[1]Centre for Resource Management, P.O. Box 56, Lincoln University, Canterbury, New Zealand. Present address: 74 Toorak
    Avenue, Christchurch 4, New Zealand.
[2] Centre for Computing and Biometrics, P.O. Box 94, Lincoln University, Canterbury, New Zealand.

A 20-YEAR RECORD OF ALPINE GRASSHOPPER ABUNDANCE, WITH INTERPRETATIONS FOR CLIMATE CHANGE.

Summary: A 20-year capture-recapture study of alpine grasshoppers spanned three distinct sequences of abundance, featuring in turn dis-equilibrium, equilibrium and secondary cyclic equilibrium. This succession of population patterns in the most abundant species, *Paprides nitidus,* retained high stability between generations. It arose via superimposed life-cycle pathways and adaptive responses between grasshopper phenologies and their environmental constraints. The responses were identified by correlation coefficient analysis across extensive matrices (11 500+ correlations) of environmental records x time-lagged grasshopper estimators. An estimator of resident population members performed better than total population estimators. The observed retention of population stability despite shifts in the patterns of abundance implies some predictability, and potential effects of climate change (increased temperature, rainfall and raindays) are examined in a context of global warming. It is concluded that flora and fauna could eventually become depleted in alpine regions due to the displacement of grasshopper populations to vegetation-scree margins where physical weathering and vegetation instability are often pronounced.

The highly flexible *P. nitidus* life cycle emphasises a high level of variation in egg phenology, whereby alternative overwintering pathways (quiescence, diapause, extended diapause) lead to variable life-cycle durations. The schematic cycle accommodates two quite different species, *Sigaus australis* and *Brachaspis nivalis,* and is probably applicable to New Zealand's alpine Orthoptera in general. Population mortality sequences are identified throughout the cycle, and the 20-year census history suggests that a classic predator-prey response may arise between a native skink species (Reptilia) and grasshoppers.

Keywords: Grasshoppers; Acrididae; abundance; alpine; life cycles; diapause; capture-recapture; climate change.

Introduction

Long-term records of insect abundance fall into two broad categories (Miller and Epstein, 1986):

a) qualitative indices derived from outbreak or collection records - such data depict population peaks better than they do annual fluctuations, e.g., 100-year overviews of grasshoppers in Kansas (Smith, 1954), larch bud moth in Switzerland (Auer, 1971), carabid beetles in the Netherlands (Turin and den Boer, 1988), and the 50-to 70-year trends of tussock grassland moths in New Zealand (White, 1991);

b) quantitative direct estimations of abundance - such data usually cover shorter periods (rarely beyond 20 years) but with greater detail of annual fluctuations, e.g., the 16- to 26-year European studies of larch bud moth (Baltensweiler, 1968), pine looper (Klomp, 1968), winter moth (Varley and Gradwell, 1968), carabid beetles (Baars and van Dijk, 1984; den Boer, 1986), and psyllid bug (Whittaker, 1985).

The only long-term records of grasshoppers (Orthoptera: Acrididae) known to fall within category (b) are the present study over 20 years, and the exceptional 32-year study of Gage and Mukerji (1977, 1978). This Canadian survey annually sampled peak adult populations for the rural districts of every arable township in Saskatchewan (representing 15.4×10^6 ha) to relate species' mean densities to climate, soil type, vegetation and crop losses. In contrast to such regional measuring of macro-populations, the localised dynamics of alpine grasshoppers have been traced at one site in detail, and can now be projected to the macro-scale using the geographic spread of abundances recorded throughout New Zealand mountains by White (1975a). Despite varying dynamics across sites (e.g., alpine topography and weather are notoriously variable), flexibilities in the alpine grasshopper life cycle act as stabilising forces to limit the magnitudes of inter-generation change.

Two analysis objectives of the present study were:

a) to investigate the 20-year dynamic in relation to
   environmental variables; and
b) to resolve the longevity of eggs laid in the soil in
   order to clarify life-cycle dynamics.

A schematic cycle is proposed for a widespread
species, and given the similar pre-Pleistocene origins of
most of New Zealand's alpine orthopteran fauna, it is
likely to be broadly representative of related taxa. Its
generality is attributed to its mode of construction using
the 20-year population dynamic of biology-environment
interactions (c.f. life-stage studies *sensu strictu)*. By
virtue of the long-term data base, the potential effects of
a changing climate are interpreted from the combined
evidence of the life cycle and from grasshopper grazing
pressures in alpine grasslands and herbfields (see White,
1974b, 1975a; reviewed in White, 1978).

Methods

A 0.177 ha plot on a sunny NNE 20 - 30∞ slope, 1490-
1530 m a.s.l., was located in *Chionochloa* Zotov tussock
grassland at Camp Stream Saddle, Craigiebum Range
(Fig. 1; grid reference NZMS1, S66 182061; also
White, 1974b, Fig. 1 for photo; White, 1975b, Fig. 1
for contour map of the 'supporting study' area). The
plot was in part defined by natural features (topography
and scree margins) that created partial barriers to
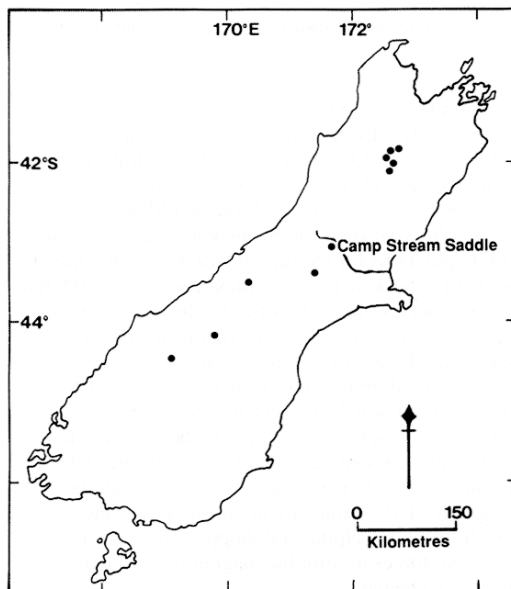grasshopper immigration and emigration. Three

Figure 1: *Location of Camp Stream Saddle study site and
comparative survey sites in South Island. New Zealand (see
text).*

flightless species were present: *Paprides nitidus*
Hutton, *Sigaus australis* (Hutton) and *Brachaspis
nivalis* (Hutton). Plant species composition in 1974 (via
point analysis) is listed by White (1975a), and nearby
meteorological stations recorded an array of climatic
data (unpublished Protection Forestry Reports, 'Climate
observations in the Craigieburn Range', 1967-1988;
unpublished DSIR Water Resources Survey records
1975-1988). The stations were Camp Stream, 1372 m
a.s.1., S aspect, 25º slope, 500 m from study plot, and
Ski Basin, 1555 m a.s.l., SE aspect, 2º slope, 1.5 km
from study plot.

