ECOLOGY AND MANAGEMENT OF MORMON CRICKET, *Anabrus simplex* Haldeman

Final report to the National Park Service

submitted by

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April, 1987

INTRODUCTION

The Mormon cricket, Anabrus simplex Haldeman, is a flightless, shield-backed grasshopper which occurs primarily in the Great Plains and sagebrush-dominated regions of the United States and Canada. It is a gregarious insect and is probably best known for its huge migratory aggregations, or bands. These typically develop in permanent breeding areas in broken, mountain habitat and then spread, by walking, to surrounding areas, including agricultural lowlands and valleys (Wakeland and Shull 1936). Dating to the early encounter in 1848 between hordes of this insect and Mormon settlers in the Salt Lake Valley - from which the name "Mormon crickets" stems - sporadic outbreaks of crickets have caused severe damage to crops, especially wheat and alfalfa (Cowan 1929, Wakeland 1959, Evans 1985). Though crickets normally feed on a wide diversity of rangeland plants, crops are highly preferred (Swain 1944). Homesteaders were forced to abandon farming in northwest Colorado due to the yearly invasions of crickets during the 1920's. Damaging numbers of crickets persisted into the late thirties, with the peak of the epidemic occurring in 1938.

Damage by crickets to rangeland plants has been much more difficult to assess than crop damage (Swain 1940, 1944). While crickets do feed on range grasses, particularly the inflorescences, they clearly prefer broad-leaf, succulent species of lesser forage value when these are present (Cowan 1929, Swain 1944, Wakeland 1959). However, Wakeland (1959) and Wakeland and Shull (1936) claimed that the economic importance of Mormon crickets arose primarily from their destruction of range grasses and the subsequent impact on cattle grazing. While true for certain areas during the 1930's, the available evidence suggests that serious range damage occurred only during a relatively short time when drought and overgrazing were severe.

Despite a scarcity of quantitative studies, the reputed destruction of rangeland has lead to extensive control campaigns in the past, and is responsible for recent control efforts in northwestern Colorado and northeastern Utah, in the vicinity of Dinosaur National Monument, where crickets have again become abundant in the last 6 to 8 years. A great deal of controversy and confusion surrounds the suppression campaigns in these areas due to ranchers' fears of a new cricket plague, and opposition from conservation agencies involved in protection of local endangered species.

Because knowledge of Mormon cricket biology is so limited, a comprehensive review of ecology and economic impact is impossible. Most of the voluminous body of literature on Mormon crickets is old (pre-1960, reviewed by Wakeland (1959)) and is primarily concerned with describing the life cycle and control measures. However, recent studies have advanced our understanding of diet composition, mating behavior, sexual selection, and biological and chemical control. These areas, along with a historical synopsis of economic importance, are highlighted in the first part of this report. The second part addresses the results of our two-year investigation of control measures and vegetation consumption by Mormon crickets. The third section outlines management recommendations for the current Mormon cricket outbreak.

PART I. DISTRIBUTION, ECOLOGY, AND HISTORICAL IMPORTANCE

TAXONOMY AND DISTRIBUTION

Anabrus is one of 22 North American genera of shield-backed grasshoppers (Tettigoniidae: Decticinae). The name "Mormon cricket" applies to *Anabrus simplex* Haldeman, though it has also been used for congeners, due to their great similarity in appearance and biology (Wakeland 1959). Presently, 4 species of *Anabrus* are recognized: *simplex* Haldeman, *cerciata* Caudell, *longipes* Caudell, and *spokan* Rehn and Hebard (Caudell 1907, Gurney 1939, Rentz and Birchim 1968).

While all are potential pests, A. *simplex* is the most widespread, occurring throughout much of western North America, and also has caused the most damage. In addition to the area indicated in Fig. 1, specimens have been reported from Tennessee, though this record may be in error (Goodwin and Powders 1970). Mormon crickets commonly occur between 1300 m and

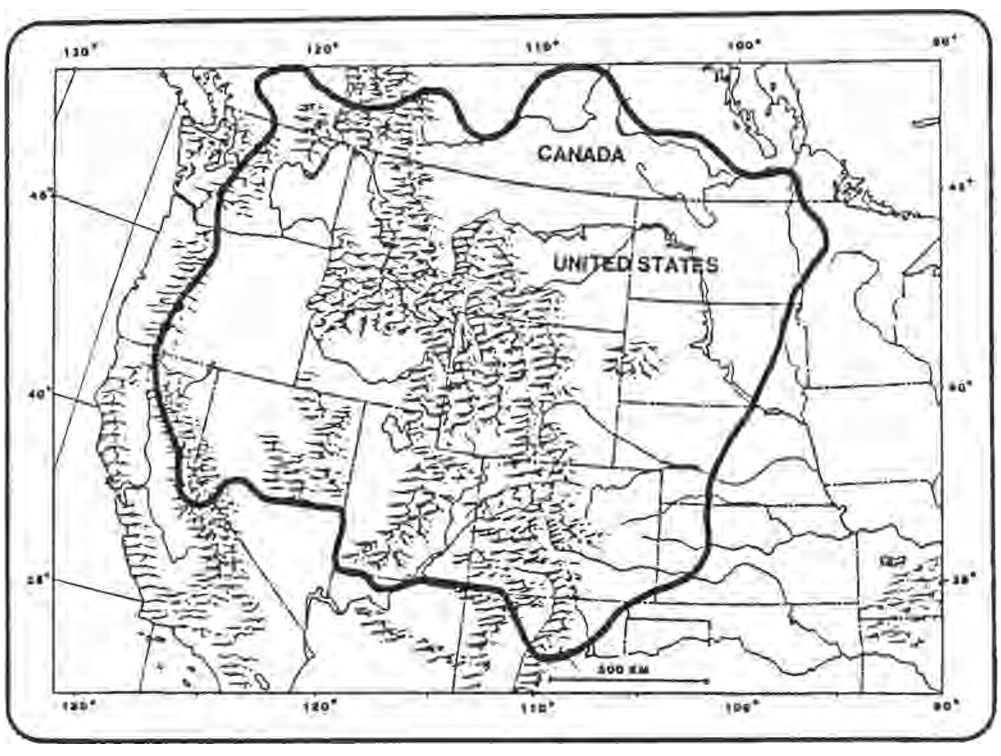


FIG. 1. Approximate geographic distribution (area enclosed by dark border) of the Mormon cricket, *Anabrus simplex* Haldeman; modified from Wakeland, 1959.

2400 m elevation (Caudell 1907, Schweis et al. 1939), but have been found as high as 4000 m in Colorado (Scudder 1898). Their habitat includes mixed, shortgrass, and sagebrush-dominated grasslands, and a variety of broadleaf and coniferous forests.

The other three species of <u>Anabrus</u> are confined to the northwestern United States. The related genus <u>Peranabrus</u> includes only P. <u>scabricollis</u> Thomas, the "coulee cricket", which occurs primarily in Washington (Caudell 1907). This species is extremely similar to A. <u>simplex</u> in appearance and habits, and has periodically achieved pest status (Snodgrass 1905, Melander and Yothers 1917).

BEHAVIOR AND ECOLOGY

Detailed descriptions of the life history of gregarious Mormon crickets are given by Gillette (1905), Corkins (1922, 1923), Criddle (1926), and Cowan (1929), so only major features will be included here. Aside from mating behavior, Mormon cricket biology has been studied only in high-density, gregarious populations. Given that mating in gregarious crickets is quite different than in solitary ones, other differences in life history traits may exist and warrant further investigation.

<u>Banding and migration</u>

Mormon crickets are univoltine, early-season insects, hatching in early spring (March to May, depending on elevation and weather) from eggs laid singly in the ground during the preceding summer. The nymphs develop through 7 stadia before the final molt to adults, with a total lifespan of about 100 days. In high-density populations, crickets display gregarious behavior throughout most of their lifetime. After the first 2 or 3 molts tney aggregate into dense migratory bands which may cover several square kilometers. During daylight hours, these large groups of insects walk in fixed directions, with individuals within the band pausing occasionally to feed (Cowan and Shipman 1943). Feeding and migrating behaviors are closely linked and generally occur under the same weather conditions: clear, sunny skies with air temperatures ranging from ca. 10° to 35°C and ground temperatures of 24° to 45°C (LaRivers 1941, 1944, Wakeland 1959). However, directional movement and feeding can occur under cloudy conditons if ambient temperature is within the specified range. At dusk, or in adverse weather (cold, rain, snow), the army-like migrations cease and crickets form dense clusters around rocks or on branches of sage and other shrubs. Under very hot conditions, crickets will climb into the plant canopy or up the culms of grasses to roost, apparently escaping high ground temperatures which often reach 50° C during the summer. A typical daily activity cycle includes morning and evening periods of movement and feeding, a mid-day period of inactive roosting, and cluster formation at night. The occurrence and timing of these events are variable and seem to be highly influenced by weather conditions. Further temporal partitioning of behavior is seen soon after the final molt to adults (end of May to mid-June) when crickets will engage in mating only during morning hours and oviposit mostly in the afternoon.

At any given moment, bands can be found criss-crossing an area in all compass directions. They may coalesce into larger units, but have also been observed maintaining their respective headings while "flowing" through each other at the intersection of their paths (Sorenson and Jeppson 1940, MacVean pers. obs.), suggesting band-specific orientation cues rather than generalized movement by an aggregation of insects. No research has been conducted to determine the causes or functions of migratory behavior, nor is the mechanism(s) which produces and maintains a band understood. Orientation to sun, wind, and conspecifics have been suggested (Cowan 1929, Swain 1944, Wakeland 1959), but none of these has been tested. The size and distribution of bands in a geographic area, as well as density within bands, are also problems which remain open for investigation. Bands of 2 to 16 km in length and 1 to 2 km in width have been reported and rates of travel of 1 to 2 km per day have been estimated.

It is not understood how or why a transition occurs from widely scattered, sedentary individuals to densely-aggregated, migratory bands of insects (Wakeland 1959, Cowan and Shipman 1943). The process bears a striking resemblance to phase transformations in the African plague locusts, *Schistocerca gregaria* (Forskal) and *Locusta migratoria migratorioides* (Reiche and Fairmaire). Historically, it accounts for the transition from an entirely benign state to outbreak and pest status. It has been noted that solitary individuals tend to be smaller and more lightly colored than their gregarious counterparts (Gwynne 1984, MacVean pers. obs.). The latter are usually black as adults, whereas solitary crickets vary from solid emerald green (except for white venter) to tan and light purple with white mottling on the abdomen.

Mating

One of the few aspects of cricket ecology which has been well studied using current ethological and evolutionary approaches is mating behavior. Gwynne (1981, 1984) has found an unusual role reversal between the sexes where, contrary to the pattern seen in most animals, males actively select among potential mates, rejecting the smaller females in the population. Females, in turn, compete among themselves for access to males. Accepted females are significantly heavier and possess a higher number of mature eggs than their rejected counterparts. Thus, it appears that males increase their fitness by mating preferentially with the more fecund females in the population (Gwynne 1981, 1984).

The evolution of this role reversal is apparently related to the unusually large investment that males make in each copulation in the form of a large spermatophore which they extrude and transfer to the female's genital opening. This large white "sac", often noted by early investigators and considered a rather awkward insemination device (Gillette 1904, Snodgrass 1905, Caudell 1908), represents up to 27% of the male's body weight, a substantial energy expenditure (Gwynne 1981, 1984). It is composed of 2 small sperm ampules and a much larger proteinaceous bulb. While the sperm are draining from the ampules into the female's spermathecae, she eats the proteinaceous mass. Subsequently, the nutrients are used in somatic tissues and for egg production. Gwynne (1984) found that the number of eggs produced is directly related to the number of spermatophores received in successive copulations. It is also possible that ovipositional stimulants, such as prostaglandins, are transferred with the spermatophore (Stanley-Samuelson et al. 1986). Female reproduction appears to be limited by access to spermatophore-bearing males, which results in female-female competition for this resource.

Role reversal is typial of high-density, gregarious, populations (5-10 adults/m or higher) but is not shown by crickets at low densities (less than 1/m9. Gwynne (1984) found that "solitary-phase" males, while producing large spermatophores, did not reject females and in fact competed for them; that is, they displayed the typical male role of most species. Also, a greater proportion of the males in a low-density population possessed well-developed spermatophores than in a high-density population. Gwynne (1984) suggested that high-density populations may be more food-limited and that the males with mature spermatophores are a limiting component of female fitness. In this scenario, sexual selection has favored large, aggressive females that compete successfully for the available males, which in turn select the larger females. Whether food is indeed limiting in high-density populations and not in the low-density ones, and how role reversal develops in the transition from solitary to gregarious states, are not known.

