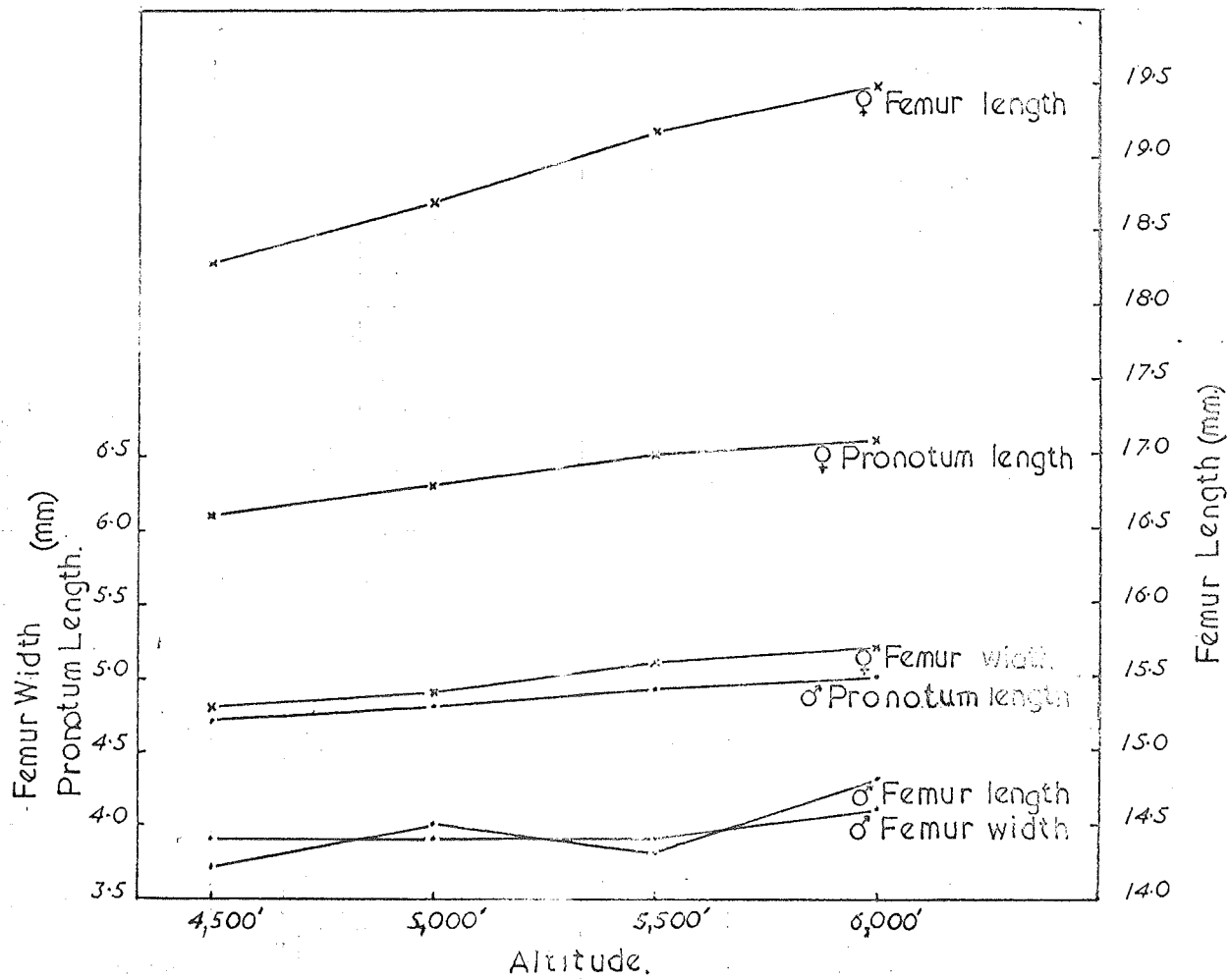


FIG3 :Mean Lengths of different Adult characters at each Altitude

TABLE 1. Calculated means, t values and probabilities for adults at 5,000' and 6,000'

<u>Character</u>	<u>Altitude</u>		<u>t</u>	<u>Probability</u>
	<u>5,000'</u>	<u>6,000'</u>		
(a) <u>Female</u>				
Femur Length (mm)	18.7	19.5	3.04	.001 < p < .005
Femur Width (mm)	4.9	5.2	3.47	.001 < p < .005
Pronotum Length (mm)	6.3	6.6	2.88	.005 < p < .01
(b) <u>Male</u>				
Femur Length (mm)	14.5	14.8	1.86	.05 < p < .1
Femur Width (mm)	3.9	4.1	3.95	p < .001
Pronotum Length (mm)	4.8	5.0	5.77	p < .001

Five out of the six characters were significantly larger at the 1% level. This effect was more marked in the female.

Following the method of Van Horn (1960) the means of the characters for each instar at the different altitudes were summed to give a size index. These results are shown for 5,000', 5,500', and 6,000' in Figure 4. A clinal increase in size with increasing altitude occurred in all instars sampled. Although samples were smaller in the younger instars, an overall trend was still suggested.