Population estimates
The Jolly-Seber capture-recapture census method was
used (Jolly, 1965; Seber, 1965) with individual capture,
uniquely coded markings and immediate release of each
grasshopper (White, 1970, 1975c). The adult
population of each species was estimated annually from
1969 to 1988 between mid-February and early March
when the recruitment of newly emerging adults and the
mortality of the senescing generation was typically
nearly complete (White 1971a, b). The populations at
this time tend to be locally stable and minimally
dispersive and represent the resident populations of
maturing nymphs (White, 1975a). The earliest plot data
(1969-71) were extracted from a 4-year continuous
census over a larger area (see White, 1975b), whereas
1972-88 data were each obtained as a single annual
census. Over these latter years, each year's estimator of
species population size ($\hat{N}$) was computed from the third
(= central) sample in a sequence of five samples
(sample 1 = marking only, samples 2, 3, 4 = marking
plus recaptures, sample 5 = recaptures only). This
approach (also used at other survey sites in Fig. 1 - see
White, 1975a) optimises estimator accuracy and
precision while limiting census durations to 3-5 working
days per year.

Jolly-Seber estimators of between-sample
population gains ($\hat{B}$) cannot distinguish between adult
recruitment (new adults from the nymph population)
and immigration; nor can estimators of population
losses (1-ϕ. where ϕ = survival rate between samples)
distinguish between emigration and deaths. Although in
the few days of each annual census it might be assumed
that recruitment and death are negligible, it does not
follow that dispersal is readily estimated, because $\hat{B}$ and
ϕ are weak statistics (e.g., see Bishop and Sheppard, A
1973; Carothers, 1973). Furthermore, the estimator $\hat{N}$
confounds resident and non-resident members in
standard applications of the method to open
populations.

Indices to standardise estimates
Two refinements were sought for the present study:
a) a residency index and residency equation to

estimate resident members alone, i.e., to estimate the adult population size 'belonging to' the plot area from egg until adult recruitment (minimal dispersal occurs throughout nymphal development, White, 1974a), and from adult recruitment until the following year's census;

b) a phenological index to standardise sample timing against biological time (since the sample ratio of old: new adults varied between years relative to variable time lags in recruitment and mortality phenologies).

In 1984, an exceptionally low level of recruitment afforded the estimation of a residency index p (Appendix 1). Thereby an approximate solution of a residency equation is:

$$R = \left(\begin{array}{c}\text{known}\\\text{new}\\\text{recruits}\end{array}\right) + \left(\begin{array}{c}\text{unidentified}\\\text{new}\\\text{recruits}\end{array}\right) + \left(\begin{array}{c}\text{total}\\\text{old}\\\text{adults}\end{array}\right) + \left(\begin{array}{c}\text{resident}\\\text{fraction}\end{array}\right)$$

In order to solve this equation, the total number of currently marked members (females plus males) over all capture samples of an annual census was partitioned as follows for each species:

r = proportion of members known to be new recruits;
y = proportion of year-old marked adults from previous year;
g = proportion of gravid female non-marked adults of previous generation;
p = 1983-84 residency index over the full year (see Appendix 1).

New recruits were recognised by the paleness/softness of the integument (□3 weeks approximately since ecdysis) and gravid females were those with indisputably enlarged abdomens. A phenological index t to standardise the census timing against the earliness/ lateness of the annual phenology was then:

$$t = r/(r + y + g) \tag{1}$$

where high t values are associated with early seasons (i.e., with high r values, low y and g) and lower t values are associated with late seasons (i.e., with low r values, and y and g varying with the degree of extended survivorship in year-old adults due to lateness of season). Multiplying the Jolly-Seber estimator N value by the appropriate proportions, we may now solve the residency equation above:

$$R = \hat{N}(r) + \hat{N}(1-r)t + \hat{N}(1-r)(1-t)p$$
$$= \hat{N}(r + t(1-r) + p(1-r)(1-t)) \tag{2}$$

$1 -r$ represents the mixed age-pool of residual grasshoppers after subtracting known new recruits from the total marked $(M;$ see Appendix 1).

$\hat{R}$ values for the years 1969-74 are few because r and g parameter values (Equation 1) were either not robust or not recorded. An analytical use of such data had never been anticipated prior to the unexpected 1984 solution of a p value.

Data analysis

Multivariate analyses and multiple regressions were inappropriate, the former because variables act serially in the course of long and overlapping life-cycles, the latter because degrees of freedom can be heavily reduced by a combination of missing data values and 0- to 5-year data lags when regressing adult abundance on the pre-adult environment data. Correlation coefficient analyses were therefore conducted using GENSTAT 5, Release 1.3 (Payne *et al.,* 1987) to iteratively explore variable time-lags across an extensive matrix of grasshopper variables x environmental variables. The matrix comprised eight environmental variables (rainfall, rain-days, mean soil temperatures at 10 cm depth, mean air temperatures, ground frost-days, screen frost-days, snow-free vegetation days from July 1 to December 31, post-snow days from latest snow to December 31, all recorded daily at 0900 h) tested against the three grasshopper species. Primary tests were based on environmental data for selected months and combinations of months (e.g., March and April separately and March + April jointly) and on annual census data with 0- to 5-year time lags (e.g., 1985 February census data were tested separately against 1979-80, 1980-81, etc. to 1984-85 rainfall data, with time lags based on a 12-month year to each January 31). A selection of different estimators was also used within each grasshopper species (e.g., estimators based on $\hat{N}, \hat{R}$ and variations of $R,$ all with females and males separately and in combination), thus yielding 11 500 primary correlations (35 estimators x 55 month or month-combinations x 6 time lags). Secondary tests (see (d) below) expanded this total.