Food habits

Mormon crickets are omnivorous insects. Food items include plants, conspecifics, other insects, livestock manure, and carrion (Wakeland, 1959). Over 400 species of food plants were reported by Swain (1944), ranging from grasses and small forbs to the foliage of large shrubs and trees. Although practically every plant species in the crickets' habitat is fed upon at one time or another, definite preferences are discernible. In their native habitat, crickets prefer succulent, herbaceous species over grasses or woody plants. Most crops, especially wheat and alfalfa, are readily eaten in preference to range vegetation (Gillette 1905, Corkins 1922, 1923, Cowan 1929, Mills 1939, Ueckert and Hansen 1970). In the most comprehensive study of cricket feeding habits conducted to date, Swain (1944) assigned all known food plants to 3 categories, ranging from most to least preferred. Forbs such as wild onion, _Allium_ spp., arrowleaf balsamroot, _Balsamorhiza sagittata_ (Pursh) Nutt., crucifers, _Sisymbrium altissimum_ L. and _Brassica_ spp, and lupine, _Lupinus_ spp., were among the most highly utilized plants, while slender wheatgrass, _Agropyron pauciflorum_ (Schwein), cheatgrass, _Bromus tectorum_ L., and Sandberg bluegrass, Poa _secunda_ Presl., were preferred grasses. Other authors have reported similar preferences in Colorado (Corkins 1923), Montana (Cowan 1929), and Nevada (Schweis et al. 1939).

Crickets also exhibit marked preferences for flowers and seeds over vegetative tissue. In this regard, cricket injury to crops can often be distinguished from that of _Melanoplus_ grasshoppers (Acrididae). In areas where crickets and grasshoppers occurred together, Swain (1944), Wakeland (1959) and Cowan (1929) found that grasshopper damage to wheat resulted in plants denuded of leaves but with intact culms, while the opposite was true for damage due to crickes.

Ueckert and Hansen (1970) and Hansen and Ueckert (1970) examined the crop contents of Mormon crickets from a population near Red Feather Lakes, Colorado, and found that plants comprising large portions of the diet made up a small proportion of the total available herbage and were thus actively selected by crickets. Grasses, clubmoss, and grasslike plants made up only 8% of the diet. Forbs represented about 50% and fungi composed 16% of the diet. The authors did not determine whether fungus consumption was the incidental result of feeding on plants bearing fungal growth, but suggested that fungus-infected plants might be preferred due to higher carbohydrate and protein content. The remaining 21% of the diet was made up of arthropod parts, most of them apparently the remains of small insects and other Mormon crickets. Diet composition varied during the season, with arthropods increasing from 10 to 20% between July and September, and forbs decreasing from about 60 to 30% in the same period. This may reflect an increased protein requirement for mating and egg production.

These studies confirm the general observations of many authors, particularly the propensity for cannibalism among Mormon crickets. Injured, weakened individuals, or those rendered vulnerable while molting are common targets of cannibalistic attacks. The cricket literature abounds with descriptions of "road slicks" caused by successive automotive slaughters of crickets congregating in the roadway to feed on the previous rash of victims. (An especially vivid description for the curious reader is given by Snodgrass (1905)).

Crickets are also known to prey upon other insects. In the earliest account of predation, Thomas (1872) reported crickets feeding on cicadas roosting in shrubs. Ueckert and Hansen (1970) found remains of aphids, ants, and lepidopterans in the crops of Mormon crickets. However, aside from these reports, predatory behavior has received no formal attention. With respect to the pest status of Mormon crickets, their cannibalistic and predatory nature, as well as scavenging on feces or carrion, deserve further study, since these components of the diet may serve to offset damage to range vegetation.

The available evidence suggests that Mormon crickets are opportunistic feeders that consume succulent, high-protein tissues or animal products without any strict regard to the species involved. Food preference patterns are variable and dependent upon the taxonomic composition of the community in which crickets occur, as well as the phenological states of potential food items. However, because Mormon crickets prefer succulent, weedy species to range grasses, they are generally predisposed not to compete with livestock for forage.

POPULATION REGULATION

The factors controlling population fluctuations are poorly understood. Though numerous predators and a few parasites and pathogens are known to occur, their function as regulating agents is largely unknown.

Predators

Probably the best studied natural enemy is Palmodes laeviventris (Cresson) (Sphecidae), a solitary digger wasp. After stinging and paralyzing a cricket, the female wasp drags it into its burrow where it serves as a food item for a developing larva (LaRivers 1944, 1945). Gwynne and Dodson (1983) found that the size of crickets taken by P. laeviventris was positively correlated with the size of the wasps, and that the sex ratio among prey was female-biased. They suggested that females may be more vulnerable to predation because they are more active and conspicuous during the morning hours when they are responding to calling males and the wasps are foraging. The sphecid wasp, Tachysphex semirufus (Cresson), is also known to provision its nest with Mormon crickets (Kurczewski and Evans 1986).

Predation by vertebrates, especially birds, has long been considered an important mortality factor. A great deal of literature and folklore surrounds the plague of crickets that invaded the Mormon settlers' crops and was allegedly arrested by huge flocks of California gulls in 1848 (Bancroft 1889, McAtee 1926, Henderson 1931, Tanner 1940, Evans 1985). Since then, the list of species known to feed on crickets has grown considerably and includes about 50 species of birds, rodents, and reptiles (Kalmbach 1918, Cowan 1929, Knowlton 1937, 1941, 1943, 1948, Knowlton et al. 1946, Wakeland 1959). Most records of predation are of nymphs and adults, though excavation of cricket egg beds by rodents and birds, presumably to feed on the eggs, has also been noted. An interesting consequence of the banded nature of cricket populations is that birds such as kestrels hover over the band and "track" it as it migrates (Wakeland 1959). Recent aerial spraying against Mormon crickets in northwestern Colorado has stimulated new interest in avian predators because of potential indirect effects on the endangered Peregrine falcon. This species is the subject of an intense recovery program in Dinosaur National Monument (NPS 1983). Declines in populations of passerine prey species following aerial application of insecticides have been noted, probably as a result of emigration from the site (Moulding 1976). In addition, toxic effects could arise through consumption of insecticide-treated crickets.

Aside from their role as a food item for wild bird species, crickets have been utilized as food for domestic fowl. Homesteading farmers found that crickets trapped in ditches (built to keep the insects out of crop fields) made a very good diet for turkeys and chickens (Cowan 1929). More recently, the nutritional value of crickets as chicken food has been investigated and found to be high (DeFoliart et al. 1982). However, commercial harvesting of crickets on open rangeland has not yet attracted the attention of industrial feed companies.

Lastly, the role of Mormon crickets in human nutrition should be mentioned. American Indians were known to herd large numbers of crickets into corrals made of sagebrush and greasewood, or to catch them in baskets as they floated down rivers, then dry and grind them. A type of flour was made from the crushed cadavers, which yielded a pasty winter food (Bancroft 1889, LaRivers 1944, Wakeland 1959, Evans 1985).

Parasites

Mormon crickets are notably free of insect parasites. Although two hymenopteran species are known to attack the eggs, their impact on population dynamics appears to be small. _Sparaison pilosum_ Ashmead (Scelionidae) occurs throughout the cricket's range, but overall percent parasitism averaged less than 3% in a 1939 survey (Wakeland 1959). However, Cowan (1929) found that in western Montana parasitism was as high 50%, and was associated with an apparent reduction in hatch. Two additional parasites have been reported. Gahan (1942) described the wasp _Oencyrtus anabrivorus_ (Encyrtidae), reared from cricket eggs collected in the Big Horn Mountains of Wyoming. Mature larvae of the flesh fly _Sarcophaga harpax_ Pandelle (as S. _tuberosa_) (Sarcophagidae) were reported from adult Mormon crickets (LaRivers 1944, 1945). Nothing is known of the distribution or importance of these two species as regulating agents.

A horsehair worm, _Gordius robustus_ Leidy (Nematomorpha), is known to infect crickets and can be abundant in localized areas near standing water. However, its efficacy as a control agent is severely limited by the scarcity of water in much of the Mormon cricket's geographic range (Thorne 1940). A nematode parasite, _Agamospirura anabri_, was described by Christie (1929) from crickets collected in Montana, but its biology is unknown.

Pathogens

The role of diseases in natural cricket population cycles is virtually unknown. The few observations of disease-related mortality found in the literature are vague and contradictory. Riley (1894) mentioned that "crickets died off by millions from disease" in the vicinity of the Snake River in Idaho. However, Wakeland and Shull (1936) claimed that "no disease is known to occur" in Mormon crickets. Attempts made to introduce _Entomophaga grylli_ Fresenius, a fungus found in many orthopterans, for cricket control were unsuccessful (Doten 1904, Ball 1915).

More recent applied studies have focused on a group of pathogens which appears to hold some promise for cricket management: the microsporidians (Protozoa: Microsporida: Nosematidae). A number of authors have suggested that Nosema locustae Canning, the best-studied microsporidian from grasshoppers, holds great potential for long-term suppression of acridids (Henry and Oma 1974, 1981, Ewen and Mukerji 1980, Henry and Onsager 1982, Erlandson et al. 1985, 1986) and Mormon crickets (Henry and Onsager 1982). This pathogen is typically acquired through transovarial infections or by ingestion of spores. N. locustae attacks the fat body, neural, and pericardial tissues of grasshoppers, but it appears to be confined to gut tissue in Mormon crickets (Canning 1962a, b, Henry and Onsager 1982). N. locustae can be easily propagated in the laboratory and applied to bran bait, which can then be spread in the field to inoculate a wild population with high levels of spores. Infected insects become weakened, resulting in slower growth, less feeding, reduced fecundity, or death. Infected insects may also be more susceptible to cannibalism, which should serve as an excellent means of transmission (Henry and Oma 1981).

After initial isolation of N. locustae from adult Mormon crickets in 1974 (Henry and Oma 1981), susceptibility of third instars to infection via application of treated bran bait was confirmed in a large-scale field test in northwestern Colorado (Henry and Onsager 1982). However, due to movement of bands into and out of the treated area and the lack of good controls, it was impossible to discern the true impact of N. locustae on the cricket population. Additional research is needed to further evaluate the effects of N. locustae on Mormon cricket survival and reproduction, and its potential as a management tool (see results of our investigation in second part of this report).

A new species of microsporidian found in Mormon crickets in 1985 (tentatively Vairimorpha sp., Henry, pers. comm., 1986) appears to hold greater potential for cricket suppression. Unlike N. locustae, it builds up extremely high spore levels in many tissues, is common in the cricket population of northwestern Colorado, and is sometimes associated with sluggish behavior and high mortality (MacVean and Capinera, unpublished data). Thus, it may be more important as a natural regulator of cricket populations.

Weather

The role of weather in cricket population dynamics is a matter of conjecture. Circumstantial evidence suggests that cold, wet conditions can adversely affect survival. Despite the crickets' ability to withstand inclement weather by clustering in protected sites (Corkins 1923), reductions in numbers have been observed during the early nymphal period (instars 1 to 4) following prolonged periods (several weeks) of rain or snow and daily lows near freezing. Other mortality factors, such as predators and parasites, were not observed during these periods, leading to the conclusion that mortality was weather-induced (Schweis et al. 1939, Wakeland 1959). The later instars appear to be less susceptible to inclement weather. Severe winter conditions appeared to be of little consequence to egg viability, as indicated by consistently high populations (Wakeland and Shull 1936). However, little can be gleaned from the sketchy observations in the literature, and the role of weather remains unclear.

PEST STATUS

Since Mormon crickets first acquired pest status by damaging wheat fields in Utah in 1848, crop losses have been recorded throughout the range of the insect at one time or another up to about 1960. From this time to the beginning of the current outbreak (ca. 1980) crickets have occurred as relatively small, localized populations, causing little damage.

Crop acreages, dollar amounts lost to crickets, and the impact on local economies for the pre-1960 era are available in the literature (Corkins 1922, Cowan and Mc Campbell 1929, Cowan 1932, Wakeland et al. 1939, Swain 1944, Wakeland and Parker 1952, Wakeland 1959). Northwestern Colorado, an area with the most prolonged cricket infestation on record (1918-1938; Wakeland 1959) witnessed a reduction in the number of farms from 420 in 1920 to 258 in 1927, due to ravages by crickets (Cowan 1929, 1932). Significant crop losses have also been documented in Montana (Strand 1937, Mills 1939, Cowan and Shipman 1943, Morrill 1983) and Utah (Sorenson and Thornley 1938).

