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CORRELATIONS BETWEEN CLIMATOLOGICAL FLUCTUATIONS AND A POPULATION OF *PHILOLITHUS DENSICOLLIS* (HORN) (COLEOPTERA: TENEBRIONIDAE)*

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INTRODUCTION

Ground-dwelling tenebrionid beetles form an obvious fraction of the fauna of the semi-arid regions of Washington, because at least on occasion, their numbers are large. In some cases, their biomass is of the order of 20 kg ha^{-1} , about an order of magnitude greater than that attained by vertebrate herbivores (W. H. Rickard *et al.*, unpublished). The species of interest here, *Philolithus densicollis* (Horn), is found in adult form only in autumn, making its emergence a notable phenological event. During the brief emergence, the adults are readily taken by carnivorous animals, particularly coyotes (*Canis latrans* L.). Coyote scats sometimes consist entirely of beetle exoskeletons. Adult beetles are herbivorous during their surface life, but apparently are not obliged to eat to live. When numerous, these and similar beetles may be the most influential grazers to which undisturbed desert vegetation is subjected.

Populations of these beetles are not constant. Pitfall trapping during the autumn emergence of the beetles have collected progressively fewer since 1963 until a minor resurgence in 1970: the total annual catch declined essentially monotonically from 1800 in 1963 to sixty in 1969. A persistent decline in numbers such as this is quite different from 'crashes' in populations occurring from one year to the next. Crashes can quite often be accounted for by considerations of peculiarly unfavourable climatic conditions (cf. Milne, Laughlin & Coggins 1965), but a steady decline might be attributable to many readily conceived biotic mechanisms, rather than climatological variation. The purpose of the investigation reported here was to determine how much or little weather conditions were related to the observed pitfall captures.

The relatively sparse information concerning the life history of these beetles is outlined in a following section. Our strategy was to use the available information to formulate several hypotheses regarding possible or probable points where climatic fluctuations might impinge upon the beetles' life cycle, then examine the evidence concerning the hypotheses using available weather data and multivariate analytical techniques. The climatological data were restricted to those affecting eggs and early instars, presumably stages most susceptible to climatic extremes. The resulting data matrix was then decomposed into principal components for correlation with the pitfall data. The purpose of this step was to reveal any linear relations between patterns of climatic fluctuations and trap catches, as opposed to simple correlations resulting from linear regressions. The third step was to use any insights from the principal component analysis to provide

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realistic criteria for selecting climatic variables as input to a multiple regression model. This approach was successful for *Philolithus densicollis*, but another autumn emergent tenebrionid, *Stenomorpha puncticollis* LeConte, which has a more or less similar life history and phenology, and occurred in the same plant community, was not amenable to similar analyses. The model is correlative, not mechanistic, but the lack of knowledge concerning *Philolithus densicollis* precluded finer analyses.

THE SITE

The study site lies in a stand of sagebrush (*Artemisia tridentata* Nuttall) on the 300 km² Arid Lands Ecology Reserve, an area set aside for ecological studies by the United States Atomic Energy Commission from its Hanford Reservation in south-central Washington.

The climate is decidedly deficient in rainfall, with an annual average of 6.3 in. (16 cm). About two-thirds of the precipitation falls between October and May—half as snow—and provides a store of soil moisture for a spring growing season. Winters are cold, but not extreme, as temperatures below 0° F (−18° C) are expected only every other year or so. Summers are hot and dry. Soil water declines steadily from a maximum in early March to a minimum in September, when the surface decimetre contains only 1 or 2% water (Rickard 1967).

The soil is a silt loam by texture. It is a young soil, formed from lake-laid deposits from a post-glacial lake behind temporary ice jams, about ten or twelve thousand years ago. The surface metre is essentially stone-free. Alkalinity increases from near neutral at the surface to a pH of about 8, with a calcareous layer, about 1 m deep. Otherwise, soil horizons are not readily recognized.

The vegetation is dominated by big sagebrush (*A. tridentata*), with a sparse understorey of perennial herbs, principally Sandberg bluegrass (*Poa sandbergii* Vasey). Annuals are scarce. Cheatgrass (*Bromus tectorum* L.), the common invader of disturbed soil in this region, is sparingly represented on the site, indicative of a long history of relatively undisturbed conditions (Daubenmire 1970). Plate 1 shows the general aspect of the site and surroundings.

