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EXPERIMENTAL MANIPULATION OF THE TIMING OF REPRODUCTION IN THE CALIFORNIA VOLE

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INTRODUCTION

The regulation of numbers in any species cannot be adequately understood until it is known how the additions of new individuals to its populations is determined. Moreover, most additions are ordinarily through reproduction. It is therefore vital that the factors which control both the timing and quantity of reproduction be carefully investigated and understood.

One species whose population dynamics has been intensively studied is the California vole, *Microtus californicus*. Yet, little is known regarding the specific environmental factors which turn on and off its reproductive efforts. In the Mediterranean climate under which it lives in central, coastal California, it normally reproduces during the wet season which extends from about October through April (GREENWALD, 1957 ; HOFFMANN, 1958 ; PEARSON, 1963, 1964 ; KREBS, 1966 ; LIDICKER, 1973). Breeding generally ceases in June when the vegetation becomes desiccated, and the species then remains non-reproductive until green vegetation is again available. This seasonal pattern of reproduction naturally suggests that the availabilities of green food and moisture may be the critical factors in determining the timing and reproduction in this region. Although this seems a reasonable hypothesis, other factors in the environment will certainly be changing concurrently with wet and dry regimes and could in fact be responsible for the reproductive changes. Furthermore, two interesting exceptions to this basic seasonal pattern of reproduction frequently occur, and suggest that the situation is significantly more complex. Sometimes breeding does occur in the dry (summer) season (BRANT, 1962; KREBS and DELONG, 1965; LIDICKER, 1973), and often there is a delay in the start of the breeding season extending from one to three or even more months after the wet season begins (KREBS, 1966; BATZLI and PITELKA, 1971; LIDICKER, 1973).

In an attempt to understand the reasons for these two recurrent modifications of the basic pattern of breeding seasons in *M. californicus* and to better assess the separate roles of green food and water on reproduction, populations of voles were grown in outdoor enclosures in which the availability of food and water could be manipulated. This report concerns three experiments (five vole populations) carried out during the three year period from 1 January, 1965 to 21 January, 1968. In all these experiments, the populations were harvested when necessary so that near-normal densities were maintained. Two additional experiments, in which no harvesting was done, will be reported elsewhere.

These experiments are part of a long-term research program on the population biology of *Microtus californicus*, a program in which field and experimental studies supplement each other. In this way, hypotheses generated by the field data can be tested under more rigorously controlled conditions. Thus, while I expect that under field conditions the timing of reproduction will be complexly determined by the interactions of a number of factors (LIDICKER, 1973), the use of experimentally manipulated enclosed populations will continue to be a powerful tool in the development of our understanding of microtine demography (e. g., FRANK, 1954; CLARKE, 1955; LOUCH, 1956; WIJNGAARDEN, 1960; HOULIHAN, 1963; CHITTY, *et al.*, 1968; GENTRY, 1968; KREBS, *et al.*, 1969; LUND, 1970; MYERS and KREBS, 1971; WIEGERT, 1972).

THE ENCLOSURES

The two enclosures utilized in this study are located at the Animal Behavior Research Station of the University of California, Berkeley. They are 9.1 m (30 ft) square giving a surface area of 83 m^2 (900 ft^2) ; see Fig. 1. The walls, constructed of reinforced concrete, are four feet (1.2 m) high and have a 15 cm overhanging lip on the inside (see Fig. 2). The floor is also concrete and slopes gradually toward drains in each of the four corners. Above the concrete wall, a wire-mesh wall continues for an additional 1.2 m, and is topped by a wire-mesh roof (see Fig. 1). Thus, these enclosures are absolutely mouse-proof, and predators are also prevented from entering.