The ratio of the length at each instar to the length at the previous instar was calculated for the femur and pronotum at 5,000' and 6,000' in order to test for differences in relative growth of the two characters at different altitudes. The

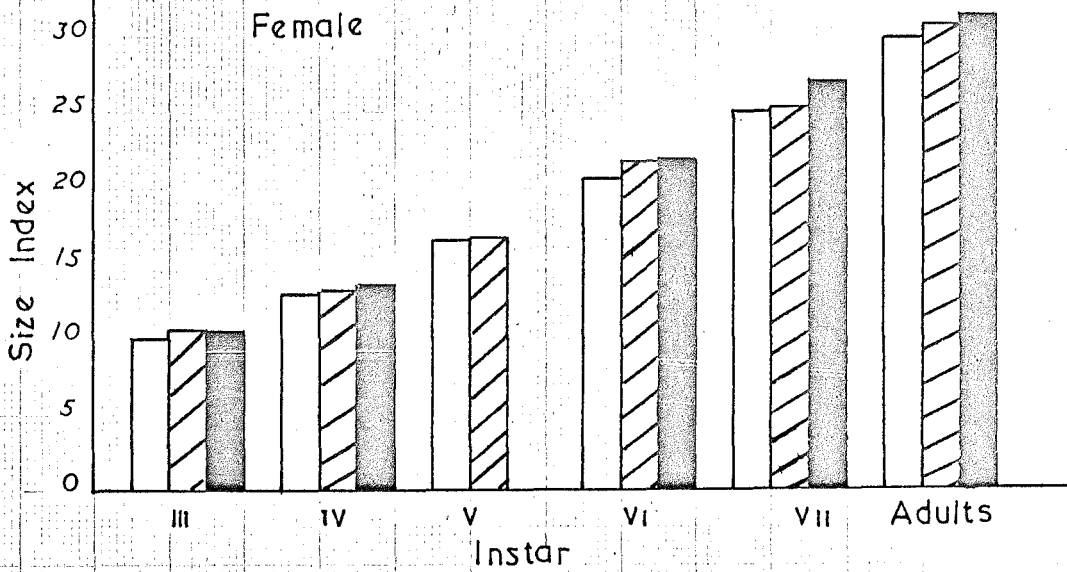
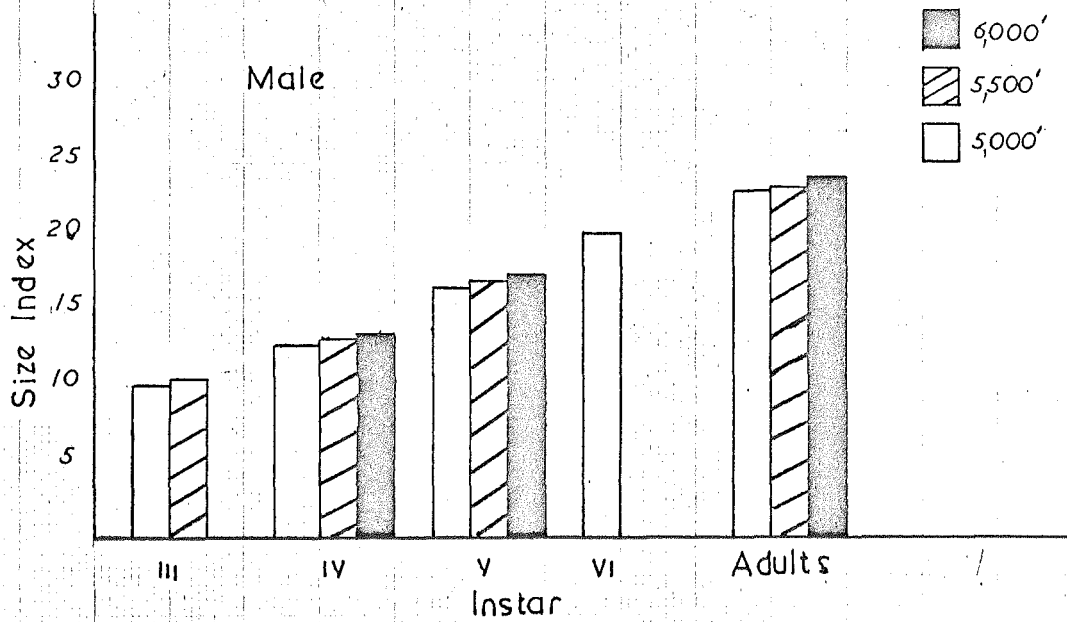


FIG 4 : Size Index at different Altitudes

characters showed a similar relationship of allomorphy to each other at both altitudes, showing that the increase in size index was not due to increase in one character relative to the other but to a general body size increase.

c. Discussion.

B. collinus increased in size with increasing altitude. This increase was reflected in all instars examined and was not merely confined to the adults. There are two possible causes of the size variation at different altitudes; it is either a direct effect of the different environment or a genetic difference produced by natural selection.

Batchelor (1967) concluded from length frequency data from Cupola Basin that B. collinus generally develops to adult stage in three years but that those caught at higher altitudes indicated a slower growth rate than the corresponding generation at lower altitudes. Samples taken from Temple Basin in February showed a similar instar distribution. Instars I and III were present in large numbers at 5,000' and instar II was caught only at 6,000'. This suggests that nymphs at lower altitudes had advanced to instar III in their first summer while at 6,000' some had only reached instar II at the time of sampling. Hence, the results show that a decreased growth rate seems to be correlated with the increased size at higher altitude.

