The Ecology of Armadillidium vulgare (Isopoda: Oniscoidea) in California Grassland: Food, Enemies, and Weather
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THE ECOLOGY OF ARMADILLIDIUM VULGARE (ISOPODA: ONISCOIDEA) IN CALIFORNIA GRASSLAND: FOOD, ENEMIES, AND WEATHER

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INTRODUCTION

The terrestrial isopod, *Armadillidium vulgare* (Latr.), is one of the most abundant macroscopic invertebrates in California coastal grassland. In areas of maximal abundance, its density is approximately 500 individuals per square meter (Paris and Pitelka 1962). Sheer numbers suggest that the species plays an important part in the dynamics of this terrestrial community. One of several studies directed at the ecology of "Mediterranean" grassland communities of the San Francisco Bay area, this investigation of *A. vulgare* populations was conducted from late 1957 through 1960. Demographic results of the study have been reported elsewhere (Paris and Pitelka 1962). The role of food, enemies, and weather in the ecology of *A. vulgare* will be considered here and a suggestion made as to the function of this isopod in these grassland communities.

STUDY AREA

The isopod populations investigated live in grassland on the west slope of San Pablo Ridge, in Tilden Regional Park, Contra Costa County. San Pablo Ridge lies to the east of the Berkeley Hills, which front on the plains on the east side of San Francisco Bay; the ridge is everywhere above 1000 ft in altitude. Grassland on the south- and west-facing slopes of the ridge alternates with chaparral on the north and east slopes, separated by ecotones of grassland and open brush. Dominant grasses are *Avena barbata* and *Bromus rigidus,* and the brush consists almost exclusively of *Baccharis pilularis* and *Rhus diversiloba.* The three most abundant forbs are *Picris echioides, Brassica campestris,* and *Achillea borealis.* For additional details on topography and vegetation see Paris and Pitelka (1962).

Most of the observations reported here were made in an intensive study area illustrated by the aerial photograph, Fig. 1. The figure shows an oblique view of the top of San Pablo Ridge, looking southwest. A fence along the crest separates range land on the east slope from ungrazed grassland of Tilden Park on the west slope. Fig. 2 is an index map for the study area located in the center of Fig. 1 and shows topographical and vegetational characters, as well as the location of study plots. The latter will be described contextually.

CLIMATOLOGY OF THE AREA

Coastal California is characterized by an annual cycle of winter rains, followed by drought lasting from late spring into the fall. In the San Francisco Bay area, precipitation typically begins in October or November and terminates by early May, although this schedule varies considerably in some years. The Bay area rarely experiences freezing weather, except

FIG. 1. Aerial view of intensive study area, looking southwest. Most sample surveys were taken in grassland on the hill in the center of the picture. Altitude of the hilltop is about 1150 feet. Location of study plots and type of vegetation are shown in Fig. 2.

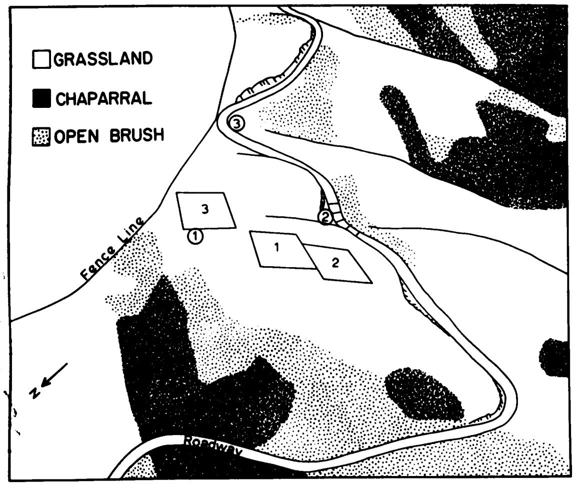

FIG. 2. Index map for Fig. 1. Numbers in quadrangles indicate quadrats in which soil samples surveys were taken. Numbers in circles indicate the location of weather stations and activity plots. The fence line follows the crest of San Pablo Ridge, separating rangeland on the east slope from ungrazed grassland on the west slope.

for occasional local frost during winter. Growth of vegetation in grassland is correlated with the annual precipitation cycle. Following the first heavy rains in the fall, growth commences and continues through the winter; a period of slow winter growth culminates with rapid spring growth, leading to the maturation of the vegetation between April and June. After termination of the rainy season, drying of the soil and vegetation proceeds rapidly, and by July most of the grassland vegetation is dead or dormant.

Terrestrial isopods are poorly adapted, morphologically and physiologically, for life in dry habitats (Waloff 1941, Edney 1954, 1960, Spencer and Edney 1954). For this reason the long period of drought experienced by isopod populations in coastal California is of special interest. A brief summary of climatological features for this period of the year is necessary for an understanding of the results reported later.

During the summer months air masses over the Central Valley of California become very warm. The Coast Range separates cool maritime air over the ocean from this warm air over the Valley, leading to a pressure difference between the two regions. This differential generates west winds that become increasingly strong as summer approaches, and from May to September a wind from the west prevails except in early morning hours (Patton 1956). These winds carry moist maritime air over land areas in the vicinity of the Bay, leading to an increase in atmospheric moisture. According to Patton (1956), the annual cycle of relative humidity is opposite that of precipitation, relative humidity being higher in summer than in winter. The area in which the present investigation was carried out lies between the 60% and 70% relative humidity isorithms (for 1200 hours) in July, according to the statistics graphed by Patton (1956).

Characteristic of the summer climate along the California coast is a diurnal cycle of low stratus, commonly referred to as "high fog," which covers land areas near the coast at night and then dissipates during the morning. Typically, several nights during which there is a stratus cover alternate with a sequence of clear nights. In the San Francisco Bay area stratus forms offshore and moves inward through the Golden Gate in late afternoon or early evening. Over land it comes into contact with the ground on hills above an altitude of about 600 ft (Patton 1956). This is particularly true of ranges which face wind streamlines, as does San Pablo Ridge. After sunrise the air above the ground is warmed, and evaporation occurs, first close to the surface and then progressively higher as warming proceeds at greater altitudes. Occasionally the stratus layer is so thick that it does not completely evaporate during the day, remaining as a blanket of "high fog" throughout the daylight hours.

On nights with a stratus cover over the area east of San Francisco Bay, the top of San Pablo Ridge is almost invariably bathed in fog. Furthermore, the top of the ridge is more or less fully exposed to westerly summer winds. As will be shown later in this paper, moist summer winds and nightly stratus play an important part in the ecology of *A. vulgare* in grassland of these coastal hills.

METHODS

SAMPLING TECHNIQUE

The isopod population was sampled using a substrate sampler which measured 6 in. to a side (enclosing an area of 232.3 cm^2); with this, soil sample blocks 5 cm deep were taken at random in study plots (to be described later). Isopods were separated from the soil samples by Tullgren funnels.

Funnel efficiency for isopods was greater than 80%, and the funnels were not selective for size classes. Species, size (length: anterior edge of profrons to tip of telson), sex, and molt condition were determined for all isopod individuals collected. The reproductive condition of females was determined, also. For additional detail on methods, see Paris and Pitelka (1962).

MICROCLIMATOLOGIC METHODS

Measurements of weather conditions in the microhabitat of *A. vulgare* were made at three stations located on the hill shown in the center of Fig. 1. The positions of the three stations are indicated by numbers in circles in Fig. 2. Station 1 was located in open grassland high on the hill and Station 2 in grassland adjacent to the roadway. Station 3 was situated on the bare road shoulder, in the saddle between two hills. At Stations 1 and 2, soil thermometers measured temperatures at depths of 1, 3, and 6 in. (2.5, 8.6, and 15.3 cm). Quick-registering mercury thermometers were used at all three stations for measuring temperature at the soil surface and, where appropriate, above the vegetation. Relative humidity determinations were made above the vegetation and, simultaneously, at the surface of the soil.

Relative humidity in microhabitats was measured colorimetrically by small pieces of tissue paper impregnated with cobalt thiocyanate, a technique developed by Solomon (1945, 1957). Paper stock was obtained from the British Drug House, and the comparator apparatus and color standards were manufactured by Tintometer, Ltd. Papers being exposed were placed in short pieces of plastic tubing (1.3 cm in diameter and 5 cm long, with both ends open) to protect them from free water. With an exposure of 2 hours, papers thus protected gave the same results as papers placed in open air. At the end of an appropriate exposure, papers were "fixed" by immersion in liquid paraffin. When changes in relative humidity was being followed over long periods, a series of papers were kept exposed, so that all papers were in the atmosphere at least 2 hours. Since the greatest change in color occurs within a few minutes of a paper's first exposure, it is reasonable to assume that the change in color of these papers followed closely the gradual change in relative humidity.

In every case, papers were exposed in triplicate. Very close agreement was obtained from the replications (usually within ±3% relative humidity). An occasional exception occurred when replicates under vegetation were exposed inadvertently to different humidity condition, in spite of the fact that the papers were very close together. Relative humidity values presented in the results are mean values from three replications.

Atmospheric temperature and moisture data have been converted to vapor pressure deficit for analyses presented later. Although there are certain theoretical objections to the use of vapor pressure deficit as an index of rate of evaporation (Thornthwaite 1940, Edney 1957), it is clearly superior to relative humidity for this purpose; its use is justified in the absence of a more satisfactory theoretical approach. Edney (1957) has pointed out that there in no body of information which conflicts with the assumption that, at constant temperature, water evaporates from arthropods at a rate proportional to vapor pressure deficit.

THE FOOD OF ARMADILLIDIUM VULGARE

FEEDING HABITS

Armadillidium vulgare is omnivorous. It has been cited as an agricultural, garden, and greenhouse pest (Pierce 1907, Essig 1926, Wiegel and St. George 1952) and is also well known as a scavenger. It is reported to eat dead leaves (Pierce 1907, Howard 1940), leafmold (Howard 1940), fungi (Pierce 1907, Healey 1941a), and dead animals (Pierce 1907).

In the present investigation, observations on the feeding activity of *Armadillidium* were made both in the daytime and at all hours of the night. It was often possible, using a hand lens, to observe the movement of the mouth parts of feeding isopods. Additional evidence of feeding came from the progressive disappearance, over a period of many days, of food items being frequented by large numbers of isopods. Its omnivorous habit in grassland was occasionally exhibited by individuals found feeding on mammalian fecal pellets and the bodies of dead invertebrates, including its own kind which had been crushed by vehicles or by the author's boots. The usual source of food, however, was dead plant material. Two species of forbs were eaten most frequently: the thistle *Silybum marianum* and the tar-weed *Picris echioides*. During the summer, of course, both *Silybum* and *Picris* became completely dead and dry. Under these conditions, isopods climbed the stems of the plants (at night) and fed on the upper dead leaves. During winter and spring, however, when the upper portions of the plants were green, isopods remained on the dead leaves at the base of the rosettes.

