Fluctuations in the numbers of the Monarch Butterfly (Danaus plexippus) in North America

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INTRODUCTION

For the past thirty-three years we have been making a rather intensive study of the migrations of the monarch butterfly and, during this period of time, we have witnessed marked fluctuations in the numbers of this species. As previously reported, (URQUHART, 1960) the monarch butterfly reached a peak of abundance in 1950 and 1951 which period was marked by countless thousands of specimens that clustered in hug masses on various species of trees during the annual fall migration. This period of peak abundance was followed by a marked reduction in numbers in 1952, and by 1953 no roosting colonies could be found and only seven specimens were collected during our summer field studies. By 1954 a few small roosting clusters were located and fifty-eight specimens were collected. By 1956 the population had once again reached a peak of abundance. This cycle occupied a period of six years.

On the basis of these data, and from previously observed cycles in 1938 and 1944, we forecasted a return to peak abundance in 1962 and 1963. This proved to be correct and, as we had anticipated, it was followed by a rapid drop in numbers in 1965.

We forecasted a peak in 1968—1969. However, in this case there was a divergence from the usual clear-cut cycle in that, although there was a population peak over most of eastern North America in 1968, the numbers dropped off in 1969 followed by a sudden and rather dramatic population peak in 1970.

We had noticed, throughout the periods of scarcity, that a disease, marked by a black, foul-smelling liquid contained in the bodies of dead specimens, seemed to be responsible for the decline. Our laboratory colonies were almost completely destroyed — as much as 98,2 % mortality — which hindered our research on other phases of the ecology of this species. During the last population decline we were able to ascertain that the pathogen involved was a polyhedrosis virus (URQUHART, 1966). This virus was later identified as a cyctoplasmic virus (HOWARD et al, 1968).

That a virus is responsible for cyclical fluctuations in other species has been previously reported on, as for example, BALCH and BIRD (1944); STEINHAUS (1948); CROW (1957); BIRD and BURKE (1962).

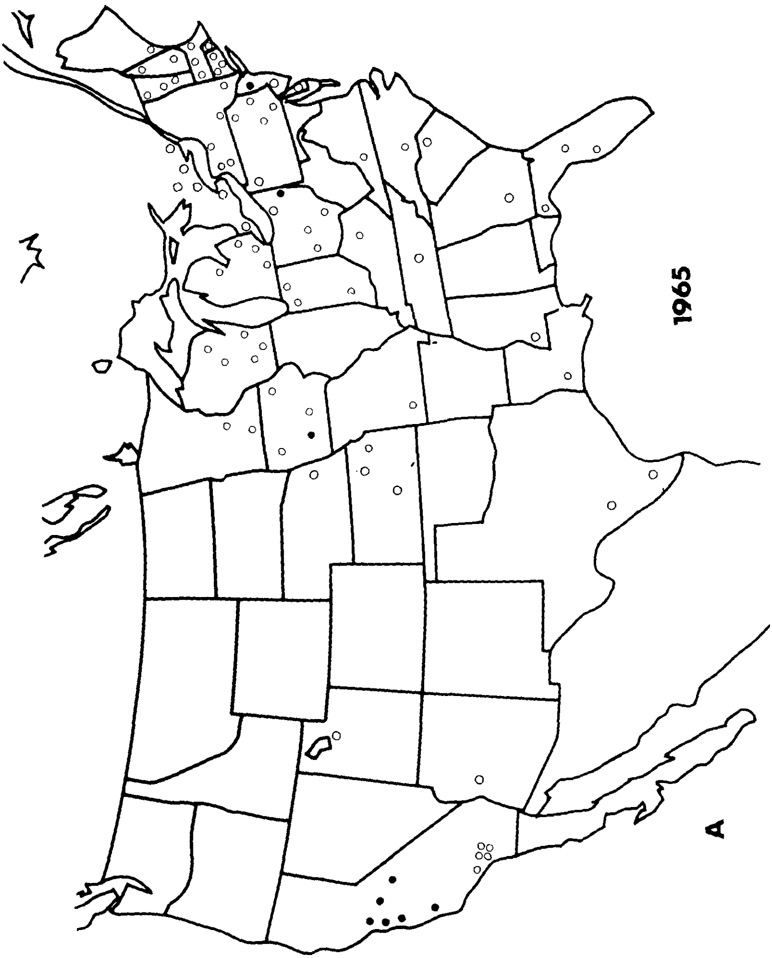
As a result of our observations we became interested in the possibility that a resistant strain of the monarch butterfly might arise in some areas of North America which strain would eventually spread over the continent giving rise to a return to a peak population. It was for this reason that we initiated a report system on the variation in abundance over the continent; the data resulting from this survey is presented in the present paper.