Ray (1960) has shown experimentally that six Drosophila species and several other poikilotherms, when raised at lower temperature, grew more slowly but attained a greater size, than did the

individuals cultured at 10°C higher. It is also well known that lowered temperatures slow egg development in many insects, and this may effect the size of the hatched nymphs.

Since the mean air temperature generally decreases with increasing altitude (Mani, 1962), it is likely that the lowered temperatures at higher altitudes are the cause of the observed increased size.

Another possibility is that a genetic difference exists between the high and low altitudinal groups. But as Ray (1960) and others point out, such a genetic difference might be a result of genetic assimilation of the environmentally acquired size characteristics, produced initially by the effect of temperature on the phenotype. This theory of genetic assimilation (Baldwin effect) is described by Waddington (1953). B.collinus as well as B. nivalis and S.australis thus fail to support Van Horn's generalisation. Therefore, size differences, and the factors causing them, need to be investigated in each particular case and general predictions cannot yet be made.

III. COLOUR AND PATTERN VARIATION

Colour and patterns are particularly important in adapting some animals to their environment. The cryptic nature of grasshopper patterns and colours has been noted by Cott (1940) and others. Two pattern forms have been described in the adults of B. collinus by Bigelow (in press) and are interesting in comparison with the relative uniformity of many of the other New Zealand species. In this study, the extent and possible significance of the variation of juveniles as well as adults was investigated in B. collinus.

a. Method

In the laboratory, the grasshoppers were killed in an atmosphere of ethyl acetate and examined immediately. The pattern, colour, instar and sex were recorded for each individual. A shorthand notation method derived from Clark (1943) was used to express the variation of colour and pattern quantitatively. The overall colour of the dorsal and lateral surfaces of the grasshoppers was noted and the detailed distribution of colour (pattern) was recorded for the following body regions: Head, Pronotum, Abdomen, Tegmina and Femur. The frequency of the different colours and patterns was then calculated for each instar. The incidence of mating between the adult colour and pattern forms was also noted in the field.

b. Results and Discussions.