THE BEETLES

Autumn-emergent darkling beetles have received little study, and the literature concerning them is primarily taxonomic. A recent taxonomic treatment of *Philolithus densicollis* discussed its relation to other tenebrionid genera, pointing out that its previously accepted ascription to the genus *Pelecyporus* was in error (Brown 1971).

Most of the life history information has been obtained by Kirby W. Brown, Curatorial Associate of Entomology, Peabody Museum, New Haven, Connecticut. The following paragraphs are a distillation of the laboratory and field observations he has generously provided for us, along with a few personal observations.

Adults emerge in late summer and early autumn, for a brief life span—about a month in the laboratory. The adults are herbivorous, but unfed adults in the laboratory survived about as long as those provided with food. The adults tend to be active in daytime, especially when the nights grow cold. Oviposition habits in the field are not well understood; from limited laboratory observations, Brown assumes the beetles oviposit perhaps a single egg each day. The eggs are relatively large—about 20% of the body length of the adult female—and deposited about 1 cm below the soil surface. A sclerotized



The pitfall trapping area. Photograph by Battelle-Northwest Photography.

(Facing p. 342)

ovipositer acts as a drill, so hard, dry soil is no deterrent to oviposition, although moist microsites are apparently preferred.

In the laboratory, *Philolithus* eggs hatch in 1–2 weeks. The first instar is an inactive grub, quickly changing to second instar. The larvae are unusual for tenebrionids, being pale, unsclerotized, readily dehydrated, and generally poorly adapted for life on the surface. By contrast, the larvae have well-developed, scoop-shaped mandibles and enlarged forelegs, providing means for easy movement through the soil. The larvae select ingestible material through their travels, and apparently are scavengers (except for cannibalistic behaviour), for no living plant material was necessary for successful laboratory rearing. The larvae do not surface after hatching until emergence as adults.

The length of the life cycle of these beetles is not known as study terminated in the early instars. Closely related but larger tenebrionids require 2 months at temperatures less than 10° C to break diapause in late instars and induce pupation, usually completing their cycle in less than 2 years, but more than 1 year, in the laboratory.

HYPOTHESES AND STATEMENTS FOR STUDY

(1) Null hypothesis: there is no relation between pitfall trapping success and climatic variables during the reproductive phase of the beetles' life cycle.

(2) Null hypothesis: no significant correlation exists between pitfall trapping success and climatic variables except those in the year of trapping, indicating activity rather than abundance.

(3) Null hypothesis: pitfall trapping success is independent of total cool-season precipitation (the principal determinant of vegetation productivity).

(4) Question for study: what evidence is there to specify whether the beetles' life cycle is of 1 year or 2 years' duration?

THE DATA

The appropriate data clearly should be related to soil surface conditions during the period of adult emergence, oviposition and hatching. Monthly averages of soil surface temperatures and precipitation seemed most appropriate as the independent variables, because the life span of the beetles, and the length of each phase of the reproductive cycle, each last approximately a month. Since interest centred on population variation between years, the total number of beetles trapped during a given year seemed best as the dependent variable.

The climatic data were from the Atmospheric Sciences Department at a station some 6 miles from the study site. The meteorological station is located on soil very similar to that at the study site (Hajek 1966), supporting vegetation that is likewise very similar. Air temperatures, precipitation and albedo also are similar at both sites (Hinds & Thorp 1969, 1971; W. T. Hinds, unpublished) so the soil temperatures at both must be similar. The temperature at 1.25 cm (0.5 in.) was selected as being representative for both adult activity and egg and early instar environments. The temperatures were averaged over daylight and darkness periods separately, to accord with the tendency of the species to daytime activity. Precipitation at the study site was closely correlated with precipitation at the meteorological station (Hinds & Thorp 1971), and monthly totals were taken directly from the meteorological records (Table 1).

METHODS

Estimates of beetle abundance were made by pitfall traps, maintained in the same plant community and visited weekly during the autumn, for nine consecutive years. Forty-nine pitfalls were arranged in a 7 × 7 grid pattern with 3-m spacing between traps. The traps consisted of metal cans, 10 cm in diameter and 25 cm deep, buried in the ground until the rim was flush with the surrounding soil surface. The pitfalls were capped at the end of the beetle emergence in late November or early December, and not visited again until the following September. All beetles were released alive at their place of capture. Although beetles were confined to the traps for up to a week, mortality in the traps was insignificant.

Pitfall traps confound abundance and activity, because an increase in either increases probability of capture. There is little hope of separating these two components of capture probability *a priori*, so this problem was set up as a null hypothesis for examination.