METHOD AND RESULTS

In our program concerned with the migratory movements of the monarch butterfly we have, over the years, organized a group of „research associates“ (Urquhart, 1960). These associates are located throughout the United States and Canada, as well as in other parts of the world where the monarch butterfly has become established. Each member of the group places alar tags on the wings of the migrating population and, at the same time, makes observations pertinent to the study. Each associate, now numbering over four hundred, was asked to fill out a form specifying whether or not the monarch butterfly was "abundant“, "scarce“, or "increasing“, in numbers. Many of these associates have been working with us for the past many years and hence were able to submit a fairly accurate report as to relative numbers.

Although the above terminology does not give exact figures which, for statistical purposes, would have been most desirable, no other means was available to us for following population trends over a continent wide area for a migrating species. Nevertheless, from a gross study point of view, the reports did indicate continent wide trends. In addition, we kept account of the abundance of the species in our particular area from year to year as well as correlating the decrease in numbers with the mortality rate in our laboratory cultures during the years of scarcity and abundance. In order to present a visual impression of the population trends, commencing from a period of scarcity to one of abundance, the results of the observational data were plotted on maps for each of the four years. Where more than one observation was submitted for a particular locality only one indication mark was used. Thus, in some areas more reports were received than would be indicated on the plotted maps. The apparent lack of information for the mountain and desert States is due to the paucity of specimens at all times in these areas except for a short period during times of maximum population in the eastern part of the continent. That more observations were submitted from the mountain and desert States during maximum population is due to the presence of more specimens at this time and the resulting enthusiasm on the part of the associate who then submitted a report but failed to do so during periods of scarcity.