FOOD PREFERENCE TESTS

Evidence of the choice of *Picris* by *A. vulgare* came from preliminary laboratory tests of food preference. In the first of these, 7 isopods were placed in each of 3 large finger bowls. The bowls were covered with glass plates and the relative humidity within them maintained near 100% by means of an open Stender dish of water placed in the center of each. Relative humidity was continuously monitored by pieces of cobalt thiocyanate paper taped to the sides of the bowls. Equally spaced around the circumference of each finger bowl were placed 4 different items which field observations had suggested might constitute isopod food: fresh *Silybum* leaves, fresh *Silybum* roots, fresh *Picris* leaves, and dead *Picris* leaves (dead *Silybum* leaves, a known dietary item, were unavailable for these tests). On 2 successive nights, beginning 24 hours after the experiment was started, the number of isopods on each of the 4 food items was determined. Isopods were counted in the darkened laboratory by light from an electric lantern equipped with a yellow lens. The presence of an isopod on a food item was considered as evidence of feeding; many were obviously feeding when counted, but of course some probably were not. Random error introduced by this fact should not affect the results, assuming that some unknown factor did not cause isopods to come to rest more often on one food item than on another. Isopods which were not on food items were not counted. The second test was designed and conducted like the first, except that 12 animals were used in each bowl, and observations were made on 3 successive nights instead of two.

Results of the food preference tests are presented in Table 1. For each test, data from all observations have been pooled. Many more isopods were found on dead *Picris* leaves than on other food items. A Friedman 2-way analysis of variance by ranks (Siegel 1956) showed that the frequencies with which animals occurred on different food items were significantly different in each test (for Test 1, P<.033; for Test 2, P<.0017). The tests indicate that *Armadillidium* feeds on dead *Picris* in preference to the other items available in these experiments.

TABLE 1. Preference of *Armadillidium* for grassland food items*

Replication	Fresh *Silybum* leaf	Fresh *Silybum* root	Fresh *Picris* leaf	Dead *Picris* leaf
Test 1:				
1......	2	0	1	7
2......	2	1	0	11
3......	2	0	2	5
Test 2:				
1......	6	0	1	18
2......	4	0	2	16
3......	3	0	4	11

* For Test 1 N=7 individuals per replication; for Test 2 N=12 individuals per replication. Data pooled from 2 observations in Test 1 and from 3 observations in Test 2.

AGGREGATIONS AT PICRIS PLANTS IN THE FIELD

Quantitative evidence of an attraction to *Picris* in the field comes from a sample survey taken on February 10, 1960. Ten samples were taken at random in Quadrat 2 (see Fig. 2); each consisted of a search for isopods on the surface (following removal of vegetation) within the confines of a 0.1 m^2 substrate sampler. Five of the samples happened to contain *Picris* plants and 5 did not.

The number of isopods taken in samples with *Picris,* and the number in plots without *Picris,* are compared in Table 2. A Mann-Whitney U test indicated that the number of isopods in samples without *Picris* was significantly less than the number in samples with *Picris* (P = .008).

PICRIS ABUNDANCE AND ISOPOD DENSITY

With this evidence for the importance of *Picris* as a food source for *A. vulgare* in grassland, it was reasoned that isopod density, or the age structure of the population, might differ in two areas which were similar except for the density of *Picris*. The density of *Picris* varies considerably from place to place in the grassland on San Pablo Ridge; in fact, this is true within the limits of the grassland shown in Fig. 1. Accordingly, 2 areas were selected in which to make such a comparison of isopod and *Picris* densities.

TABLE 2. Isopods in samples with and without *Picris.*

SAMPLES WITH *Picris*		SAMPLES WITHOUT *Picris*	
Sample number	Number of isopods	Sample number	Number of isopods
1	23	2	1
3	5	4	4
5	27	7	9
6	33	9	16
8	56	10	0
	$\bar{X}$=28.8		$\bar{X}$= 6.0

Two quadrats, each measuring 10 m. to the side, were laid out at about the level of the western border of Quadrat 2 (see Fig. 2). The quadrats were at the same altitude, with about the same slope. They were separated by a distance of approximately 25 m. In one of them *Picris* density was very high (Quadrat A), and in the other it was low (Quadrat B). Both isopod density and *Picris* density were quantitatively assayed in the 2 plots. Nine randomly located line transects were laid across each quadrat in a west to east direction, and the *Picris* plant intersects of each were determined. Isopod density was assayed by 10 randomly located soil samples taken in each quadrat.

The results are given in Table 3. A Mann-Whitney U test showed the number of *Picris* plants to be significantly greater in Quadrat A than in Quadrat B (P<.002). On the other hand, the number of isopods taken in the 2 quadrats did not differ

TABLE 3. Isopod numbers in areas with high and with low *Picris* density.

QUADRAT A		QUADRAT B	
Number isopods in each of 10 samples	Number plants intersected by each of 9 transects	Number isopods in each of 10 samples	Number plants intersected by each of 9 transects
7	69	16	1
24	70	12	5
6	56	14	3
3	43	10	1
14	55	2	1
22	41	4	3
12	18	18	3
3	39	6	2
7	25	6	1
20		10	
$\bar{X}$=11.8	$\bar{X}$=46.2	$\bar{X}$= 9.8	$\bar{X}$=2.2

significantly. In fact, experience from other sample surveys suggests that the insignificant difference in isopod numbers was what would have been expected in 2 similar sample sets taken in the same, vegetationally homogeneous, quadrat. Furthermore, the age structure of the 2 groups of animals taken in the 2 quadrats was very similar (for a discussion of age structure in these isopod populations, see Paris and Pitelka 1962).

It does not appear that a difference in abundance of the favorite food, *Picris,* affects *Armadillidium* density in these grasslands. More casual observations elsewhere on San Pablo Ridge indicate that these results are not surprising. Isopods were present in large numbers both in areas in which *Picris* was present, and in areas without *Picris.* The conclusion which must be drawn seems clear; where *Picris* is available isopods utilize it as a principal food source, but in the absence of *Picris* they turn to other dietary items. Mention has already been made of the fact that isopods were often seen feeding on *Silybum marianum. Silybum,* however, is primarily characteristic of disturbed areas, such as road shoulders; only widely scattered individuals of this species occur in grassland proper. Several times isopods were seen feeding on culms of dead *Avena barbata* which had been crushed by trucks driving onto grassland. Except for these instances, isopods were never seen feeding on grass. On the other hand, they were seen often feeding on unidentifiable pieces of litter and duff. Indeed, the very diversity of their diet in areas without *Picris* perhaps has played a part in the failure to identify other specific food items.

ENEMIES OF *A. VULGARE*

PREDATORS

Many biologists have assumed that terrestrial isopods commonly are subjected to heavy predation. In a discussion of the physiological ecology of woodlice of the San Francisco Bay Area, Miller (1938) expressed the belief that they suffered heavy pressure from predators such as salamanders, lizards, birds, and spiders. Actually, the literature now available does not indicate heavy mortality of isopods from predation. Centipedes do not readily eat isopods (Cole 1946, and personal communication with Dr. D. E. Bowers); the only actual observation known to me of a centipede attacking an isopod was reported by Cloudsley-Thompson (1958). Isopods apparently are distasteful to spiders (Bristowe 1941, Gorvett 1956) and to shrews (Brereton 1956). Gorvett showed this tastefulness to result from secretions of the tegumental glands and suggested that these glands, which do not occur in aquatic isopods, had evolved in terrestrial species as a defensive mechanism. Carabid beetles, on the other hand, will eat small isopods (Cole 1946). Several salamanders (Miller 1938, Anderson 1960) and lizards (Miller 1938, Hamilton and Pollack 1961) are known to eat isopods, also.

The abundance and conspicuousness of isopods in the grassland areas studied made them seem a suitable prey for a number of potential predators, and hence an examination of this aspect of their ecology was made. Feeding trials with centipedes and lycosid spiders gave negative results, confirming the observations of others. Carabid and cicindellid beetles captured on San Pablo Ridge occasionally ate small isopods in the laboratory, as did the salamander *Aneides lugubris* and the lizard *Gerrhonotus caeruleus.* In addition, the stomachs of two specimens of *G. multicarinatus* from San Pablo Ridge (provided by Dr. O. P. Pearson) yielded 8 isopods along with a great bulk of other material. In spite of this evidence that beetles, salamanders, and lizards would eat isopods, a routine search for evidence of predation in the field during the investigation produced negative results. The only birds commonly encountered in the research area were meadowlarks *(Sturnella neglecta);* their collection was not permitted and it is not known whether they were feeding on isopods. More data will be required before a meaningful estimate can be made of the amount of isopod mortality attributable to predators.

PARASITES

Terrestrial isopods are known to be hosts of several tachinid (Diptera) parasites (Brues 1903, O'Mahoney 1931, Thompson 1934, Brereton 1956). Thompson (1934) listed *Porcellio scaber, Oniscus asellus, Metaponorthus pruinosus,* and *Armadillidium vulgare* as woodlice in which these parasites occur. Thompson had never found an infested specimen of *A. vulgare,* but Donisthorpe (cited by Thompson) reported collecting one individual of this species on the Isle of Wight, from which a *Phyto melanocephala* emerged. Brereton (1956) likewise obtained a single *P. melanocephala* from an *A. vulgare* specimen. *Phyto melanocephala* also parasitizes *Porcellio scaber* (Thompson 1934). Thompson found *P. scaber* to be the most frequently parasitized woodlouse; for all species of parasites combined, he reported an average frequency of 9.1% parasitization for it. This compares with a frequency of 1.3% obtained by Brereton (1956) for *P. scaber.* In addition to tachinids, acanthocephalan parasites have been reported for *A. vulgare* (Thompson 1934, who cites H. A. Baylis in personal communication). Thompson suggested that the low incidence of tachinid parasitization in *A. vulgare* was because of their heavy exoskeleton which made it difficult for the fly larvae to gain entrance. It was his conclusion that, in general, the low incidence of parasitization, plus the inefficiency of the parasites, make it unlikely that they are of major importance in the control of isopod numbers.

In my study no evidence indicated parasitization in the *Armadillidium* population. In the winter of 1960 a sudden high mortality suggested the possibility of a parasite infestation. Sick or recently deceased isopods were collected, and 75 of them were dissected; parasites were found in none of them. Healthy isopods collected at bait sites with dead and ill individuals were maintained in the laboratory in mass cultures without additional mortality taking place; this also suggests that parasites or disease were not responsible for the mortality observed in the field. The cause of this high winter mortality is discussed later.

CANNIBALISM

Cannibalism frequently has been observed in laboratory cultures of terrestrial isopods (Thompson 1934, Heeley 1941b, Brereton 1956). Usually it involved adults eating newly released young. Studying survivorship in relation to density in laboratory populations of *Porcellio scaber,* Brereton (1956) found a high rate of disappearance of young which he could explain only on the basis of cannibalism. The rate of mortality of the young appeared to be correlated with the density of adults in his cultures, but he was never able to get individual adults to eat young at a rate high enough to account for the rate of disappearance in the survivorship experiments. Although a high mortality rate was characteristic of young *Porcellio* in the field also, Brereton never observed cannibalism in nature.

Heeley (1941b) found that, of the several species cultured by him, *A. vulgare* was least apt to eat its young. In 3 years experience with laboratory cultures, I failed to find a high incidence of cannibalism. Occasional disappearance from group culture perhaps can be attributed to cannibalism, but in general mortality from this cause was low. It was mentioned earlier that *A. vulgare* was seen in the field feeding on bodies of others of their own species, but in every case the victims had been killed by being trampled or run over by a vehicle. Evidence of cannibalism in nature was never found.

