Occurence of Grasshoppers as Accidentals in the Rocky Mountains of Northern Colorado

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OCCURRENCE OF GRASSHOPPERS AS ACCIDENTALS IN THE ROCKY MOUNTAINS OF NORTHERN COLORADO

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In 1951, in a paper on the occurrence of Acrididae at high altitudes, I listed a number of species that occur as accidentals in the alpine zone of the Colorado Rockies. The term was used with the meaning long accepted by ornithologists, an accidental being an individual outside its normal resident range. This term was used, and is used here again instead of another of similar connotation, because its use has been, to some extent, standardized.

In a mountainous region, we must recognize 2 types of accidentals among insects. They may be individuals that occur completely outside the resident altitudinal range of the species, or they may be adults that appear within the total range but at a given elevation before adults resident at this (higher) altitude could have matured. In either case, these individuals necessarily matured elsewhere and must have arrived at the particular altitude through their own activity or by passive transport.

Field work in the Colorado Rockies in recent years has convinced me that accidentals among grasshoppers are much more frequent than was previously assumed, and that, for a few species, the phenomenon may have more significance than could be attributed to the chance occurrence of a few stragglers (Alexander 1960). Rare stragglers should be recognized as such, of course, and should not be used in defining the normal altitudinal or geographical limits of a species. But when such extralimital individuals are particularly numerous for a given species they constitute a pioneer fringe of its population, a fringe that can be of major importance in determining year-to-year fluctuations in the resident limits of that species.

Factors Involved in Altitudinal Movements

All grasshoppers involved in extensive wandering are competent fliers. Short-winged and wingless species do move about, but their movements are relatively insignificant in comparison with those of species with well-developed wings. Those best known for long flights are the migratory grasshoppers, or locusts, but their movements, which have had special treatment by many authors (Kennedy 1951) and have been considered in all major discussions of insect migration (Fraenkel 1932; Williams 1958; Schneider 1962) are only indirectly related to the observations included here. The few reports of mass flights of mixed species that are typically nonmigratory, as in Carbonell's (1957) observations in Uruguay, are also only indirectly pertinent. Early observations of high altitude accidentals in Colorado (e.g., Hayden 1874) and Gurney's (1952) account of the Grasshopper Glacier of Montana indicate mass flights of migratory grasshoppers, but the accidentals considered here reflect the activities of individual insects only. To use Schneider's (1962) terminology, we are dealing here with "dispersal" rather than "collective displacement."

Most grasshoppers are nonmigratory—even if we accept Williams's (1958) definition, broad as that is, that migration is movement in a definite direction with "movement and direction . . . under the control of the animal concerned." Distance movements of nonmigratory grasshoppers, though aided by their own activities, are probably not in a definite direction or completely under the control—as to direction—of the insects. Such movements are more likely to be the result of a combination of flight and active transport by wind.

A long-winged grasshopper is readily air-borne, but even strong fliers are not necessarily transported by wind. Species behavior is an important factor, some species controlling their activities to such an extent that they are rarely subject to accidental transport. If a species is a "wanderer," however—and some appear to be—the direction of movement and, to some extent, the distance traveled are undoubtedly determined in part by the direction and velocity of air movement. Even migratory species, which fly into the wind when the velocity is low, are, according to Kennedy (1951), carried with the wind when the rate of air flow reaches 9 or more miles per hour.

During the summer the prevailing direction of air flow relatively near the ground in mountains is upward during the day, downward at night. This is an indirect result of the effect of insolation on the gradient of air density, and this air current near the ground may move in a direction opposite that of the prevailing winds aloft—as, in fact, it does on the eastern slope of the Rocky Mountains. If there is a reservoir of low altitude insects nearby, these, if readily air-borne, may be carried upward by such rising air currents.

Holdhaus (1929), discussing insect movement in relation to distribution, emphasized the role of wind in the passive transport of flying insects in mountains. One kind of evidence he gave was the occurrence of insects frozen or immobilized in snow and ice at high altitudes. He pointed out that low altitude insects active during the day are often transported to high altitudes by rising air currents, but that high altitude insects are seldom carried to low altitudes because temperatures are so low at night, when the downdrafts occur, that there is little or no insect activity. In my observations I have never found a montane grasshopper more than a few hundred feet below its normal altitudinal range but have collected many species one to several thousand feet above normal breeding range.

Several observers have been impressed by the large numbers of low altitude insects caught in snowbanks at high altitudes. A remarkable observation of this sort was recently reported by Mani (1962), who recorded, at the time of the southwest monsoon, approximately 400 specimens of air-borne insects deposited in 20 min in an area of 10 m^2 of snow field on the south side of a range in the northwest Himalaya. Caudell (1902) published a list of 78 species of insects collected in one day during the summer of 1901 from 2 small snowbanks near the summit of Pikes Peak, Colorado. He noted the absence of alpine insects in the snow, and he stated that all trapped insects were from lower altitudes—though he observed insects native to the alpine tundra common and active near the snow. Similar observations can be made every summer in the Front Range of the Colorado Rockies, with grasshoppers among the insects immobilized in the snow. The abundance of snow-trapped insects is attested to by the behavior of the brown-capped rosy finch—its flocks regularly working across alpine snow fields during July and August, feeding on the chilled insects.