As census data are targeted at the new adult generation, correlations of step by step time lags of current census data against the environmental data of earlier years eventually reach back to all years of earlier life stages. A given lag (e.g., 27 months before a current February census) was identified with a specific life stage (e.g., the egg) based on a count-back of life stage phenologies through a life cycle. Various life cycle postulates (3-year; 4-year; a 3- and 4-year mix; a 3-year progressing to 4-year in the course of the study - see Discussion) were each assessed within the 35 estimators. Only 3- and 4-year alternatives could be tested by direct correlations of $\hat{N}$ and $\hat{R}$ with environmental variables, but all postulates could be expressed as progeny/parent indices, e.g., the index:

(female + male census in 'year of progeny')/
(female census in 'year of parents')

can be used to express different postulates of a parent-progeny lag, assuming if necessary. a 'switchover' year between 3- and 4-year life cycles (e.g., 1977 was used for one of the *Paprides nitidus R* estimators, based on an observed decline in abundance in 1980).

The assumption underlying all time-lag

expressions is inter-generational stability, i.e., progeny abundance on reaching the adult stage is assumed broadly comparable to parent abundance. Because the life-cycle postulates above are all plurivoltine (multiple years), inter-generational stability can still be present when inter-mixed years of higher and lower abundance arise from parent: progeny successions out of phase with one another, i.e., from overlapping 'broods' 12 months apart. Despite differences in the abundances of broods, the assumed stability means that variations are less frequent across the generation sequences of any one brood-line (e.g., in a 4-year life cycle, similar brood-years would be predicted in years $x, x + 4, x + 8$, etc.). In turn, the pattern and sum of life-table mortalities (intra-generational) are also assumed to be broadly similar between generations, such that counting time-lagged correlates backwards from the censused new adult stage is biologically comparable for the broods of different years.

No formalised guidelines exist to distinguish a spurious high correlation (low causality) from a valid correlation (where causality is probable). However, given the large number of correlations over sequences of related and unrelated estimators, it was possible to distinguish *repeating patterns* in the occurrences of high correlations (as reinforcing evidence of causality) from *random patterns* of occurrence (as non-reinforcing and therefore 'suspect' evidence). The weight of evidence within the matrix was therefore screened for significance to select the overall best performing estimator(s) for each species via the following steps, in order:

a) consistency of strong correlations with known biology;

b) evidence of causality in the pattern of spread of strong correlations across related grasshopper estimators (c.f. high correlations for an estimator in isolation);

c) comparisons of differing grasshopper estimators based on each estimator's mean coefficient value across a selection of the top 10 correlations that fulfilled steps (a) and (b);

d) time-series truncations (omitting some data years, as necessary) to standardise degrees of freedom in comparisons of high-performance estimators;

e) assessment of data robustness (including graphic techniques of plotting regressions) across selected estimators and correlations;

f) life-cycle consistency across all selected correlations of the best-performing estimator(s).

Results

Population Estimates

In total, 7849 grasshoppers were coded from 1972-88 ($\bar{x}$ = 491 year^{-1}, annual ranges 371 - 752), and yielded

4408 recapture records ($\bar{x}$ = 276 year^{-1}, range 185-397). Two statistics of the selected central samples 1972-88 (combined species) are the proportion recaptured, α ($\bar{x}$= 0.31, range 0.19 - 0.41) and the probability of capture, $\hat{P}$ (8 = 0.21, range 0.16 - 0.33). A further 5728 adults had been coded in the 1968-72 continuous census, and in keeping with the long-term annual census, $\hat{N}$ is computed for 1969-71 using only selected data sub-sets and a modified analysis to correct for dispersal rates (see White, 1975b).

The Jolly-Seber $\hat{N}$ estimators for *P. nitidus* (Fig. 2A) suggest three temporal sequences of abundance, 1969-1988:

Sequence 1 (to 1972) - dis-equilibrium between consecutive broods;

Sequence 2 (1973-78) - equilibrium across consecutive broods;

Sequence 3 (from 1979) - secondary cyclic phasing of broods ('secondary' because brood overlap contributes more strongly than parent: progeny successions).

There was no 1976 census (Fig. 2A) but field observations of late-instar nymph abundance in the February 1975 adult census of *P. nitidus* pointed to a prevailing stability through 1976 (supported also by an independent census of nymphs in two other plots in November 1974 -November 1975). Likewise, in February 1988, the small numbers of mid-ins tar nymphs forecast a low adult recruitment for 1989 to reinforce the prevailing cyclic sequence for yet a further year.

The less numerous species (Fig. 2C, 2D) could not be analysed in this way because $\hat{N}$ estimators and Equation 1 parameter values were robust in some years only. The total numbers marked *(M* values) were therefore plotted and over most years tend to reflect relative abundances. Only in years of higher abundance was *M* notably limited by sampling effort. Fig. 2C has, in addition, an analytical problem for *N* values. The small numbers of *S. australis* necessitated the combining of the sexes despite a known failure in the capture-recapture assumption of equal catch ability in the original 1968-72 study (see White, 1975b). It is likely, however, that $\hat{N}$ biases are smaller in the annual census context of five closely-spaced samples.

Indexed population estimates

The residency estimator $\hat{R}$ (Fig. 2B) strongly reduces the above 1978-79 abundances of *P. nitidus* and . highlights in particular a pronounced divergence of the 1979 sex ratio in favour of females. The Sequence 3 cyclic phasing of $\hat{R}$ is also more marked, but is clearly waning by 1987 (note the failure of female abundance to increase substantially). Sex ratios strongly favouring males are evident for the peak years 1983 and 1987.