THE EFFECT OF WEATHER ON *ARMADILLIDIUM* POPULATIONS

DISTRIBUTION DURING RAINY SEASON

During the rainy season, *A. vulgare* populations are confined to the soil surface and upper layer of loose soil. This was demonstrated by samples taken in the fall and winter of 1957, in which each sample consisted of two parts: one included the upper 4 cm of soil, and the other the next lower 4 cm of soil. Less than 3% of the total number of *Armadillidium* captured came from the deeper part. It is doubtful that even this much of the population occurs below 4 cm; the manner in which the split samples were taken did not entirely preclude the possibility of animals falling into the lower part of the sample as the upper part was being removed.

Microclimatic conditions experienced by isopods in grassland during the rainy season were estimated from relative humidity and temperature determinations made beneath the vegetation at various places and times during the winter and spring of 1959 and 1960. Relative humidity measurements were usually above 65%, and most were above 70%. Temperature at the surface varied considerably, according to season and weather conditions. Examples of vapor pressure deficit calculated from relative humidity and temperature determinations follow: 1.80 mm Hg on morning of March 30, 1958; 7.69 mm Hg on afternoon of April 12, 1958; 6.17 mm Hg at noon on May 18, 1958; 2.90 mm Hg in late afternoon on March 30, 1960.

These are suboptimal vapor pressure deficit values for *A. vulgare,* since it can survive for long periods only in a saturated atmosphere (Miller 1938, Waloff 1941). Undoubtedly, however, the relative humidity to which the cobalt thiocyanate papers were exposed in these observations was less than that experienced by isopods crawling on the damp soil in the same area. Furthermore, *A. vulgare* can compensate for evaporative water loss by imbibition of water from a moist substrate (Spencer and Edney 1954). Such substrates are readily available to isopods during the rainy season. Desiccation does not appear to pose a significant threat to the population during the wet months.

DISTRIBUTION DURING ANNUAL DROUGHT

With the termination of winter rains in the spring and subsequent drying of the soil and vegetation, there begins a period during which moisture availability plays an increasingly critical role in isopod ecology. This fact is reflected in a change in distribution and behavior of the population during the dry months. As drying of the habitat proceeds, isopods take refuge at day in the upper layer of loose, moist soil. The adobe soil of the region shrinks and cracks upon drying, and when the surface soil becomes dry, isopods migrate downward into the fissures thus formed, and into rodent burrows.

This downward migration is reflected in a decrease in the number of isopods taken in soil samples during the spring months. Results from monthly sample surveys during January through July, 1959, (Table 4) illustrate this fact. These surveys were taken in the area shown in Fig. 1. Monthly rainfall totals recorded at the Berkeley weather station are also given in Table 4.

TABLE 4. Isopod numbers in soil samples from monthly surveys and monthly rainfall, January-July, 1959.

Date of survey	Number samples taken	Number isopods per sample ($\bar{X}\pm SD$)	Rainfall during month (total inches)
Jan. 23......	8	11.3±10.0	4.69
Feb. 21......	4	16.3±15.7	4.53
Mar. 22......	12	8.8± 7.7	0.58
Apr. 18......	20	12.7± 9.5	0.36
May 16......	20	9.4± 5.4	0.03
June 10......	20	1.2± 2.0	0.00
July 17......	10	0	0.00

Beginning in March rainfall was light, and none fell after May. At the time samples were taken on March 22, rain was falling. By April 18 the soil had undergone some drying, but it remained moist beneath the surface layer; at this time isopods were deeper in the soil than at any time earlier in the spring. On May 16 the upper 5 cm of soil was fairly dry and grass had begun to die. On this occasion several isopods were seen at the bottom of the soil blocks as they were being collected. By June 10 both soil and vegetation were quite dry; no isopods were seen when the samples were collected, but a few specimens were separated from them in the laboratory. Finally, the samples taken on July 17 yielded no isopods.

In order to ascertain the extent of the vertical descent of isopods into subsurface soil spaces, a series of pits were dug in the study area during the summers of 1958 and 1959. In each case, a pit was dug to a depth of 50 to 60 cm; then, under a prescribed surface area adjacent to the pit, the wall of the pit was carefully broken away. This procedure exposed isopods in crevices without dislodging them, making possible a determination of their depth beneath the surface. The results from three such pits dug during the fall, 1959, drought are illustrated in Table 5. Each of these extended to a depth of 60 cm under a surface area 50 x 50 cm.

TABLE 5. Depth of isopods in soil during Fall, 1959, drought.

Depth of isopods (to nearest 5 cm.)	NUMBER OF ISOPODS FOUND IN PIT (Size of pit: 50×50 cm)		
	Nov. 5	Nov. 27	Dec. 9
0	0	0	0
5	13	0	0
10	6	4	0
15	4	7	49
20	33	36	12
25	2	8	17
30	2	2	4
35	0	2	10
40	0	0	2
45	0	0	2
50	0	0	0
55	0	0	0
60	0	0	0

Generally, isopods were found at depths ranging from 5 to 30 cm; the greatest number occurred from 15 to 25 cm. The 1959 drought was unusually long, extending into December, and isopods retreated to greater depths as the soil continued to lose moisture during November and December. On December 9, some were found as deep as 45 cm, although most were still between 15 and 25 cm deep. In the subsurface soil spaces, isopods occurred singly and in small aggregations. There was no indication that they fed while underground; they were never near food when uncovered in the pit studies.

Large aggregations of isopods were found in rodent burrows on September 20 and again on October 4, 1958. These two aggregations were located in blind side chambers to main burrows; the chambers were filled with loose, slightly moist material which consisted of a high proportion of isopod fecal pellets. Of 56 animals taken in the collection on September 20, 74% were young individuals, and 97% of 261 collected on October 4 were young animals. Although scattered individuals were frequently found in rodent burrows at other times, attempts to find additional aggregations in burrows failed.

These aggregations must be advantageous by reducing rate of evaporation from isopods in them; Allee (1926) has shown that isopod aggregations serve such a function. Of added significance is the fact that the groups in rodent burrows consisted largely of young individuals, which are more susceptible to desiccation than adults (Heeley 1941b). It does not appear, however, that such aggregations are a regular feature in the ecology of isopod populations in these grasslands.

In other situations, however, aggregations are common. During the summer small areas of surface soil are kept moist by precipitation of water of condensation from leaves and branches of the bush *Baccharis pilularis;* an area of moist soil at the base of a bush is illustrated in Fig. 3. Condensed water is also channeled down the dead stalks of the tall forb *Brassica campestris* (Fig. 4), to wet small areas at the base of the plants. *Baccharis* is confined to chaparral and chaparral-grassland ecotones, but *Brassica* is common in open grassland.

The size and commonness of isopod aggregations at the base of *Brassica* stalks was investigated by a sample survey on September 2, 1959, in which paired samples were taken; one of each pair enclosed *Brassica,* while the other sampled an adjacent area without *Brassica.* The samples were taken at widely separated sites on the hill in the center of Fig. 1. Results are given in Table 6.

Isopods occurred in all samples taken at the base of *Brassica* stems and were numerous in most of them, but the animals were absent or scarce in samples without stems. A sign test indicated the number of isopods in samples with stems to be greater than the number in samples without stems, at the .002 level of significance. In addition, in two unpaired samples

FIG. 3. Base of a *Baccharis* bush. The area of dark soil was kept moist by precipitation of moisture of condensation from leaves and branches. Isopods aggregated here during drought.

FIG. 4. Stalks of dead *Brassica* in open grassland. Water, condensed on the branches, is channeled down the stalks to moisten a small area of soil at the base of the plants; isopods aggregate in these moist areas in large numbers during drought.

TABLE 6. Isopods in samples with and without *Brassica* stems.

Samples with stems (isopod numbers)	Samples without stems (isopod numbers)
77	1
16	0
20	2
9	0
78	0
5	0
43	1
71	3
6	0

which enclosed *Brassica* stems, there were, respectively, 58 and 46 isopods.

Of the 429 individuals taken in the samples with *Brassica* stems, 87% were young (i.e., individuals from broods produced that year). A comparison (Table 7) with other samples taken in the same general area in the fall of 1959 suggests that this is a higher proportion of young than occurs under grass without *Brassica*. Surveys used for this comparison were taken at night (except the one taken on September 19, which followed an unseasonable rain storm). The proportion of young from each survey was compared with the proportion from the *Brassica* stem survey, using a normal approximation test for equal proportions. In all surveys except one the proportion of young were significantly less than in the *Brassica* stem sample set.

TABLE 7. Proportion of young in aggregations at base of *Brassica* and in population under grass without *Brassica*.

Location of sample	Date of survey	Number of individuals	Proportion of young
At base of *Brassica* stems	Sept. 2	429	.87
Under grass without *Brassica*	Aug. 18-19	130	.45**
	Sept. 19	112	.53**
	Nov. 6-7	81	.89
	Dec. 9-10	227	.72*

* Differs significantly from 0.87 at .05 level.
** Differs significantly from 0.87 at .001 level.

It appears that the small areas of moist soil at the base of *Brassica* stems may be foci for breeding or release of young, or that survival of young may be better here. Perhaps both factors account for the high proportion of young. No sampling was done beneath *Baccharis* bushes, but observations indicated that here, too, young isopods were very abundant during drought.

The retreat of isopods during the summer and fall into small areas of moist surface soil and deep into soil fissures is not accompanied by estivation, as has been suggested for California terrestrial isopods (Miller 1938). Observations made at night during the summer and fall of 1959 showed that isopods emerge at night from their daytime retreats and are active on the surface. Feeding occurs at this time. To document this noctural emergence, a survey of 10 randomly located samples was taken in Quadrat 2 (Fig. 2) between 2200 and 2330 hours PST on July 16, 1959. This was compared with another survey of 10 random samples taken in this quadrat between 1500 and 1630 hours on July 17. The results, presented in a contingency table (Table 8), indicate a significant difference in the number of daytime samples which contained isopods as opposed to the number of nighttime samples containing them (P = .00036). Although absent from the upper soil during the day, isopods were taken in 8 of 10 night samples.

TABLE 8. Occurrence of isopods in soil samples taken in July during the day and at night.

	Samples with isopods	Samples without isopods	
Day	0	10	10
Night	8	2	10
	8	12	20

Fisher Exact Probability:

$$p=\frac{10!\,10!\,8!\,12!}{20!\,0!\,10!\,8!\,2!}=0.00036$$

DIEL PERIODICITY IN ISOPOD BEHAVIOR

SURVEY METHODS. The diel periodic behavior of *Armadillidium* was studied by surveys in which isopod activity was observed at different times during the 24-hour cycle. Measurements of microclimatic conditions were made at the same time and place. Observations were made at the weather stations described in METHODS. Estimates of isopod activity were obtained from counts of the individuals present in 50 x 50 cm plots adjacent to the weather stations. Activity Plots 1 (Fig. 5) and 3 were adjacent to Weather Stations 1 and 3, respectively; Activity Plots 2 and 4 were both adjacent to Weather Station 2 (Fig. 6).