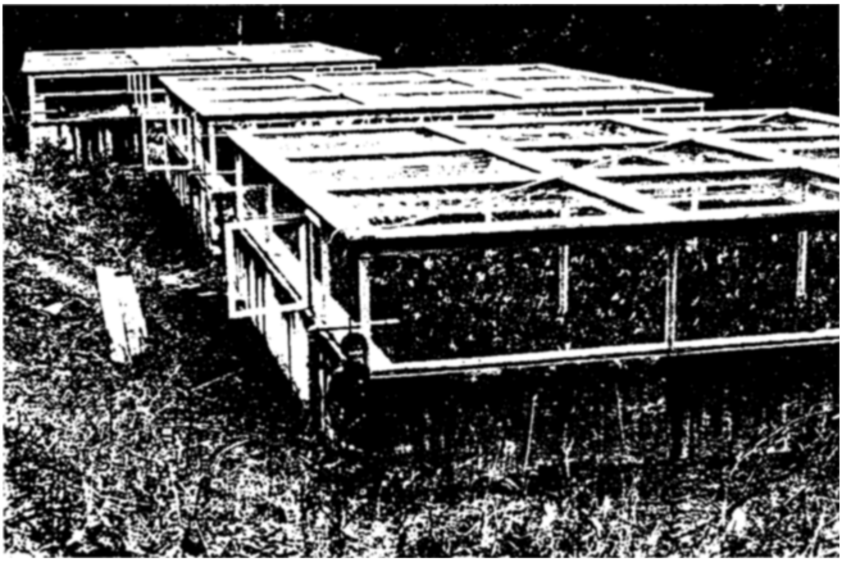

Fig. 1. The two enclosures used in this study. Photo taken on 1 November, 1964.

Fig. 2. View of inside of enclosure, showing overhanging lip on concrete walls, and other details of construction. Photo taken 2 April, 1966 when lush perennial grasses and clover were present (experiment 2B).

The enclosures were prepared for the growing of vole populations by first filling them to a depth of 15 cm with coarse gravel and then placing 45 cm of topsoil on top of the gravel. This still left 60 cm of concrete wall above the soil surface. The rich top soil permitted growth of lush vegetation in the enclosures (see Fig. 2). The gravel and drainage system prevented flooding during heavy rains. One of the enclosures was fitted with watering devices to simulate rainfall. Trampling of vegetation was kept to a minimum by walking on the wall ledges whenever possible.

GENERAL PROCEDURES

In each experiment, the populations were initiated by introducing two pairs of adult mice. The enclosures were live-trapped at frequent intervals and all voles were individually marked by toe-clipping. Upon capture, voles were weighed, checked for external reproductive sign, and examined for wounds and scars. When harvesting was necessary, individuals were chosen randomly from within various sex and age categories. The number removed in each category was determined so as to minimally upset the sex and age structure of the population. All harvested individuals were autopsied for reproductive data. At the end of each experiment, all voles were removed and autopsied.

EXPERIMENT 1

The plan of this first experiment was to grow two populations simultaneously so that they were reproducing vigorously as the dry season began. Then the vegetation in one enclosure would be watered in an effort to keep it growing. In this way it would be determined whether reproduction would continue into the summer if the vegetation did not desiccate. Moreover, a detailed analysis of weight and reproductive changes under drying conditions could be made.

The two populations were founded in January after a lush growth of volunteer vegetation (local grasses and forbs) had been established in the enclosures. Watering of the vegetation in one enclosure (B) was begun in early May and continued into early August. Because the vegetation was composed largely of annuals, it was possible only to extend the period of drying vegetation in the watered enclosure a little over one month beyond that in the control enclosure. Major events in this experiment and the body weights of various cohorts are presented in Figs. 3 and 4.