1. The extent of variation.

Figure 5 illustrates the percent distribution of patterns and

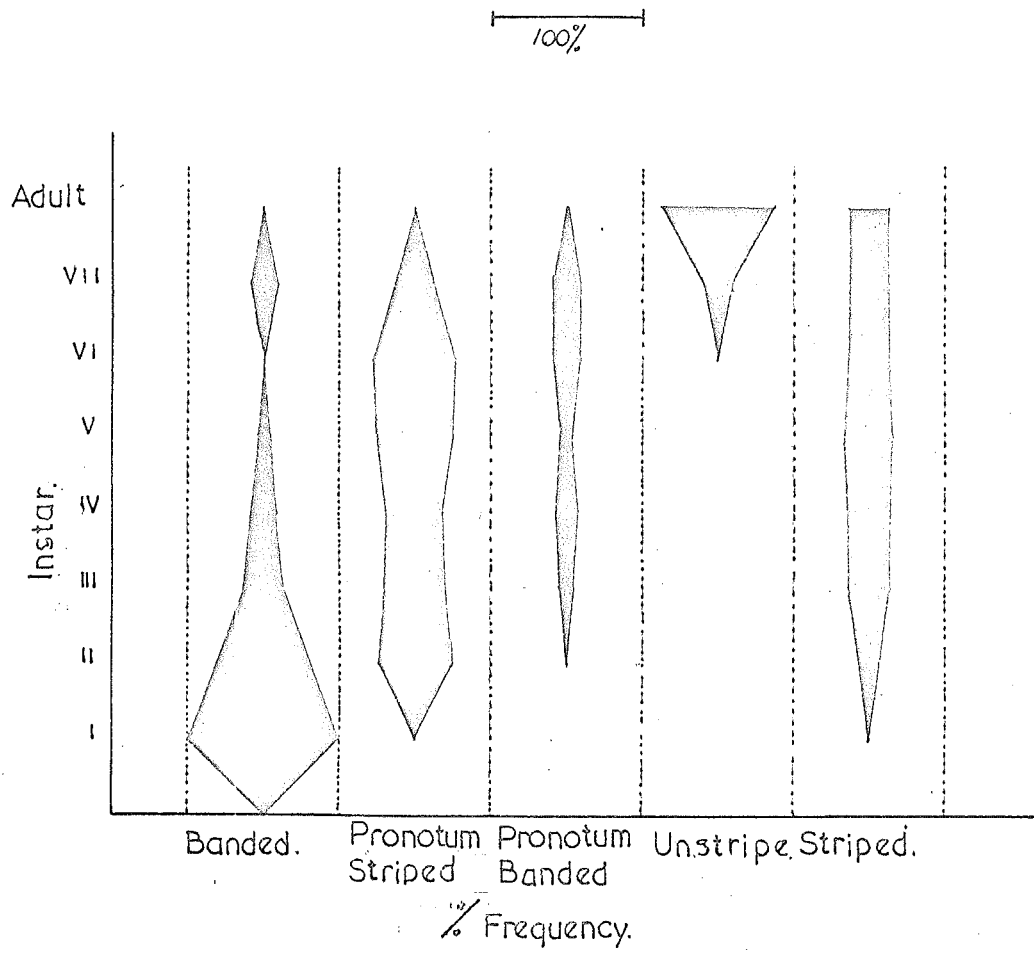


FIG 5 : Percent Frequency of Patterns in each Instar

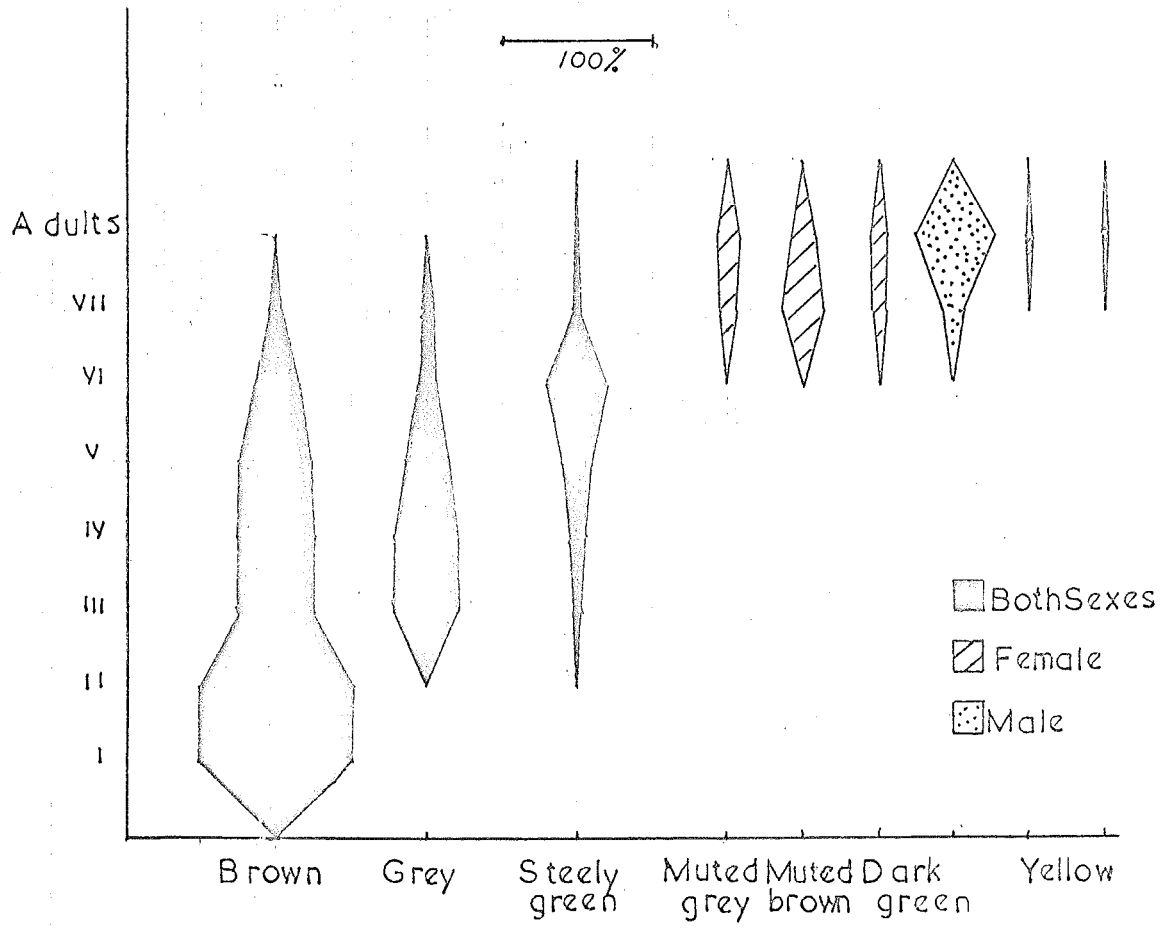


FIG 6. Percent Frequency of Colours in each Instar

Figure 6 the dorsal colours within each instar for the pooled 'intermediate' samples (frequencies are given in Appendix 2). These show that there is a considerable variation within each instar and that juveniles differ markedly from adults.

Variation of Juveniles: Four main pattern forms were recognised, viz:-

Banded - pale longitudinal band extending along dorsal surface.

Pronotum Banded - pale band only on head and pronotum.

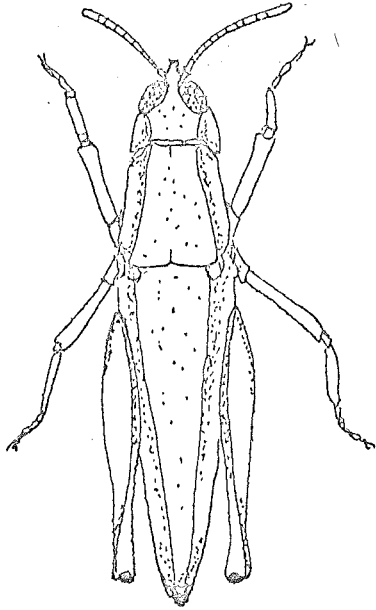
Striped - two longitudinal stripes along body.

Pronotum Striped - stripes on pronotum and sometimes on head. (These are shown in Figure 7).