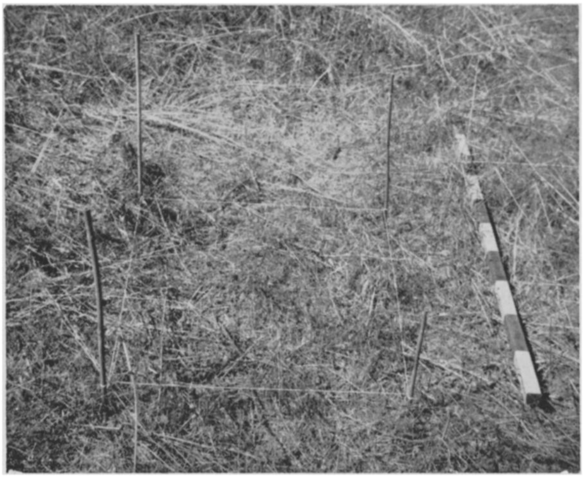

FIG. 5. Activity Plot 1. The plot was 50 x 50 cm. The photograph was taken during drought and illustrates the sparse, dead vegetation present at this time of year. The stick is marked in decimeter intervals.

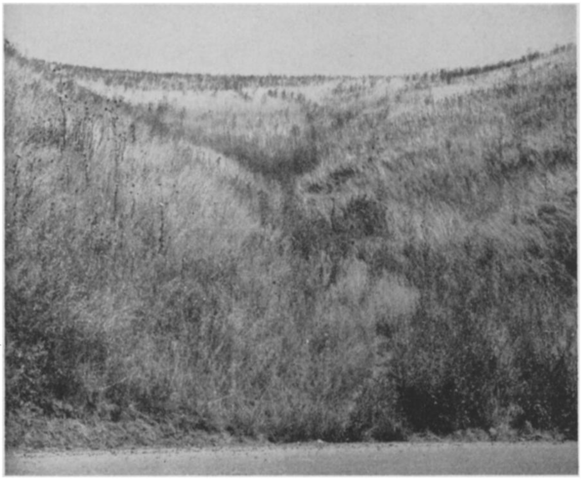

FIG. 6. Location of Weather Station 2 and Activity Plots 2 and 4. These study sites were situated in the grass above the road, at the lower right center of the picture. The lighter vegetation is grass, and the darker is *Brassica campestris* (with the large flowerheads) and *Picris echioides*.

A hand counter was used to enumerate the isopods in the plots. An electric lantern provided illumination at night. Under sudden exposure to this light, isopods either showed no immediate alarm reaction, or else they rolled up quickly; in either case some individuals usually began to crawl away from the light within a few seconds. This movement was slow, however, and rapid work with the counter permitted an accurate determination of the number of isopods present. One or more hours of undisturbed darkness elapsed between observations; there was no evidence that the brief disturbance at each observation affected the number of isopods at subsequent countings.

Soil samples were taken in Quadrat 3 (Fig. 2) during each survey, also. Four sets of five samples each were taken at different times. The location of each sample in the quadrat, and the set in which it fell, were at random. In surveys during the dry season, the 1st set was taken about 2300 hours, the 2nd about 0300 hours, the 3rd about 0630 hours (at dawn), and the 4th between 1000 and 1200 hours. In the survey taken during the rainy season, sample sets were taken at 2200, 0600, 1030, and 1400 hours.

Finally, for the survey taken in the rainy season, four additional activity plots were set up on the roadway adjacent to Weather Station 2 and Activity Plots 2 and 4. Each roadway plot was 15 m in length and included the width of the asphalt surface (Figs. 2 and 7). Relative humidity and temperature were determined at the surface on the edge of the road each time a count was made of the isopods in the plots (it was impossible to expose humidity papers on the roadway itself because of occasional vehicular traffic).

FIG. 7. Location of Roadway Plots. The plots were contiguous, each measuring 15 m in length and including the asphalt surface of the road. Weather Station 2 and Activity Plots 2 and 4 were located in grassland just out of the picture to the right.

DRY SEASON RESULTS. It is convenient to consider the results from dry season surveys separately from those taken during the rainy season. Climatological data from Weather Stations 1 and 2 for all surveys are given in Table 9. Surveys 1-4 were taken during drought, 1 and 3 being taken on nights when the atmosphere was very dry, and 2 and 4 on nights when the air was moist. On the night of Survey 2 a dense stratus enveloped the ridge. During Survey 4 the sky was clear; a very moist wind was blowing from over San Francisco Bay, however, and dewpoint

TABLE 9. Weather data from stations 1 and 2 for all diel surveys.

Number and date of survey	STATION 1			STATION 2		
	Time PST	Temp. °C.	R. H. %	Time PST	Temp. °C.	R. H. %
Survey 1 Aug. 6 and 7, 1959	1900	25.1	40	1910	25.4	35
	2200	16.0	62	2145	15.7	67
	0300	20.1	47	2230	16.0	69
	0430	16.3	65	2310	16.0	70
	0650	18.0	70	0130	17.7	55
	1100	28.8	37	0515	17.1	66
	1215	33.8	37	0710	17.0	75
				1050	28.0	33
Survey 2 Aug. 18 and 19, 1959	1900	12.2	85	1910	14.2	80
	2145	11.2	90	2135	12.1	85
	2305	11.2	89	2325	12.1	87
	0315	11.0	93	0250	11.6	90
	0610	10.3	92	0555	11.2	90
	0740	10.3	92	0730	11.7	91
	1035	11.7	88	1025	13.0	85
	1135	16.3	70	1155	18.4	65
Survey 3 Nov. 6 and 7, 1959	1800	15.1	40	1815	14.3	40
	2100	14.5	50	2115	13.1	42
	2230	10.6	43	2245	12.0	47
	0200	10.8	47	0140	13.1	42
	0400	10.6	40	0415	12.1	48
	0600	9.0	47	0545	11.8	50
	0745	13.0	40	0800	13.1	48
	1045	20.1	32	1030	18.9	21
Survey 4 Dec. 9 and 10, 1959	1800	8.3	86	1810	8.3	86
	2100	9.0	95	2030	9.9	92
	2315	9.2	93	2330	9.2	90
	0215	8.0	95	0200	8.9	91
	0400	8.7	88	0415	9.2	89
	0645	8.0	85	0630	8.8	86
	0945	11.2	74	1000	13.9	65
Survey 5 Mar. 31 and Apr. 1, 1960	1700	11.0	82	1645	13.5	77
	2100	10.5	93	2030	12.1	91
	2230	10.4	90	2330	10.6	94
	0515	9.5	94	0500	10.3	94
	0715	9.9	92	0645	10.4	88
	1000	22.3	50	0945	23.5	47
	1400	22.0	45	1115	32.0	25
				1430	32.8	37
				1545	23.9	53

was reached early in the evening. The relative humidity on wet nights was consistently above 85% and usually above 90%. In contrast, on dry nights it varied between 40 and 70%.

The highest relative humidity obtained during Survey 2 was 93%, in spite of the fact that the area was enveloped in a dense fog. The occurrence of relative humidity determinations less than 100% in a fog may result from two causes. The 1st is inherent error in the technique of measurement; this has been analyzed by Solomon (1957). According to him, the greatest error probably comes from the cobalt thiocyanate papers being read at a temperature which differs from that at which they were exposed: at 100% relative humidity this may contribute an error of ± 4%. It is still possible, however, that the humidity in the stratus layer was actually not 100%, since stratus formation occurs regularly at a humidity only slightly greater than 90% (Patton 1956).

Air temperature varied more on dry nights, dropping after sundown to a minimum before midnight; generally this low level was maintained, with fluctuation, until shortly after dawn. At that time temperature began to rise sharply. Soil temperatures (not given) underwent gradual changes, following the trend of air temperature with a lag of approximately two hours at a depth of 15 cm.

Isopod activity at Plots 1 and 2 are shown in Fig. 8; vapor pressure deficits computed from data taken at the adjacent weather stations are also graphed.

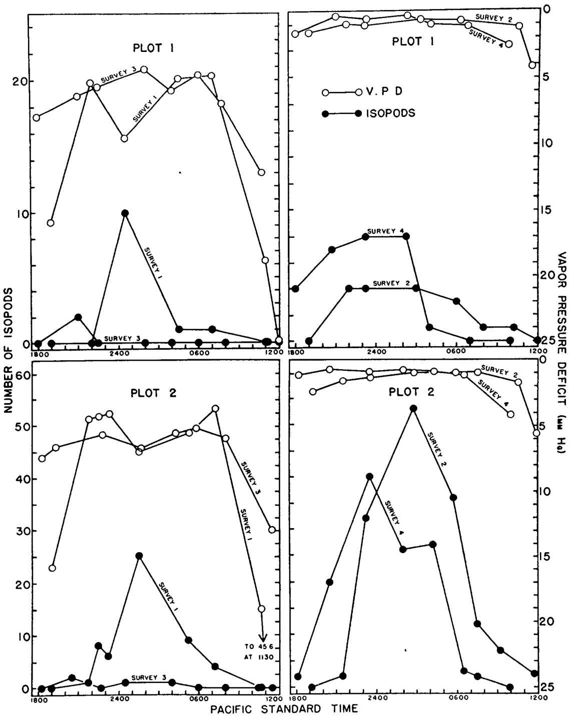

FIG. 8. Results from Diel Surveys 1-4 for Activity Plots 1 and 2. All four surveys were taken during drought (see Table 9). The left-hand graphs show results from dry nights; those on the right show results from moist nights. Vapor pressure deficit was computed from relative humidity and temperature recorded in air above the vegetation. The scales for isopod numbers have been made different for Plots 1 and 2 because of a difference in isopod density in the two areas.

Relative humidity and temperature determinations made at the surface of the vegetation were used for these calculations, since at the time of these surveys vegetation in the activity plots was sparse and isopods essentially were exposed to open air. Plots 1 and 2 were used in all surveys, but Plot 3 was used only during Surveys 1 and 2 and Plot 4 during Surveys 3 and 4. Observations at Plots 3 and 4 (and adjacent weather stations, 3 and 2, respectively) are presented in Table 10.

In general, the number of isopods present in the

TABLE 10. Dry season diel survey results from Plots 3 and 4.

	PLOT 3				PLOT 4		
	Time PST	VPD mm/Hg	Number isopods		Time PST	VPD mm/Hg	Number isopods
Survey 1	1900	—	0	Survey 3	1815	7.33	0
	2130	7.09	0		2115	6.55	0
	2215	6.74	2		2245	5.58	1
	2245	6.62	4		0130	6.56	1
	0145	9.23	5		0415	5.51	1
	0530	8.24	1		0545	5.19	0
	0730	4.77	0		0800	5.87	0
	1045	16.33	0		1030	12.93	0
	1245	24.52	0		—	—	—
Survey 2	1900	2.57	0	Survey 4	1800	1.15	1
	2130	1.89	0		2030	0.73	10
	2340	1.58	18		2330	0.88	51
	0230	1.50	18		0200	0.77	45
	0545	1.50	13		0415	0.96	60
	0715	1.48	0		0630	1.19	21
	1015	0.79	0		0730	—	4
	1155	—	0		1000	4.17	1

activity plots, and the length of time that they remained exposed, were greater on wet nights than on dry nights. Data from all surveys made during drought were pooled for each activity plot and for each weather station, and a Spearman rank correlation coefficient for number of isopods with vapor pressure deficit was computed for each plot. To reduce confounding with photic responses, only data taken during hours of darkness were used for the calculation. The results were: for Plot 1, $r_s=-.40$ ($N=19$, $P=.05$); for Plot 2, $r_s=-.66$ ($N=21$, $P=.01$); for Plot 3, $r_s=-.60$ ($N=9$, $P=.05$); for Plot 4, $r_s=-.67$ ($N=10$, $P=.05$). A significant negative correlation of number of isopods present on the surface with vapor pressure deficit was obtained for each activity plot.