In contrast, forage loss on rangeland and the associated monetary costs are much more difficult to document. Only two studies exist in the literature which attempt to quantify range damage due to crickets. They suggest that while total consumption by crickets is potentially damaging, only a few relatively small areas have experienced serious losses. Since evidence of the Mormon cricket's damage potential in croplands is well documented, and because the current controversy over cricket control centers on damage to rangelands, the remainder of this discussion will focus on the latter problem.

Based on consumption studies with caged insects, Cowan and Shipman (1947) concluded that during a 4-month period (the approximate lifespan of a cricket) crickets at a constant density of 12/m' would consume 4.4 times the amount of forage taken by cattle under proper stocking rates, i.e., 4 head of cattle per 100 ha for 9 months (10 head of cattle/section for 9 months). Furthermore, they pointed out that the plant species most frequently consumed by crickets, *Bromus tectorum, Lupinus caudatus* Kellogg, Poa sp., and *Balsamorhiza sagittata*, were also the most important forage species in Nevada (although lupine is generally considered a poor forage plant). Thus, the likelihood for competition between crickets and livestock was high, and had in fact forced ranchers to move livestock out of infested areas.

However, Swain (1944) found that severe damage due to crickets was rare and localized. Using visual estimations of consumption (calibrated with hand balances) in replicated, 9.3-m^2 open plots in the areas of worst cricket infestations in Nevada and Idaho, total amounts of herbage removed by crickets were calculated. The relative losses of forage for livestock, based on "proper-use factors" and species composition, were also computed. Total dry weight removed by the end of the season ranged from 1 to 56% of the total current year's growth, and averaged 15% (averages of data given by Swain (1944)). Loss in forage available for livestock (i.e., the fraction of the total year's growth which can be removed without overgrazing) ranged from 1 to 100%, but averaged 35% for cows and horses, and 40% for sheep and goAts. In 7 of 36 transects (each transect consisting of ten 9.3-m^2 plots) relative losses approached 100%. Three of these transects were dominated by broadleaf trees which possess little forage value, but where even moderate feeding by crickets can remove 100% of the utilizable plant growth. Excluding these locations, only 4 of 36 study sites, or 11%, experienced loss of all the forage available for livestock.

Clearly, even the most severely damaged areas in Swain's study suffered much less damage than Cowan and Shipman's (1947) data would have predicted, i.e., removal of all utilizable plant growth in any heavily infested area. The discrepancy can probably be explained by two major factors: cricket density over time (cricket-days) and diet composition. Wht,le a few transect sites experienced cricket densities of 6-24/m^2 during the entire season, most areas were occupied and injured by crickets for only 3-4 successive days (Swain 1944). Cowan and Shipman (1947) claimed that bands of crickets covering a given area at a density of 12/m^2 for an entire season (required for their damage projections) were not uncommon, but gave no supporting data. More likely, as suggested by Swain's study (1944), such infestations are rare. Secondly, Cowan and Shipman (1947) estimated forage loss by extrapolating consumption of lettuce or alfalfa leaves by caged crickets. As pointed out earlier, the predatory, cannibalistic', and scavenging components of cricket feeding behavior may well reduce forage consumption, and are probably reflected in the lower consumption values found by Swain (1944).

Swain (1944) also discussed cricket injury to range plants with respect to major vegetation types. The transect studies were conducted in "northern desert shrub" areas (Oregon, Nevada, Idaho, Utah), where the worst cricket outbreaks were occurring in 1938-39 and where estimates of total available plant biomass per unit area were much lower than in the "mixed prairie grassland" in the eastern portion of the crickets' range (portions of South Dakota, Nebraska, Montana, Wyoming). In the latter areas, Swain (1944) estimated green clipped weight at ca. 400 g/m^2, compared to 55 g/m^2 in typical sagebrush vegetation of Nevada. Based on transect data, losses in the mixed prairie areas were barely detectable (less than 5% of total biomass) with weedy species suffering most of the damage (*Taraxacum, Tragopogon, Penstemon*). These plants made up a small proportion of the total vegetation, but were preferred over grasses such as *Stipa comata* Trin. and Rupr., *Festuca* spp. and *Agropyron* spp. Swain (1944) thus pointed out the importance of total biomass availability and species composition in determining the pest status of Mormon crickets. When succulent forbs are available, most feeding will be confined to them, and to a lesser extent, the inflorescences of grasses. However, in areas of high shrub density, crickets will utilize grass foliage and inflorescences more heavily.

Cricket densities have generally remained lowest in the eastern part of the species' range. While economic damage has occurred in eastern Colorado, the Dakotas, Nebraska and Montana, (Cowan and McCampbell 1929, Swain 1944, Wakeland 1959, Morrill 1983), the major outbreaks have always been reported west of the shortgrass and mixedgrass regions.

While quantitative assessments of cricket damage to rangeland were scarce, control campaigns were widespread throughout the infested area for many years (Fig. 9.1). Wakeland (1951, 1959) provides an excellent review of the evolution of control measures, from mechanical barriers such as trenches, sheet metal fences, or oil-on-water traps designed to divert or capture migrating bands of crickets, to arsenite dusts, baits, and finally to aerial sprays. In part, control measures were conducted in the immediate vicinity of crop lands, but most of the effort was directed at cricket control on open rangeland, where infested acreages were much greater (Wakeland and Parker 1952). In 1939, almost 19 million acres were estimated to be infested (Wakeland 1951).

The claim was often made that cricket injury to rangeland and loss of stock carrying capacity was significant and warranted control (Schweis et al. 1939, Cowan and Shipman 1943, Wakeland 1959, Cowan and Wakeland 1962). While undoubtedly true for certain areas, it seems likely that damage was overestimated in many instances. Evidence for this view is seen in the limited amounts of damage in many of Swain's (1944) study sites, despite their location in areas of worst cricket infestations. Even in agricultural areas with higher monetary value than open rangeland, control campaigns were sometimes conducted at an expense greater than the value of the crop (Wakeland and Shull 1936, Wakeland 1959). However, the psychological impact of huge hordes of large, black crickets traversing not only the range but also invading houses and barns (Johnson 1905, Corkins 1922), destroying vegetable gardens and contaminating well water with thousands of dead bodies (Wakeland 1959) cannot be underestimated.

Drought conditions during the 1930's and overgrazing on most western rangelands (Wakeland and Shull 1936, Voigt 1976) certainly worsened the impact of cricket herbivory, making control measures necessary where they might not have been required due to crickets alone. The worst cricket outbreak peaked in 1938-39, soon after the Dust Bowl drought years (LaRivers 1944, Wakeland 1951, Navarra 1979). It also coincided with a time when overgrazing by sheep and cattle was at its height and just beginning to draw attention by land management agencies (Wakeland and Shull 1936, Foss 1960, Voigt 1976). Prior to the Dust Bowl era, it appears that Mormon crickets had no significant detrimental effects on rangeland, even during outbreak years. Doten (1904) could find no trace of feeding damage despite the fact that "crickets fairly covered the higher mountain slopes" in Nevada. Corkins (1922, 1923), working in Colorado, reported that "so long as this insect confines itself to its native habitat, the sagebrush covered hills, little harm results." In the early thirties Cowan (1932) also found that "crickets do not make very appreciable inroads on range grass" in northwestern Colorado. Thus, it appears that during the outbreak of the late thirties, drought and overgrazing aggravated an otherwise tolerable, perhaps inconsequential, level of herbivory by crickets with respect to livestock carrying capacities.

The current outbreak in northwestern Colorado and northeastern Utah has again triggered strong action by ranchers and government to control crickets. In 1985, the Animal and Plant Health Inspection Service (APHIS) conducted aerial ULV applications of Sevin-4-Oil (carbaryl) on 23,700 ha of rangeland. The campaign immediately came under legal scrutiny for potential damage to endangered species, primarily the American peregrine falcon, and no spraying was conducted in 1986. Control efforts in 1985 were partly in response to claims that range damage was occurring, partly for prevention of crop damage by bands of crickets migrating from nearby uplands, and perhaps most significantly from apprehension that an uncontrolled population would reach epidemic proportions, as in the 1930's.

PART II. RESULTS OF 2-YEAR STUDY IN DINOSAUR NATIONAL MONUMENT

In 1984, we began a 2-year study to evaluate several approaches to Mormon cricket control, particularly the use of pathogens in bait formulations, and to obtain information on damage to rangeland plants caused by Mormon crickets. The results of this study are presented in the following section.

The control agents tested were a) a parasitic nematode, *Steinernema feltiae* Filipjvev (= *Neoaplectana carpocapsae* Weiser), which has been shown to be infective to a wide range of insects; b) carbaryl insecticide (Sevin); and c) *Nosema locustae* Canning, a protozoan parasite known to occur naturally in Mormon crickets and other grasshoppers (discussed in the pathogen section above). S. *feltiae* and carbaryl are both known to produce very rapid mortality (within 48-72 hrs), while N. *locustae* requires a period of several weeks to exert pathogenic effects.

All three control agents were tested in bait formulations. Both the nematodes and spores of *Nosema* commonly infect the host via ingestion, and thus require bait formulations, and carbaryl is more efficiently delivered in a bait than in an aerial ULV application. *Steinernema* and *Nosema* were evaluated in both laboratory and field experiments, while carbaryl was tested only in the field. Each test conducted with these three control agents is discussed below.

Preparation of field site

Since crickets move large distances during the course of even a few days, we found it necessary to enclose test populations of crickets within outdoor "arenas" in order to monitor the insects' survival and development following treatment with the control agents. In 1985, 16 large experimental enclosures (10 x 10 m, made of 14-inch high galvanized tin) were constructed near Echo

FIGURE 2.

SURVIVAL IN FIELD PENS
INOCULATION OF INSTARS 6-7

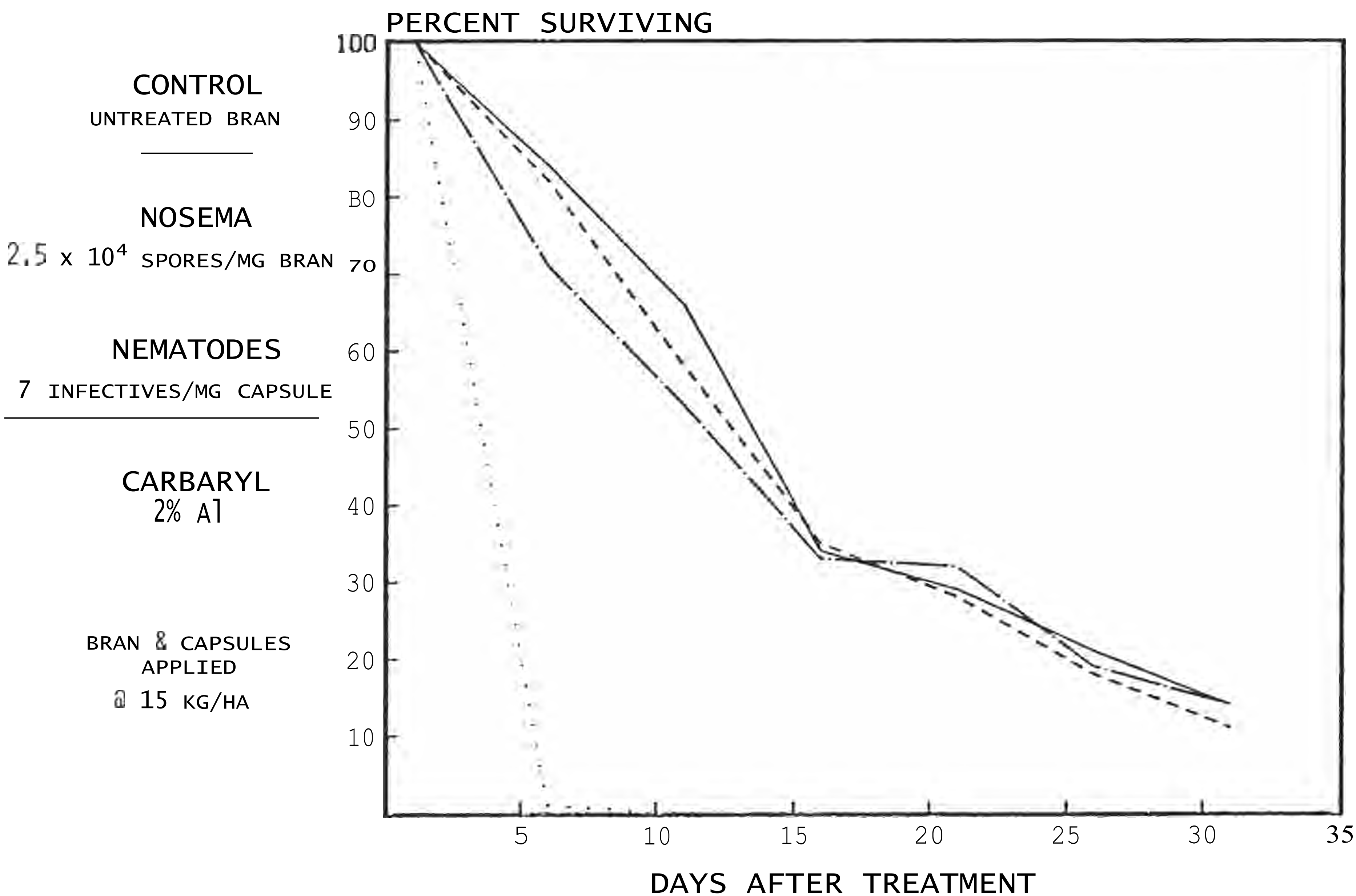


FIGURE 3.