We should note that observations such as these cannot be made in a mountain area far removed from lowlands. Accidentals are infrequent in the interior ranges of Colorado. They are most likely to appear in the Front Range, where the large population of high plains insects is only 10 to 20 miles away, by air, from alpine tundra and the snow fields.

Accidentals are most likely to appear, of course, when strong winds toward the mountains prevail, or when hot dry weather at the lower elevations increases the diurnal updraft. That such condi-

tions are important is suggested by the coincidence of weather conditions and my largest collection of accidentals in one locality on a single day. On July 13, 1936, at an elevation of 11,400 ft on Niwot Ridge, 14 miles west of Boulder, I collected 50 accidentals, representing 8 species (Alexander 1951). These were 1,500 to 5,000 ft above their normal upper resident limits. July that year was a month in which light dust storms were carried by easterly winds across the eastern borders of Colorado and Wyoming. It was an unusually warm month, the mean monthly temperature at the Denver weather bureau being 5° above normal. Maximum wind velocity at Denver was 24 mph, and that was recorded from the southeast July 9 (Weather Bureau 1936), just 4 days before the large collection of accidentals on Niwot Ridge. Hot dry weather on the plains and prevailing winds in the direction of the mountains are obvious factors contributing to the high incidence of accidentals in this particular collection. Gurney (1952) noted a similar correlation of grasshopper movements with weather conditions in Montana.

Possible Significance of Accidentals

The observations of low altitude insects in alpine snowbanks have contributed a great deal to our awareness of accidentals. Unfortunately, we have been inclined to underestimate their importance, considering them either novelties—and therefore rare—or chilled and dying individuals of no further significance for the species involved.

Accidentals are not necessarily rare, however, and not all insects carried upward in rising air currents are immobilized in ice and snow. Even in alpine areas, in spite of the fact that downdrafts are more frequent over snow fields than over exposed tundra, many insects drop down on the tundra or exposed soil. And, what is probably more important, many insects drop out at intermediate elevations along the way; they are not all carried to alpine areas.

When we consider the fact that accidentals are spread over a wide gradient of altitude we see that the occurrence of insects in alpine snowbanks is only an isolated expression of a much more extensive phenomenon. This observation has as one corollary the conclusion that many published records of presumed normal altitudinal distribution should be questioned. The finding of an adult insect at a given altitude is not prima-facie evidence that it is resident there. Accidentals occur at all altitudes, and at the higher altitudes the proportion of species occurring as accidentals to those that are resident may be quite high. Total records for the Front Range of the Rocky Mountains near Boulder, Colorado, with numbers of species tabulated by altitudinal bands, demonstrate this quite clearly (Table I).

Table I. Numbers of species of Acrididae recorded as residents and as accidentals in different altitudinal bands in the Boulder, Colorado, region, 1931-1960

Altitude range (in feet above sea level)	Numbers of species[a]		
	Total	Residents	Accidentals
5,000— 6,000	67	61	6
6,000— 7,000	56	51	5
7,000— 8,000	43	31	12
8,000— 9,000	41	25	16
9,000—10,000	34	19	15
10,000—11,000	29	17	12
11,000—12,000	20	9	11
12,000—13,000	9	3	6
13,000—14,000	4	2	2
over 14,000	1	0	1

[a] The total number of species is 74.

Another corollary of this observation is more significant ecologically, however. If numerous individuals of a given species appear regularly at altitudes above normal range, that species is continuously exerting a pressure for maintenance at its upper ecological boundary and for establishment at even higher levels. Such numerous accidentals constitute a fringe of pioneers ready to establish the species at the highest altitudes at which survival is possible in any given season. In an unfavorable season, the upper limit of the resident population is pushed downward; in a favorable season, the boundary may advance upward. In other words, the upper altitudinal limit of distribution of a highly vagile species is continually shifting, this boundary reflecting year-to-year changes in factors essential for survival.

We are not dealing here with permanent invasion of new territory (Chopard 1938; Elton 1958). Nor does this appear to be a mechanism of gradual extension of range, as argued so admirably by Grinnell (1922) in his discussion of accidentals among birds—except, of course, during a long period of time, with progressive change in climatic conditions. Instead, we are dealing with population pressure and year-to-year survival under the relatively unstable conditions of the range limits of a species. We are dealing, in fact, with range oscillation in response to changes in ecological factors (Andrewartha and Birch 1954; Ross 1962).

The contrast between this fluctuating, upper altitudinal limit and that occurring at the northern boundary of a species with a wide distribution at low altitudes is primarily in the distances involved. Replacement of a population decimated or exterminated at the northern edge of a range that extends many miles at the same altitude may be a long

process, because the bulk of the surviving population may be hundreds of miles south. But where there is a steep altitudinal gradient, an analogous climatic gradient occupies a distance of only a few miles. When the season is favorable, replacement of the population at its upper limit in mountains can take place in a single year, accidentals providing the nucleus for the replacement. Eggs and young may be available every year at altitudes above those at which the species normally reaches maturity, the eggs having been deposited not by individuals that developed at that altitude but by accidentals that came in from lower altitudes.

All accidentals cannot be considered pioneers capable of establishing the species when conditions are favorable. Some species are relatively sedentary, having only an occasional vagrant. Other species do not wander at all. The possible significance of accidentals becomes more apparent, however, when all such types are compared, and since appropriate data are available for all species in the area of this study they will all be considered. The more detailed accounts will, however, be devoted to those species with numerous accidentals; these are clearly of greatest significance in a consideration of factors affecting distribution.