Cloudsley-Thompson (1958) has shown a relation between wind velocity and the number of *A. vulgare* present on a wall beside a bay on the west coast of England; he found isopods less numerous when wind velocity was high. Although I did not make measurements of wind velocity, it has been pointed out that a strong west wind is characteristic of the San Francisco Bay area in summer. Wind velocities recorded at the weather station on the University of California campus, Berkeley, indicated that the lowest velocity on any diel survey night prevailed during Survey 1 from 2200 to 0200 hours. During this period a brief emergence of isopods occurred in all plots in spite of a high vapor pressure deficit (see Fig. 8). Perhaps the sudden drop in wind velocity contributed to this phenomenon. The highest wind velocity occurred, however, on the two wet nights. In general, the strongest winds at night prevail when there is a stratus cover, and it is on such nights that isopods emerge in greatest numbers.

Whatever the influence of wind (and other environmental factors) on the nightly emergence of isopods during the months of drought, a clear correlation has been shown to exist between isopod activity and atmospheric moisture. Moisture conditions appear to be the overriding environmental factor affecting this diel periodic behavior of isopod populations in these dry grasslands.

Results from soil sample surveys taken during the diel periodicity studies are given in Table 11.

TABLE 11. Soil sample results from diel surveys.

Survey and sample set* number	Time	Number isopods ($\bar{X}\pm$SD)	VPD mm/Hg
Survey 1:			
Set 1.........	2245	0.8± 1.8	11.15
Set 2.........	0315	0.2± 0.4	7.97
Set 3.........	0515	0.4± 0.6	6.41
Set 4.........	1030	0.2± 0.4	18.93
Survey 2:			
Set 1.........	2130	4.8± 4.9	1.77
Set 2.........	0245	6.6± 3.8	1.21
Set 3.........	0545	8.2± 3.8	0.96
Set 4.........	1000	6.4± 6.1	1.35
Survey 3:			
Set 1.........	2215	4.4± 6.0	5.95
Set 2.........	0230	2.2± 3.0	5.69
Set 3.........	0630	7.2± 8.0	5.50
Set 4.........	1000	4.8± 4.3	12.00
Survey 4:			
Set 1.........	2130	4.6± 4.6	2.19
Set 2.........	0300	13.4±13.0	1.69
Set 3.........	0730	22.6±12.5	0.83
Set 4.........	1015	4.8± 4.3	2.15
Survey 5:			
Set 1.........	2200	19.2±11.1	1.00
Set 2.........	0600	13.0± 5.1	0.74
Set 3.........	1030	9.6± 3.4	1.50
Set 4.........	1500	14.8± 8.7	3.38

* Each set consists of 5 samples.

Isopod numbers are mean number of isopods ± standard deviation for each set of five samples. Vapor pressure deficits were calculated from data taken at Weather Station 1, located next to the quadrat in which the samples were taken; these values are based on relative humidity readings at the soil surface and temperatures recorded at a depth of 1 in. (2.4 cm). Vapor pressure deficit computed in this way probably approximates moisture conditions in the air spaces of the upper soil layers. Generally, saturation deficit thus obtained was greater than in open air. This is not surprising since the soil was very dry at the time Surveys 1-4 were taken; furthermore, in dry habitats relative humidity under vegetation is often lower than in the open air above it (Geiger 1957: 300).

Soil sample data for Surveys 1-4 were pooled, and a Spearman rank correlation coefficient was computed for mean number of isopods per sample with vapor pressure deficit at the time the sample was taken. A significant negative correlation was indicated ($r_s = -.78$; $P = .01$).

The number of isopods taken by the soil samples in each survey varies considerably from set to set. A Kruskall-Wallis analysis of variance by ranks (Siegel 1956; 184 ff.) indicates a significant displacement among the distribution of isopods numbers for the sample sets within each survey ($P = .001$ in each case). In surveys 2, 3, and 4 the greatest number of isopods was taken at dawn, at a time when the number on the surface had decreased markedly from a maximum in the middle of the night. Recall that at this time of year isopods descend in soil fissures during the day to depths of 15-45 cm. The total number of isopods taken in the diel periodicity soil sample surveys (when compared with one another, and when compared with surveys taken in the same area during the rainy season: *cf.* Survey 5) indicates that on different nights a varying proportion of the population was high enough in the soil to be sampled. Perhaps, then, the high numbers taken in samples at dawn reflects an accumulation of isopods in the upper soil layer at this time in the 24-hour cycle because of: (1) the presence of individuals which had been on the surface during the night, but which had commenced a downward migration in search of refuge for the day, and (2) the presence of individuals that were located very deep during the preceding day, and which had begun an upward migration during the night without getting to the surface before dawn. It would be desirable to investigate this possibility by means of pit studies conducted at various times during the hours of darkness.

RAINY SEASON RESULTS. Since we have just considered soil sample data from the dry season surveys, it is convenient to discuss rainy season survey results by first considering soil samples. During the rainy season, the population is located at or near the surface at all times; this is illustrated in the results for Survey 5 (Table 11). This survey extended over a full 24-hour period. Compared to summer and fall surveys, the mean number of isopods per sample was high at all hours. There is an apparent peak in isopod numbers at 2200 hours, but in the set taken at that time there was a sample producing 37 individuals. This was 12 more than was taken in the next largest sample (in the set taken at 1400 hours); if this unusually large sample is omitted from the 2200-hours set, the remaining 4 samples give a mean of 14.8 isopods, which approaches the means of the sets taken at other hours.

On the night of Survey 5, a dense stratus covered the hill until just before dawn; the following day was clear and dry (see Table 9). Activity plot results and vapor pressure deficit values are given in Fig. 9. Since the soil was moist at the time of the survey, and the vegetation green and in luxuriant growth, vapor pressure deficits were computed from relative humidity and temperature measurements made beneath the vegetation.

In Plot 1 isopod activity was greatest during the middle of the night. The number of individuals actively crawling about on the surface of the plots decreased before dawn and remained low during the day. The general pattern is similar to that for dry season surveys, except that isopods did not disappear from the surface during the day. In Plots 2 and 4, however, an opposite trend occurred: fewer isopods were found at night than during the day. Data from Plots 2 and 4 were parallel throughout the 24-hour period, indicating a general trend in the area of these plots. An explanation for this apparent enigma is developed below.

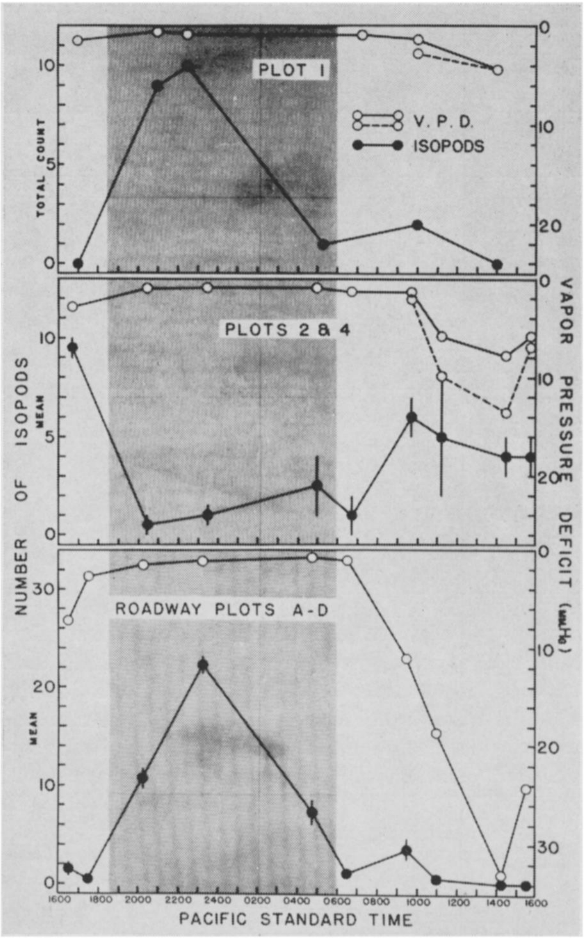

FIG. 9. Results from Diel Survey 5. This survey was taken during the rainy season. Plots 2 and 4 were in grassland adjacent to the Roadway Plots. Shading indicates the period from sunset to sunrise. Solid vapor pressure deficit lines in the two top graphs are from observations taken beneath the vegetation, and broken lines are from observations taken in air above the vegetation. Weather data on the roadway were taken at the surface of the road. Vertical lines through points for isopod numbers in the lower graphs indicate standard error.

On many occasions *A. vulgare* was observed to crawl on the roadway and other exposed areas during clear, sunny mornings. Cloudsley-Thompson (1951) has reported that *A. vulgare* occurred in greatest numbers on a roadway in England (in May) during midmorning. His results are presented as a generalized curve which indicates a sharp rise in number of isopods beginning about 0800 hours, reaching a peak about 1000 hours, and followed by a decline during the afternoon. Temperature and relative humidity were graphed, also, from which I estimate a vapor pressure deficit of about 4 mm Hg during the period of greatest activity. Cloudsley-Thompson (1951, 1952) concluded that the diurnal locomotory rhythm of *A. vulgare* was not correlated with humidity and temperature. Since this appears to be in contradiction to my findings, the activity of *A. vulgare* on the roadway (see Fig. 2) was followed during Survey 5.

Roadway plot results are presented in Fig. 9. The statistics given are mean number of isopods per plot ± standard error, and vapor pressure deficit at the surface on the edge of the road. The pattern of activity on the roadway was similar to that obtained for Activity Plot 1, which was located in grassland 75 m from the road. Activity Plots 2 and 4, however, were less than 5 m from the edge of the road, and here a reverse pattern was obtained. The decline in numbers of isopods in these two plots during the night appears to represent an emigration of isopods from roadside grassland onto the road. Nothing on the surface of the road appeared to be attracting isopods; almost all observed there were crawling, apparently aimlessly. The weather conditions on the road during the night were essentially similar to those in the adjacent grassland (compare vapor pressure deficit statistics for the two areas). It seems likely that random movements of isopods, during the period of high locomotory activity at night, carry them onto the road. The roadway, thus, is a habitat which can be entered by isopods only periodically, on the occasion of a very low ambient vapor pressure deficit.

Vapor pressure deficit at the surface of the road increased precipitously after sunrise on the morning of Survey 5, reaching a maximum in mid-afternoon. By noon there had been a complete evacuation of the roadway by isopods. A slight increase in their number occurred between 0630 and 0930, which may or may not reflect the phenomenon reported by Cloudsley-Thompson (1951). These results do not confirm Cloudsley-Thompson's observations, although a complete knowledge of microclimatic events and the physiology of the isopods in the two locations would be necessary before they could be claimed to be contradictory. Observations at other times during the rainy season indicated that the behavioral pattern found in Survey 5 occurs regularly on moist nights. On dry nights during the winter and spring, on the other hand, isopods do not appear on the road in great numbers. The conclusion by Cloudsley-Thompson (1951, 1952) that the diurnal activity of *A. vulgare* is not controlled by temperature and moisture cannot, therefore, be considered a valid generality.