In both populations, litters were produced promptly and regularly. Those born before April grew rapidly and matured reproductively at a normal weight (25 to 30 g). Litters born after this, grew more slowly and failed to mature reproductively. In the unwatered enclosure (A), body weights levelled off or declined during the drying

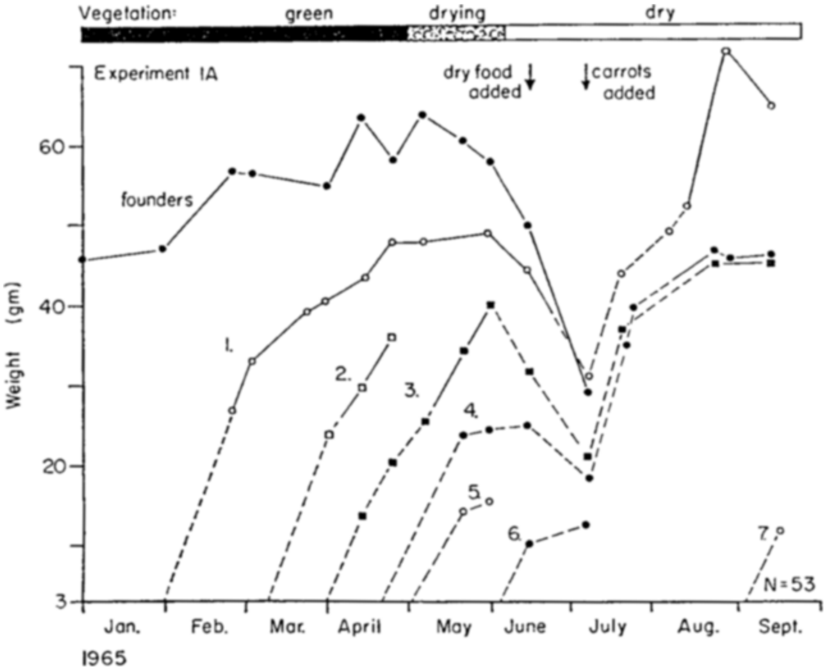

Fig. 3. Changes in mean body weight (g) for the various cohorts of voles in experiment 1A. Arabic numerals refer to successive litters born in the enclosures (in some cases more than one litter may be unavoidably combined into a single cohort). The status of the vegetation and various other important events are indicated across the top. Solid lines connecting dots indicate that at least some of the cohort is reproductively competent; dashed lines indicate that none of the group is reproductively active. Intentional cropping of the population during the active growth period caused the premature termination of some cohorts.

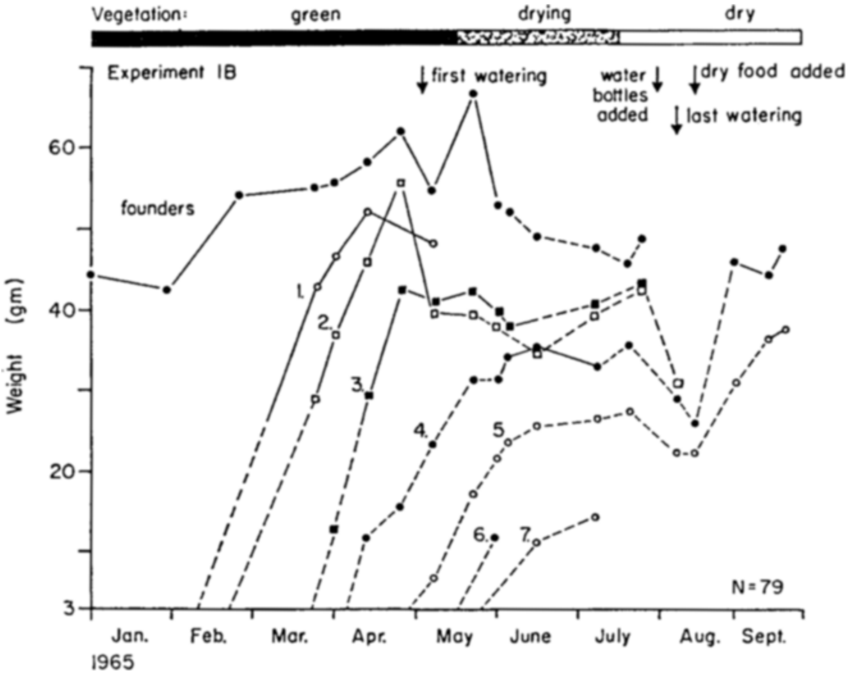

Fig. 4. Changes in mean body weight for the various cohorts of voles in experiment 1B. Symbols as in Fig. 3.