SURVIVAL IN LAB NEMATODE TRIAL

INOCULATION OF ADULT CRICKETS

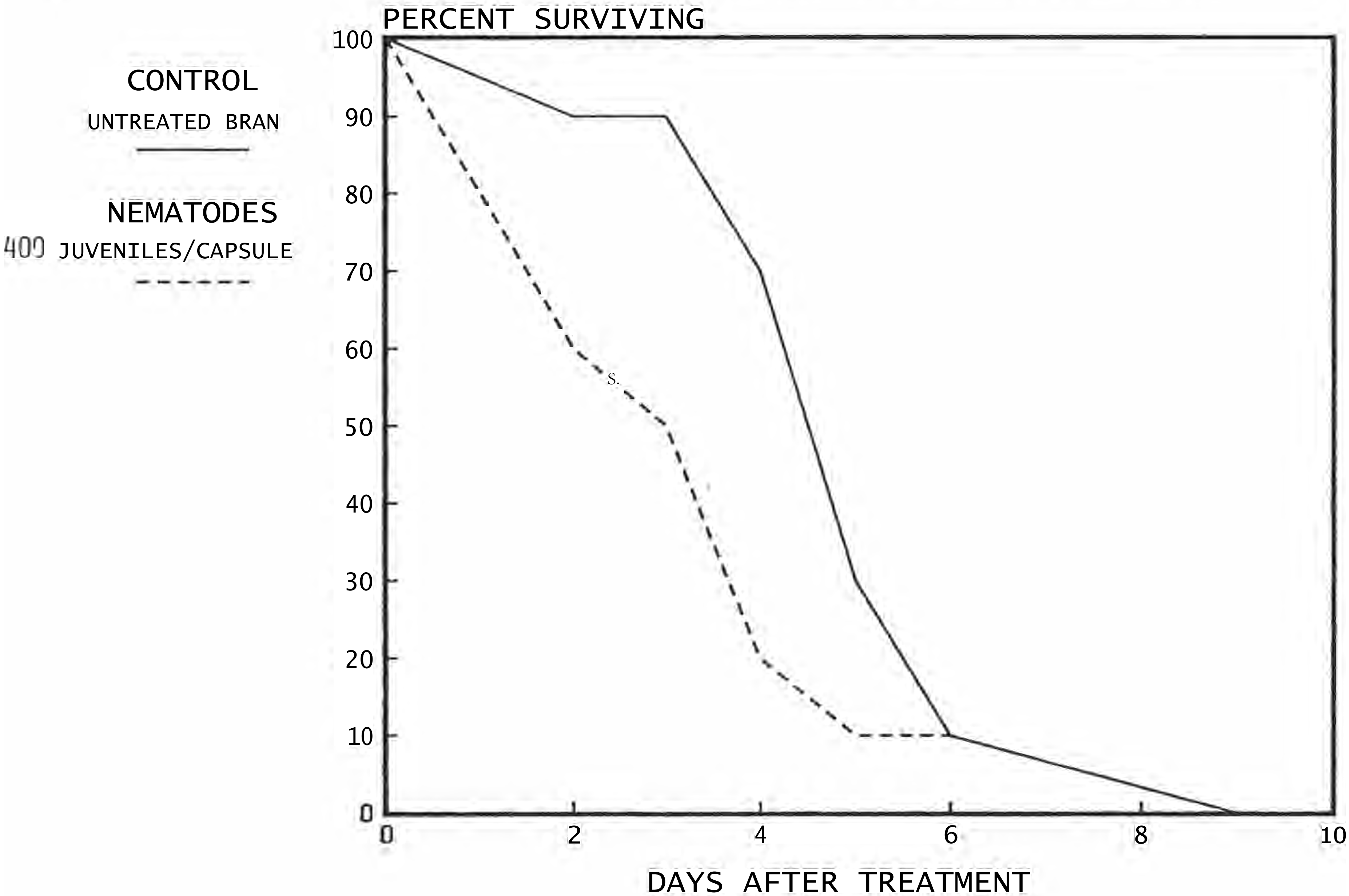
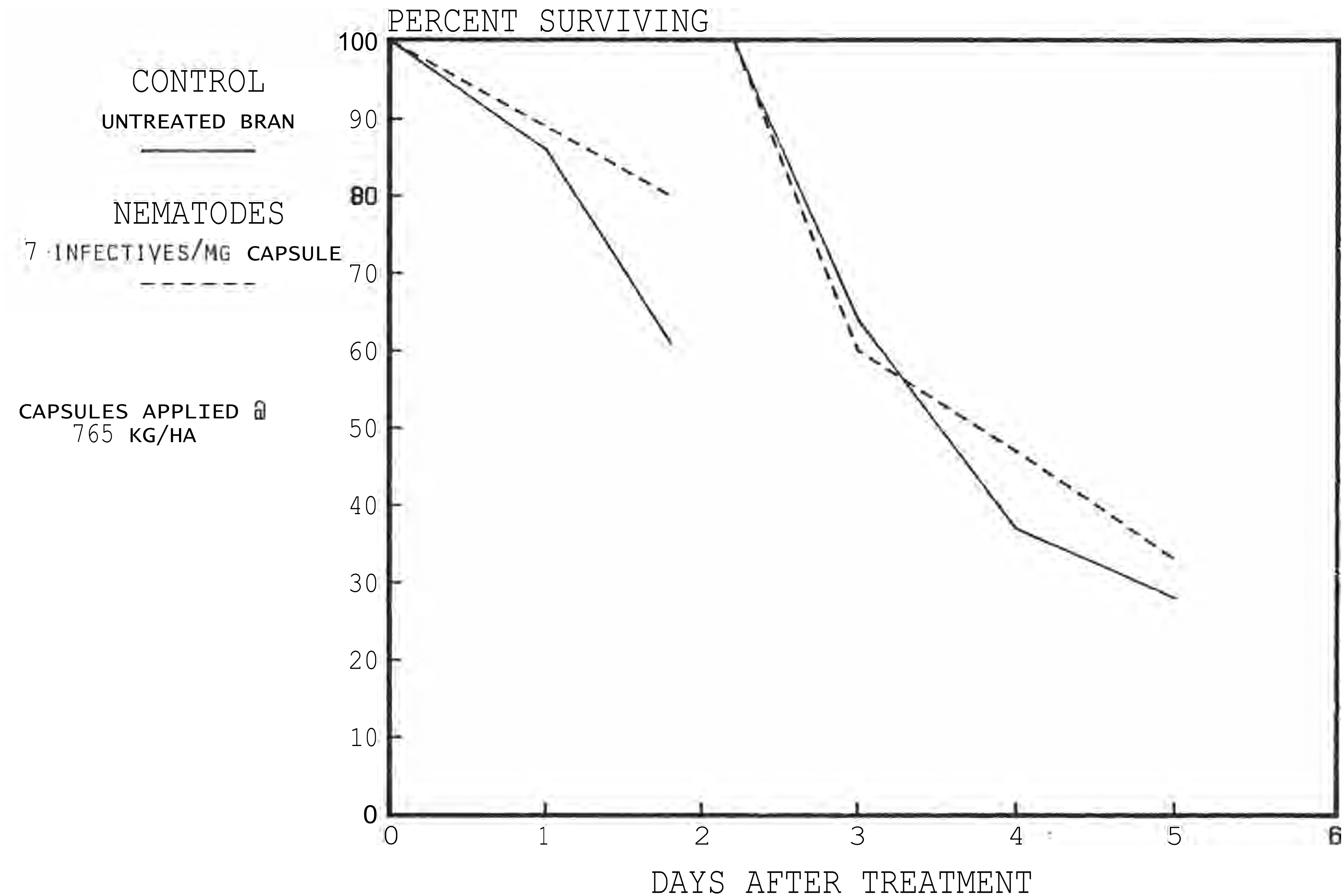


FIGURE 4.

SURVIVAL IN SMALL FIELD PENS

INOCULATION OF ADULT CRICKETS



Park Overlook, in Dinosaur National Monument. Known numbers of crickets were introduced into each enclosure to serve as experimental populations. Each control agent was applied with 4 replications (4 enclosures).

In addition to the large "pens" described above, 21 small enclosures (2 m^2 area) were also constructed at the same site in 1985 and were used for further tests with nematodes and carbaryl, with 7 replications of each, as will be discussed below.

Nematodes

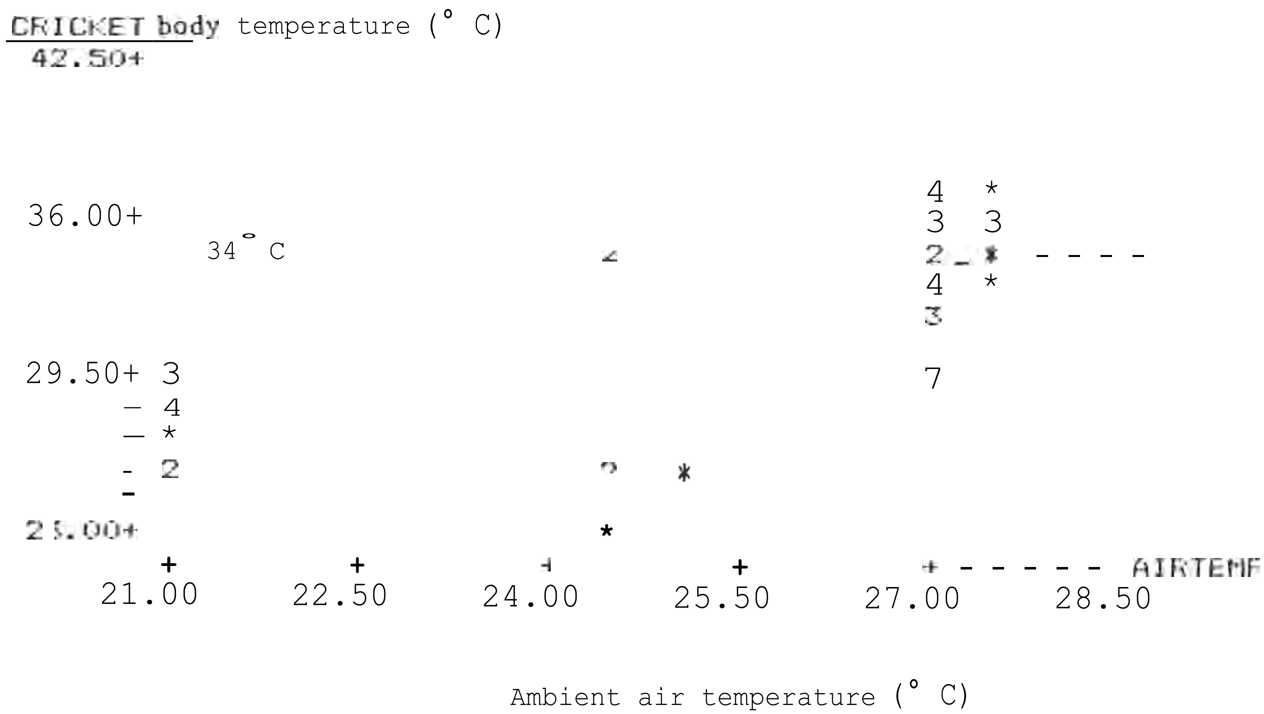
Parasitic nematodes were applied in soft, moisture-retaining capsules to the test populations of crickets. The infective stages of Steinernema are extremely sensitive to desiccation and require some free water for successful infection of the host. A calcium alginate capsule formulation with a high water content, containing wheat bran as a bait, was provided by Plant Genetics, of Davis, California. In the first test of nematodes, the capsules (containing 7 nematodes/mg) were applied at the rate of 15 kg/ha to field populations of 800 6th and 7th-instar crickets in the large pens. The application was made at mid-morning during the crickets' peak feeding period.