In *P. nitidus,* annual values for the Equation 2 terms *t(1-r)* and *p(1-r)(1-t)* were respectively in the
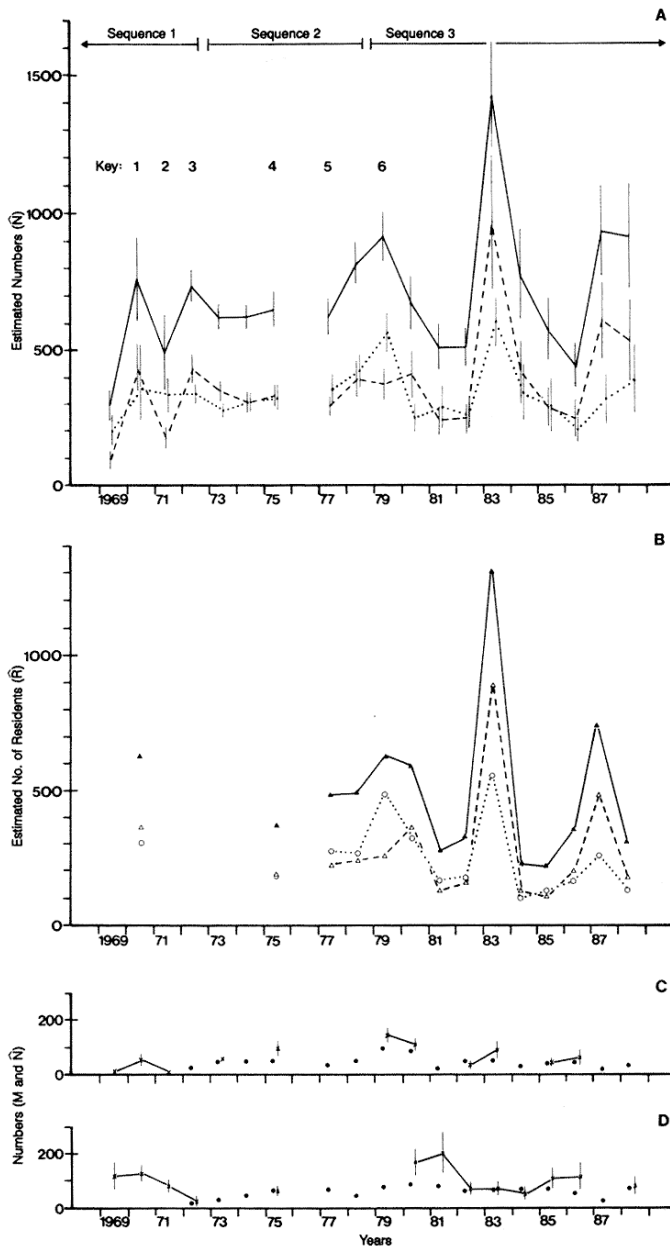
Figure 2: *Estimates and standard errors of population sizes 1969-88. (A)* Paprides nitidus: *Jolly-Seber estimates by sexes, indicating three sequences of abundance and a key to notable environmental variables (see below); (B)* P. nitidus: *residency estimates by sexes; (C)* Sigaus austral is *and (D)* Brachaspis nivalis: *Jolly-Seber estimates and numbers marked (M, solid circles).*
Key: *...... female,- - - male, -combined sexes (joint estimator, not a summing of separate estimates). 1 - Many female adults recruited October 1969; 2 - Heavy emigration (?) to slopes of southerly aspect November 1970; 3 - Late snows in spring and summer 1971; 4 - Regular rains and vegetation vigour pronounced 1974-75; 5 - Late snows to December 1976; 6 - Heavy Chionochloa flowering February 1979, and peak skink abundance.*

ranges 0.136 - 0.699 and 0.012 - 0.134 (range limits that were exceeded by the other two species only when data were weak). The effect of annual variations in the residency index p is therefore low, and the residency equation estimate $\hat{R}$ is influenced mainly by r and t. As their respective values for *P. nitidus* were in the ranges 0.03 - 0.27 $(\bar{r} = 0.10)$ and 0.14 - 0.90 $(t = 0.56)$, $\hat{R}$ is most influenced by *1-r*.

Data analysis

The screening steps (a) - (0 (see Methods) identified *P. nitidus* $\hat{R}$ estimators based on the Equation 1 phenological index as marginally superior to a similar series of estimators weighted towards female parameter values (using a different phenological index), and superior to $\hat{N}$-based estimators. Overall, the highest correlation coefficients belonged to $\hat{R}$ progeny/parent indices that were based on an assumed 4-year life cycle (Table 1), i.e., within the available data span 1975-88 (Fig.2B). A nearly comparable estimator was the $\hat{R}$ index based on a 1977 'switchover' year between 3 and 4-year life cycles (i.e., maturation of the progeny of 1977 new adults was split between 1980 and 1981), while one set of correlations favoured $\hat{R}$ values directly (see Table 1). Such results tend to endorse the validity of $\hat{R}$ estimation procedures. A striking feature of the analyses was that most significance focused on the egg stage (i.e., 2- to 4-year lagging of estimators). A composite life cycle based on significant correlations and published evidence is proposed for *P. nitidus* in Fig. 3. Key mortality sources are also shown. The cycle basically takes 3 years, but Table 1 evidence suggests that this seldom occurs with the present climate. White (1975a, 1978) stated 3 years assuming a 1-year egg stage, but correlations now suggest that this may rarely happen, at least for most members of most broods. Note that nymphal development between egg and adult is in most years completed within 12-13 months.

The prime determinant of a minimum life-cycle duration is the March + April soil temperature regime (Table 1, Fig. 3). Temperature effects occur 22-23 months before the adult census and, because the best performing correlate is $\hat{R}$ *rather than* the $\hat{R}$ progeny/parent index, higher soil temperatures favour the completion of egg development *independent of brood.* i.e., of egg age. Analysis of the *P. nitidus* matrix further points to an extended diapause because two November correlates are lagged 27 months before the February census: mean monthly air temperatures and numbers of screen frosts (Table 1). As eggs are in the soil, low air temperatures and many frosts at this time appear to postpone hatching by forcing development through an extra annual cycle. Such variable seasonal events tend to be specific to some broods but not others and thus the grasshopper correlate here is an $\hat{R}$ progeny/

parent index (rather than *R,* as above).

The remaining *P. nitidus* correlations of Table 1 identify key mortalities in the life cycle. The mortalities relate principally to the egg stage and are determined indirectly from rainfall and mean air temperature correlations. November-January rainfall (i.e., over the normal period of oviposition; White, 1974a, Fig. 6) is correlated with $\hat{R}$ progeny/parent 4-year indices that have been lagged by 37-39 months before progeny census. The highest correlation with an individual month is for January $(r = 0.89, p = 0.001,$ n = 9), and correlations between $\hat{N}$ and January rainfall are equally strong and more robust $(r = 0.72, p = 0.007,$ n = 17). As positive correlations imply survivorship, it follows that egg *mortalities* are negatively correlated with rainfall. Table 1 also shows February air temperatures to be inversely correlated with $\hat{R}$ progeny/parent 4-year indices, lagged by 36 months, while post-snow days to December 31 are similarly inversely correlated but lagged by 2-4 months. An inverse relationship implies a possible year's delay in adult recruitment in late snow years proportional to snow-lie duration (Fig. 3), and on extreme occasions late-instar nymph mortalities may occur (White 1974b, p. 363).

Sigaus australis correlations (Table 1) reflect the lack of suitable $\hat{R}$ estimators (Fig. 2C). The negative correlation with rainfall when *M* is lagged 50-51 months hints at a 5-year cycle, c.f. the positive correlation 12 months later for *P. nitidus*. In contrast, the timing of the negative air temperature correlation (Table 1) implies an extended diapause as in *P. nitidus* (Fig. 3), and coincides in part with November raindays via their cooler temperatures $(r = -0.667, P < 0.05,$ n = 11). The actions of these correlations appear tied to 4-year cycles, and they do not coincide with the high rainfall years that delay life cycles (see Discussion).