Behavioural changes in the population at risk may cause serious errors in pitfall trapping success. Behavioural changes must ordinarily be expected between instars

Table 1. *Climatic and pitfall trapping data*

Year	October			November			Total winter precip. (mm)	Total annual catch of <i>Philolithus</i>
	Precip. (mm)	Av. max. <i>T</i> (° C)	Av. min. <i>T</i> (° C)	Precip. (mm)	Av. max. <i>T</i> (° C)	Av. min. <i>T</i> (° C)		
1961	2	28.7	5.3	12	13.8	-2.1	109	
1962	24	26.4	6.3	17	14.1	2.1	151	
1963	1	26.2	8.8	19	11.9	3.4	63	1803
1964	7	28.6	5.8	24	8.3	1.3	124	918
1965	Trace	32.6	7.7	30	13.4	3.7	70	297
1966	10	24.2	7.3	57	12.9	3.5	131	101
1967	3	27.0	7.8	4	14.2	1.1	58	62
1968	24	25.9	5.9	31	12.1	2.4	178	120
1969	3	23.4	5.1	3	11.1	1.3	152	58
1970	6	25.1	3.6	18	10.3	0.1	104	427
1971	5	26.1	4.2	12	10.4	0.3		238

Note: in the text, *O* = October, *N* = November, *P* = precipitation, *T* = temperature; subscript 2 = 2 years before trapping, subscript 1 = 1 year before trapping, subscript *x* = maximum temperature, subscript *n* = minimum temperature.

(Gilbert 1958). However, behaviour should be constant within species between generations. The use of total annual catch as samples of succeeding generations of univoltine insects as an index to the population at risk should keep behavioural changes to a minimum.

Trapping efficiency apparently changes with soil moisture under laboratory conditions, but no changes due to this could be detected in field conditions (Mitchell 1963). Soil moisture varied strongly throughout the season in our study, but soil moisture trends between years are relatively constant on the site, being quite dry in September and quite moist in December. So, no between-year bias can be expected.

Different species are trapped in differing proportions (Greenslade 1964) primarily because of behavioural aspects of activity in relation to surface cover density. Maintaining the traps at the same site for several years removed this problem, under the simple and realistic assumption that the relative proportion trapped remained constant between years except insofar as environmentally controlled activity responses were concerned.

Problems of trapping constancy between habitats were nonexistent, because the traps remained in one habitat.

From all the above considerations, it seems likely that pitfall trapping was approximately equally efficient between years except insofar as climate might alter activity; the null hypothesis mentioned earlier.

We chose a square root transformation of the pitfall data, a common approach for count data (Bliss 1967), to equalize variance. Ordinarily, population analyses use a logarithmic transformation because of the geometric nature of population changes (Morris 1960) and because of an assumed multiplicative nature of variables (Mitchell 1963). These considerations are most applicable to population variation within years for multivoltine insects, and are less appropriate for considerations of abundance of univoltine insects between years, because any climatological stresses reducing the population tend to be density-independent (Thompson 1956). We therefore chose to use the climatic data untransformed.

Multivariate methods offered the most efficient analysis of the data. However, simply exploring the many dimensions of possible regression models is intellectually unsavoury without some rational basis for choosing variables (Watt 1962). We therefore subjected the climatic data to a principal component analysis, then used the components as independent variables in a regression analysis with the pitfall data. The rationale and implications of this approach deserve some amplification.

Principal components are mutually uncorrelated linear combinations of the independent data which, in sum, reproduce all of the variance in the original data (Morrison 1967). Data with disparate dimensions, such as we have here (degrees Fahrenheit, inches of precipitation) suggest that the correlation matrix, calculated from the variance-covariance matrix of the original data, provides the most reasonable starting point. In the correlation matrix, all data variability has been reduced to standard scores in the range -1 to 1 .

The first principal component (eigenvector) is that linear combination of the correlations that accounts for the maximum amount of variability in the correlation matrix. The second principal component is that linear combination of the correlations which accounts for the next largest proportion of variability in the correlation matrix, subject to the constraint that the second component must be completely uncorrelated with the first . . . not overlapping in 'explained' variability. This procedure may be continued until a satisfactory proportion of the total variability in the correlation matrix has been attributed to the several (or few) principal components. The advantage to this procedure is that the variability in our 18×18 climatic data correlation matrix can be reproduced within 2% with only seven components, each of which represents an individual pattern of variability within the climatic data. Thus, instead of eighteen variables with correlations among themselves, only seven variables remain, having no correlation with each other, each representing a pattern of climatic occurrences.