As shown in Fig. 2, no statistically significant reductions in survival resulted from the nematode application relative to controls (untreated crickets). Survival was determined by direct counts of the crickets in the pens and analyzed by calculating the area under the curve for each replicate followed by analysis of variance on these data. Crickets were collected from the pens and brought to the laboratory to determine infection rates. No infection was found (n = 195). At least 2 factors were responsible for the lack of infection. First, high ground temperatures (40-50° C) caused desiccation of the capsules and death of the infective nematodes within about 1 hour of application. Secondly, the capsules were unpalatable to crickets and very few insects fed on them, despite the bran bait which alone is highly palatable.

A second set of nematode tests was conducted in the small field pens, as well as in a laboratory experiment. Each field pen was stocked with 50 adult crickets and nematodes were again applied in calcium alginate capsules, but at a much higher rate of 765 kg/ha. Application of capsules was done in late evening (7 pm) and early the next morning (7 am) (2-part application) to avoid the high daytime temperatures. Viability of the nematodes was greatly increased relative to the first trial; live nematodes were recovered from capsules examined 3 hours following the 7 am application. In the laboratory test, crickets were held in groups of 10 (3 replicates) and provided with an unrestricted supply of fresh capsules (more than could be consumed) for a period of 48 hours.

The results of these tests are shown in Figures 3 and 4. Although no infection was found in the lab trial (n = 50), there was a significant reduction in survival associated with the nematode treatments ($t = 5.0$, $P < .01$). Steinernema sometimes can invade and kill its host without reproducing (the usual

FIGURE 5. Cricket internal body temperature as a function of ambient air temperature. Dashed line (34 C) indicates lethal limit of *Steinernema* nematodes.



criterion for infection), which is apparently the case here. However, the field trial showed no significant reductions in survival, and only 4% infection (n = 138). As in the first field trial, little feeding was observed on the nematode capsules.

Survival curves in the field test are shown separately for days 1-2 and days 2-5. At day 2, a sample of 15 crickets was removed from each of the nematode-treated plots for determination of infection rates. This removal would ordinarily cause the survival curves for the nematode plots to automatically (and artificially) drop about 45% lower than the controls, from which crickets were not removed. Thus, survival among the crickets remaining in each pen after removals was analyzed with separate curves. There were no significant differences in survival between nematode-treated crickets and controls in either time period.

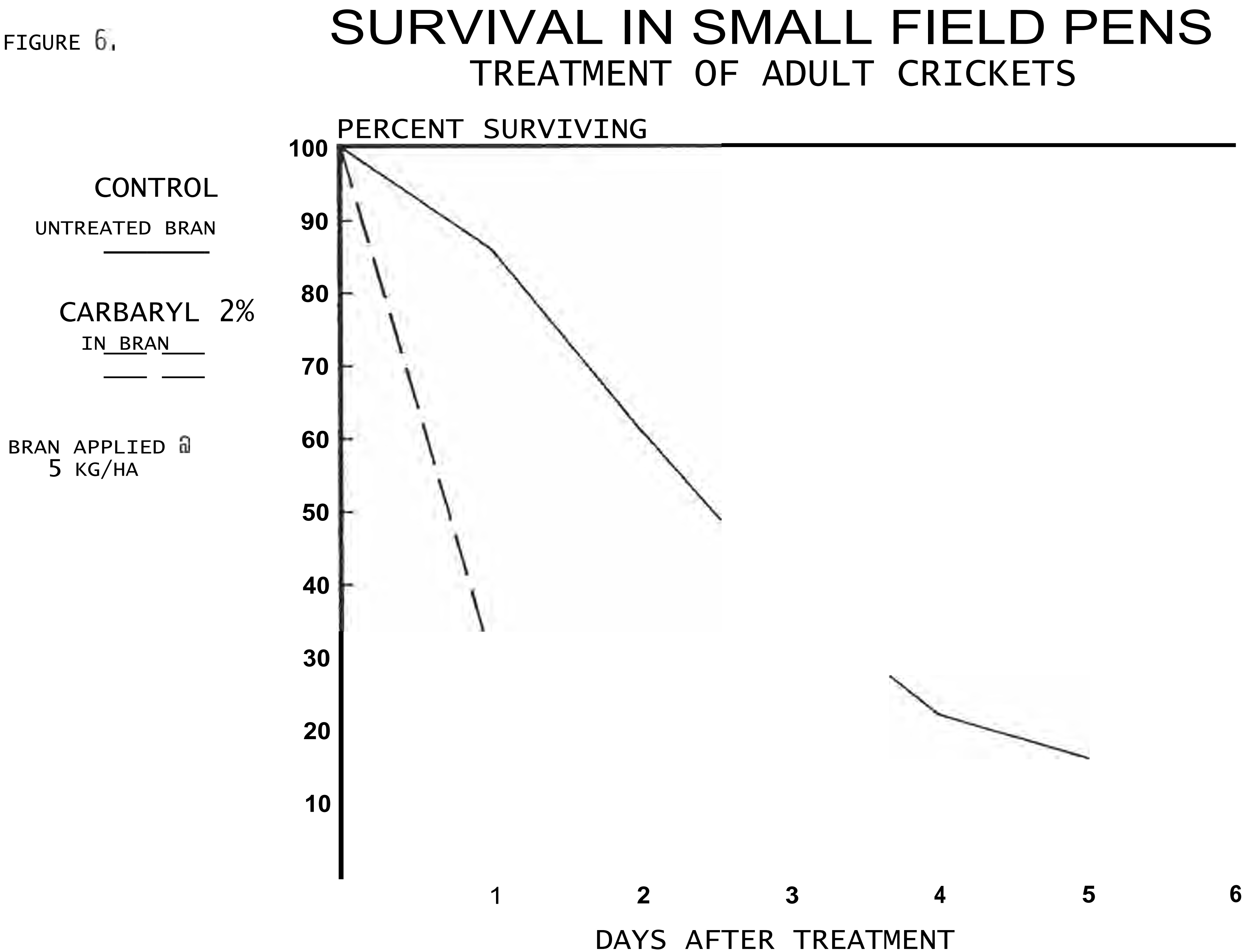
In addition to the problems of unpalatability of capsules and desiccation due to high ground temperatures, the internal body temperature of crickets may also pose a barrier to successful infection by Steinernema nematodes. Heat death of infective stages begins at 34^{o} C, and body temperatures of adult Mormon crickets often surpass this limit, as shown in Fig. 5, which plots body temperature in relation to ambient air temperature (body temperature was determined by inserting a hypodermic thermocouple probe into the abdomen, immediately behind the metathoracic leg). Since nematodes must invade the body cavity in order to infect the host insect, high temperatures are a potential barrier.

A further drawback to the use of Steinernema in dry environments was presented by Kaya and Nelsen (1985). They showed that nematodes in capsules were only able to infect insects (armyworms) feeding in a moist environment. The study suggested that nematodes must first be released from the capsules into a moist environment before they can successfully attack the host insect.

All of these difficulties suggest that Steinernema feltiae is not well suited for biological control of Mormon crickets, at least not in the current capsule formulation. While the capsules represent the best available protection against desiccation, they are not very palatable to crickets and are thus ineffective as a bait formulation. Significant mortality due to nematodes occurred in the laboratory, which demonstrates inherent pathogenicity, but this was not expressed in a field environment. Nematodes might prove to be an effective control agent early in the summer season when ground temperatures and cricket body temperatures are less likely to exceed the lethal limit of the nematodes. Further research is required to develop a highly palatable formulation of nematodes which could be tested under these conditions.

Nevertheless, it is clear that the open rangelands in which crickets occur constitute a harsh environment for a delicate parasite like Steinernema. Efforts should be more profitably committed toward further research on parasites which are better adapted to this environment, such as microsporidan pathogens (i.e., Nosema, Vairimorpha).

FIGURE 6.


SURVIVAL IN SMALL FIELD PENS
TREATMENT OF ADULT CRICKETS
PERCENT SURVIVING
CONTROL
UNTREATED BRAN
CARBARYL 2%
IN BRAN
BRAN APPLIED @
5 KG/HA
100
90
80
70
60
50
40
30
20
10
1
2
3
4
5
6
DAYS AFTER TREATMENT

Carbaryl

A bran bait containing 2% AI carbaryl by weight (Sevin-4-Oil, applied undiluted to bran) was very effective in reducing cricket survival, whether applied at 15 kg/ha (Fig. 2, $F = 27.82$, $P < .01$) or 5 kg/ha (Fig. 6, $t = 12.32$, $P < .01$). These results indicate that wheat bran is an effective bait material and confirm the findings of Foster et al. (1979), who showed that an application of 2% carbaryl bait at 5.6 kg/ha was sufficient for control of adult crickets at densities between 12 and $24/m^2$. Our tests with an application rate of 5 kg/ha were conducted with adult cricket densities of 20/m and yielded ca. 90% control after 48 hours (adjusted for control mortality). Crickets feed readily on bran flakes, and there is little doubt that a carbaryl bran bait is an effective control agent. It provides rapid reductions of either nymphal or adult Mormon crickets.

Nosema locustae

The first test of N. locustae was conducted in 1985 using 6th-7th instar crickets in the large field enclosures (simultaneous with pematode and carbaryl treatments). Bran bait containing 2.5 x 10 spores/mg (2.5 x 10 /kg) was applied at 15 kg/ha. This application rate was calculated to provide an amount of bait in excess of the maximum consumption by 6th-7th instars over a period of 2 days. As with nematode and carbaryl treatments, survival following treatment was determined via direct counts of crickets within the experimental enclosures.

Fig. 2 shows that the Nosema application caused no significant differences in survival relative to controls. Neither was there a significant difference in the number of eggs produced by control vs. Nosema-treated females brought into the lab and held individually after mating (26 vs. 31, respectively, $t = -.87$, $P = .39$). Lastly, we have been unable to detect spores of N. locustae in the midgut tissues or in fecal pellets from treated insects (as discussed above in the section on pathogens, N. locustae infections in Mormon crickets are limited to midgut tissues). It appears that this parasite undergoes very little reproduction in Mormon crickets, thus leading to very low (undetectable in our studies) numbers of new spores being produced. As will be shown below, this does not preclude short-term pathogenic effects, but does raise the question of transmission potential to other crickets, either horizontally (to other members of the population during the current season) or vertically (to members of the following year's generation).

Data from this first trial showed that treatment of 6th-7th instars with N. locustae is ineffective in reducing survival or fecundity. Most grasshoppers (Acrididae) are not highly susceptible to infection by this parasite in the late instars, and this is true of Mormon crickets as well.