Discussion

Population dynamics

The dis-equilibrium of Sequence 1 in Fig. 2A coincided with the 4-year intensive study (White, 1975b) (a salutary caution for any short study), and probably reflects in particular the temporal and spatial disruptions of late snows. Temporal disruption is evident in the atypical recruitment of many female adults in October 1969 (Fig. 2A, Note 1). Females include one more nymphal instar than the smaller-bodied male (Hudson, 1970) and their completion of development lags males by several weeks (Fig. 1 in White, 1974a). Thus the 1969 census of females under-represented brood size because many maturing nymphs deferred their final ecdysis until after the 1969 winter. The 1970 census was in turn enlarged by the combined recruitment of broods from both 1969 and 1970. At no other time in the 20-year record is .such a pronounced brood-merger

Table 1: *Correlations between population abundance estimators and environmental variables, selected via six screening steps for each grasshopper species (see text). Correlates are ordered within species by the count-back sequence of months (i.e., correlation lag time) before the February adult census. $\hat{R}$ = residency estimator; $\hat{R}^{PP}$ = progeny/parent index based on $\hat{R}$ values and a 4-year life-cycle postulate; M = annual number of adults marked; $\hat{N}$ = annual estimate of population size including non-residents; N/A = not applicable; r = correlation coefficient; p = probability level; n = sample size (years of correlated data, i.e., excluding years lost as lag time).*

Species	Estimator	Life-cycle postulate	Correlate	Lag (months)	r	p	n
P. nitidus	$\hat{R}^{PP}$	4-year	Nov + Jan rainfall	37-39	0.94	<0.01	7
	$\hat{R}^{PP}$	4-year	Feb air temperature	36	-0.79	<0.01	10
	$\hat{R}^{PP}$	4-year	Nov air temperature	27	-0.87	0.001	10
	$\hat{R}^{PP}$	4-year	Nov screen frosts	27	0.85	<0.01	10
	$\hat{R}$	N/A	Mar + Apr soil temperature	22-23	0.84	<0.001	12
	$\hat{R}^{PP}$	4-year	Post-snow days to Dec 31	2-4-	0.91	<0.01	8
S. australis	M	N/A	Nov + Dec rainfall	50-51	-0.81	<0.01	11
	M	N/A	Nov + Dec air temperature	26-27	-0.70	<0.01	14
	M	N/A	Nov raindays	27	0.73	<0.01	12
	$\hat{N}$	N/A	Feb raindays	24	-0.90	<0.01	8
B. nivalis	M	N/A	Nov + Dec soil temperature	26-27	-0.81	<0.001	13

suspected.

Spatial disruption may also occur owing to snow (Fig. 2A, Notes 2-3). The study area lies below a saddle that acts as a spring dispersal route for grasshoppers moving from the north to the south slopes (White 1975b, pp. 177-178) and snows lie longer below the south edge of the saddle. Whereas spring conditions favoured dispersal in 1970-71 (shown by a low 1971 census for the study area), late spring and summer snows in 1971- 72 may have blocked some dispersal to give a high 1972 census due to retention of would-be dispersers. In 1979 (Fig. 2A, Note 6), a different spatial mechanism of retention may have similarly contributed to a census peak. Heavy flowering of the physiognomic dominant *Chionochloa* (tall tussock) created unfavourable heavy shading within the south aspect canopy and may have 'forced' dispersing grasshoppers back to !.he north study area. Both mechanisms illustrate that *N* estimators are prone to spatial disruptions and therefore fail to standardise residency across the years.

The reasons for a 1979 peak may not, however, be explainable by a single factor. The increasing grasshopper numbers during the last part of Sequence 2 include a year of notable vegetation vigour (Fig. 2A, Note 4), four years before the 1979 peak. If a 4-year life cycle is assumed, the diets available to females recruited in 1975 could have increased their maturing progeny numbers (3.33 per parent female, based on *R*) for a high 1979 census. Had there not also been late spring snows in 1976 (Fig. 2A, Note 5) with their sequel of another possible brood-merger (1977 + 1978, thereby increasing the 1978 census), the margin of the 1979 peak above the 1978 census could well have been greater. The initiation of Sequence 3 may therefore have resulted indirectly via the chance sequencing of

two favourable weather factors: regular rains in 1974-75 and, three years later, high cumulative temperatures in 1977-78, necessary for induction of the mast flowering of *Chionochloa* in 1979 (see Mark, 1968). A

For *Sigaus australis.* the two estimators $\hat{N}$ and *M* in combination suggest similarities with the dynamics of *P. nitidus* over the period 1969-84, but a quite different 20-year dynamic is apparent in *Brachaspis nivalis.* While *P. nitidus* and S. *australis* share biological and ecological similarities as vegetation dwellers, *B. nivalis* inhabits the vegetation-scree ecotones and appears capable of multiple ovipositions (Mason, 1971). Furthermore, censuses of *B. nivalis* are prone to greater sampling errors because scree rock makes physical capture of grasshoppers difficult and because the population was concentrated along plot margins (and beyond) rather than spread throughout the study area. Interpretations of Fig. 2D should therefore give weight only to major trends.