Criteria for Recognition of Accidentals

As previously stated, an adult grasshopper that appears at an altitude at which it does not complete its life cycle is considered an accidental. (Example: In northern Colorado, *Melanoplus sanguinipes* [Fabr.] may complete its life cycle up to an altitude of 10,000 ft, rarely higher. Adults, however, are frequently found much higher; many have been collected above 13,000 ft and some even above 14,000 ft. These are accidentals. This species, incidentally, has been called *M. mexicanus* or *M. bilituratus* in most of the recent literature, but Gurney [1962] has summarized and corrected the nomenclature.)

We may say further that if an adult grasshopper appears at a given elevation before juveniles at that elevation can have become mature, it also is an accidental. (Example: Adults of *M. sanguinipes* appear at 10,000 feet as much as 2 weeks before 5th [last] instar juveniles at the same altitude. These early adults matured at lower elevations and flew or were carried to the higher altitudes.)

These criteria can be applied only after one determines the altitudinal breeding range of each species involved, and that implies ability to identify the juveniles. In this study a few species were reared, but such a program is not necessary for identification of late juvenile instars. The last juvenile instars are, for most species, readily identifiable by comparison with adults, and recognition of the last juvenile stage is all that is necessary to establish a species as resident for juveniles are flightless at all stages.

Species that are flightless as adults do not appear as accidentals. They are resident wherever they occur. They do move short distances but not the distances that make their occurrence noteworthy. (Example: A brachypterous form such as *Melanoplus dodgei* [Thomas] occurs only at elevations where juveniles of this species are present and, incidentally, where juveniles invariably appear before the adults.)

Objective evidence for the difference in dispersal between short- and long-winged grasshoppers is scanty, but there is some evidence for this in Stalheim's (1960) studies. She found greater recovery of marked and released specimens of short-winged grasshoppers than of long-winged species handled in the same way. Several factors other than wing length are involved in such movements, however, and even a single species is not necessarily consistent in its behavior. *Melanoplus sanguinipes,* which is known at times to move distances of many miles (Monro and Saugstad 1938), and even to migrate in swarms (Parker *et al.* 1955), may sometimes be quite sedentary (Edwards 1961). We are probably safe in assuming, however, that short-winged species are invariably sedentary.

Resident status has been presumed for one other group of species, those in which one sex is flightless and the other has moderately well-developed wings. This interpretation may be questioned, but it seems justified by the fact that juveniles of such species have been collected at all altitudes where adults occur, and the adults have not been collected on dates earlier than those on which they could have matured at the altitude in question. (Example: *Aeropedellus clavatus* [Thomas], in which females are short-winged and flightless but males have wings of moderate size.)

Collections and Observations

Scattered early observations, chiefly my own and those of Fehlmann (1950), were used in my earlier reference to accidentals (1951). These will be referred to when appropriate, but the recognition of relatively large numbers of such individuals in some species has come only from regular and extensive collections during several recent seasons.

Data presented here are from collections made during 1958, 1959, and 1960. During these 3 seasons intensive and regular collections were made in northern Colorado over a wide altitudinal gradient in the front range of the Rocky Mountains

near Boulder. The collecting localities were between 39° 35′ and 40° 05′ N and between 105° 05′ and 105° 50′ W, and the altitudinal range extended from 5,100 to 14,200 ft (1,550 to 4,320 m) above sea level. The collections were made as part of a general study of altitudinal distribution of Orthoptera, and this report developed as a corollary of the more general observations.

The lowest stations were in the upper edge of the grassland, the lower edge of pine forest being about 6,000 ft above sea level. From this elevation to upper timber line, at about 11,000 ft, the predominant vegetation is coniferous forest, with spruce-fir giving way to tundra at timber line. Although the forested area has its characteristic Orthoptera, our largest collections at intermediate elevations were in the more extensive open areas within the forest.

Specimens collected, identified, and recorded by altitude, age, and (if adult) sex totaled 11,407 in 1958, 28,586 in 1959, and 18,948 in 1960. More than 50,000 of these were Acrididae, true grasshoppers.

These data are extensive, of course, but the total number of specimens is less significant than the ratio of accidentals to resident individuals in certain species. The best example of a species with high incidence of accidental occurrence is *Melanoplus sanguinipes*. In one season, 1959, we processed 4,881 specimens of this species. Of these, 2,401 were adults, and of these adults 266 were collected at or above 12,000 ft. These 266, as well as others taken at lower altitudes before the season of maturity at such altitudes, were accidentals. During 1959 alone approximately 400 accidentals of this species were collected at altitudes at and above 10,000 ft. Thus, in this species, more than 15% of the adults collected along the entire altitudinal gradient were accidentals.

The records are less impressive for less abundant species, naturally, but the conclusions drawn from observations of normally abundant species may be applicable in principle to others in which accidentals occur less frequently but regularly.

We have records of 74 species of Acrididae in this area of special study, the records beginning in 1931. That this sample is adequate taxonomically is demonstrated by the fact that among the more than 40,000 specimens collected in 1959 and 1960, no species was represented that had not been previously collected in the area.

Two of the 74 species, *Trachyrhachis aspera* Scudder and *Melanoplus gladstoni* Scudder, are known from only one and 2 specimens, respectively—adults collected at the upper edge of the plains. These were presumably accidental from resident populations outside the area and at a lower altitude.