FIGURE 7

SURVIVAL IN LABORATORY

INOCULATION OF INSTARS 4-5

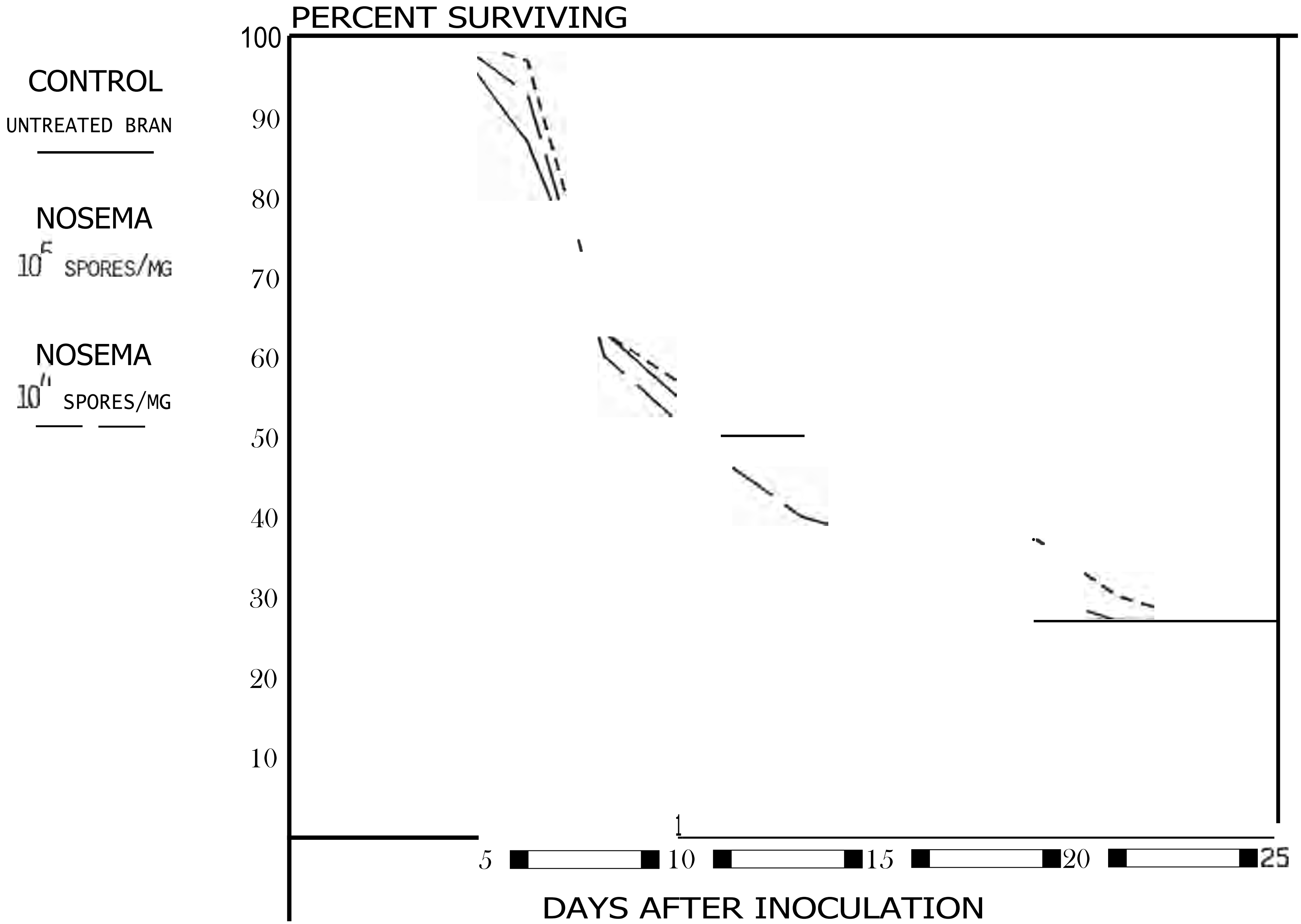


FIGURE 8.

INSTAR DISTRIBUTION

LAB INOCULATION OF INSTARS 4-5

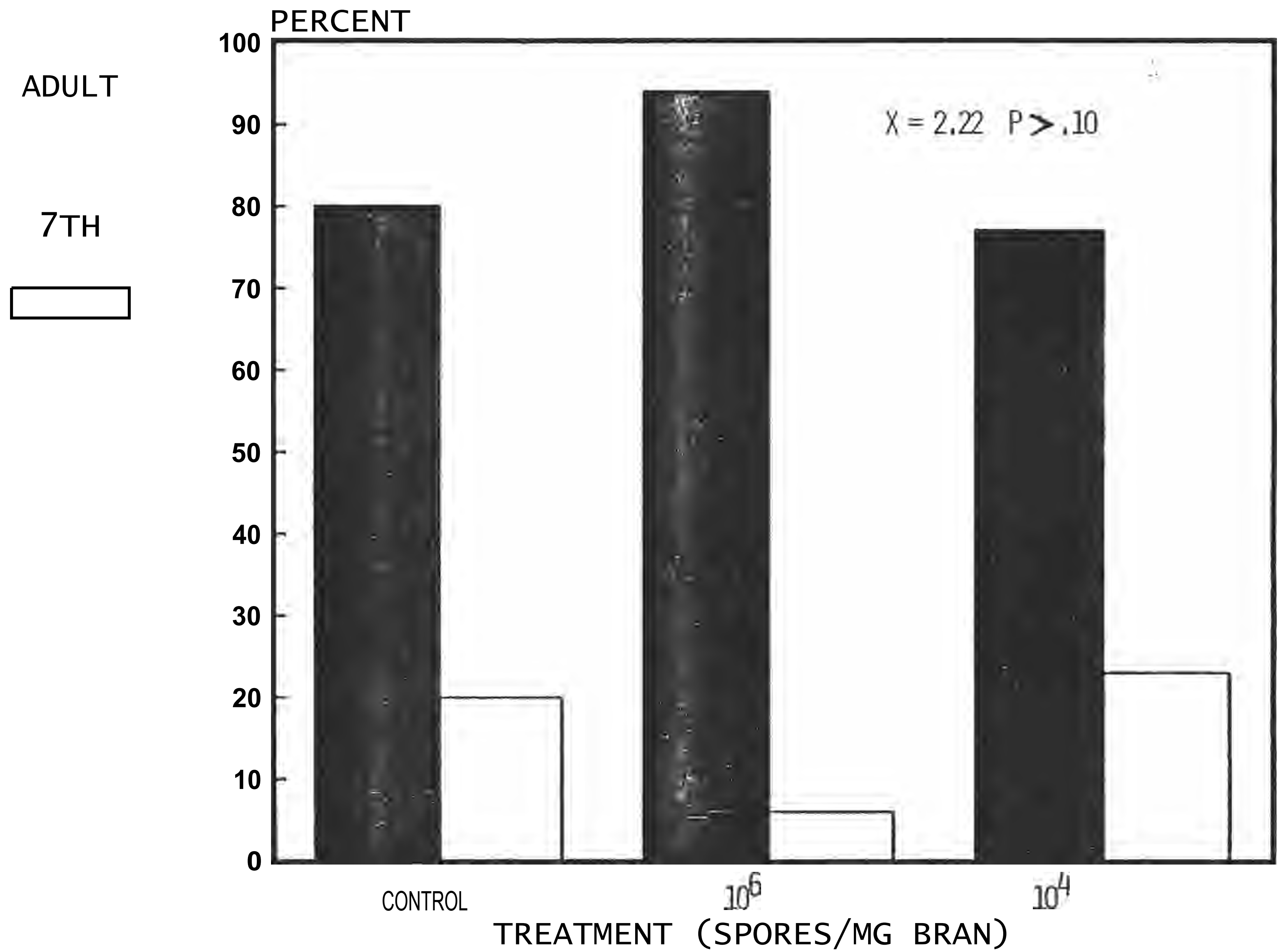


FIGURE 9.

SURVIVAL IN FIELD PENS

INOCULATION OF INSTARS 4-5

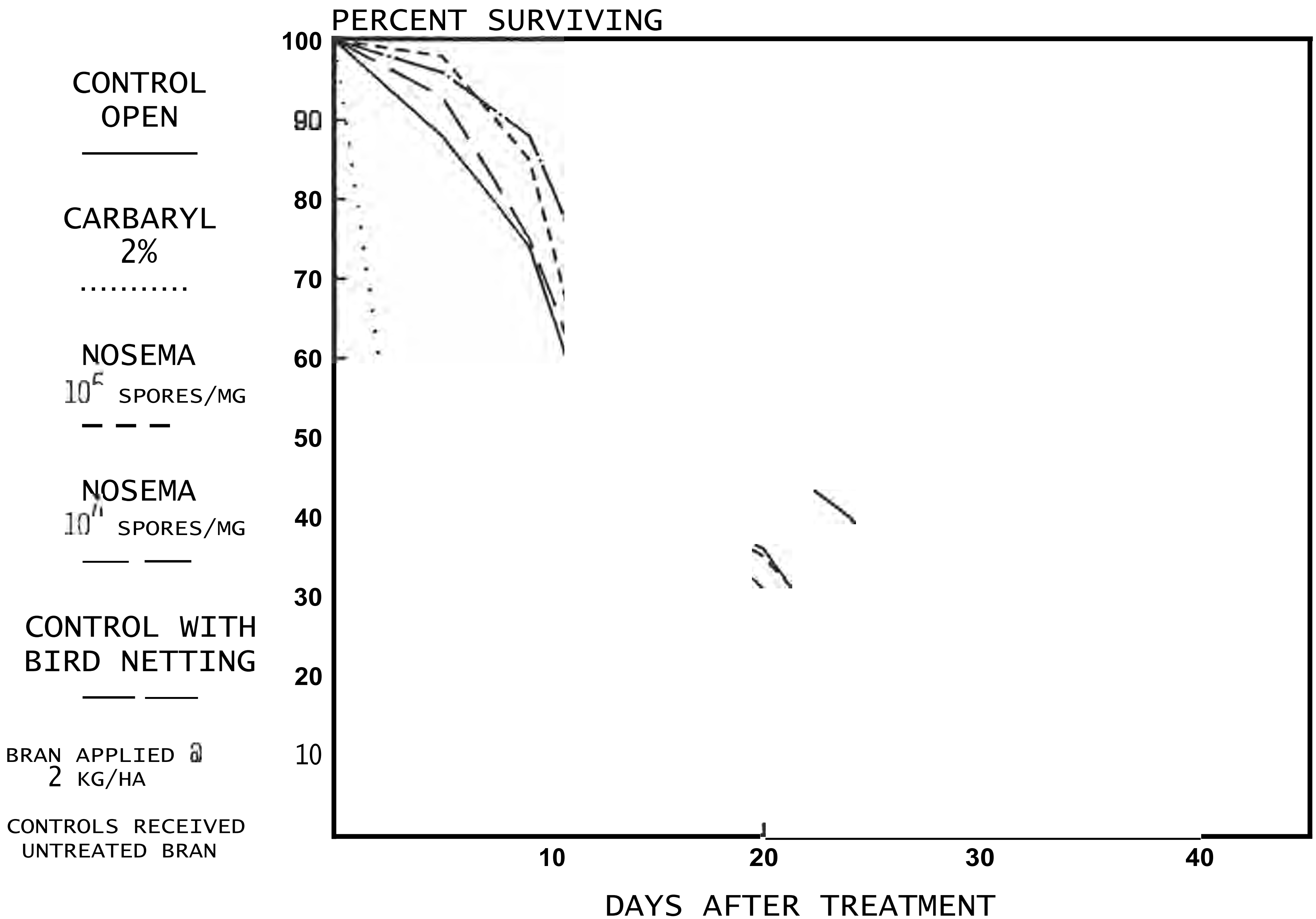


FIGURE 10.