Egg biology and the life cycle

Figure 3 allows that warmer autumn soils may permit the pre-diapause embryo to develop in full (up to the completion of anatrepsis; Mason, 1971) within 3-5 months of oviposition. In laboratory conditions, Mason (1971) observed *P. nitidus* anatrepsis from 54 days, but also recorded apparently healthy embryos at 24 months. Early oviposition (from November; White, 1974a, Fig. 6) is thereby likely to favour a 3-year life cycle if rates of egg development are not arrested by cool March + April soil temperatures; in consequence, the probability of broods being split between 3- and 4-year life cycles appears high due to the lateness of some oviposition. Favourable conditions may not guarantee pre-diapause completion, however, and late ovipositions (if not all
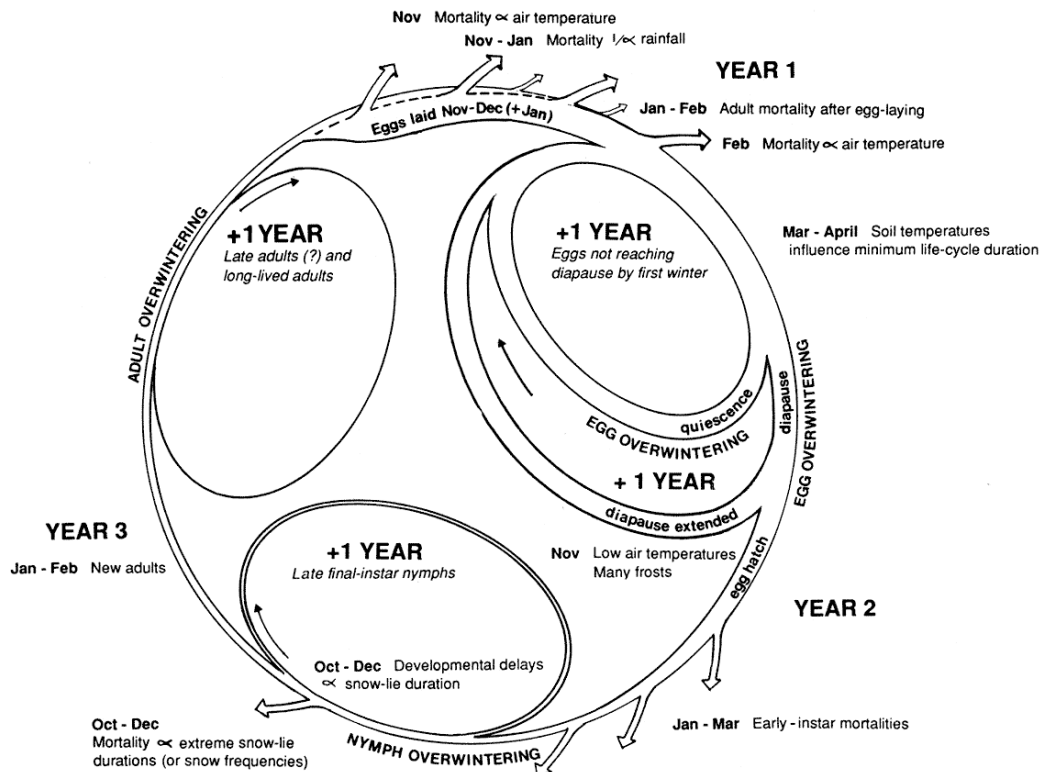
Figure 3: *Proposed life cycle of* Paprides nitidus *populations, based on field records of marked individuals and environmental correlations with abundance estimates.*

oviposition in some brood-years) may commit the minimum life cycle to 4 years. Overwintering eggs become quiescent if diapause has not been reached (Fig. 3), and proceed to a second (diapause) winter.

Post-diapause development is known to be temperature-related and may take 3 months until eggs hatch (Mason, 1971, for *Brachaspis).* In *P. nitidus,* the postponement of summer hatching by a full year due to unfavourable November temperatures and frosts (Fig. 3, Table I) occurs within 3 months of calendar hatching dates. In agreement, the Table 1 selection of the 4-year life cycle index as the superior postulate based on correlation analysis implies that eggs at least one year old must be dominant in the extended diapause pathway. Nothing is implied, however, about the relative importance of the extended diapause and quiescence pathways, nor about their relative frequencies of use, but the majority of eggs of most or of all broods cycled via one or other over the years 1975-88. When conditions dictate, a brood might logically split and use both pathways simultaneously; and if the major pathway over most years was that of extended diapause, presumably this could be by-passed in some years of non-limiting November conditions to

achieve 3-year life cycles. However, because evidence of 3-year cycles is weak, for the November conditions in most years were not unfavourable, it appears more likely that quiescence is frequently the norm.

The likelihood of some eggs not hatching until a third summer is unknown, but 3-year durations have been recorded for several alpine acridid species in North America (see Ushatinskaya, 1984, Table 1). Figure 3 is unchanged by this possibility, which could arise if an egg was quiescent in the first winter, in diapause for the second, but then blocked in its post-diapause development by unfavourable November conditions. Deferred diapause termination is presumably optimal for survival because a nymph hatched from an egg in late summer or autumn would be unable to complete the minimum development to enter overwintering nymphal quiescence (as 3rd and 4th instars; White, 1974a, 1978). Sensitive stages of development must be synchronised with favourable conditions (Ingrisch, 1990).

Late-instar nymphs and adults are also capable of extended life cycles (Fig. 3; White, 1974a) but in most years relatively few individuals have prolonged longevities. The adaptability clearly permits gene-flow between broods and on occasions may strongly favour

brood survival, e.g., females in 1969 (see Population dynamics).

Key mortalities in the egg stage of *P. nitidus* (see Results) might be explained by egg-pod desiccation after laying, and heavier predation favoured by drier soil and/or drier weather conditions. However, recorded alpine rain frequencies make egg-pod desiccation unlikely (see review of soil moisture effects on North American Acrididae; Hewitt, 1985), although dry soil surface temperatures are presumed to be high on occasions. Predation, therefore, appears the more likely possibility, as also implied by the February air temperature correlation with a 36-month lag (Table 1). An increase in predation must occur in conditions more favourable (i.e., warmer) for predator activity, for a higher temperature-lower survival relationship here would contravene developmental physiology over normal temperature ranges. Note also that if a 3-year life cycle occurred (i.e., no extended diapause), the higher November temperatures that break diapause (Fig 3, year 2) would at the same time favour predation on newly-laid eggs (Fig. 3, year 1). The primary and only known egg parasitoid is the wasp *Scelio* sp. (Hymenoptera: Scelionidae; Mason, 1971). Species of this worldwide genus all have similar biologies: adults are active during sunny periods, predation occurs soon after the grasshopper egg pod is laid, and all eggs in the pod eventually suffer mortality (Baker, 1983). Other potential egg predators (e.g., birds, lizards, mice) appear to be few, but of possible interest are casual observations of the skink *Leiolopisma nigriplantare* (Peters) *(sensu lato;* Reptilia: Scincidae). Its numbers were most conspicuous during the latter years of Sequence 2 (Fig. 2A), with an apparent peak in 1979-82. Although the skink's dietary preference is unknown, the steady 1973-79 equilibrium phasing of grasshopper broods might have induced a classical lagged predator-prey response, peaking as grasshopper numbers fell at the onset of Sequence 3.