One species, *Dissosteira longipennis* (Thomas), which can easily be recognized at sight, was observed but could not be collected. Two specimens were seen flying near my home in Boulder in August 1938, during one of the major outbreaks of this species (Wakeland 1958). They were undoubtedly accidentals, for the nearest areas of egg deposition that year were still 100 miles or more to the southeast.

A fourth species, *Melanoplus angustipennis* (Dodge), has been collected in the area on several occasions, even up to 9,000 ft, but all of the few specimens taken have been adults. They undoubtedly wandered into the area from farther east.

These 4 species, though probably all accidentals in the area, are all relatively rare and because of this will be disregarded in further discussion. Of the other 70 species, 19 are brachypterous in either or both sexes and may be presumed to be resident wherever found. The remaining 51 macropterous species include 22 that are apparently sedentary in behavior and 29 species that have appeared as accidentals. In some species these accidentals are infrequent, but in others they are abundant.

SPECIES NOT RECORDED AS OF ACCIDENTAL OCCURRENCE

Brachypterous species

The 19 short-winged species collected in the area of this study are the following (names in alphabetic rather than taxonomic sequence): *Aeropedellus clavatus* (Thomas), *Boopedon nubilum* (Say), *Brachystola magna* (Girard), *Bruneria brunnea* (Thomas), *Chloealtis conspersa* Harris, *Chorthippus longicornis* (Latreille), *Dactylotum pictum* (Thomas), *Hesperotettix speciosa* (Scudder), *Hypochlora alba* (Dodge), *Melanoplus borealis* (Fieber), *M. dawsoni* (Scudder), *M. dodgei* (Thomas), *M. fasciatus* (F. Walker), *M. lakinus* (Scudder), *M. marshalli* (Thomas), *Neopodismopsis abdominalis* (Thomas), *Paropomala wyomingensis* (Thomas), *Phoetaliotes nebrascensis* (Thomas), *Tropidolophus formosus* (Say). This list includes those species in which only one sex is strictly brachypterous as well as species in which both sexes are short-winged.

No species on this list is considered a wanderer. Adults of *Melanoplus fasciatus,* a species that probably does not deposit its eggs above timber line, does, however, occasionally wander by hopping a short distance into the tundra. I have collected some adults on the tundra but always near the edge of the timber.

One species on the list, *Melanoplus dawsoni,* occasionally appears in macropterous form. A few

long-winged individuals of *M. dawsoni* have been collected in our area, and at least one of these was an accidental. A long-winged female (identification verified by Ashley Gurney) was collected by Donald H. Van Horn August 11, 1958, at 12,200 ft, approximately 2,000 ft above its upper altitudinal limit as a resident. The fact that the only accidental taken of this relatively abundant montane species was macropterous indicates the necessity for well-developed wings in wanderers.

Macropterous species

The 22 species with wings moderately to well-developed in both sexes that have been collected only at altitudes where they are resident are as follows: *Aerochoreutes carlinianus* (Thomas), *Arphia conspersa* Scudder, *Chortophaga viridifasciata* (DeGeer), *Cordillacris occipitalis* (Thomas), *Encoptolophus sordidus costalis* (Scudder), *Eritettix simplex tricarinatus* (Thomas), *Hippiscus rugosus* (Scudder), *Melanoplus alpinus* Scudder, *M. infantilis* Scudder, *M. keeleri luridus* (Dodge), *Mermiria maculipennis macclungi* Rehn, *M. neomexicana* (Thomas), *Mestobregma plattei* (Thomas), *Opeia obscura* (Thomas), *Orphulella speciosa* (Scudder), *Pardalophora apiculata* (Harris), *Phlibostroma quadrimaculatum* (Thomas), *Psoloessa delicatula* (Scudder), *Schistocerca lineata* Scudder, *Trimerotropis humile* (Morse), *T. suffusa* Scudder, *Xanthippus corallipes* (Haldemann).

Several species in this group are weak fliers, but others, unquestionably, are strong fliers. Even in the latter group, however, there has been no tendency for any species to move out of the altitudinal range in which it normally completes its life cycle. It is particularly interesting to see on this list so many Oedipodinae which usually are strong fliers. This observation suggests that possession of well-developed wings is not the only trait that predisposes a species to wandering. A certain type of behavior is also essential.

Aerochoreutes carlinianus is one of the strongest fliers in our area, as, in fact, its generic name suggests. It has a rather large population on Gunbarrel Hill, an extensive, slightly elevated area (about 5,300 ft in altitude) a few miles northeast of Boulder. But this species has not been collected as an accidental even in the foothills. The presence of another species on the list, *Schistocerca lineata,* is perhaps even more surprising, because its eastern relative, *S. americana* (Drury), is a notorious wanderer, often recorded far north of its normal range. *S. lineata,* though locally common, seems to be restricted to certain areas on the plains and in the foothills, and it is resident in those places.

One might assume that the list is made up of the rarer species. Although a few are not common, in general these species are no less common than those that appear as accidentals. Actually, several of the species that seem to be sedentary in behavior are quite common, and it would indeed be remarkable if some of these did not occasionally appear as accidentals. Hebard (1929) reported *Arphia conspersa* above timber line in Colorado. This occurrence was probably above resident range, but I have not collected this species or any other on this list outside its breeding range.