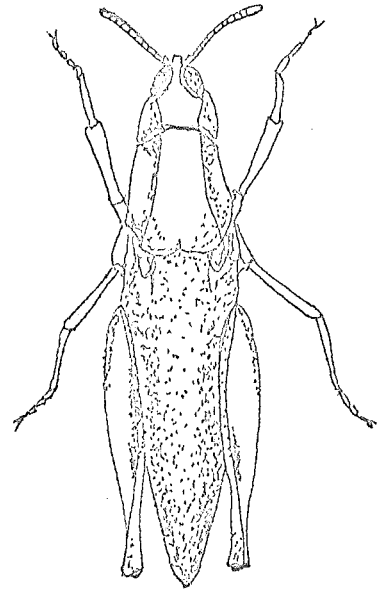
All instar I examined were banded. Five instar II were recorded, of which two were striped and three pronotum-striped. (The stripe appeared to be developed by the deposition of darker pigment along the mid dorsal line of the band as seen in the striped species Paprides nitidus). The four juvenile patterns were present in instar III and were exhibited in all subsequent instars. Thus a wide variety of patterns occur and these appear to develop after instar I.

The younger instars were predominantly greys and browns with variable amounts of fine black spots. An increased proportion were steely green in later instars, and in instar VII some individuals exhibited adult colouration.

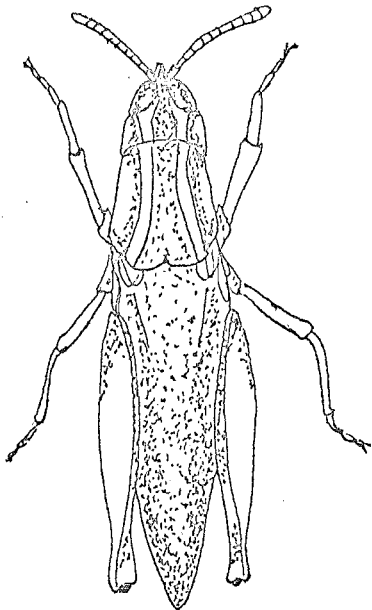
Comparisons of samples from different habitats showed that juveniles were usually more numerous on screes and bare shingle



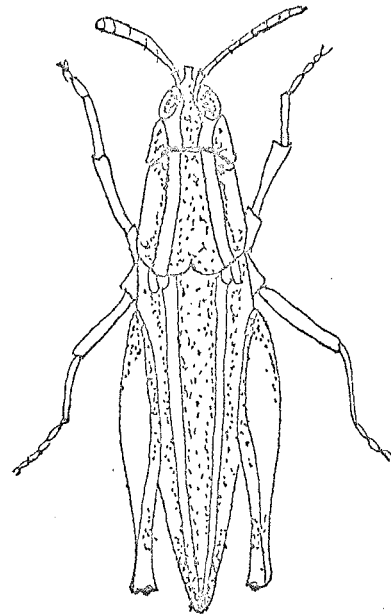
Banded



Pronotum Banded



Pronotum Striped



Striped.

FIG 7: Pattern Forms of Juveniles.

patches. The grey and brown integument resembled the colour of the shingle and the patterns broke the outline, thereby camouflaging the hoppers. Obliterative shading, consisting of a gradation of dark to light on the lateral surfaces, gave an illusory effect of flatness. It is therefore reasonable to consider the colours and patterns of the juvenile in terms of cryptic value to the hoppers in their favoured habitat.

Adult variation: Only two pattern forms exist in adults, but a wide range of distinctive colours are present. The two adult pattern forms are striped and unstriped (Fig. 8a, b). The stripes are more obvious in adults than in juveniles due to contrasting colours of the stripe and body. The unstriped category included some individuals with inconspicuous patches on the abdomen.

The frequency of striped forms relative to the unstriped in the adults was the same as that observed for the distinctly striped form relative to the other patterns in all instars ($\chi^2 = 1.02$, $p \doteq .95$). It is likely that striped sub-adults become striped adults and that all the other juvenile patterns become unstriped in the second-to-last and last moults. This is supported by the observation that several unstriped adults had faint patterns discernable on the head and pronotum which were masked by the total body colouration.

The colours of the females ranged from muted brown, muted grey (tinged with green), green (striped forms) to yellow. Males ranged from dark green to black and a few contained yellow especially on the lateral surfaces. Figure 6 shows the frequencies

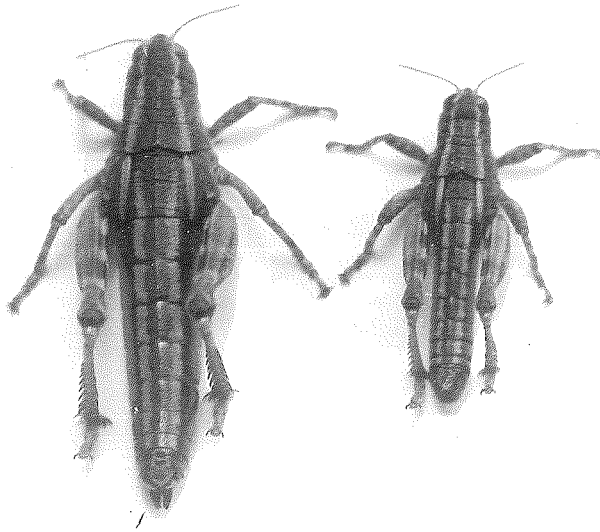


Fig. 8a. Adults of Striped Form of B. collinus
(Left, female; right, male)