It would appear from the data obtained that the population in California


1965
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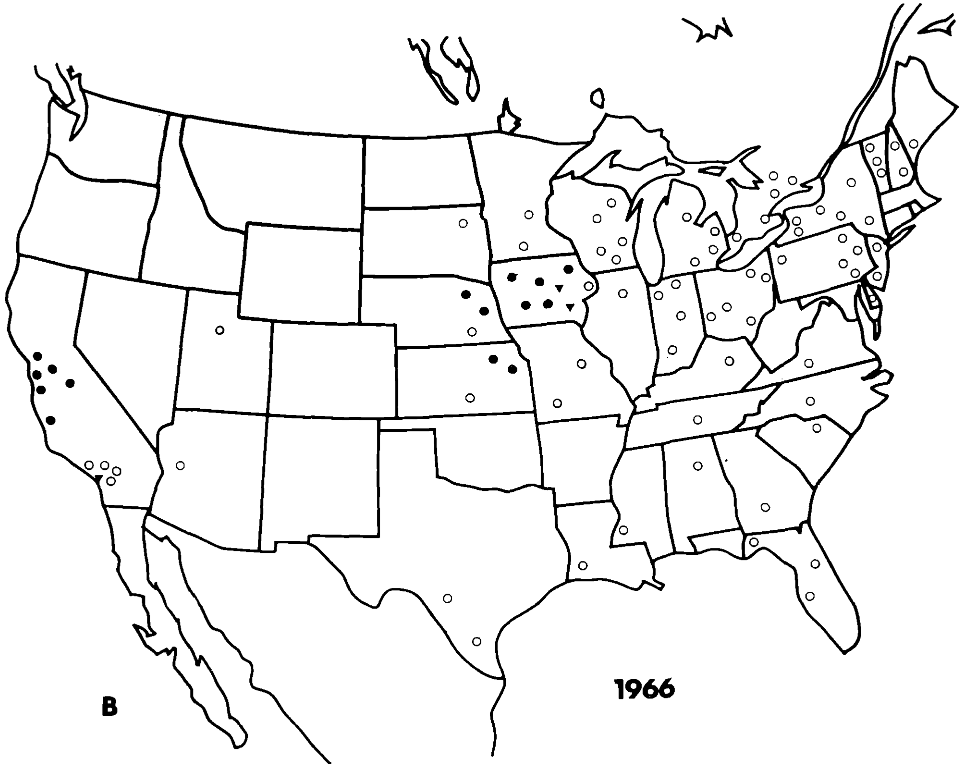
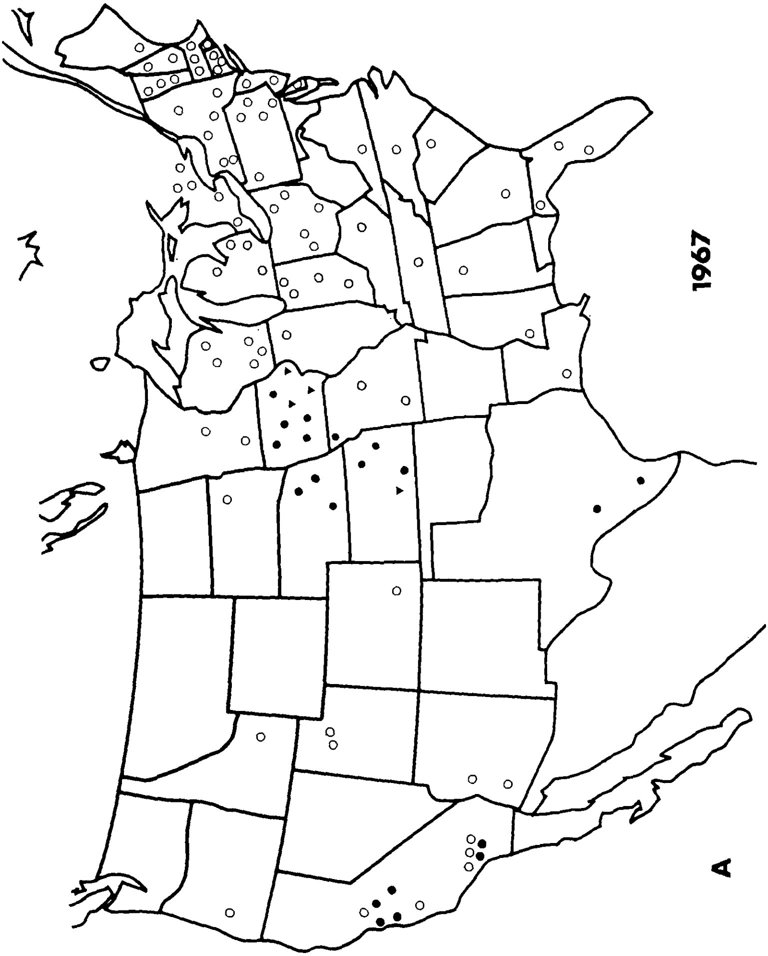