SPECIES APPEARING AS ACCIDENTALS

At altitudes below resident range

As previously stated, few species appear at altitudes below the range in which they are resident, and none has been found very far below. There are only 4 species in this category, all being Oedipodinae characteristic of clearings in the foothills and montane areas. These 4 have all been collected a few times each on a grassy mesa at about 5,700 ft in altitude, only 100 ft in vertical range below the nearest timbered areas in which they normally occur.

These 4 species are: *Camnula pellucida* Scudder, *Cratypedes neglectus* (Thomas), *Trimerotropis campestris* McNeill, and *T. cincta* (Thomas). Their occurrence a short distance below normal range is not very significant; it merely reflects the movements associated with the characteristic mating displays of these strong fliers. I have no evidence of the occurrence of these species above resident range, but it is quite probable that they do wander upward short distances as well. All are relatively common, *Camnula pellucida* being one of the most abundant montane species in northern Colorado.

At altitudes above resident range

Twenty-five species have been represented in the area of study by clearly defined accidentals, all of these appearing well above the normal upper altitudinal limits of resident range. One cannot attribute much significance, however, to the appearance of only an occasional vagrant. Hence, for purposes of considering possible significance, I have arbitrarily grouped these species in 2 categories, those with fewer than 10 records as accidentals during the seasons for which most extensive records are available, and those with more than 10 records. Those in the first group are said to have "infrequent accidentals," and those in the 2d group are referred to as having "relatively frequent accidentals." It is obvious that an accumulation of only 10 records does not indicate a high frequency. We may presume, however, that actual

TABLE II. Summary of records of species with fewer than 10 records as accidentals in an altitudinal gradient near Boulder, Colorado, 1931-1960

Name of species	Upper resident altitudinal limit	Altitudes and occurrence of accidentals
Acrolophitus hirtipes (Say)	5,700′	6,700′(3), 7,200′(1), 9,500′(1)[a]
Aeoloplus turnbulli (Thomas)	6,700′	7,700′(1), 12,100′(1)
Amphitornus coloradus (Thomas)	7,600′	8,500′(2), 9,500′(1), 9,800′(1), 11,400′(2)
Arphia pseudonietana (Thomas)	6,700′	7,600′(2), 8,000′(1), 8,500′(1), 10,000′(2)
Circotettix rabula (Rehn & Hebard)	10,500′	11,300′(1), 11,500′(1), 11,600′(7)
Derotmema haydenii (Thomas)	6,700′	7,700′(1)
Dissosteira carolina (Linn.)	6,700′	8,100′(1), 8,500′(1), 9,100′(1), 10,000′(1), 10,500′(1)
Drepanopterna femoratum (Scudder)	6,800′	8,500′(1)
Hadrotettix trifasciatus (Say)	6,700′	7,700′(4), 9,000′(1), 9,200′(3)
Hesperotettix viridis (Thomas)	8,500′ or lower	9,200′(1), 9,500′(1), 10,800′(1), 11,400′(1), 11,500′(1)
Melanoplus differentialis (Thomas)	5,700′	8,200′(1), 10,500′(1)
Orphulella pelidna (Burmeister)	6,800′	7,200′(1), 7,600′(1), 8,500′(1)
Spharagemon collare (Scudder)	6,700′	7,500′(1), 8,500′(1), 9,200′(1) 9,500′(2), 10,000′(1), 12,200′(1)
Spharagemon equale (Say)	5,300′	6,700′(3)—may be resident
Trimerotropis pallidipennis Burmeister)	5,300′	8,000′(1), 8,500′(1), 9,400′(1)

[a] The number in parenthesis after the figure for altitude indicates the number of specimens taken at that altitude. All altitudes are in feet above sea level.

occurrence involves many more individuals than the few taken in our relatively small samples of the total populations.

Species with infrequent accidentals.—Fifteen species fall into this category. Records of accidental occurrence of these are summarized in Table II and will not be discussed in detail.

The species here are those in which accidentals are rare vagrants of little or no significance in the normal species distribution. With one exception, all these species are relatively common at the altitudes where they are resident. In one species, however, the low frequency of accidentals does probably reflect a small population. This is *Melanoplus differentialis,* which is not the abundant grasshopper that it is farther east. Its close relative, *M. bivittatus,* tends to replace it in the west. *M. bivittatus* is a much more abundant species in the Boulder area, and it has a relatively high incidence of accidentals.

Species with relatively frequent accidentals.—The 10 species for which we have records of more than 10 accidentals have all been collected well above their normal resident range in several different seasons. Accidentals are certainly not of equal significance in these 10 species, however. In a few cases it is doubtful if the number of accidentals indicates any population pressure at higher than resident altitudes, even though we may assume that our sample is small. In other cases the evidence is clear that there is an annual reservoir of pioneers ready to establish the species at the highest possible altitude each year. The extent of vertical dispersal and its possible significance will be considered for each species individually, considering them in alphabetic order.

Ageneotettix deorum (Scudder) has been collected 16 times at altitudes at least 1,000 ft above its apparent upper resident limit (about 7,500 ft). It has been collected 11 times between 8,500 and 9,500 ft and 5 times above 9,500 ft —one specimen having been collected above timber line (at 11,300 ft). Though a small grasshopper, it is a vigorous flier near the ground. The upper resident limit of this species probably fluctuates from year to year, the species being much less abundant at and above 7,000 ft than below, and its dispersal above 8,500 ft is probably merely an indication of a modest and perhaps irregular population pressure at the upper altitudinal limit.