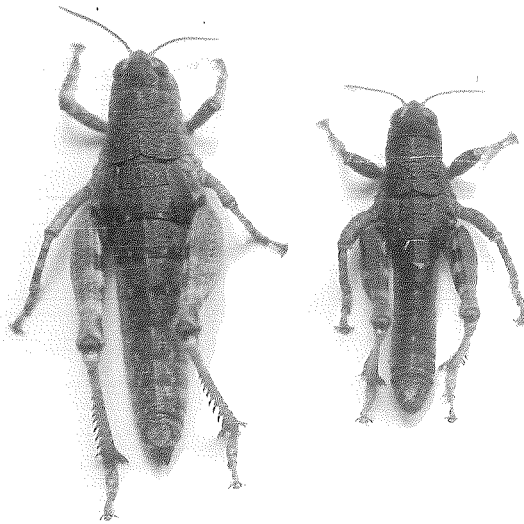


Fig. 8b. Adults of Unstriped Form of B. collinus
(Left, female; right, male)

of these colours in an intermediate habitat, the dorsal surface being used as an index to general body colour. It can be seen that the commonest colours in the females are muted brown and grey and dark green, and in the males, dark green. Although it is not shown in the figure, the presence of stripes in the females was associated with a greener body colour. Stripe colour ranged from dark brown, through orange to straw and yellow. All these colours in the adults closely resembled those seen in the general background of the study area, both in the tussock grassland and in the scree, (e.g., Snow tussock - green, orange, yellow and straw; Dead vegetation, leaves and twigs - grey; Bare earth - fawny-brown; Shingle scree - black, brown and grey).

The presence of such colour and pattern forms caused by genes at intermediate frequencies in a population of individuals is generally referred to as polymorphism (Falconer, 1964). The colour and pattern of the phenotypes observed appeared to be more cryptic against certain backgrounds or substrates than against others. The colours of the unstriped form, particularly those of the female and darker males, camouflaged motionless grasshoppers on shingle, on eroded bare soil patches, and on areas of dead vegetation (Fig. 9a). The striped form was more effectively concealed in the snow tussocks, especially when the longitudinal stripes on the body were aligned with the leaf blades, as the grasshoppers backed down toward the leaf bases. This was a common escape behaviour, after being disturbed (Fig. 9b).

Yellow in the integument of either striped or unstriped forms

Fig. 9: Different forms of adult *B. collinus* on different Backgrounds



(a) Dark unstriped
male on scree



(b) Striped male in
Chionochloa sp.

Fig. 9 Cont'd.



(c) Yellow striped female from grassland placed on scree.



(d) Dark striped female on scree.

made the grasshoppers particularly conspicuous on the scree (Fig. 9c)

On the present field evidence the observed variation can be associated with the heterogeneity of the environment which B. collinus inhabits. A variety of substrates were encountered as the adults basked on the screes, rocks and bare soil patches but moved to neighbouring plants to feed. Whatever substrate was considered, some of the individuals were camouflaged. The close resemblance of the colours and pattern of the striped form to grass suggests a selective (cryptic) advantage in grassland, while the unstriped form would be favoured on the screes and bare ground. Selective agents could be insectivorous birds such as pipits, Anthus novaeseelandiae (12 observed in study area), rock wrens, Xenicus gilviventris (3 observed) and Southern Black Gulls which are known predators on alpine grasshoppers, while Keas, Nestor notabilis and New Zealand Falcons (Falco novaeseelandiae) could be included as possible predators. Today's predators are not necessarily the same as those that acted as selective agents in the past. It is well known that the relationship between different colour forms is often complicated by the pleiotropic effects of genes associated with physiological characteristics (Mayr 1963). In these cases natural selection could act through the physiological advantages as well as through predation.

If disruptive selection is acting, different selective mortality of the forms would be expected in extreme habitats. This should be detectable from the relative frequencies of the forms in

these habitats. Hence, the frequency of striped to unstriped patterns and the frequency of the different colour forms were determined for the scree, intermediate and grassland habitats at 5,000'. These results are given in Table 2a.

TABLE 2a. Frequency of striped and unstriped adults in different habitats at 5,000'.

Habitat	Female Striped	Male Striped	Female Unstriped	Male Unstriped	Striped	Unstriped	Total
Grassland	23	18	56	64	41	120	161
Scree	7	20	23	49	27	72	99
Intermediate	3	5	10	16	8	26	34

TABLE 2b. Frequency of striped and unstriped adults at different altitudes.

Altitude	Female Striped	Male Striped	Female Unstriped	Male Unstriped	Striped	Unstriped	Total
4,500'	4	5	21	21	9	42	51
5,000'	3	5	10	16	8	26	34
5,500'	6	6	24	22	12	46	58
6,000'	5	4	10	13	9	23	32

No significant difference in relative frequency of pattern occurred over all habitats ($\chi^2 = 0.213$, $p \doteq 0.98$). It was also noted (Table 2b) that the relative frequency of the forms was the same

throughout the study area as shown by the comparison of samples at different altitudes ($\chi^2 = 1.368$, $p. \neq 0.7$). The relative proportions were about 1 striped to 3 unstriped, in both sexes. A difference in relative frequencies of colours was recorded, however, in samples taken from the grass and scree. Specimens taken from scree were darker in stripe and body colour and fewer yellow forms were present. (Figure 10 compares two females, one from grassland and one from the scree showing the colour difference.) The colour change does not necessarily indicate differences in selection; it may be the direct result of environmental differences on pigment formation (e.g., temperature, food or background colour). The constant pattern frequency suggests either that no selective difference between the phenotypes exists, or that the selective pressure was too slight to be detected or that other factors cancelled out the effect. One such factor could be individual movement from one habitat to the other (200 yards) but the observed change in frequency of colour forms does not support this. Another factor could be that the melanism rendered the stripe less conspicuous on the scree (Fig. 9d). Further, the results show that no preferred habitat is behaviourally selected by the two pattern forms of this species.