The relation between the principal components and the pitfall data was determined by applying multiple regression techniques to the principal components and the pitfall trapping data. In this fashion, the components best correlated with the pitfall data were found and examined for their characteristics in terms of climatic variables. This step illuminated patterns of climatic interactions with populations, allowing a more reasonable approach to otherwise rather arbitrary selections of variables for multiple regression analysis. To be sure, the original selection of climatic variables for the principal component analysis itself was guided only by Brown's life history information, the ecological

principle that reproductive phases of organisms's lives tend to be easiest to disrupt, and intuition.

In the final analysis, the principal component analysis and multiple regressions contain the same information, so this approach does not in fact increase the total information relating populations to environment. However, principal components often lend themselves to interpretation, due to dominance within a component of a few variables. The advantages, if any, devolve from the independent nature of the combinations in each principal component—such independence is by no means either necessary (Mead 1971) or common in independent variables for regression analyses.

The search for relationships between climate and populations described here bears more than a passing resemblance to modern dendrochronological analysis (cf. Fritts *et al.* 1971). In both cases, the rationale for interaction between climate and population indices already existed (Fritts 1970; Solomon 1957; Thompson 1956), so the multivariate techniques were employed to optimize the picking and choosing amongst competing variables, and to quantify the basis for choice.

RESULTS FROM PRINCIPAL COMPONENT ANALYSES

Seven components were found associated with 98% of the variance in the climatological data. The components were characterized according to the fewest variables providing 50% or more of the total weights of the component. The average weighting of the 'dominant' variables was about 12% each, whereas the remainder were weighted about 3% each. In the following discussion, the less important contributors to each component will be ignored.

Table 2. *Principal components found to be correlated with pitfall trapping data*

Step no.	Component no.	Associated climatic variance (%)	Associated increase of explained variance of pitfall data (%)	Cumulative variance of pitfall data accounted for (R^2)
1	6	8	52	0.52
2	7	3	25	0.77
3	3	15	14	0.91

Each component has a specific value for each specific combination of climatic data (that is, each year). These values for each year were used as independent variables in a stepwise regression of pitfall data on climate, with the results summarized in Table 2. The characteristics (or patterns) within each component are displayed in Fig. 1, with the components found to be related to the pitfall data separated from the components uncorrelated with the pitfall data. From Table 2, it is clear that the components most closely tied to the pitfall data are those accounting for the least of the climatic variability. This must imply that much of the variability in climate has little bearing on pitfall trapping success, and according to Morrison (1967, p. 229) may imply that specific climatic variables are individually responsible for the variability in trapping data. Note, too, that the high degree of variance accounted for by these three components indicates that climatic fluctuations must indeed be closely related to the pitfall data.

Fig. 1 bears examination. The three components separated on the top half of the figure are those entering the regression equation. Note especially the paucity of influence of

climatic data from one year before trapping. This suggests that climatic variables observed one year before eclosion have very little relation to pitfall data, and therefore provides substantial evidence that the larvae reside in the soil two seasons, an answer to the question posed earlier.

A further point emerges from Fig. 1: only a single precipitation datum enters the components related to pitfall data, and that is in the year prior to trapping. Apparently precipitation patterns are not a particularly influential factor, for one of the components that is not related to the pitfall data contains nothing but precipitation variables in its make-up.

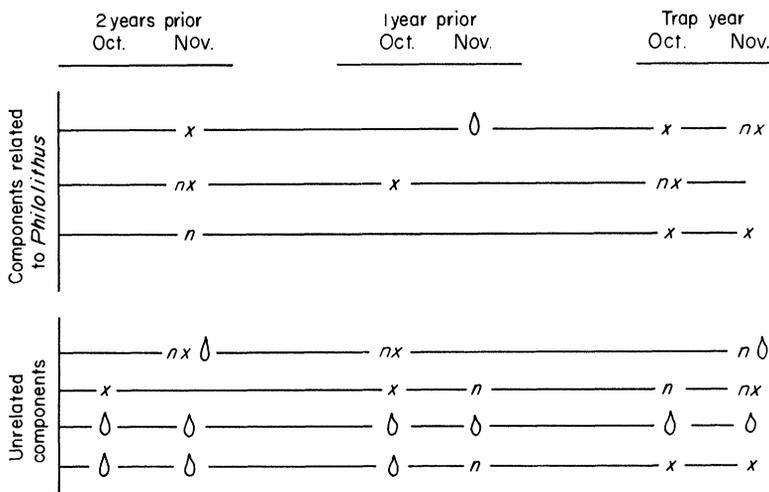


FIG. 1. Results from multiple regression using principal components of the climatic data as independent variables and pitfall trapping data as the dependent variable. The dominant climatological parameters within each component are indicated. *x*, Maximum temperature; *n*, minimum temperature. The rain drop indicates precipitation.