Aulocara elliotti (Thomas), like the preceding species, is a small grasshopper but a vigorous flier near the ground. It has appeared somewhat more frequently as an accidental than *Ageneotettix,* 36 adult specimens having been collected well above the resident upper limit (about 5,700 ft). Five were taken at altitudes from 6,800 to 9,000 ft, 13 between 9,000 and 11,000 ft, and 18 above 11,000 ft (15 of these on the record day in 1936, previously mentioned). The distribution of *Aulocara* on the plains appears to be more restricted in the Boulder region than does that of *Ageneotettix;* hence the vagrants, though more numerous, are probably of no more significance than for *Ageneotettix.*

Melanoplus bivittatus (Say), which is second only to *M. sanguinipes* in frequency of accidentals, is, like it, an abundant crop pest on the high plains of Colorado. It is a clumsy insect and not a very strong flier, but it has been collected with fair regularity in the neighborhood of timber line and above. Our highest record of an accidental is at Summit Lake, on Mount Evans, at an elevation of 12,800 ft. The highest altitude at which a juvenile has been collected is 10,000 ft, but we have not yet collected the last juvenile instar at this elevation. The fact that juveniles are regularly collected at 10,000 ft suggests, however, that the species could establish itself at that altitude with a slightly longer growing season. Its normal upper resident limit is probably about 9,000 ft above sea level. Records of this species for the 3 seasons, 1958, 1959, and 1960, have been summarized in a graph (Fig. 1).

Melanoplus confusus Scudder, the first *Melanoplus* to mature in the spring in the Boulder region (hatching before the end of May), does not develop, according to our observations, above an altitude of about 7,000 ft. Accidentals occur as high as 10,000 ft, and so early in the season that confusion with *M. sanguinipes* (from which females, but not males, are practically indistinguishable) is hardly possible.

In 1959 we collected 6 adults (4 of them males) at 10,000 ft above sea level before the end of June. Most of the accidentals of this species were recorded that season before the end of the 3d week in July. Accidentals have been rather frequent early in the season. Juveniles are not easily determined, however, and it is possible to confuse them with those of *M. sanguinipes.* The actual upper resident limit of this species may be higher than our estimate, therefore, but on the basis of the occurrence of accidentals early in the season, before any juvenile

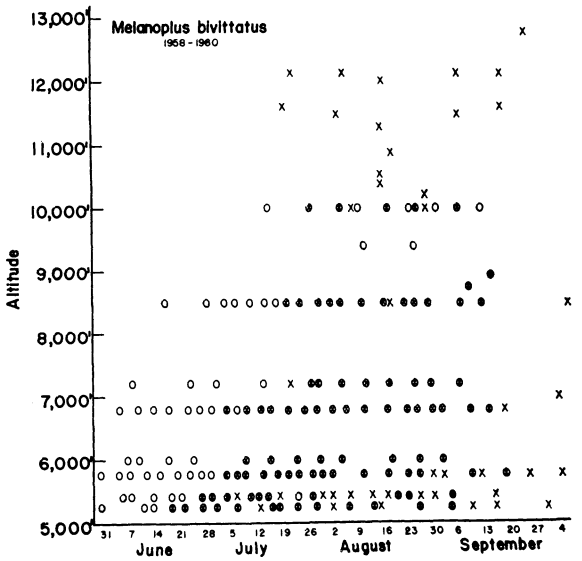

FIG. 1. Summary of all collections of *Melanoplus bivittatus* (Say) in the Boulder, Colorado, region during 3 seasons, 1958, 1959, and 1960. Five thousand forty-two juveniles and 1,518 adults form the basis for this graph, but datum symbols that would overlap on the graph have been omitted to avoid confusion. Each symbol refers to a collection; this may, rarely, have been based on a single specimen, but most collections involved several specimens and some included 50 or more. Explanation of symbols: O, collection containing juveniles only; X, collection containing adults only; the combined symbol, collection containing both juveniles and adults.

Melanopli appear, it seems safe to assume that the actual upper resident limit is not particularly high.

Melanoplus femur-rubrum (DeGeer), in marked contrast with *M. confusus,* is the last *Melanoplus* to mature each season in our area. Its upper resident limit is not likely to be high, therefore. This appears to be at about 7,600 ft. High altitude accidentals of this species appear late in the season, so late, in fact that wanderers could hardly constitute a very effective fringe of an expanding population. Only 2 accidentals of this species have been collected before August.

Late accidentals can, of course, deposit eggs, but the late hatching dates characteristic of this species would be still further postponed by the effect of increasing altitude. It is therefore difficult to believe that this species could mature at an elevation much above that which we consider its upper resident limit.

Melanoplus packardii Scudder is similar to *M. bivittatus* in altitudinal distribution and in frequency of accidentals. It matures regularly not much higher than about 8,500 ft, though a 3d instar juvenile has been collected at 10,000 ft. Nine accidentals have been collected in our area above 10,000 ft, 4 of these at 11,400. (Fehlmann [1950] collected one adult male above 12,000 ft in southern Colorado.) In the altitudinal band from about 8,500 to 10,000 ft, annual wanderers provide the nucleus of a population that might become established under favorable conditions up to about 10,000 ft.