CONCLUSIONS. A clear correlation exists between atmospheric moisture and isopod behavior during the summer and fall drought. *Armadillidium* seeks refuge from desiccation during the day by descending deep into soil fissures; from these it emerges on nights when there is a low ambient vapor pressure deficit. During the winter and spring, on the other hand, moist soil enables the population to remain near the surface both day and night, but maximal activity again occurs during hours of darkness. Probably this, also, is related to moisture conditions. The fact that the animals anticipate daylight by a diminishing of activity before dawn suggests an intrinsic rhythmicity in behavior, but such an intrinsic behavioral pattern, if present, is overridden by the influence of atmospheric moisture. In conclusion, the activity of the *A. vulgare* population in this grassland habitat is governed largely by moisture availability.

FIELD BEHAVIOR AND THE PHYSIOLOGY OF A. VULGARE

Results of this study are interesting in light of the work of others on the environmental physiology of *A. vulgare*. The survival rate of *A. vulgare* at suboptimal vapor pressure deficits was determined by Miller (1934, 1938). Isopods I observed in nature remained exposed to high vapor pressure deficits for much shorter periods than the average survival times obtained by Miller under similar moisture conditions. To illustrate, in Diel Survey 1, a general emergence of isopods occurred between 2300 and 0500 hours, during which the vapor pressure deficit (at Weather Station 1) was as high as 9.35 mm Hg. This emergence lasted less than 7 hours, and according to Miller the survival time at such a saturation deficit is approximately 20 hours. Exposure times under natural conditions would not be expected to approach survival times, provided shelter is available; presumably isopods would seek shelter before entering desiccation stress. Furthermore, the actual survival times of *A. vulgare* may be less than those reported by Miller (1934, 1938); Edney (1954) has pointed out that the isopods in Miller's experiments were allowed to aggregate, which reduces evaporation (Allee 1926) and increases survival rate (Miller, cited by Edney 1960). Finally, the presence of wind in the field would greatly increase evaporation and hence reduce survival time. Consequently it is to be expected that the lengths of exposure to suboptimal moisture conditions tolerated by isopods in the field are considerably less than the mean survival times obtained under similar moisture conditions in the laboratory.

The upper thermolethal point for *A. vulgare* is about 37° C, but temperature as high as 46° C can be survived briefly if relative humidity is sufficiently low to permit evaporative cooling (Edney 1951). In California coastal grassland surface temperature near 40° C is not uncommon in the summer and fall. The highest recorded by me was 43.6° C, on July 25, 1959 (1730 hours) at Weather Station 1; at a depth of 8 cm, the temperature was only 27.2°, and at 15 cm it was 24.1°C. The highest temperature to which isopods were found exposed was 26.5° C, on the surface of the road during Survey 5 at 1100 hours; the vapor pressure deficit at the time was 18.7 mm Hg. Shortly after this observation isopods had disappeared from the roadway. At 1430 hours they were numerous in grassland adjacent to the road, where temperature under the vegetation was

24.0° C and saturation deficit was 7.8 mm Hg. The soil was moist, hence the animals could imbibe water. As in the case of suboptimal moisture conditions, isopods undoubtedly take refuge from adverse temperature before their thermolethal point is approached.

Why do isopods appear in exposed areas, such as the surface of roads, in bright sunlight and suboptimal moisture conditions? Edney (1953) has suggested that they may do so to raise their body temperature in cool weather, or to escape a lethal temperature in combination with high humidity in warm weather. Neither explanation seems to account for observations made in this study. For example, in Diel Survey 5 the greatest number of isopods on the road during daylight occurred at 0930 hours, when air temperature at the surface was 20.8° C. Under the vegetation in the adjacent grassland the temperature was only 21.5° C. The vapor pressure deficit on the road was 11.1 mm Hg and in the vegetation 1.4 mm Hg. An alternative explanation has been advanced by Cloudsley-Thompson (1952). On the basis of a reported change from a negative to positive phototaxis by isopods as they become desiccated, he suggested that woodlice emerge from daytime retreats when these dry out, and then wander until another moist refuge is encountered. This does not account for many instances when isopods were found on the roadway, either. For example, on March 19, 1960, isopods were present on the road in bright sunlight at 1100 hours; the temperature at the surface was 25.0° C, and the vapor pressure deficit was 14.2 mm Hg. Under stones on the road shoulder, where isopods were present also, the temperature was 11.5° C and the vapor pressure deficit 0.8 mm Hg. Additional observations failed to show any evidence of drying out of the roadside retreats.

The mechanisms invoked by Edney and Cloudsley-Thompson to explain the presence of isopods in exposed situations during the day may operate under appropriate circumstances, but they do not satisfactorily explain many instances of this phenomenon I observed. A simpler explanation can account for much of this daytime activity. A peak in locomotory activity has been shown to occur on moist nights. Furthermore, *A. vulgare* has a surprising vagility in these habitats (Paris and Pitelka 1962). Perhaps the general displacement of the population during the peak of locomotory activity at night carried isopods into exposed situations, and by morning many exposed individuals had not yet found suitable daytime shelter. Thus, isopods present on the roadway during the morning represented a remnant from the preceding night's activity.

WEATHER AND MORTALITY

DEATH FROM DESICCATION. Although the summer and fall drought in California has a profound influence on the distribution and behavior of *A. vulgare,* there is little direct evidence of its effect on survivorship. In the pit studies described earlier, small *cul-de-sacs* were sometimes discovered in the upper soil layers, in which young isopods, and occasionally some adults, were found dead. Perhaps these animals had taken refuge there during the day, only to die as the soil warmed and the vapor pressure deficit or temperature in the soil spaces rose above the lethal limit. From time to time a few dead adult individuals were found in roadside culverts, where apparently they were caught by a rapidly rising vapor pressure deficit or temperature on mornings following moist nights, with death resulting before they could seek refuge. Yet the magnitude of these findings did not suggest a high mortality from desiccation, at least among adults. This view is supported by demographic results of this investigation, which did not show a high adult mortality during the summer (Paris and Pitelka 1962). Apparently most of the adult population is able to avoid desiccation during drought.

In spite of the fact that few dead young were found, demographic data showed a high mortality rate for the youngest generation between April and October 1 (Paris and Pitelka 1962). Death from predation or cannibalism could result in total destruction of carcasses, of course, and probably some of this occurred. On the other hand, if young isopods were killed by physical factors, they still might not be found because of the difficulty in seeing their tiny bodies among soil particles. Furthermore, the exoskeletons of the young are extremely fragile, and it is unlikely that they would remain intact for long following death.

Heeley (1941a) has noted that newly released isopods are more susceptible to desiccation than older individuals. Laboratory observations made in the present study confirm this. On *a priori* ground we may assume that the young cannot move from adverse microclimates to more favorable ones as readily as adults. Indeed, it was noted in the pit surveys that young individuals were confined generally to the upper 15 to 20 cm of soil, even in late fall when adults were seeking refuge as deep as 35 to 45 cm. It is reasonable to assume, therefore, that some of the summer mortality of young, and perhaps much of it, results from desiccation.

DEATH FROM DROWNING. Extensive mortality in *A. vulgare* population following heavy rains has been reported by Pierce (1907) in Texas. He also observed individuals of this species taking refuge on a fence and beneath the clapboards of a house during summer storms. Both Abbott (1918) and Cole (1946) have reported *Porcellio scaber* taking refuge on plants above ground when the soil beneath was flooded. Finally, Heeley (1941b) observed that specimens of *A. vulgare* could not tolerate having the pleopods flooded.

In January, 1960, large numbers of dead or ill isopods were found at bait sites in the study area. Additional observations revealed that dead adult isopods were common throughout grasslands of the region. Prior to this, during summer and fall, dead isopods were encountered very rarely. Clearly some new mortality factor had suddenly come into operation.

The possibility of a sudden infestation by parasites or infectious disease was considered. The evidence on parasitism has been examined and dismissed in the section on ENEMIES OF A. VULGARE. The possibility that the population was diseased seems ruled out by the fact that healthy animals which were collected at bait sites, along with sick and dead ones, continued to live in apparent good health in crowded laboratory cultures.

Since the mortality occurred shortly after the onset of winter rains in mid-December, the possibility that the observed deaths resulted from drowning was investigated. Observations of isopods in the field during heavy rains revealed that many were actively seeking shelter. In areas where water was running over the surface, numerous individuals were found clinging to stalks of vegetation, a behavioral pattern not normally found in *Armadillidium* in this grassland habitat. Elsewhere the animals were aggregated in dense vegetation, in an apparent attempt to take shelter from the driving rain.

During a storm on February 7, 1960, many isopods were observed attempting to take shelter from rain on the lee side of the wall of a roadway culvert (Fig. 7). Every available recess in the wall was filled with isopods; there were clearly more isopods than available shelter sites, so that many individuals were trapped in streams of water running down the surface of the wall. On the day following the storm, 111 recently killed individuals were found at the base of the culvert wall. (Recently killed isopods can be distinguished easily from those which have been dead for some time, because drying and blanching of the carcasses begin a few days after death). The number of isopods on and about this culvert decreased markedly during the winter. Thus, in a storm lasting from March 8 to 11, 1950, few isopods were taking refuge on the culvert wall. Following the storm, only 35 dead individuals were found on the floor of the culvert.

These observations indicate that flooding winter rains pose a serious threat to the population. Deaths observed during the winter are believed to result chiefly from drowning.

EXPERIMENTAL DROWNING. In addition to dead animals, many obviously ill animals were also found during the winter. Was submergence by flooding rains causing death in some individuals, but only illness in others? To investigate this question, and to determine the length of submergence required to kill isopods, a drowning experiment was carried out in the laboratory.

From a stock of animals collected at bait sites on February 7 and 8, 1960, sixty individuals ranging in length from 5 to 15 mm were selected for the experiment. Ten of these were placed in each of 6 Stender dishes, size classes being equally apportioned to each dish. The dishes were then randomly assigned to 6 experimental conditions. Experimental treatments involved flooding the dishes with pond water for periods ranging from 0.5 to 7 hours, except for one dish which was an unflooded control. Wads of wet tissue paper were placed in each dish (including the control) to enable the animals to crawl off the wet dish bottom after water had been drained from it. Submergence times and results are given in Table 12.

TABLE 12. Drowning among isopods subjected to varying periods of submergence in pond water.

	LENGTH OF PERIOD OF SUBMERGENCE (hours):					
	0	½	1	2	4	7
Number dead:						
7 hours from beginning of experiment	0	0	0	1	3	4
19 hours from beginning of experiment	0	0	0	2	3	6
43 hours from beginning of experiment	0	0	0	2	5	8

All animals subjected to 1 hour or less of submergence survived, although those which were under water for an hour were quite sluggish at the time water was drained from the dish. Following removal of water, the isopods flexed their abdomens, a movement which apparently expresses water from the pleopods (Fischbach 1951). Of the animals submerged for 7 hours, only 2 were living 43 hours after the start of the experiment. Note that at the time water was drained from this dish, only 4 animals were dead; the difference between this number and that of 8 dead after 43 hours represents ill isopods. Sick animals which later died were also present in dishes given 2 and 4 hours submergence. The behavior of these ill animals was similar to that observed in sick animals collected in the field: they were nearly or completely incapacitated, and they responded to probing with only feeble movement of the appendages. Finally, it was noted that several of the dead animals in the experiment had an everted anus. The same symptom had been observed in a number of dead animals collected in the field following rain storms.