period, except for litter 3 which continued to grow until the end of May. In order to keep population A at about 15 individuals, a total of 30 voles was removed during this growth phase. With the complete drying of the vegetation, and with no drinking water provided, the mice began to lose weight rapidly, and many deaths occurred. Dry food (commercial lab mouse chow) was added in mid-June, but this failed to stop or slow the weight losses. Those mice that had matured reproductively began to lose reproductive competence, the youngest ones first. Then in early July, carrots were provided. Only four voles had survived this period of severe weight loss. They gained weight rapidly, and in five weeks had become reproductively competent. Thus, it is clear that dehydration rather than starvation was the primary cause of the losses. Litter number 7 was born in early September, which is long before the usual breeding season begins.

In enclosure B, body weights levelled off through the drying out period, and reproductive competence was gradually lost. The last litter was actually born in late May near the beginning of the drying period. A total of 63 mice was killed in order to keep the population density comparable to that in population A. Severe weight losses, accompanied by high mortality rates, did not begin until late July, almost two months later than in the control population. These losses were not due to dehydration as this population was never without water. It was provided in the form of frequent artificial rainfall, by water bottles, or both (carrots were not provided). When dry food was provided, the four survivors immediately started to gain weight rapidly and achieved reproductive maturity within a month (two weeks in the case of one male). In both populations, the survivors of the stressful period did not include members of litters born during the drying out phase.

Not surprisingly, this experiment has shown that either insufficient food or water can cause the termination of the breeding season, weight losses, and eventually death. It is interesting, however, that the recovery of reproductive competence seems to be a little quicker after starvation than after dehydration. Finally, it is worth mentioning that even desiccated and partially eaten vegetation was able to sustain a very dense population (15 voles equals about 725 per acre; 1750 per hectare) into late July.

EXPERIMENT 2

This experiment was designed to replicate Experiment 1 with the important exception that perennial grasses (*Lolium*, *Poa*) and clover (*Trifolium*) were planted in the enclosures (Fig. 2). With this change from annual to perennial vegetation, it was anticipated that watering would succeed in maintaining green vegetation for a longer time into the dry season than was achieved in the first experiment.

The populations were initiated in late March, and watering of the vegetation began in mid-May. In enclosure A, watering was terminated on 10 June, and the vegetation allowed to dry out. In B, watering was continued throughout the experiment. The history of these two populations, and body weight changes are presented in Figs. 5 and 6. Litter production began promptly in both populations as at least one of the founding females in each case was already pregnant.

Fig. 5. Changes in mean body weight for the various cohorts of voles in experiment 2A. Symbols as in Fig. 3.