fig. 1 POPULATION DENSITY: ○- abundant, ▲- increasing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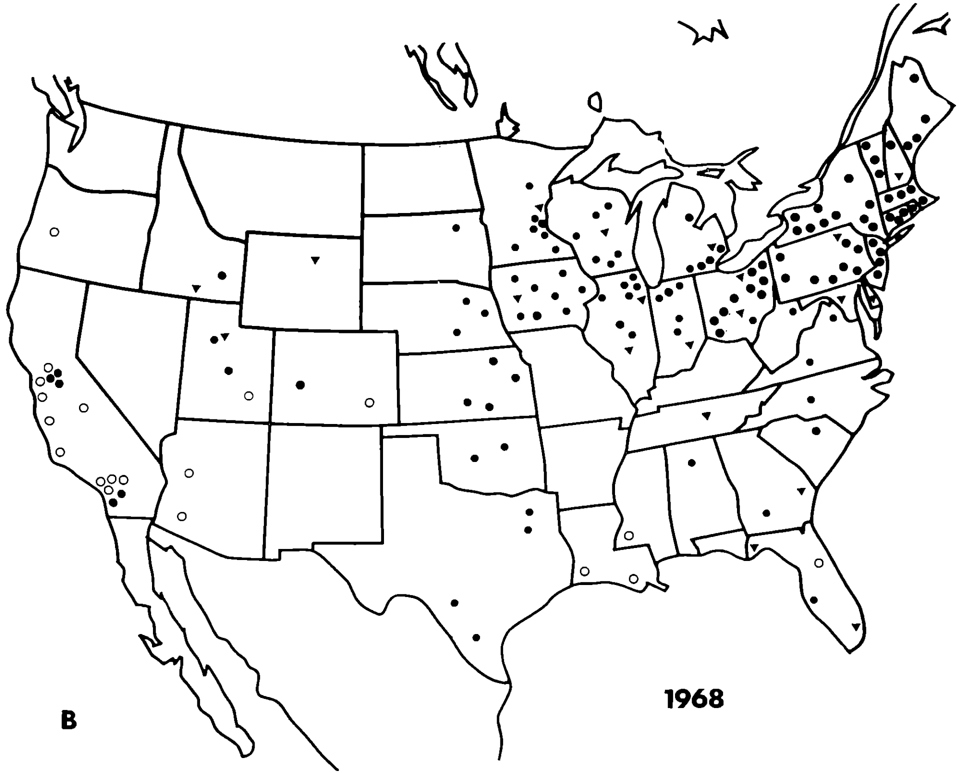

fig. 2 POPULATION DENSITY: ○- abundant, ▲- increasing

did not follow the same trend as for the rest of the continent. Hence, in presenting the results, the California population and that for the eastern United States and Eastern Canada are considered separately.

Eastern United States and Eastern Canada

With but three exceptions, which were single reports, all information received indicated scarcity over the entire eastern United States and Canada in 1965 (Fig. 1 A).

In 1966 (Fig. 1 B) twelve reports of abundance were received from Iowa, together with six reports indicating increasing numbers and one report of scarcity. In Nebraska, the State adjoining Iowa, three reports of abundance and one of scarcity were received. In Kansas, immediately south of Nebraska, five reports of abundance and one of scarcity were received. With these exceptions, the entire area of the eastern United States, eastern Canada, and the south-western States (Oklahoma and Texas) reported scarcity. In many cases the report of scarcity submitted by the associate was argumented by actual counts or statements concerning complete failure to obtain specimens.

By 1967 (Fig. 2 A) many reports were received indicating either abundance or increased numbers in Iowa, Nebraska and Kansas together with reports of abundance and increasing numbers in Oklahoma and Texas.

By 1968 (Fig. 2 B), with but few reports to the contrary, all associates reported abundance or increased numbers.

This pattern for the eastern United States and eastern Canada agreed with our field studies and our laboratory colonies. During 1965—1967 we were unable to obtain sufficient field specimens for our research and no roosting colonies could be located. In the laboratory we experienced great difficulty in maintaining our colonies.

California

In 1965 (Fig. 1 A) reports of abundance were received from northern California (north of Cape Mendocino and the Sacramento Valley) and scarcity in the south.

In 1966 (Fig. 1 B) the northern population remained abundant while in the south there was an indication of increasing numbers which persisted through 1967 and 1968 (Fig. 2, A, B). In the north, however, a few reports of scarcity were received in 1967 and numerous reports of scarcity in 1968.

DISCUSSION

It would appear from these data that a species of migrating butterfly may fluctuate in numbers from year to year and that, in the case of the monarch butterfly, this is due to a virus epizootic. The cycle period is approximately six years.