This experiment has shown that the symptoms of dead or ill animals found in the field following storms can be duplicated in the laboratory by drowning. It has demonstrated, also, that the length of submergence required to drown individuals is in the range of periods of flooding expected during winter storms. The length of California winter storms is usually one to 3 or more days. These storms are characterized by intermittent heavy rain, followed by periods of light showers or brief cessation of precipitation. The heavy rainfalls commonly lead to extensive soil flooding, and they often last for two or more hours. Hence, isopods in the field which are unable to find refuge during storms are undoubtedly sometimes subjected to sufficiently long periods of submergence to cause their death.

DROWNING MORTALITY IN THE FIELD. Searches for dead animals at many places in grassland during the winter of 1960 indicated that large numbers of animals were being killed throughout the area. It was desirable, therefore, to obtain some estimate of the amount of mortality attributable to winter storms. The following sample survey attempted to obtain such an estimate.

After a 0.77-in. (1.9-cm) rain (measured in a rain gauge on the hill in the center of Fig. 1) on February 8 and 9, 1960, 10 random samples of dead and living isopods were taken in Quadrat 2 (Fig. 2). Each sample consisted of all the isopods which could be found on the surface after vegetation had been cleared from within the confines of a 0.1 m^2 circular substrate sampler. The total number of isopods taken in each sample, and the number of these which had recently died, are given in Table 13. Only living plus recently killed individuals were counted; sufficient time had elapsed since earlier rains to insure that individuals drowned prior to the storm in question would not be counted.

TABLE 13. Drowning mortality due to one storm.

	Number isopods in samples	Number recently killed
	28	5
	1	0
	8	3
	8	4
	29	2
	36	3
	9	0
	65	9
	19	3
	1	1
Totals:	204	27

Per cent killed (from pooled data) = 14.7.

Results from pooled data indicated that 14.7% of the individuals taken in the survey were dead, presumably killed during the storm on the 2 preceding days. The maximum possible range of proportion of dead animals was encountered in the samples; hence it is difficult to estimate the reliability of the percentage figure. In spite of this the results indicate that a moderately large fraction of the population was killed in this single storm. The storm was of medium severity, and it appears certain that high mortalities such as this occur repeatedly during the winter, in other storms. Therefore, a large proportion of the population is probably killed by winter storms.

Nearly all dead individuals collected during the winter were adults. This may be due, in part, to the difficulty in seeing dead young individuals. On the other hand demographic results have shown a high mortality among adults during the winter (Paris and Pitelka 1962). Furthermore, in the drowning experiment it was noted that the first individuals to become incapacitated by submergence were large adults. The 2 animals which survived 7 hours of submergence were young individuals. This suggests that young animals have a greater tolerance to submergence than adults. Furthermore, it seems probable that small individuals are more successful in finding refuge from flooding than large ones, simply because they require a smaller shelter site. Hence, it is believed that there is a higher incidence of storm mortality in the adult age-classes than in the youngest generation. Although the available data are sufficient for no more than a provisional estimate of the extent of mortality caused by winter storms, the generalization that drowning mortality takes a heavy toll of the *A. vulgare* population in California grassland appears justified.

DISCUSSION

The only hypothesis known to me for a population regulating mechanism of terrestrial isopods has come from the study by Brereton (1956) of *Porcellio scaber* in England. He dismissed food availability, predation, parasitism, interference by other species, and weather as regulative mechanisms. He observed a high mortality rate of young in laboratory populations, however, which he assumed to be caused by cannibalistic adults. On the basis of this, Brereton advanced the hypothesis that *P. scaber* has evolved cannibalism as a self-regulating mechanism in natural populations.

The present study of *A. vulgare* has not shown cannibalism to be an important mortality factor, either in the field or in the laboratory. Other types of predation certainly occur in nature, particularly by lizards, salamanders, beetles, and perhaps birds, but their impact on the population has not been precisely determined. *Armadillidium vulgare,* however, occurs in California grassland in densities as great as 500 per m^2 (Paris and Pitelka 1962). During peaks of activity great numbers (often as many as 200 per m^2) can be observed on the surface at one time, apparently openly exposed to would-be predators. In spite of this, no evidence of heavy predation on the population was obtained. On the basis of evidence available at this time, it appears that predation plays a minor role in the regulation of *Armadillidium* numbers in this habitat.

Food as a factor affecting population numbers of isopods has received little attention. It is axiomatic that availability of food plays a part in determining the distribution and abundance of animals; it does not follow, however, that food is of primary importance in limiting a population in any given habitat. Other environmental factors may hold the population below the level at which a food shortage develops. Although direct evidence on the importance of food in regulating *A. vulgare* populations is not available, observations on the kind and abundance of the food of these isopods offer a basis for relevant speculation.

In the grassland areas studied in this research, *A. vulgare* ate dead plant material almost exclusively. Although a preference was shown for *Picris echioides,* the abundance of *Picris* did not affect the isopod population. Other kinds of dead vegetation apparently served equally well as food. If food availability affects isopod numbers in these grasslands, it probably does so by influencing fecundity rather than mortality. There was no evidence that isopods were starving; the only observable cause of non-predatory mortality was drowning. I believe that an abundant food supply is available to the *Armadillidium* populations in the area studied. In fact, it is possible that terrestrial isopods, in general, live in the presence of a plentiful food supply and that their success in the terrestrial environment can be attributed largely to this fact.

Their success on land is the more striking when it is realized that in several respects isopods are poorly adapted for life on land. Their ability to live in a relatively dry environment depends primarily on behavioral mechanisms which enable them to avoid the rigors typical of terrestrial habitats (Edney 1954, 1957, 1960). Edney (1954) has suggested that this fact is related to the manner in which isopods entered the terrestrial environment from the sea. He believes that the Oniscoidea invaded the land not via fresh-water, but rather by way of the littoral zone. In so doing they were subjected to the high temperatures often characteristic of exposed intertidal areas. In order to survive these high temperatures, it was necessary for them to evolve some mechanism for cooling the body. This was accomplished by maintaining an integument permeable to water, so that evaporative cooling could occur. Thus isopods moved onto land with the disadvantage of a pronounced susceptibility to desiccation. With such a physiological handicap, what was the selective advantage of the isopods' invasion of the terrestrial environment?

In general, terrestrial isopods are scavengers of dead organic matter, and dead vegetation in particular. Oniscoidea which are known to utilize dead plant material as a part of their diet include *Trichoniscus pusillus* (Heeley 1941b) and *Protracheoniscus politus* (Gere 1956), which feed on decaying leaves, and *Porcellio scaber* (Brereton 1956), which will eat dead wood. In addition, I have observed that *A. vulgare, A. nasatum,* and *Ligidium longicaudatum* in North Carolina utilize dead leaves as a major food source. In fact, the feeding habits of terrestrial isopods, considered in the light of their abundance, suggest that these organisms may play a significant role in the trophic dynamics of many land habitats, by hastening decomposition of dead vegetation. Gere (1956, 1957) has shown this for isopods in oak woodlands of Europe. In the grasslands studied by the author, isopods were the only abundant macroscopic organisms feeding on dead vegetation. A similar observation has been made in other grasslands by A. Macfadyen (personal communication). Examination of the friable surface soil collected during the investigation revealed that a high proportion of it consisted of isopod fecal pellets. Apparently *A. vulgare* populations function as an important first link in decomposer chains of California coastal grassland communities.

The feeding habit of modern terrestrial isopods probably was inherited from their marine littoral ancestors. Modern isopods which live in the littoral zone of the sea are scavengers, and it is reasonable to assume that those which gave rise to terrestrial species were scavengers, also. Today, littoral isopods probably compete for food with a variety of other scavenging organisms, including worms, snails, amphipods, crabs, etc. This competition for dead food in the littoral zone was probably as true prior to the invasion of land by isopods as it is today. The earliest fossil terrestrial isopods known are from the Eocene (Edney 1954); invasion of land by isopods undoubtedly occurred at a time when terrestrial communities were already characterized by an abundance of vegetable litter. Perhaps, then, isopods invaded the land under pressure of competition for food in the littoral habitat. By moving onto land, they made available to themselves a plentiful supply of dead plant material which was being utilized by few organisms that could give them serious competition. Even today, there are few macroscopic terrestrial animals which utilize dead, decaying herbaceous vegetation as a major part of their diet. The invasion of land by isopods probably represented an occupation by them of an ecological niche less efficiently used by previous occupants.

At the present there appear to be land habitats in which this niche is still readily accessible to isopods. The rapid and widespread establishment of exotic isopod species in North America since its occupation by white man attests to this fact. In California grassland, for example, *A. vulgare* is a relatively recent invader; there is evidence that its introduction and dispersal may have occurred as late as the early part of the 20th century. Essig, in 1926 (q.v.), reported that the species had become recently established in the San Francisco Bay region, in the vicinity of human habitations. A few years earlier, Kendall (1915), who studied the distribution of terrestrial isopods of the Bay area in relation to certain behavioral and physiological responses, worked with 5 species which he said "were all that could be located in the bay region." *Armadillidium vulgare* was not among these. It is now common in the areas in which Kendall collected, however, and apparently was so at the time of Miller's (1934) work on the terrestrial isopods of the San Francisco Bay area. Thus, in less than 50 years this species has become established as one of the most common and abundant animals in these grasslands. Such rapid occupation of a niche strongly supports the argument of an abundant food supply during the period of invasion. My observations on the feeding biology of *A. vulgare* in this habitat suggest that there still is ample food available to them.

In contrast to enemies and food, weather has been shown to have some profound influences on certain population parameters. The behavior and distribution of the population during drought is determined primarily by moisture of soil and atmosphere; this, of course, is related to survivorship, and possibly to natality as well. The highest death rate occurs during the first 6 months of life (Paris and Pitelka 1962). The young, which are very susceptible to desiccation, are released into the habitat during the driest period of the year; hence, perhaps much of this early mortality results from desiccation. Finally, a heavy adult mortality has been shown to result from flooding winter rains. Is weather, then, a factor which limits *A. vulgare* numbers in these grasslands?

Theoretical objections to weather as a population regulating factor have been advanced, principally by Nicholson (1933, 1954, 1957), on the grounds that weather cannot act in a density-dependent fashion. Most students, however, apparently accept weather as a possible controlling mechanism by recognizing that it can act in conjunction with other factors (notably shelter site availability) in a density-dependent manner (Smith 1935, Macfadyen 1957, Odum 1959). Indeed, a careful review of the argument on weather as a density-dependent factor reveals the problem to be more semantic than ecological.

With regard to isopod populations and weather, Brereton (1956) dismissed any consideration of climatic effects with the claim that animals, in general, have wide tolerance limits to physical factors; he believes that normally they live well within the range of these limits, behaving, to a large degree, independently of weather. In terms of the range of moisture conditions characteristic of terrestrial habitats, however, it has unequivocally been demonstrated that the Oniscoidea do not have wide tolerance limits (Edney 1957, 1960). Furthermore, this investigation has shown that much of the activity of *A. vulgare* (one of the woodlice best adapted for life on land) is very closely dependent on weather. Indeed, the fact that Brereton (1956, 1957) found (1) a diel periodicity in the behavior of *Porcellio scaber*, (2) that their activity at night was low when it was dry or when it was raining, and (3) that the greatest numbers could be found when both temperature and humidity were high, suggest that *Porcellio's* behavior may also be dependent on weather.