Mayr (1963) expressed the opinion that in most cases, genuine polymorphism in natural populations is maintained by superiority of the heterozygotes, regardless of any additional factors such as mosaicism of the environment that may contribute to the genetic diversity. The possibility of heterosis within B.collinus cannot



Fig. 10. Two striped female B. collinus showing lighter colouration of grassland specimen (left) compared with scree (right).

be overlooked. The genes causing the observed differences in colour and pattern, which could be linked to physiological characteristics, would be retained in the population at intermediate frequencies if selection was favouring the heterozygotes. The result that no difference in relative frequency of striped to non-striped forms exists between instars and adults in all habitats can be more easily explained in terms of heterosis rather than in terms of selective mortality on the different substrates.

However, both heterogeneity of the environment and heterosis are likely to be acting, giving a wide variation of discernable adult colour forms and two pattern forms with obvious cryptic value against certain substrates thereby adapting the population as a whole to the mosaic of habitats present.

The relative importance of the two components could be further investigated by the study of populations from different geographic localities. An extensive collection with information on the percentage vegetation cover and scree could determine the degree of correlation of striped forms with extent of vegetation and of unstriped forms with scree. At Cupola Basin (Nelson) the ratio of striped to unstriped was 1:1.5 (Wren Q. Green, pers. comm.) as compared with 1:3 from Temple Basin. This higher relative frequency of striped forms in Cupola Basin may be correlated with the reported observation (C. Burrows, pers. comm.) of a slighter higher percentage of grass coverage there than in Temple Basin. No striped forms were recorded, however, in specimens from near the northern periphery of the species range studied by Bigelow (in

press), which suggests that some factor other than the mosaicism of the environment is maintaining the polymorphism in B. collinus.

Since alpine grasshoppers are difficult to rear in the laboratory and may take about three years per generation, breeding experiments could not be carried out in this study. However, individuals did mate in captivity and eggs were deposited. Perfection of a rearing technique would greatly facilitate the genetical analysis of the colour and pattern variation. Laboratory selection tests on visibly different phenotypes in terms of physiological adaptations and cryptic advantages would also be interesting, and might throw more light on the ecological and evolutionary significance of the variation.

2. Mating between Colour and Pattern Forms.

The incidence of mating between the colour and pattern forms has a direct bearing on the taxonomic relationship of the different forms in a population and on the presence or absence of definite preferences in the choice of mates which would affect the frequencies of phenotypes produced.

In order to calculate the expected incidence of random mating between forms of B. collinus the sex ratio at the time of mating and the relative frequencies of the forms must be known. 31 pairs of grasshoppers in copula were noted in four days in February, but only 8 pairs were observed during a similar period later in March. This suggests that ovipositing activity is greater in February. Further, the sex ratio of adults in February was 88 ♀♀ to 92 ♂♂, and none of the constituent samples differed significantly from a 1:1

ratio ($\chi^2 = 1.99$, $p \doteq 0.6$). In March the sex ratio was significantly different on the scree ($\chi^2 = 16$, $p \doteq .005$), with a deficit of females. This could indicate that females were either diapausing or dying after laying, as suggested by Batchelor (1967) for B. collinus in Cupola Basin. However, at the time of highest ovipositing activity the sex ratio was 1:1.

The calculated ratio of striped to unstriped adults was 1:3 with no significant changes over the study area.

From these ratios the expected probabilities of the different pattern forms mating (if no mating preference existed) could be calculated. A population of 100 adults would consist of 76 unstriped (38 of each sex) and 24 striped (12 of each sex).

The expected probabilities of forms mating would be:-

$$u \times u = (0.76)^2 = \underline{0.578}$$

$$u \times s = 2(0.76)(0.24) = \underline{0.365}$$

$$s \times s = (0.24)^2 = \underline{0.058}$$

u = unstriped

s = striped

31 pairs of B. collinus were observed in copula in February; 15 were unstriped-unstriped (18 expected), 2 were striped-striped (2 expected) and 14 unstriped-striped (11.3 expected). The observed values did not differ significantly from the expected ($\chi^2 = 0.996$, $p \doteq 0.6$), indicating that mating was random between the forms. The observed incidences of mating in terms of colour were not large enough for statistical analysis but colour forms

were seen in most combinations in copula.

The observed variation in colour and pattern, then, was not the result of non random mating and must be maintained by other mechanisms in the interbreeding population. A strict morphological definition of a species might allot the different forms to separate species, but on biological criteria both forms must be considered as B. collinus, and the variation described in the present study is in fact a striking example of intraspecific variation within one population.