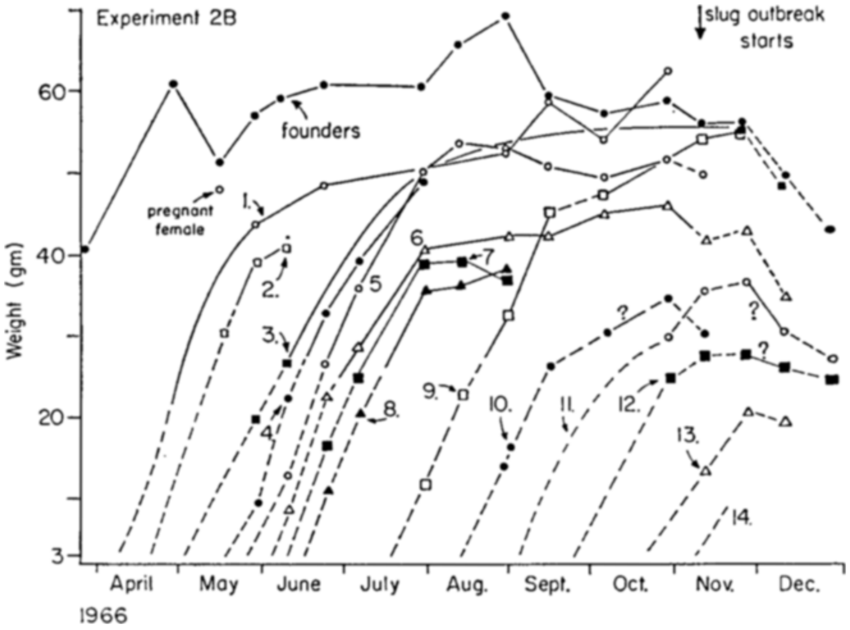

Fig. 6. Changes in mean body weight for the various cohorts of voles in experiment 2B. Symbols as in Fig. 3. Litter 10 is almost certainly a multiple litter. Question marks associated with litters 10, 11, and 12 refer to the doubtful achievement of reproductive competence at the times indicated.

In population A, litters born during the period of green vegetation grew rapidly, and, with the inexplicable exception of litter 3, matured at a normal rate (two females from litter 3 seemed to begin cycling at usual weights and then stopped). Litter 5 entered the drying period at less than 20 g and subsequently grew more slowly. Litter 6 grew slowly and did not survive into August. Twenty-one individuals were removed from the population during this spring and early summer. Weight losses and high mortality rates characterized the drying period. When water bottles were provided in mid-August, only four survivors remained. They immediately gained weight suggesting that as in experiment 1A the cause of the weight losses and deaths was primarily dehydration.

In marked contrast to Experiment 1A, the four survivors (one male and three females) did not continue to gain weight after their recovery from dehydration and did not become reproductively competent after a five-week delay. In mid-September I added dry food (lab mouse chow and sunflower seeds) to test the possibility that these survivors were not adequately fed. This produced little or no weight gains, and no changes in reproductive status. Until April, these four remained in this stunted condition (35 to 40 g). Then suddenly, they gained weight and started to reproduce. This was an eight month delay between recovery from dehydration and the start of reproduction. The voles were then over ten months of age, and the two members of litter 4 had previously achieved reproductive competence. This delay is longer than, but otherwise apparently similar to, the delays in reproduction following the start of the rainy season reported for eleven years on nearby Brooks Island (LIDICKER, 1973).

In population B, numerous litters were produced through June and then steadily but at a reduced rate into November. The first nine litters grew repidly, and matured normally. After that, initial growth rates were still good, but growth tended to level off at 30 g or less and reproductive maturity was not definitely achieved (questionable cases occurred in litters 10, 11, and 12). A total of 64 individuals were harvested from this population in an attempt to keep total numbers to around 15.

By early November it was obvious that a massive outbreak of an introduced European slug, *Milax gagates* (Limacidae), was occurring in enclosure B. Thousands of these slugs were present and soon had a devastating effect on green vegetation. The amount of green growth was greatly reduced even though this was the rainy season. Their effect on the voles can be seen (Fig. 6) about one month before they became obvious to me. There are weight losses and the loss of reproductive competence in some individuals. By late November, the entire population of voles was losing weight rapidly, and mortality increased greatly. At the end of the experiment in late December, only three survivors remained, and none of them was in reproductive condition. The most obvious explanation for these events is that the voles were suffering from lack of food. Unfortunately, this idea was not tested by the addition of dry food to the enclosures.

From this experiment we can see that breeding can continue throughout the dry summer period if green food is available, and that it can terminate even during the normal breeding season if slugs eat up most of the food supply. Furthermore, we see again in experiment 2A that dehydration can stop reproduction, and that recovery entails a delay in the return of reproduction. In this case a delay of eight months was observed. It is not known whether the reduction in growth and delay in maturation shown by litters 10, 11, and 12 (B) were the result of the slugs being present even in low numbers in this enclosure or by some other factor arising from the fact that these litters were born in a normally non-reproductive season. The reduced rate of litter production from July on also suggests that some seasonal factor may be operating which is independent of food and water.