RESULTS FROM REGRESSION ON CLIMATIC VARIABLES

As mentioned earlier, each principal component contains a contribution from each of the input climatic variables. Even though to this point each component has been characterized by the dominant few climatic variables in its make-up, still the reality is that all components contain a considerable 'noise' from the remaining climatic variables in addition to the relatively clear-cut contributions from the dominants. However, the patterns from the principal components' regression provide a criterion for selection of specific climatic variables to be used as independent variables in a regression analysis: the data should come only from the year of trapping and two years prior to trapping.

Table 3. Stepwise multiple regression of pitfall data on climatic variables

Step	Variable	Increase in variance of pitfall data (R^2)	Intercept	Standard error of estimate	Regression coefficient	Standard error of coefficient
1	N_2T_n	0.43			-6.221	1.00
2	OT_n	0.26			2.652	0.65
3	O_2P	0.21			0.574	0.18
	A11	0.90	-45.562	4.63		

The results of the stepwise regression are summarized in Table 3, and the relative success of the resulting model in reproducing the observed population decline is shown in Fig. 2, from the equation

$$N^{1/2} = -45.562 - 6.221 N_2 T_n + 0.574 O_2 P + 2.652 OT_x.$$

Examination of Table 3 and Fig. 2 shows clearly that a very high proportion of the total variance of the pitfall trapping data is associated with specific climatic parameters, and that most of the variance accounted for is from two years before trapping (64%). In contrast, the variance related to the year of trapping is 26%, and unexplained variance is 10%. The clear implication is that nearly two-thirds of the observed decline in pitfall trapping success is related to climatic variations during adult emergence and reproduction, and about one-quarter is due to changes in activity of the beetles between years.

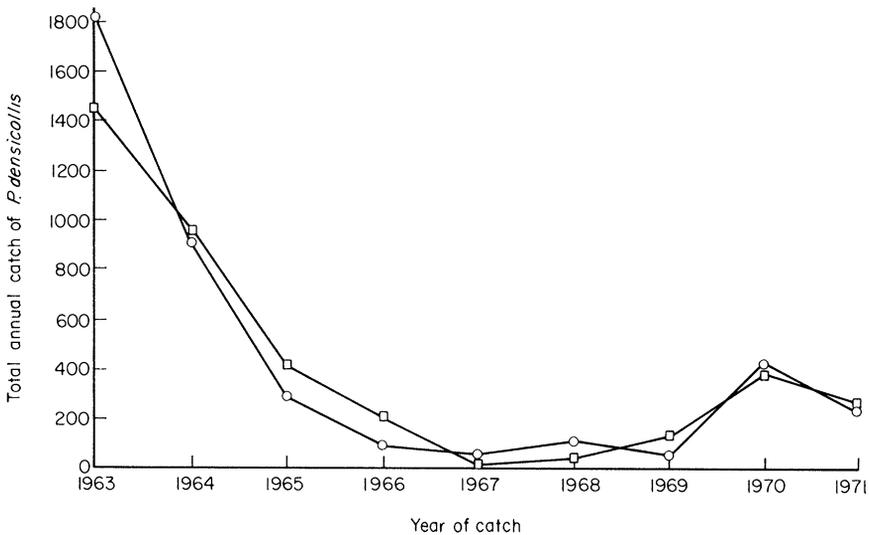


FIG. 2. Comparison of stepwise regression equation with pitfall trapping data. The regression used unmodified climatic data; after three steps, R^2 was 0.90. ○, Observed; □, regression.

DISCUSSION

Several mechanisms exist which could conceivably act to reduce the total catch of the beetles but have not yet been considered; their potential significance is briefly assessed here.

Pesticide drift. The study site is buffered by several miles of reserved lands in all directions. The nearest agricultural lands are dryland wheat fields six miles upwind and 2500 ft higher in elevation. The potential for drift over this distance is nil, due to restrictions on pesticide applications during windy conditions.