My data do not permit an incontrovertible answer to the question of regulation of *Armadillidium* numbers by weather in California coastal grassland. We have shown that weather affects distribution, behavior, access to food, and mortality, but we have no accurate measure of the relative importance of these effects on overall population dynamics. Nevertheless, it seems more desirable to advance a tentative hypothesis of population control on the basis of the available information, than to offer none at all.

Weather could regulate *Armadillidium* populations in a density-dependent manner by interacting with population numbers and shelter site availability. Such an effect would probably operate through mortality, resulting from death by desiccation (mostly in the young) during the summer and death by drowning (mostly in adults) during the winter. The relative importance of these two mortality factors is unknown; perhaps in different years their relative importance changes, each varying because of variations in weather pattern and shelter availability. The density-dependent action of these factors would thus vary in degree from year to year. Their severity in any given year would depend on the vicissitudes of weather, and hence would be a chance event; however, these vagaries of weather are confined within definite limits by meteorological factors which determine the regional climate. The prevailing climate, therefore, would provide the basis for long-term regulation of isopod numbers.

Numbers of *Armadillidium* in these grasslands might also be influenced by the effect of weather on the accessibility of food during the summer. Dead vegetation at the soil surface is available to the population only when atmospheric moisture conditions are favorable. When isopods take refuge underground, apparently there is no food available to them. Although isopods can go for long periods without food (Heeley 1941a, Marshall and Orr 1960), perhaps the degree to which surface food is available to the populations has an effect on natality. The severity of this factor would depend on meteorological events, and would be subject to chance variation within climatic limits.

The view taken here is rather similar to that adopted by Andrewartha and Birch on weather as a population regulating factor (Andrewartha and Birch 1954, Birch 1957). These authors, however, do not accept the concept of density-dependence; they argue that in some sense all factors affecting animal numbers can be considered as density-dependent, and hence the term becomes useless. In the usual sense, however, a density-dependent factor is one whose severity in depressing the population increases as population numbers increase. Factors which interact with population density in any other way are not to be considered as density-dependent. On *a priori* grounds, population numbers, shelter site availability, and adverse weather could interact in a density-dependent way. It is true, as maintained by Nicholson (1957), that population density does not affect the severity of weather, and herein lies the element of chance involved in the action of weather as a population controlling factor. The effect of weather on a population, however, may very well depend on population density.

Theoretical objections to the invocation of chance as an element in population regulating mechanisms, as proposed by Andrewartha and Birch (1954), have been advanced (Elton 1955) on the grounds that the observable order in natural communities could not have evolved through the operation of chance. On the contrary, however, elements of chance are involved in all organic evolution. Furthermore, it is axiomatic that in every population regulating system a point is reached where the probability of some event is independent of population numbers. The directness, magnitude, and frequency of these events vary in different systems. Some of the most direct, and hence the most obvious, events of this kind are meteorological ones.

My agreement with certain aspects of the interpretation placed by Andrewartha and Birch on weather as a population regulating mechanism should not be interpreted as an endorsement of their "general theory" of population limitation (Andrewartha and Birch 1954, 660 ff.). Their theory consists of three main points: animal numbers may be regulated by (1) a shortage of resources, (2) by the inaccessibility of resources relative to the animals' capacity for finding them, and (3) by a shortage of time when the intrinsic rate of increase is positive. Fluctuations in intrinsic rate, they say, may be caused by weather, predation, or "any other component of environment which influences the rate of increase." It is my opinion that this misinterprets intrinsic rate of increase. Intrinsic rate, the parameter *r* in the exponential growth equation, simply describes the instantaneous rate at which the slope of the growth curve changes. It is meaningful, therefore, to invoke intrinsic rate as having a causal relation to population numbers only in a population which is growing in an unlimited environment. Under these circumstances the intrinsic rate is determined by the animals' physiology and represents a product of their evolution (Smith 1954). Otherwise the value of *r* simply describes rate of increase, nothing more.

An interesting approach to the problem of population control is taken by Hairston, Smith, and Slobodkin (1960); they consider the regulation of population numbers according to trophic levels. On the basis of general observations, they suggest that primary consumers are, on the whole, limited by predators. Producers, carnivores, and decomposers are, on the other hand, usually limited by shortage of resources. They dismiss weather as a possible controlling factor of herbivore populations, primarily on the basis of observed outbreaks of introduced herbivores which result in depletion of vegetation. They argue that the invocation of weather as a factor controlling primary consumers would require, in order to explain invader outbreaks, the implication that the probability of a pre-adaptation to weather by invaders is greater than the likelihood of an evolutionary adaptation by native species.

This investigation of California populations of *Armadillidium* is relevant to their arguments, since it represents an invading herbivore which has been highly successful in establishing itself in a foreign habitat. In a sense, then, it must have been pre-adapted to the California coastal climate. There are undoubtedly all degrees of pre-adaptation, however, and there is no evidence that *A. vulgare* is sufficiently pre-adapted to allow population growth to the point of food depletion. The pattern of population control conceived by Hairston, Smith, and Slobodkin does not account for introduced species such as this which are able to maintain themselves under the prevailing climate but at the same time may be controlled by it. General observation may well underestimate the incidence of events of this kind relative to the incidence of outbreaks by invader populations, since outbreaks are far more apt to attract attention.

By the same token the importance placed on invader outbreaks in these authors' argument on herbivore population control may be out of proportion. The occasional outbreak of invaders which leads to defoliation does not necessarily imply that pre-adaptation is more likely than ordinary adaptation, as they suggest. Rather, it is more probable that vast numbers of species are introduced regularly into foreign environments, but their prompt destruction by a climate to which they are totally unadapted prevents our ever becoming aware of their introduction. Therefore the occurrence of outbreaks by invaders, albeit by reason of a pre-adaptation, probably represents a very rare event, indeed. Furthermore, even if it could be shown that invader outbreaks occurred more commonly than outbreaks by native species, this would not imply that the likelihood of ordinary adaptation to weather is less than that of pre-adaptation. The evolutionary release from control by weather provides the opportunity for the evolution of other control factors. Thus, predator populations may evolve in response to a gradually enlarging food supply, and eventually come to effect control before the herbivore over-exploits its resource. In fact, this may have occurred in the case of the majority of herbivores, as Hairston, Smith, and Slobodkin suggest, but it does not mean that all native herbivore species have undergone evolutionary release from weather.

Weather is not a single variable to which an animal must react, of course. An animal must evolve an adaptation to several environmental components which we group under the term weather; it must evolve, also, to the interactions of these components, and to the interactions of weather components with non-weather components of its environment. It is perhaps not infrequent that the extent to which a species can evolve an adaptation to one factor is limited by the necessity of an adaptation to another. For example, the evolution of a cooling mechanism (a water-permeable integument) by terrestrial isopods limits their adaptation for utilization of land habitats.

Finally, long-term climate is not constant. Any species which adapts to weather may sooner or later again find itself threatened by weather because of climatic change. It may evolve an adaptation to weather again, but not until weather first becomes adverse. Among the nearly 1,000,000 known species of animals on the earth, we should expect occasionally to encounter some which are not totally adapted to the climate in which they live.

The hypothesis advanced here is that *A. vulgare* populations in California coastal grasslands are controlled in a density-dependent manner by the interaction of population numbers, shelter-site availability, and weather. This regulation prevents their expansion to a level beyond which their food supply is depleted. It is recognized, also, that there is a point at which weather affects *A. vulgare* populations as a chance event, independent of their density; weather has this relationship to all populations of organisms, although the manifestation of the relationship varies with time, locality, and species. My hypothesis for a population controlling mechanism for *A. vulgare* in California grassland can be confirmed or refuted, I believe, only by the design and conduct of field experiments which would modify the effect of weather on these populations. The effect of food availability and of predation, likewise, could profitably be approached by field experiments. Clearly, however, additional basic information on food and predation is needed before such experiments can be adequately designed. Since this information has proved difficult to obtain through ordinary observations and techniques, radioisotopes are now being employed in an effort to elucidate the trophic dynamics of these isopod populations.

On the whole, ecological experimentation and ecological field observations have for too long been separated by laboratory walls. Undoubtedly this may be attributed, in part, to the unsuitable nature of many animal populations for experimental study. Nevertheless, judicious selection of research material and careful analysis of population dynamics, followed by field experiments, should help eliminate some of the ambiguity which so often characterizes research on the regulation of natural populations. It is hoped that future investigations of isopod population dynamics will make contributions in this direction.

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SUMMARY

1. The role of food, enemies, and weather in the ecology of *Armadillidium vulgare,* one of the most abundant macroscopic invertebrates in California coastal grassland, was studied.

2. The principal food of *A. vulgare* in this habitat is dead vegetation, especially leaves of the tar-weed, *Picris echioides;* isopods aggregate at *Picris* plants in the field, and they chose dead *Picris* leaves in preference to other food items in laboratory feeding trials.

3. The abundance of *Picris* in the field, however, does not affect isopod density or population age structure. In the absence of *Picris,* isopods turn to other dead vegetation for food.

4. Salamanders, lizards, and predaceous beetles occasionally ate isopods in laboratory feeding trials, but negative results were obtained in trials with centipedes and spiders.

5. No evidence of heavy predation on isopod populations was obtained in the field.

6. Parasitism, disease, and cannibalism were not important mortality factors.

7. Weather has a profound effect on isopod distribution, behavior, and mortality. During the annual rainy season, isopods live on or near the soil surface, but during drought they seek refuge from desiccation by descending into soil fissures to depths as great as 45 cm.

8. Isopods also take refuge from desiccation in small areas of soil kept moist by the precipitation of water of condensation from certain tall plants; the condensation results from low stratus which periodically envelopes the California Coast Range at night.

9. Isopods emerge from these retreats on nights when saturation deficit is low; this most commonly occurs when low stratus is present. Feeding takes place during these periods of emergence.

10. On mornings following moist nights, isopods often crawl about in exposed areas, where vapor pressure deficit is high. This behavior can be explained most simply as resulting from some individuals not having found shelter since the preceding night's activity.

11. Young isopods, which hatch during the spring and summer, suffer a high mortality rate during the first 6 months of life; much of the death during this period probably results from desiccation, since small individuals are less capable of finding moist retreats than are adults.

12. During the winter months the greatest mortality rate is among adults; field observations and laboratory experimentation showed this to result from drowning during flooding rains. Young individuals are less susceptible to drowning than are adults.

13. Food and weather are considered as possible population regulating factors.

14. It is argued that food probably is available in plentiful supply. Further, it is hypothesized that isopods invaded the terrestrial environment, in spite of a physiological handicap for life on land, to take advantage of an easily accessible trophic niche offered by dead vegetation. The rapid spread and establishment of introduced land isopods, such as *A. vulgare* in California, supports the argument of a readily accessible and abundant food supply.

15. An hypothesis for the regulation of *A. vulgare* populations in a density-dependent manner, through the interaction of weather, shelter site availability, and isopod numbers is suggested.

16. The intensity of this density-dependent action must vary from year-to-year, as weather varies, but this fluctuation occurs within limits imposed by factors which determine regional climate; hence, the survival and long-term control of population depends on regional climate and ultimately is a product of chance.

17. It is argued that in all population regulating systems there are factors influencing population numbers which operate, in the history of the population, as chance events.

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