EXPERIMENT 3

Only one enclosure was used in this experiment, which was an attempt to repeat experiment 2B, but with a shift in timing to two months later in the year. Perennial vegetation was again planted, and watered regularly. The population was founded in May when green vegetation was abundant. I wanted to see if rapid production of litters would occur in June through August as it did in April through June in 2B.

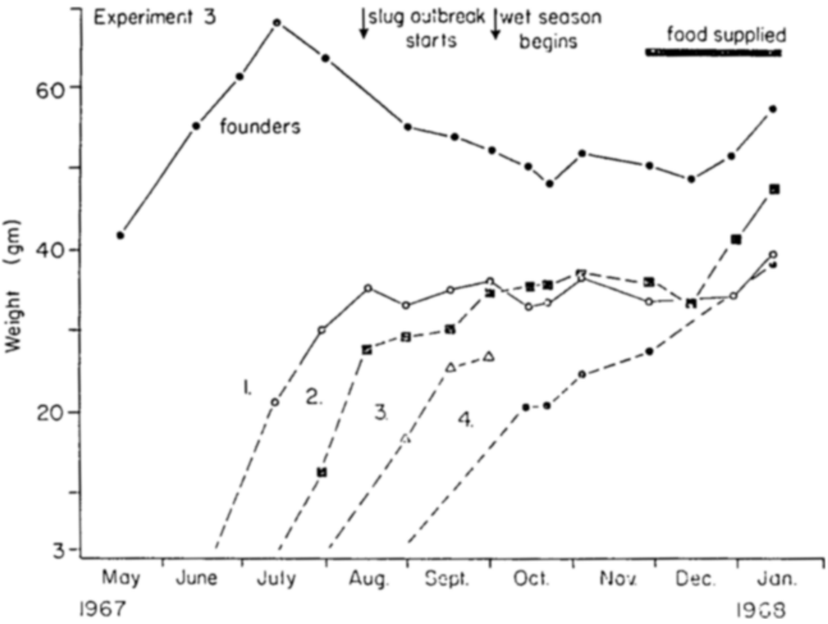

Fig. 7. Changes in mean body weight for the various cohorts of voles in experiment 3. Symbols as in Fig. 3.

The results are shown in Fig. 7.

Only four litters were produced in this experiment (average litter size only 2.8). They were well spaced, none showed maximal growth rates, all became stunted, and only the first matured normally. No harvesting was found to be necessary. These poor results were almost certainly caused by another severe outbreak of *Milax*. This time it was evident by mid-August, although it was apparently affecting the voles for at least a month earlier. This is suggested by the relatively slow growth of litters 1 and 2, the failure of litter 2 to mature reproductively (even though experiment 2B demonstrated that this was possible in July), and the loss of weight suffered by the founding adults beginning in mid-July. By late September the vegetation was showing obvious effects of depredation by slugs. In mid-October, the grasses above ground were almost all dead, although numerous green forbs remained available to the mice. At the end of November, new grass shoots again were appearing.

Although it is not apparent from the figure, the inhibiting effect of the slugs seemed to be affecting females more severely than males. Among the two surviving founders, the male remained in reproductive condition throughout. The female, however, was inactive for the three months October through December. Also the females of litter 1 became inactive after the end of July while the males of this litter remained reproductively competent to the end of the experiment. Both sexes failed to mature in the other three litters. HOULIHAN (1963) also found that inadequate food supplies quickly reduced reproduction in females.

From early October through early December, a program of slug poisoning and manual removal of slugs was carried out. Slug poison was placed in containers so that voles did not have access to it. During this interval over 3.5 kg of slugs were removed from the enclosure (7081+individuals). This seemed to have little effect on slug numbers although the age structure was apparently reduced.

Finally, at the very end of November both dry and succulent food was supplied to the population. Although it seemed likely that as in experiment 2B, insufficient food was causing the stunting of growth and lack of reproduction, a test of this hypothesis was needed. The addition of food was followed by a week of freezing temperatures. In spite of this, all voles showed substantial weight gains after mid-December. The terminal autopsy in mid-January showed that four of five females had begun to cycle and all four males were also reproductively active. Thus, even after five months of stunting, recovery was relatively rapid.