Melanoplus occidentalis (Thomas) is a special case. Its extensive movements have been referred to elsewhere (LaRivers 1948; Alexander 1951). Apparently all the adults for which we have records in the mountains west of Boulder are accidentals, for we have taken no juveniles. In this respect this species is like *M. angustipennis* but is much more common; in any case, it apparently hatches on the plains.

Twenty-two of our records are from above 9,500 ft, and there are many others from lower altitudes but above 7,000 ft. Only *M. sanguinipes* has been collected at a higher altitude; a male of *M. occidentalis* was collected by Robert J. Niedrach at 13,600 ft on Mount Evans, August 10, 1933. Perhaps this species does mature in the foothills, but our available data suggest that the accidentals reflect a wandering propensity of the species and are not related to its establishment in the mountains.

Melanoplus sanguinipes (Fabricius) (*M. mexicanus* in my 1951 paper and *M. bilituratus* in much recent literature) is the species in which continuous dispersal is best indicated by abundant accidentals. Although a high frequency of accidentals was suggested in my earlier paper, observations up to that time were meager indeed compared to those made in the seasons 1958, 1959, and 1960.

As previously stated, more than 400 accidentals of this species were collected in a single season in the area of our study. All collections of this species during that season, 1959, have been tabulated in a graph, Figure 2, indicating distribution by altitude and distinguishing between records of juvenile and adult specimens. It is apparent from this graph that normal resident range extends upward to about 10,000 ft, but that occasional juveniles appear up to 12,000 ft.

With this species several observations can be cited to support the theory that an abundance of accidentals implies population pressure by a fringe of high altitude pioneers ready to become established under temporarily favorable conditions. Egg deposition and even mating may occur at altitudes well above resident range. I have ob-

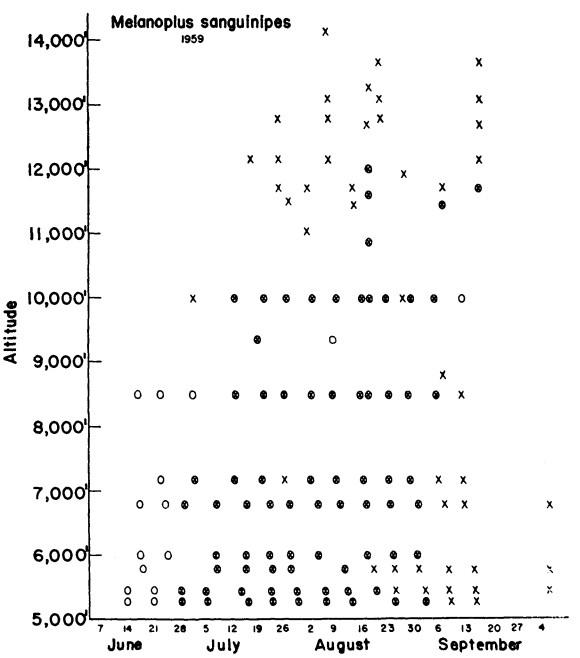

FIG. 2. Altitudinal and seasonal distribution of collections of *Melanoplus sanguinipes* (Fabr.) in the Boulder, Colorado, region in 1959. Two thousand four hundred eighty-one juveniles and 2,400 adults are incorporated in this graph. Explanation of symbols: O, collection containing juveniles only; X, collection containing adults only; the combined symbol, collection containing both juveniles and adults.

served copulation in this species at altitudes up to 11,800 ft, and juveniles, as evident in the graph, have been collected up to 12,000 ft. This highest collection of juveniles was made August 20 in a particularly favorable location, a south-facing slope, between Waldorf (a deserted mining camp west of Georgetown) and Argentine Pass. Thirteen adults and 12 juveniles were collected; only one of the juveniles was in the 5th (last) juvenile instar, so it is probable that most, if not all, of the adults collected were accidentals. Fourteen additional adults were collected the same day on the way up to Argentine Pass, 13,130 ft in altitude, but no other juveniles were collected above 12,000 ft. These observations suggest that under particularly favorable circumstances an occasional specimen of *M. sanguinipes* may mature at altitudes as high as 12,000 ft.

In contrast, an observation made in 1960 suggests that in a year of exceptionally early cold weather the upper resident limit may be depressed to an altitude even below 10,000 ft. On August 18, 1960, on arrival at our regular collecting station at 10,000 ft (the C-1 Weather Station of the Institute of Arctic and Alpine Research, University of Colorado), we saw evidence of a recent hard freeze. The leaves of the golden banner (*Thermopsis*), one of the most conspicuous herbs in the area, were blackened, and the plants were wilted. We found that the temperature at the weather station had dropped to 18° F two nights before. On the collecting date, however, we did take 4 adults and 5 juveniles of *M. sanguinipes,* one juvenile being in the 5th instar. But 6 days later, on August 24, intensive search for about an hour by several collectors revealed only one specimen, an adult female. The species was practically eliminated, probably not by cold but by destruction of forage. In both 1958 and 1959 collections of adults and juveniles were made regularly and in fair numbers at this same station as late as the end of August 1958 and into the 2d week of September 1959. It was apparent that the species completed its life cycle at 10,000 ft during both these seasons. In each of these 2 years the first freeze recorded at the weather station came after September 1.