In the population for the eastern United States and eastern Canada, a strain resistant to the virus apparently arose and made its appearance, in terms of increased abundance, in the states of Iowa, Nebraska and Kansas — although it is admitted that if more reports had been received from states to the east the resistant strain may have covered a much wider area. This resistant strain persisted during 1967 causing an increased area of abundance through Oklahoma and Texas. By 1968, since the monarch butterfly is a migrant, the resistant strain by remigration populated the entire area of the eastern United States and eastern Canada causing a return to abundance. However, the peak did not carry through to the following year and there was a definite decline in numbers, over most of the continent followed by a return to a maximum in 1970. During the period of 1968—1969 we experienced difficulty in maintaining our laboratory colonies. However, field specimens received in the spring of 1970 gave rise to a laboratory population in which there was only a slight mortality rate — less than five percent, indicating that a resistant strain had developed. Food material treated with virus, taken from the bodies of specimens that had died as a result of the disease in our previous laboratory cultures, had a negligible lethal effect (2,2 %).

The effect of this epizootic was not apparent in northern California in 1965—1966 but was indicated in 1967 and became obvious in 1968. It would appear that the virus did not penetrate the northern California population until 1966 and was not of epizootic potential until 1968. The population in southern California followed a trend similar to the eastern United States and eastern Canada. This has led to conjecture that perhaps the northern population has a weak gene flow with the eastern population while the southern one is stronger. Further reports on the population variation in California are now being studied with this idea in mind.

CONCLUSION

It is concluded that a virus epizootic may be responsible for marked fluctuations in populations and that, as a result of this, one can expect to record years of heavy migration of certain species when the population is at a maximum and years of light migration when the population is at a minimum. Crow (1957) has pointed out that the cycles of population is a response to virus infection followed by a host strain resistance. It would appear, from these observational data, that a resistant strain may occur in a well-defined geographical area and that, if the species is a migrant, this will result in the reappearance of the species where it had been absent for a period of time.

It would be of considerable interest to those of us involved in migration studies to have comparative data on the fluctuations in numbers of those species that are not well-defined migrants or are not remigrants such as species that enter areas formerly unoccupied by them. An examination of reared specimens of other migrants during periods of low population density may indicate an epizootic similar to that here described and perhaps follow a cycle similar to that of the monarch butterfly both in time and duration. There is also the possibility that the distance travelled during migration varies with population density, with greater distances during maximum and lesser during minimum density.

The data obtained for the monarch butterfly, although admittedly not of an exact nature to allow for statistical analysis, is pressented so that others interested in following the movements of migrant insects may wish to carry out a similar study.

ACKNOWLEDGEMENT

This investigation, which is a small part of a much larger study on the ecology and physiology of *Danaus plexippus*, was made possible by a grant from the National Geographic Society.

Zusammenfassung

VON KURT HARZ

Durch 33 Jahre wurden vom Autor und seinen Mitarbeitern die Populationsschwankungen des Wanderschmetterlings Monarch *(Danaus plexippus)* in Nordamerika und Kanada untersucht. Hier wird das Fluktuieren der Populationen von 1950 bis 1970 geschildert. Die Zyklen verliefen so regelmäßig, daß für 1962 und 1963 ein Höhepunkt des Auftretens vorausgesagt werden konnte, der ebenso eintraf wie die Vorhersage für 1968. Im Jahre 1969 erfolgte jedoch ein Absinken der Zahlen, dem 1970 wieder ein starker Anstieg folgte. Es zeigte sich, daß die Populationen Floridas dem allgemeinen Trend auf dem übrigen Kontinent nicht folgten. Die Abbildungen lassen diese Unterschiede sowie die Populationsschwankungen in den Jahren von 1965 bis 1968 gut erkennen, wobei ein heller Kreis spärliches, ein dunkler Kreis starkes Auftreten und ein dunkles Dreieck zunehmende Vermehrung bedeutet. Dem spärlichen Auftreten in den östlichen Gebieten der Vereinigten Staaten und Kanadas sowie Süd-Kaliforniens 1965 (1A) folgt Zunahme und verstärktes Auftreten 1966 (1B) in Iowa, Nebraska und Kansas, das sich 1967 (2A) noch steigert und auf Oklahoma und Texas und in Kalifornien auf den Süden übergreift. Die Vermehrung steigert sich bis auf wenige Ausnahmen 1968 noch (2B) und erreicht einen Höhepunkt.