INSTAR DISTRIBUTION

FIELD INOCULATION OF INSTARS 4-5

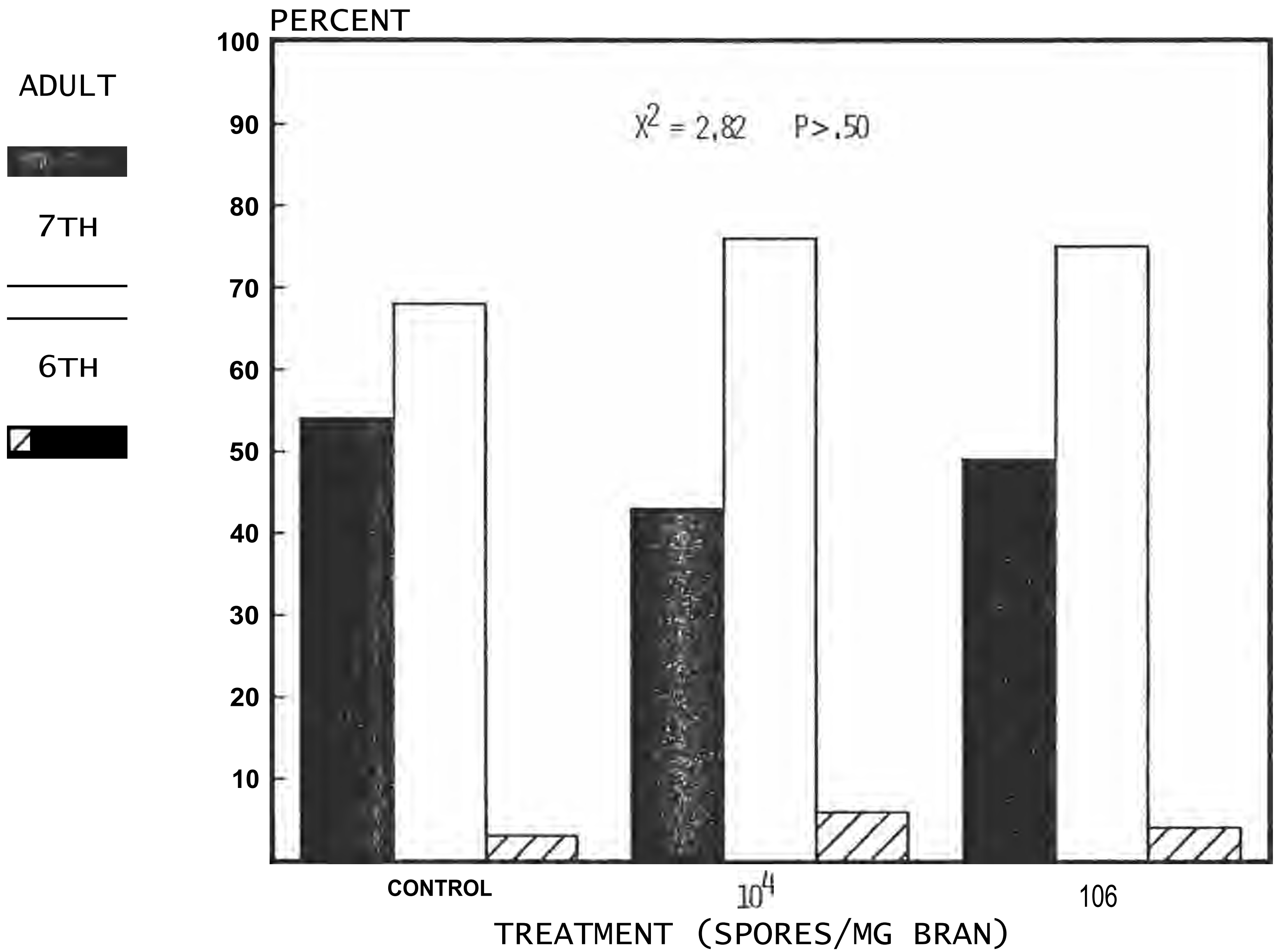


FIGURE 11.

SURVIVAL IN LABORATORY

INOCULATION OF INSTARS 1-3

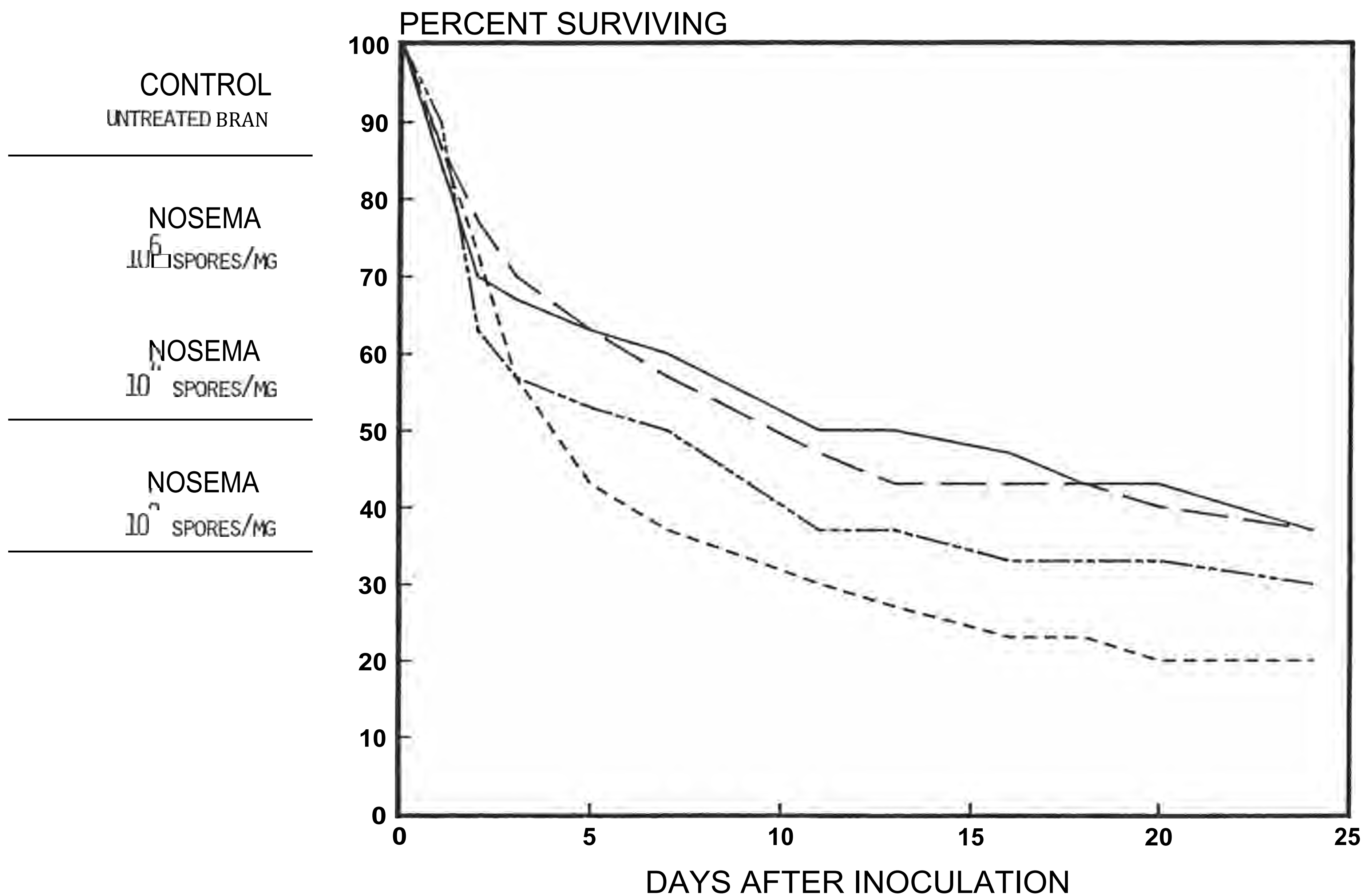
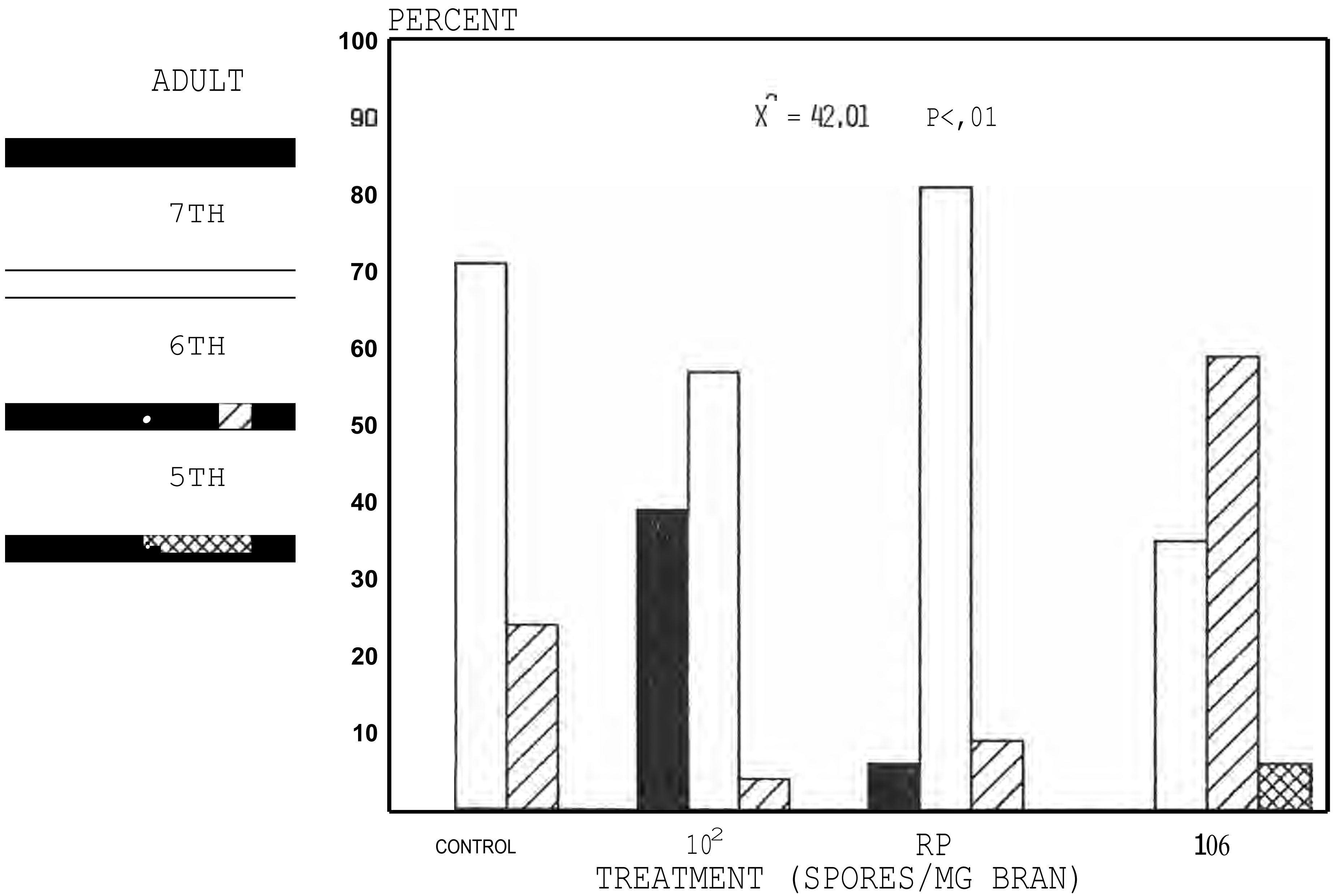


FIGURE 12.

INSTAR DISTRIBUTION
LAB INOCULATION OF INSTARS 1-3



Studies continued in 1986 with a younger age group, instars 4-5, which were tested in both lab and field experiments. Lab studies were conducted with field-collected crickets held in grpups of 30/cage, inoculated at two levels of spores, 10^4 and 10^6/mg bran. Each group (3 replicates per treatment level and controls) was given the amount of bran that could be consumed in a 48-hour period, followed by measurements of survival and development. Since Nosema is known to retard growth, we assessed the number of insects developing to each instar in treated vs. control groups ca. 4 weeks after inoculation. These age distributions were examined using contingency table chi-square statistics.

Unfortunately, as indicated in Figs. 7 and 8, no significant differences were caused by Nosema treatment in either survival or development. Similar proportions of the insects in each treatment group reached the adult stage by the end of the experiment. These data suggest that instars 4-5, like instars 6-7, are not detectably susceptible to pathogenic effects by N. locustae.

A field test with instar 4-5 was conducted simultaneous with the lab trial. Experimental populations of 1600 crickets were introduced into each 10 x 10 m pen and the same spore concentrations were applied as in the lab trial at 2 kg bran/ha (4 replications per treatment level). In order to assess the role of bird predation in the rapid decline in penned-cricket numbers, a set of 4 control pens was covered with bird netting (and were otherwise treated like un-netted controls, i.e., received untreated bran). The results of measurements of survival and development are shown in Figs. 9 and 10. As in the lab trial, no significant differences due to Nosema were observed in survival or in the proportion of insects reaching the adult or 7th instars. However, survival in the pens covered with bird netting was significantly higher than in open control pens ($F = 11.32$, $P < .01$), indicating an important role of bird predation on the penned populations.

A third age group, instars 1-3, was tested (in the lab only) in 1986 for susceptibility to pathogenic effects by Nosema. This experiment was conducted similarly to the lab test with instars 4-5, but included 3 spore concentrations: 10^2, 10^4, and 10^6 spores/mg bran, covering the range of concentrations reported in the grasshopper literature.