Predation. Little is known concerning predation of the adult beetles, beyond the observations that they may be readily taken by coyotes, and probably by gallinaceous birds. Predation by other arthropods is probably slight, because only black widow spiders are known to be able to kill the adults. Carabid beetles (*Calosoma luxatum* Say) are spring emergents in this region and may prey upon larvae. Nothing is known concerning predation upon the larvae, either at the time of hatch or during their residence in the soil.

Fire, grazing and other surface disturbance. The study site has for 30 years been little disturbed in any manner. Grazing by domestic livestock apparently was never a strong disturbance at this site, and was completely eliminated in 1960. The study site has not been burned for a century or more, as evidenced by long dead stubs and branches of sagebrush at the site. The oldest living sagebrush in the area probably approach 70 years of age, based on ring-counts in similar sites.

Although the 'explained' variance in Table 3 is high, still it is a correlative rather than a mechanistic model—we may only say, for example, that moist Octobers two years ago tend to increase pitfall trapping success this year, and so on. There is no evidence for specific biotic mechanisms, whether physiological or behavioural, that might account for the changes in abundance noted (and attributed to climatic variation). However, the relatively simple regression, and the high correlation, provide a tempting ground for speculation into specific mechanisms involved. We will more or less stoutly resist the temptation, and offer instead a few obvious interpretations.

First, the regression model requires rejection of the first null hypothesis.

Secondly, the importance of climate in the year of trapping is restricted to October maximum temperature, an indicator of activity. This variable accounts for only a quarter of the total variability, whereas variables during the second year prior account for nearly three times as much variability. Therefore, the second null hypothesis, that there is no significant correlation between pitfall trapping and climate except due to changes in activity, must be rejected—most of the variability is due to true changes in abundance.

Third, the relative lack of importance of precipitation deduced from the principal component analysis is seen to apply only in general; specifically, October precipitation in the year of oviposition accounts for about 20% of the variability observed two years later. Apparently soil moisture has little to do with trapping efficiency, as noted earlier, but it is of some importance for reproduction.

However, a direct examination of the importance of total winter precipitation in the regression analysis indicated there was no correlation whatsoever with pitfall trapping success. Thus, the third null hypothesis, that the variability in trapping success was independent of cool-season precipitation, and therefore plant productivity, cannot be rejected. This corroborates Brown's observations that the larvae are scavengers (decomposers) in the ecosystem, rather than herbivores (consumers).

The importance of November minimum temperatures is somewhat an enigma, even though it accounts for nearly half the total variability of trapping. Note that the relation is negative—warm November nights during reproduction are related to a decrease in trapping success 2 years later. There is no obvious ecological interpretation, but there is a wealth of speculative potential in this result. It seems likely that this would be a profitable point to begin research into the behaviour and physiology of the beetle.

CONCLUSIONS

From the foregoing analysis, the following conclusions seem appropriate.

- (1) *Philolithus densicollis* resides 2 years in the soil in larval instars, whose function in the ecosystem is as a decomposer rather than herbivore.
- (2) The observed decline in pitfall trapping of *P. densicollis* is due primarily to a real decline in abundance, rather than to changes in activity.
- (3) The decline in abundance is primarily related to climatological variation, princi-

pally November minimum soil temperatures and October precipitation during oviposition of the generation to be trapped, and secondarily October maximum soil temperatures in the year of trapping. About 90% of the variability in pitfall trapping is related to these three variables.

SUMMARY

(1) A population of a common tenebrionid beetle, *Philolithus densicollis* (Horn) was trapped and trapping success dropped steadily, from 1800 beetles in 1963 to 60 in 1969, with no readily observed reason.

(2) The beetles emerge in autumn, laying eggs that hatch in 1 or 2 weeks.

(3) Three principal components were found (by multiple regression) to be associated with 91% of the pitfall trapping data. The dominant characteristics of the components related to trapping success were climatic data from the year of trapping and 2 years prior to trapping.

(4) By this criterion, multiple regression using untransformed climatic data from the year of trapping and 2 years prior to trapping yielded a regression equation accounting for 90% of the pitfall trapping variability.

(5) The decline in pitfall trapping success was primarily due to a real decline in abundance; the numbers of beetles 2 years after oviposition are negatively correlated with November night temperatures and positively correlated with October precipitation in the year of oviposition; and the decade-long decline was principally due to climatic fluctuations.

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