Von der Forschungsstelle in Toronto im gleichen Zeitraum durchgeführte Laboratoriums-Zuchten und Felduntersuchungen spiegelten diese Vorgänge im Kleinen wider. Alle Untersuchungsergebnisse ließen vermuten, daß in

erster Linie ein Epidemien erzeugender Virus für die in einem etwa sechsjährigen Zyklus ablaufenden Populationsschwankungen von *Danaus plexippus* verantwortlich ist. Es wird angenommen, daß ein geringer Prozentsatz der Populationen des östlichen Nordamerika und Kanadas gegen den Virus resistent ist, sich vermehrt, ausbreitet und schließlich wieder einen Höhepunkt herbeiführt. Während des Gipfels 1970 durchgeführte Laboratoriumsversuche zeigten, daß von Faltern die infiszierte Nahrung aufnahmen nur 2,2 % starben. Im Norden Floridas war bis 1966 kein Einfluß der Seuche erkennbar, erst 1967 deutete er sich an und wurde 1968 klar erkennbar, wogegen die Population des Südens einen ähnlichen Ablauf des Geschehens wie im Osten der USA und Kanadas zeigten.
Die Vermutungen über den Einfluß von Viren auf die Populationsschwankungen werden von den Feststellungen CROW's (1957) bestärkt, der zeigte, daß Populationszyklen und Virenbefall in Beziehung stehen können und daß verstärkte Infektion von verstärkter Resistenz der Wirte gefolgt wird. Wahrscheinlich gibt es in bestimmten Gebieten resistente Stämme und handelt es sich dabei wie im Fall des Monarchen um eine wandernde Art, ergibt sich daraus zwangsläufig das Wiedererscheinen in Gebieten, in denen sie für einige Zeit fehlten. Es wäre sehr interessant Daten von Populationsschwankungen solcher Arten zum Vergleich heranzuziehen, die keine ausgesprochenen Wanderer sind oder von überhaupt nicht wandernden Arten, die neue Gebiete besiedeln. Zuchten anderer Wanderarten während der Perioden geringer Populationsdichte zeigen vielleicht ähnliche Erscheinungen und Zyklen wie die hier vom Monarch beschriebenen.

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Zu vorstehendem Beitrag

Die hochinteressanten Forschungsergebnisse unseres verehrten Kollegen FRED A. URQUHART, dessen Erforschung von Wanderungen und Leben des Monarchs einfach beispielhaft sind — ich verweise auf das Buch „The Monarch Butterfly", Toronto 1960 — hat hier neue Gedanken aufgeworfen, die auch für unsere Arbeit bedeutungsvoll sind und ihr weitere Impulse geben. Wer hat nicht schon beim Züchten vom Distelfalter, *Vanessa cardui* und der Gamma-Eule, *Autographa gamma,* nicht schon schwere bis 100 %ige Verluste erlebt? Wenn hier auch nur Puppen bzw. Raupen betroffen werden, so ist es im Endeffekt doch das gleiche. Im Jahre 1966 gingen mir 5000 bis 8000 Raupen von *gamma* an Polyedrose ein; im folgenden Jahr in den gleichen, nicht desinfiszierten Behältern durchgeführte Zuchten blieben praktisch verlustlos. Also auch hier eine erhöhte Resistenz nach dem Zusammenbruch, wenngleich es sich hier allerdings um andere Stämme handelte. Ähnliche Vermehrungszyklen zeigt bei uns auch der Große Kohlweißling, *Pieris brassicae,* die zwischen Massenauftreten bis völligem Fehlen in einzelnen Gebieten schwanken können, wobei aber offenbar Parasiten vor Viren wirksam sind. Auch bei ganz anderen Tieren, z. B. Feldmäusen, gibt es Zyklen, die von spärlichem Auftreten bis zur Massenvermehrung mit anschließendem Zusammenbruch infolge Virosen reichen, man vergleiche die Arbeiten des finnischen Forschers KALELA. Natürlich gibt es auch Kreisläufe im Auf und Ab des Auftretens, die nicht periodisch verlaufen, Populationsdynamik ist ja oft ein sehr komplexes Geschehen. Wir werden dieser Erscheinung jedenfalls erhöhte Aufmerksamkeit zuwenden und bitten besonders auch die Züchter unter unseren Mitarbeitern diese zu verfolgen und darüber zu berichten.

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