These observations suggest that the upper altitudinal limit at which *M. sanguinipes* can complete its life cycle varies from below 10,000 ft in an "unfavorable" year to about 12,000 ft under exceptionally favorable circumstances. It should be noted, however, that even in a year that is unfavorable for the species there are usually viable egg pods in the ground up to 12,000 ft and above, these having been deposited by adults that moved up from lower altitudes. This reservoir of eggs provides juveniles at and above the upper altitudinal limit every year.

Metator pardalinus (Saussure) is one of the few Oedipodinae with what we might call vagrant tendencies. Its apparent upper resident altitude is at the upper edge of the plains, about 5,800 ft above sea level. Nevertheless, 13 accidentals have been collected, 3 of these up to 9,000 ft, 7 between 9,000 and 11,000 ft, and 3 at 11,400 ft. Perhaps there is some potential for a fluctuating upper limit involving appropriate grassy areas in the foothills, but thus far we have collected no juveniles above the plains stations.

Trachyrhachis kiowa (Thomas) is unique among the species we have studied. This tiny oedipode is an inveterate wanderer; but the remarkable aspect of this species is that the parent population producing the accidentals is somewhere on the plains east of Boulder, not far east of the lowest stations we visited regularly. That this major population is not far away is suggested by the fact that the zone of oscillation marking the upper boundary of the resident population involves our lowest stations.

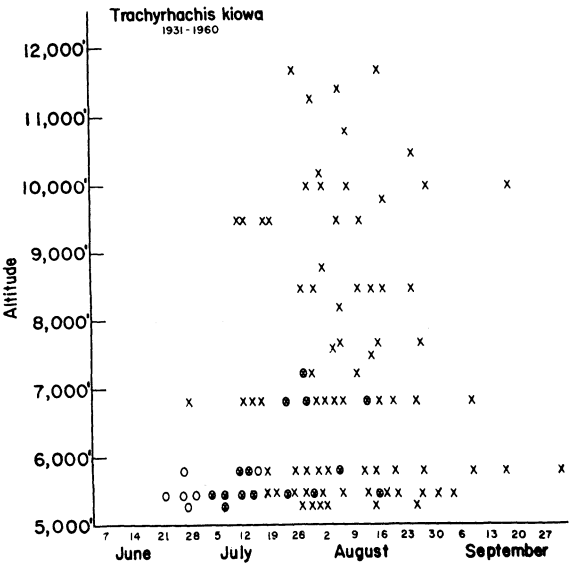

FIG. 3. Summary of all collections of *Trachyrhachis kiowa* (Thomas) in the Boulder, Colorado, region from 1931 to 1960, inclusive. Sixty-three juveniles and 143 adults are incorporated in the graph. Explanation of symbols: O, collection containing juveniles only; X, collection containing adults only; the combined symbol, collection containing both juveniles and adults.

All records for the species, for the entire period from 1931 through 1960, are summarized in Figure 3. What is apparent from this graph is that all records above an altitude of about 7,000 ft are for adults. This might imply that 7,000 ft is the upper resident limit, but the average upper limit is actually much lower. Though not apparent from the graph, but revealed in year-by-year examination of the records, is the fact that in many seasons only adults were collected along our entire altitudinal gradient. In some seasons, in other words, there was apparently no resident population in our area. But we still collected adults, presumably accidentals from lower elevations; the potential was always present.

Juveniles were collected at those stations in the upper edge of the plains (i.e., below 6,000 ft) in most, but not all, years of intensive collecting. In only a few seasons were juveniles taken in the lower foothills. But adults turned up every year in which intensive collecting was carried on. The fluctuating resident population of *Trachyrhachis kiowa* appears to be at the upper edge of the plains and in the lower foothills. Its stable population is on the plains at somewhat lower altitudes. The pattern of distribution of this species is similar to that observed with *M. sanguinipes* but with one major difference; the altitude of this fluctuating upper boundary is some 5,000 ft lower.

SUMMARY

1. Two kinds of accidentals occur among grasshoppers in mountains, individuals outside their resident range, and adults that appear at higher altitudes within the normal range but before adults can have matured at such altitudes.

2. Accidentals occur only among species with well-developed wings, being apparently dependent upon both flight and transport by wind. The

diurnal updraft characteristic of mountains and adjacence of lowland source-habitats are important factors.

3. Accidentals occur along the whole gradient of altitude. Many species are involved, species known only from accidentals being as numerous as resident species at some altitudes.

4. If accidentals of a given species are numerous, that species is continuously exerting a pressure for maintenance at its ecological limits—and for temporary establishment when conditions are favorable above its normal range. Accidentals constitute a reservoir of reproductive adults every year at altitudes above those at which the species normally completes its life cycle. Eggs and juveniles are thus available every year to establish the population beyond normal limits.

5. Seventy-four species of Acrididae have been collected in the northern Colorado Rockies since 1931. Nineteen are short-winged and do not appear as accidentals. Of the 55 other species, 22 are essentially sedentary in behavior, but the other 33 (including 4 relatively rare species) have been collected as accidentals. In some species the frequency of accidentals is high.

6. Species with a high frequency of accidentals (e.g., *Melanoplus bivittatus, M. sanguinipes, Trachyrhachis kiowa*) clearly show an oscillating upper altitudinal limit, advancing to higher altitudes in favorable seasons and being depressed to lower altitudes in unfavorable seasons.

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