IV. CONCLUSIONS

Size, colour and pattern are variable in B. collinus. A mean clinal increase in size in all instars was observed with increasing altitude. Analysis of the instar distribution suggested that the increase size at higher altitudes was correlated with a retardation of development. It is likely that these phenotypic variations are the result of lowered mean temperature at higher altitude.

Colour and pattern were considerably variable within each instar but marked changes through to the adults was observed. The variation of juveniles was correlated with the preferred shingle habitat and appeared to be cryptic in function. In contrast to the juveniles, only two adult pattern forms were present; one of which (striped) appeared to be derived directly from striped juveniles, whereas the other (unstriped) appeared to result from the obliteration of the various other juvenile patterns. Colour and pattern variation in the adults closely resembled different aspects of the mosaic environment. The obviously cryptic nature of the different forms suggested selective advantage of the different forms on appropriate substrates. The colour and pattern forms were mating at random in the population.

Therefore the variation appeared to be an adaptation of the population as a whole to the variation of the environment which it inhabits.

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APPENDIX I. Table of calculated means of Femur Length (FL) Pronotum Length (PL) and Femur Width (FW) for each instar at different altitudes. (n = number in sample at right hand top of cell; units = mm.)

		4,500 ft		5,000 ft		5,500 ft		6,000 ft	
Adult	FL	14.2 \pm .17	(13)	14.5 \pm .11	(30)	14.3 \pm .08	(29)	14.8 \pm .08	(16)
	FW	3.9 \pm .04		3.9 \pm .03		3.9 \pm .05		4.1 \pm .02	
	PL	4.7 \pm .04		4.8 \pm .04		4.9 \pm .03		5.0 \pm .04	
VI	FL	11.9 \pm .04	(3)	12.1 \pm .06	(14)				
	FW	3.5 \pm .05		3.5 \pm .04					
	PL	4.4 \pm .07		4.5 \pm .04					
V	FL	9.5 \pm .07	(2)	10.0 \pm .15	(9)	10.0 \pm .15	(3)	10.4 \pm 1.3	(2)
	FW	2.8 \pm .02		3.0 \pm .08		3.0 \pm .06		3.3 \pm .16	
	PL	3.6 \pm .07		3.6 \pm .07		3.6 \pm .06		3.7 \pm .04	
IV	FL			7.8 \pm .04	(24)	8.0 \pm .12	(7)	8.1	(2)
	FW			2.3 \pm .02		2.4 \pm .03		2.3	
	PL			2.8 \pm .03		2.8 \pm .06		2.9	
III	FL			6.2 \pm .10	(7)	6.4 \pm .1	(6)		
	FW			1.9 \pm .01		2.0 \pm .07			
	PL			2.0 \pm .03		2.2 \pm .07			
II	FL							4.6	(1)
	FW							1.4	
	PL							1.4	
I	FL	3.3	(1)	3.6 \pm .05	(4)				
	FW	1.2		1.2 \pm .05					
	PL	1.3		1.2 \pm .01					

B. FEMALES

		4,500 ft	5,000 ft	5,500 ft	6,000 ft
Adult	FL	18.3±.17 (18)	18.7±.21 (15)	19.2±.10 (25)	19.5±.13 (13)
	FW	4.8±.06	4.9±.07	5.1±.03	5.2±.05
	PL	6.1±.03	6.3±.08	6.5±.03	6.6±.06
VII	FL		15.4±.12 (10)	15.3 (1)	16.5±.26 (3)
	FW		4.2±.06	4.5	4.8±.02
	PL		5.5±.09	5.3	5.8±.02
VI	FL		12.6±.13 (6)	13.2 (1)	13.0 (1)
	FW		3.6±.03	3.9	4.1
	PL		4.4±.04	4.7	4.7
V	FL		10.1±.07 (6)	10.1±.11 (3)	
	FW		3.0±.02	3.0±.06	
	PL		3.5±.08	3.6±.11	
IV	FL		7.9±.06 (22)	8.0±.13 (7)	8.1±.12 (3)
	FW		2.3±.02	2.5±.02	2.6±.03
	PL		2.7±.03	2.7±.05	2.9±.04
III	FL		6.2±.08 (5)	6.5±.08 (2)	6.3±.04 (2)
	FW		1.9±.01	2.0±.10	2.0±.04
	PL		2.0±.03	2.2±.02	2.2±.07
II	FL				4.8 (1)
	FW				1.6
	PL				1.6
I	FL				
	FW				
	PL				

APPENDIX 2. Frequency distributions of colours and patterns.

(i) Colour frequency of dorsal surface for all instars.

Dorsal Surface	Instar										
	I	II	III	IV	V	VI		VII		Adult	
					♀	♀	♂	♀	♂	♀	♂
Brown	9	5	11	28	5	4	3	1	2	-	-
Grey			9	24	3	2	1	-	3	-	-
Steely green			1	5	2	4	5	1	1	1	-
Muted grey								3		24	-
Muted brown								9		21	-
Dark green					1		2	2	4	14	68
Greeny yellow										2	1

(ii) Frequency of patterns in each instar.

Pattern	Instar								Adult
	I	II	III	IV	V	VI	VII		
Striped		2	6	17	4	6	8	106	
Pronotum striped			9	22	6	12	8	-	
Banded	9	3	6	10	1	-	3	-	
Pronotum banded			1	9	1	4	5	-	
Unstriped			-	-	-	-	5	432	