As in experiment 2B, we see again that summer reproduction is possible, and that high slug density can terminate reproduction and growth even in a normally wet season. Of particular significance in this case is the rapid recovery of the voles when supplemental food was provided.

DISCUSSION

These experiments permit several tentative conclusions regarding the role of food and water in controlling the normal breeding season in the California vole. The termination of reproduction in early summer can, it is clear, be caused by insufficient food or water. The fact that in the field this occurs when the vegetation becomes dry, and over a very wide range of population densities further emphasizes the probable importance of these two factors. Lack of water seems likely to be more important than starvation in producing initial weight losses and heavy mortality. Furthermore, it seems plausible that the rate at which dehydrating conditions develop may critically influence the responses of the vole. Notice that in experiment 1A, severe weight losses due to dehydration were followed by complete recovery in five weeks. In 2A, on the other hand, dehydration was followed by eight months of stunted growth and reproduction. This difference seems most likely related to the relatively gradual period of drying in 1A as compared to the more abrupt dehydration of the vegetation in 2A (see Figs. 3 and 5). Another possibility is that the carrots provided as a source of water in 1A but not in 2A, contain some vitamin or hormone-like substance that is stimulating to the voles. The potential importance of such substances, such as found in newly sprouted vegetation, for reproduction in *M. montanus* has been shown by PINTER and NEGUS (1965). From extensive experience with laboratory colonies, I know that *M. californicus* reproduces well when fed on a diet of only dry food and carrots.

It is also of interest that the average size of eleven litters born in the summer and autumn period was only 3.7 (range 1-6). This is consistent with the annual cycle in litter sizes reported by HOFFMANN (1958) and LIDICKER (1973: Fig. 6), a recurring pattern which appears to be independent of population density or vole condition.

With the return of the wet season, conditions again become favorable for reproduction. However, the fact that pregnancies frequently occur promptly after heavy rainfalls (LIDICKER and ANDERSON, 1962) and may even precede the appearance of green vegetation (KREBS, 1966; BATZLI and PITELKA, 1971) suggest again that moisture may be a more important trigger than food supply. Whereas food conditions would not improve until at least five days after the first heavy rainfall of the autumn season, moisture conditions often are alleviated much sooner. Heavy dews begin to occur in September and then some light rainfall may precede the first soaking storm. PEARSON (1960) has shown that in the dry season the daily above-ground activity pattern is closely correlated with the availability of dew. Thus, if the voles are responding to an improved moisture situation, this could explain both the rapid response to the start of the rainy season, and the occasional pre-rainfall pregnancies. Of course, if the animals are also starving, they will not respond reproductively until green food is again available.

These experiments have also resulted in some improvement in our understanding of the mysterious and often prolonged delays in reproduction and growth that sometimes occur after the rainy season begins. In the field these delays have been observed to last up to three months (LIDICKER, 1973) and in these experiments eight months. It is now apparent that recovery from stunting due to inadequate food is relatively rapid, that is one month or less in these experiments (1B, 3). In contrast, stunting caused by dehydration produced delays of five weeks (1A) and eight months (2A). I suspect, therefore, that sub-optimal moisture conditions have more severe effects on the physiology of *M. californicus* than do sub-optimal food supplies. CHURCH (1966) has shown that this species of vole is only poorly adapted for arid conditions. It can slightly reduce urinary-fecal losses by increasing water turn-over time, but mainly it copes with arid conditions by reducing its body mass. Actual tissue dehydration is not tolerated. This means that once its fat reserves are gone, it begins to metabolize its body proteins while reducing its food intake. As much as fifty percent of body weight may be lost.