The *Sigaus australis* evidence of egg mortality due directly to rains (Table I) is clearly contrary to *P. nitidus* biology (Fig. 3) and also contrary to typical acridid biology in well-drained soils (e.g., Hewitt, 1985). It is therefore concluded that high November + December rainfall must interfere with S. *australis* oviposition, and in support, White (1974a) has noted the delayed onset of oviposition and more stringent temperature and insolation responses in this species. Note further that the site represents the species' northern distributional limit and the maxima of its geographical and altitudinal clines in body-size (Bigelow, 1967). Seemingly, the species may not be very successful in oviposition in some years and, if 5-year cycling reflects extended nymph development (as in Fig. 3), then February raindays (Table 1) may reduce and delay the success of its nymph broods. This is not surprising for a species with large-bodied females that are tightly

constrained by the energetics of life-cycle completion, for if final instars are not delayed, they need to achieve the highest known production efficiencies in Orthoptera in order to complete their nymphal growth over 8 weeks of summer (White, 1978). Thus, some overlap of 4- and 5-year broods may be implied for this species.

The *Brachaspis nivalis* correlation (Table 1) may not be open to direct interpretation using Fig. 3 because of likely differences in biology, including multiple oviposition (see Mason, 1971), and a total lack of field knowledge on oviposition sites (e.g., White, 1974a). The species' oviposition possibly occurs out of sight in the scree subsoils below rock, and hence soil temperatures may be a better micro-environment index of the rock interstices than are external air temperatures. If true, this correlation might parallel the *P. nitidus* November correlations of Fig. 3 and lead to extended diapause, assuming that similar species' adaptations occur in the breaking of diapause.

Egg diapause and population dynamics

Egg biology has been inferred from long-term adult censuses. In population terms, a biology of superimposed life-cycle pathways is virtually indeterminable by direct field studies of the egg, given the physical, biological and temporal complexities of the alpine conditions. The evidence of correlations must therefore suffice as a field-based extension of the laboratory studies of Mason (1971), subject to interpretative caution. In support, the correlations make sense against the limited details of egg biology in the orthopteran literature.

The crux of acridid egg biologies is the unresolved nature of diapause-regulating processes. Hilbert, Logan and Swift (1985) proposed and simulated regulation as non-linear functions of temperature for *Melanoplus sanguinipes* in both its bivoltine (southern U.S.A.) and univoltine (northern) populations. Under their hypothesis of two processes acting in parallel, "the mean rates of the diapause regulating process and morphological development relative to each other determine whether or not morphogenesis is interrupted, and the length of the resulting diapause". The non-diapause/diapause model interprets the function of diapause at higher latitudes as the prevention of autumn hatching with its consequent certainty of winter nymph mortality. In Fig. 3, the extended diapause of high-altitude species also implies similar prevention, and moreover, because unfavourable hatching conditions may recur over consecutive springs, extended diapause might repeatedly block morphogenesis and repeatedly add to life-cycle duration. In long-horned grasshoppers (Tettigoniidae), prolonged diapause is known to add up to 6 years beyond the minimum life-cycle duration (Ingrisch, 1986, Fig. 12).

The *M. sanguinipes* model emphasises process

rates and thereby corresponds well with the March + April soil temperature correlate of *P. nitidus* (Fig. 3) acting as an autumnal marker of developmental degree-days since oviposition. Thus soil temperature regimes may reflect the relative progressions of the diapause regulatory process and of morphological development as anatrepsis nears completion in readiness for diapause. In such a threshold mechanism the earliest-laid eggs have a clear advantage, provided the March + April temperatures permit attainment of diapause-readiness. In present climate conditions, the likelihood of a 3-year life cycle appears marginal for *P. nitidus,* but may be realised occasionally for partial if not whole broods. The model of Hilbert *et al.* (1985) further accommodates the variable voltinism observed in *M. sanguinipes,* including the cases of split broods and of species with 'strong' diapause. New Zealand alpine grasshoppers have 'strong' diapause and their biologies appear to fit well within the model hypothesis if it is extended to explain the adaptations of plurivoltine life cycles. The eggs of such life cycles can include up to two independent diapause stages (Ingrisch, 1990).

It remains to demonstrate positively the biological mechanisms that end orthopteran diapause. Diapause induction mechanisms have received close attention (e.g., Dean, 1982; Saunders, 1982) but inferences that some acridid species require two cold periods to break diapause (e.g., Kreasky, 1960; Mason, 1971; Burleson, 1974) are now shown to be suspect. Figure 3 pathways clearly illustrate that environmental circumstances can explain two (or more) cold periods in the above observations without an obligatory requirement for dual exposures. Observations must discriminate between the inherent biological factors breaking diapause and the limiting environmental factors so often present. Given a process-rate model, it may be that diapause completion is more a function of elapsed diapause development and its phenological timing than of specific diapause-breaking stimuli (see Tauber and Tauber, 1976).

Examples of diapause among indigenous New Zealand insects are few, and the current evidence supports Morris (1989) in re-opening questions of diapause incidence and value in the temperate, oceanic climate. His review includes egg diapause in lowland acridid and gryllid species, and taken in conjunction with the alpine data of Mason (1971) and of this study, a widespread incidence of orthopteran diapause appears likely (d. Ramsay, 1978; Roberts, 1978). Mason concluded that its probable origins are pre-Pleistocene, and Fig. 3 demonstrates that it confers survival value against un favourable climatic conditions (c.f. Dumbleton, 1967). This benefit is conferred through the egg stage to subsequent life stages. Thus, moderately strong life-cycle synchronisation appears to be more an outcome and means of survival (see Ingrisch, 1990) than a pre-determining reason (c.f. Morris, 1989).

The inter-generational stabilities of the present grasshopper species are only partly explained in terms of their phenologies being adaptable within the short-term annual environment, for the vagaries of alpine weather acting on such phenologies might still lead to population instabilities across the years. The observed stabilities are also achieved by delaying compensatory responses (e.g., deferring the completion of egg development for a full year when conditions are unfavourable) because life cycles are long and brood-splitting can occur across consecutive years. The lags of compensatory responses offset the disrupting impact of a temporarily unfavourable environment (e.g., see Takahashi, 1977), and the low grasshopper fecundities also restrict ranges of abundance. Food is not usually limiting (White 1974b, 1975a, 1978) and feeding selection appears to be adapted to a marginally positive daily energy balance (White, 1978). This conservative energy strategy (and nutrient balancing?) may further contribute to the observed population stabilities.