If, however, inadequate moisture is the primary cause of these growth and reproductive delays occurring under apparently good conditions, we might expect that they would occur in low density as well as high density populations. The evidence so far suggests that they characterize only populations which enter the dry season at high densities (LIDICKER, 1973). Perhaps there are small supplies of succulent foods that are available through the summer which are adequate for low densities, but completely insufficient for large numbers. HOULIHAN (1963) has observed a lack of reproduction and growth in an enclosed population for four months following a crash in numbers. These survivors exhibited a significant thyroid inhibition, and he suggests that prolonged metabolic disorder may follow any severely stressful period such as one producing a population crash.

An unexpected observation from these studies is that populations of the slug *Milax gagates* also respond to prolonged periods of green vegetation. In large numbers, they clearly were competing with *Microtus* for green forage, and were able to cause reductions in the vole populations even in the wet season (experiments 2 and 3). Their intrusion into these experiments provided examples, in addition to experiment 1B, of vole population response to inadequate food. It is conceivable that these slugs also may have affected the voles through toxic substances in their mucous secretions. When the slugs were abundant, these secretions were so ubiquitous that it must have been impossible for the voles to avoid contacting it on their food.

Finally, I would like to point out that the actual control of reproduction under natural conditions may be more complex than suggested by these experiments. They do not explain, for example, reduced litter sizes in the normally non-breeding season or the lowered rate of litter production seen through the summer and fall in experiment 2B. The nutritive value of carrots as compared to green vegetation, also needs to be investigated. Furthermore, in all these experiments, densities were high but fairly uniform, and dispersal was of course not possible. The natural regulation of numbers, moreover, involves mortality as well as natality rates, and in this species is suspected to involve at least six interacting factors, the quantity of food and water being only one of these (LIDICKER, 1973).

SUMMARY

The potential role of food and water in determining 1) the timing of the normal breeding season in the California vole, and 2) two frequently occurring exceptions to this normal pattern, are explored by using experimentally manipulated enclosed populations. Hypotheses derived from field observations were tested in the enclosed populations by the manipulation of green food, dry food, water, and vole density. The results of three experiments involving five populations are reported. In all populations densities were maintained at near-normal levels (475 to 1750 per ha).

In all three experiments, it was shown that breeding was possible in the summer if sufficient food and water were available, although perhaps with reduced litter sizes and rates of growth and reproductive maturation of young. In two cases, severe weight losses and high mortality were induced by insufficient water. When water was provided, survivors recovered weight and reproductive competency in between five weeks and eight months. In three populations, starvation induced weight losses and mortality. In these cases recovery of the voles took only one month or less. In two of these last, the inadequate food situation was produced during the normally wet season by outbreaks of a European slug.

It is concluded that available moisture is the most important factor in triggering both the end and beginning of the normal breeding season. Of course, inadequately fed mice do not breed at any season. Summer (dry season) breeding can occur when food and water conditions are adequate due to locally favorable conditions or very low population densities. Prolonged delays in growth and reproduction following the return of favorable conditions are most likely the consequence of chronic and severe water deprivation.

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California vole の繁殖時期の実験的解析

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ハタネズミの1種 California vole の繁殖時期の決定における食物や水の役割を調べるため，閉鎖個体群を用いた一連の実験を行なった。実験個体群の密度はいずれも正常に近いレベル（475～1750/ha）に維持された。食物と水が十分あれば，夏季（乾季）であっても繁殖が可能であることがすべての実験で示されたが，litter size や仔の発育速度は減少すると思われた。水が不足した個体群の場合には著しい体重減少と高い死亡率がもたらされ，水分補給を行なうと5週間から8カ月の間に生残者の体重および繁殖能力の回復がみられた。食物不足の場合にも体重減少と死亡は起こったが，この場合は補給後わずか1カ月以内で回復した。結論として正常繁殖期の終了および開始の引き金となる最も重要な要因は利用可能な水分量であるといえる。もちろん食物が不十分であればどの時期にも繁殖は不可能であるが，好適条件に戻った後の発育や繁殖の長期の遅延は慢性的かつきびしい水不足の後効果である可能性が高い。