Climate change

In a context of climate change, specialist adaptations can be sensitive to relatively subtle disturbances. Despite the flexibilities and depth of evolutionary adaptations, current population dynamics reveal propensities for fundamental shifts (e.g., the three sequences of Fig. 2A) in response to particular environmental conditions. Gradual climate changes might also affect density regimes. The range of recorded densities of grasshoppers for some of the more highly populated alpine grasslands/herbfields of New Zealand (Fig. 1) is 1779 - 18 866 adults ha^{-1} (= c. 3000 - 53700 adults ha^{-1} of living ground-cover; White, 1975a). A 20-year interpretation of the population limits represented by these ranges (Appendix 2) places the present study in geographic context.

In the following interpretations, the Fig. 3 life cycle is used to anticipate possible effects of specific climate changes. In the event of warming temperatures (e.g., see Salinger *et al.,* 1989; Anon, 1990), outcomes might include:

* life-cycle durations more frequently of minimum length;
* higher egg mortalities;
* lower nymph mortalities given the more favourable developmental temperatures, offset (possibly) by more favourable conditions for predators;
* increased population displacement to vegetation margins to escape denser plant canopies (if climate not arid), leading to further increases of grazing pressures along vegetation-
* scree ecotones (see White, 1974b, p. 366); population movement to higher altitudes to offset the higher respiration costs of temperature increases and to thereby avoid negative energy

balance due to feeding strategies that restrict daily food intake and energy gains (see White, 1978);

* greater grazing pressures on upslope vegetation since alpine substrates limit upslope spreading and occupancy by plants. The greatest consumer-producer imbalance in the survey of White (l975a) occurred at upper vegetation limits where the highest grasshopper densities on record depleted herb-fields the most aggressively.

In a case of greater rainfall and more raindays (e.g., see Salinger *et al.,* 1989; Anon, 1990), the seasonal distribution of rainfall would be an important determinant of grasshopper dynamics. Assuming rains were spread throughout the active grasshopper season (spring to autumn) and were combined with a higher temperature regime as described above, outcomes might include:

* more life-cycle delays (and therefore a move away from minimal durations) unless rain is frequently interspersed with favourable dry warm spells to sustain the development cycle, and/or the active season is lengthened;
* possible interference with oviposition (see comments on S. *australis* above) and thereby the regional distributions of species;
* lower egg mortalities from predation (c.f. disease, below);
* higher nymph mortalities among early instars unless summer rains tend to be brief and frequently interspersed with feeding opportunities;
* an increase in grasshopper pathogens, nematode worms (Mermithidae) and mite pardSites (Trombidiformes) from the currently low to negligible levels recorded by Mason (1971) (see also Baker, 1983; Hewitt, 1985);
* a greater vegetation vigour and food quality but, less favourably, greater canopy shading within tall swards, further increasing population displacement towards vegetation-scree ecotones (see temperature projections above).

Note that both sets of projections have in common the following:

* population displacement to the vegetation-scree margins where physical weathering and vegetation instability are often pronounced;
* upslope movement towards the least productive upper vegetation (herbfield) limits.

In the openness of such boundary habitats, any net increases in grasshopper numbers beyond current levels are potentially destabilising for many already fragile systems of plants. It follows that the projections may apply only to the initial consequences of climate change and not necessarily to the attainment of new equilibria. Their eventual outcome could be a more depleted endemic flora and fauna at the altitudinal extreme (see also Hay, 1990). Moreover, as a dominant herbivore, the sun-loving grasshopper may be a key indicator of climate-induced change for other faunal elements in the sub-alpine/alpine zone.

Acknowledgements

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Appendix overleaf

Appendix 1: *Derivation of the 1983-4 residency index* p, *illustrated by the combined data of the three grasshopper species. Small-sample bias is lessened by combination of consecutive samples (within years) to obtain between-year comparisons.*

1984 (female + male)

No. of newly marked grasshoppers, all samples (m_1)	= 496
No. of 1983-marked grasshoppers, all samples (m_1)	= 32
Total no. of marked grasshoppers (M)	= 528
Proportion ofml recaptured, all samples	= 0.38
Proportion of M recaptured, all samples	= 0.36

1983 (female + male)

Proportion of M recaptured, all samples	= 0.42

The 1984 recapture statistics 0.38 and 0.36 confirm equal catchability of newly-marked and 1983-marked members $(M$ is cited in lieu of m_0 because few 1982-marked individuals were captured in 1983). Not many members of m_1 in 1984 were newly recruited, and body size and colour suggested most others had been adults at the time of the 1983 census (but not necessarily in the study area).

A guesstimate of 1984 recruitment is 10% of $M,$ i.e., 90% of total members are assumed to be ≥1 year old. An index of marked + non-marked survivors that had retained residency over the 1983-4 year is:

$$p \approx (1/0.42 \times 32/528)/0.90$$
$$\approx 0.16$$

where retention of residency ('belonging to' the plot area) does not exclude temporary emigration in the course of the year.

Appendix 2: *A temporal interpretation of the survey densities of White, 1975a.*

The $\hat{R}$ maximum numerical difference between consecutive years is 5.5x for *P. nitidus* (1983-84, Fig. 28) and the 20-year mean using $\hat{N}$ values is 1.49x (Fig. 2A, maximum 2.80x). As equation 1 and 2 parameter values are highly site-specific, $\hat{N}$ relativities alone might hold for other survey sites (Fig. 1 and White 1975a). If it is assumed that the 1973 and 1974 survey data fall within similar 20-year relativities site by site, then individual site limits can be approximated to be somewhere between $\hat{N}/2.80$ and $\hat{N} \times 2.80$. Hence upper and lower boundary survey estimates now become 635 - 4981 adults ha^{-1} (lowest site $\hat{N} = 1779$) to 6738 - 52 825 adults ha^{-1} (highest site $\hat{N} = 18 866$). The highest extreme corresponds closely to the survey maximum of 53 700 adults ha^{-1} of living ground cover, and probably represents a maximum attainable density for the site conditions (see Climate change). At this same site, narrowed limits might therefore be approximated as 6738 - 18 866 adults ha^{-1}, or 19 200 - 53 700 adults ha^{-1} of living ground cover. At remaining sites, the wider unmodified boundary estimates afford the only definable limits over a 20-year term (the lowest extreme represents 1070 adults ha^{-1} of living ground cover). As tentative confidence limits, the estimates represent the likely temporal variation for sites surveyed and compared on a single occasion. Individual site limits can be calculated from Table 1 of White, 1975a, and converted to grasshopper consumption and grazing pressuress via the listed species and site indices. The consumption calculations should then be doubled (see the energy budget factor of White, 1978), and the same calculation procedures can be repeated to relate grasshopper consumption to other vegetation productivity scenarios.