Again, measurements of survival and development were made following inoculation and are presented in Figs. 11 and 12. Unlike the previous age groups, survival among these very young crickets was significantly affected by inoculation with Nosema ($F = 8.46$, $P < .05$). A significant reduction in survival, ca. 50%, was apparent 4 weeks after inoculation at the highest dose, with smaller reductions caused by the other dosages. Furthermore, a significant effect on development was also apparent: at the highest spore concentration, no insects reached the adult stage and fewer reached the 7th instar than in the other treatments. A higher proportion of insects remained as 6th instars. Thus, the high dose of N. locustae significantly retarded the normal rate of moulting. It is not clear why the highest proportion of adults was found in the low-Nosema treatment group. This experiment should be repeated to verify this effect and the others mentioned above.

The results above suggest that an early application (w hin a few weeks of hatch) of a high concentration of spores (10' /kg bran) should produce a significant reduction in survival in the field and should result in a lower proportion of insects reaching reproductive (adult) age. It should be noted that this concentration of spores is much higher than that usually found to exert pathogenic effects on acridid grasshoppers (about 100-1000 times higher), suggesting that Mormon crickets are much less susceptible hosts than acridids. Also, the potential for transmission of *Nosema* within the population, and its establishment as a regulating agent, are questionable due to the extremely low level of spores produced in infected insects. Short-term effects within the season of application are more likely to be obtained. However, a field test with instars 1-3 is necessary to corroborate the laboratory data presented above.

New pathogen, *Vairimorpha* sp.

In 1985, a band of crickets exhibiting lethargic, sickly behavior was found to contain individuals heavily infected with a microsporidan pathogen. Samples were sent to Dr. John Henry, of the Rangeland Insect Lab, Bozeman, MT, who confirmed that the parasite is a new species, tentatively *Vairimorpha* n. sp.

In 1986 further sampling was conducted at various locations throughout the cricket-infested area. Many of these samples are still being processed, but infected individuals have been collected from Blue Mountain, Diamond Mountain, Pot Creek, West Cactus Flat and near Elk Springs. Incidence of infection varies from 50-100% and is detectable by the presence of spores in both nymphs and adults.

Levels of infection within individuals also vary, but are generally high in many tissues such as the fat body, as discussed in Part I above. Unlike N. *locustae*, transmission potential for *Vairimorpha* n. sp. appears to be high due to the large numbers of spores produced. We are currently working with Drs. John Henry and Doug Streett (Rangeland Insect Lab) on taxonomic description of this new species, and on the survey of natural incidence begun in 1986. We plan to carry out lab and field tests in 1987 to assess its pathogenicity and potential application as a biocontrol agent for Mormon crickets.

Evaluation of damage to vegetation

Estimates of plant biomass removed by crickets were obtained in 1986 through a paired-sample technique employed in the 10 x 10 m field pens. The procedure consisted in comparing a 1/2 m^2 plot which had been exposed to cricket feeding to a virtually identical paired plot from which crickets had been excluded by means of a galvanized metal ring (12" high). Four such pairs of plots were established in each pen at the beginning of the 1986 *Nosema* experiments described above. The biomass within each plot was determined by a visual estimation procedure known as double

FIGURE 13. Actual dry weight of grasses as a function of estimated fresh weight

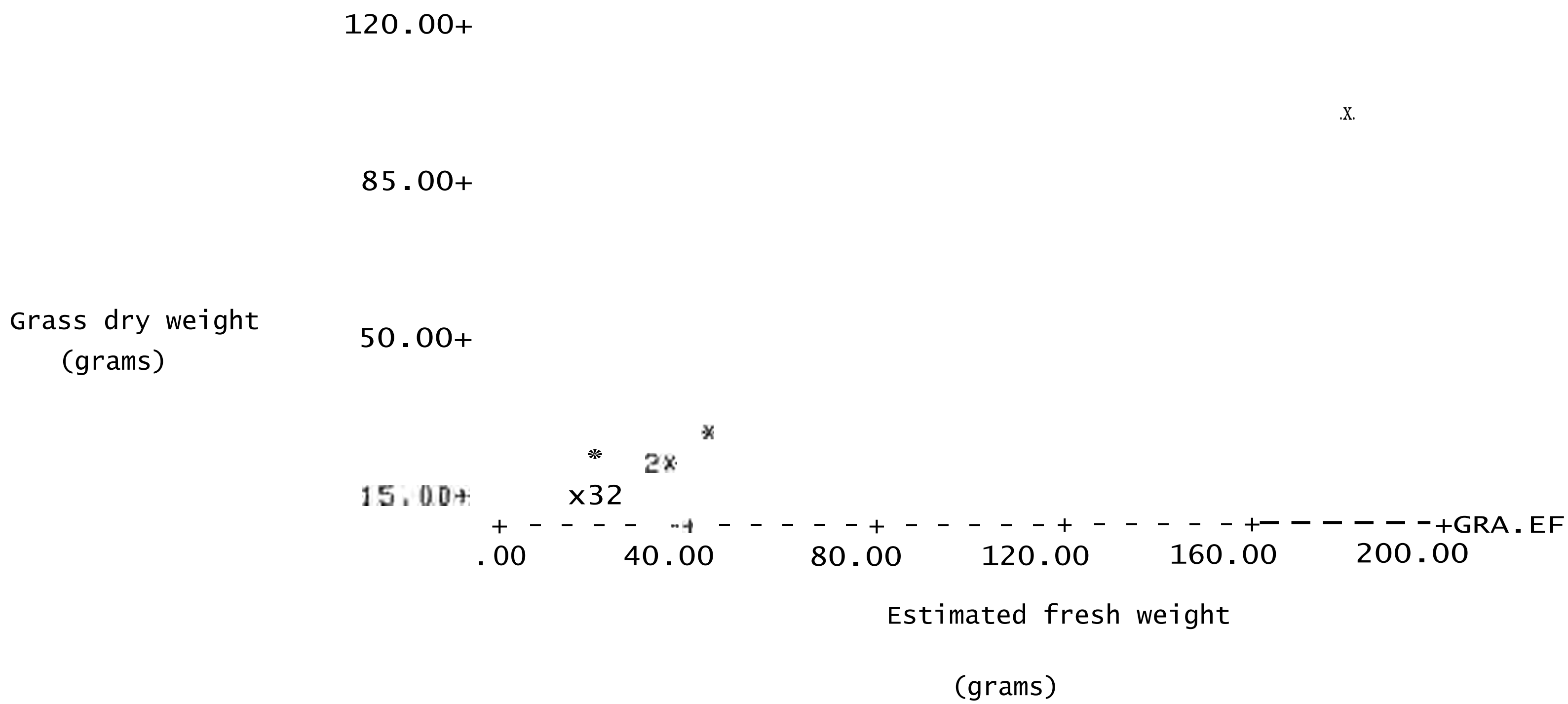
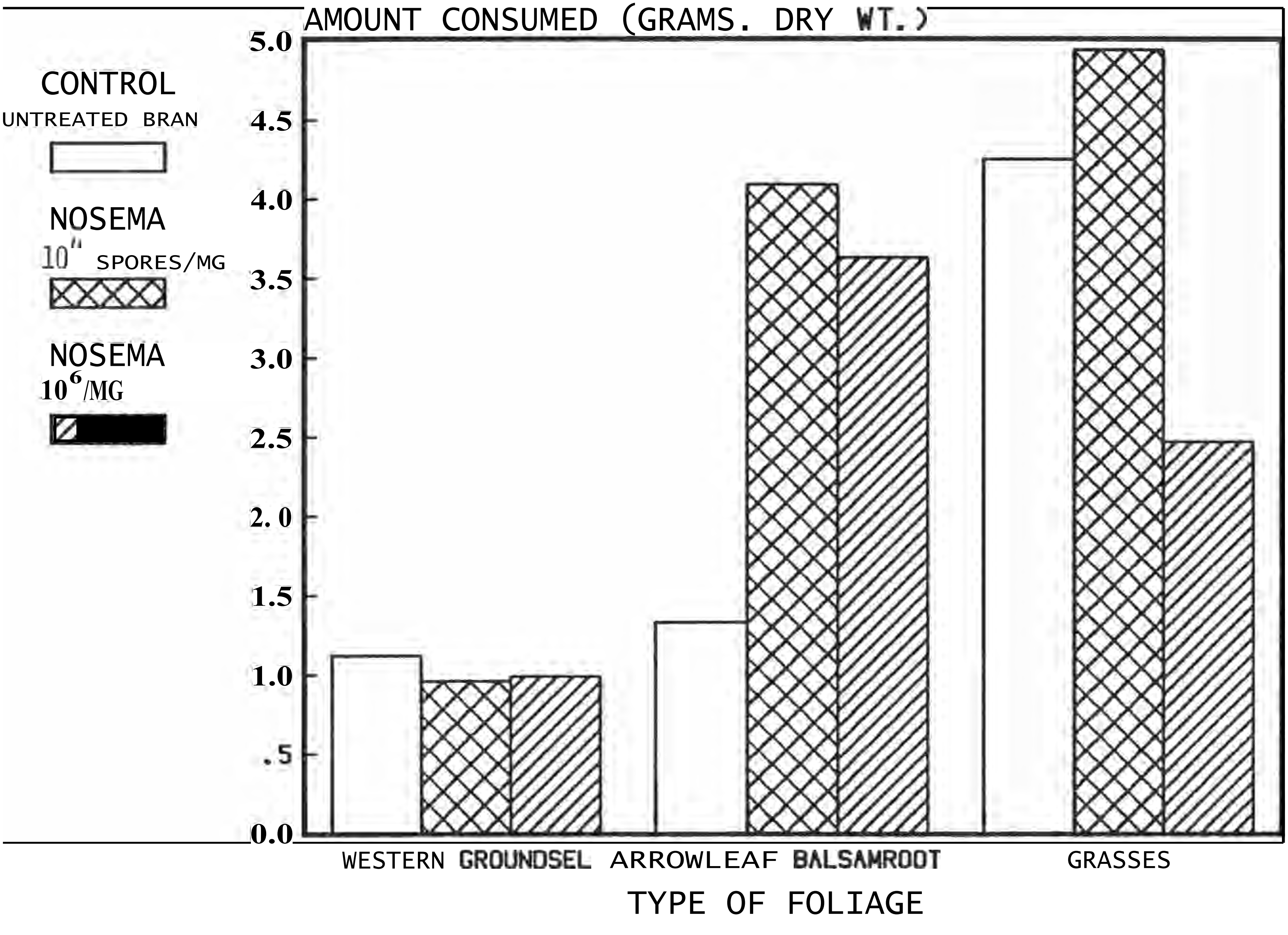


FIGURE 14.

DRY-WEIGHT CONSUMPTION/. 5 M SO.
BY CRICKETS IN FIELD ENCLOSURES



sampling, where plots outside of the cricket pens were both visually estimated and then clipped and weighed, serving as a means of calibrating the estimates within the pens. An example of a calibration curve is shown in Fig. 13, which relates visual estimates of fresh weights of grasses to the actual dry weights of the same samples. After conversion of all estimates to dry weights, the difference between the biomass in exclosure plots (no cricket feeding) and the paired open plots (with cricket feeding) was calculated to provide an estimate of biomass removed by crickets. Separate estimates were made for a) arrowleaf balsamroot, *Balsamorrhiza sagittata*, a dominant forb in the study area; b) grasses, primarily needle-and-thread, Stipa *comata*, sandberg bluegrass, Poa *secunda*, bottlebrush, *Sitanion hystrix*, and junegrass, *Koeleria cristata*, all species taken together into one biomass estimate; and c) western groundsel, *Senecio integerrimus*, a small and relatively uncommon forb which is nonetheless one of the few plants ever to show severe defoliation by crickets.

The data obtained from this study allow preliminary discussion of 2 questions: a) is there a measurable and significant amount of consumption of the vegetation categories mentioned above by crickets held in experimental enclsures?; and b) is consumption significantly affected by *Nosema* treatment (of 4th-5th instars)?

The data obtained so far suggest "yes" and "no" answers, respectively, and are shown in Fig. 14. Comparison of exclosure plots and paired open plots yielded differences that were significantly different from 0, i.e. the exclosures contained slightly higher biomasses of arrowleaf balsamroot, grasses and western groundsel after approximately 3 weeks of cricket feeding. These values are presented in Fig. 14 as gram amounts (dry weight) of consumption/.5 m^2 plot. However, no significant differences in consumption were found between Nosema-treated and control plots within a given type of foliage.

It must be pointed out that while the data show a significantly higher biomass in exclosure plots than open ones, this may not be entirely attributable to cricket feeding in the open plots, but may be due instead to an "exclosure effect". That is, the galvanized metal ring may have altered micro-site conditions (shading, moisture relations) in a manner which increased plant growth relative to the open plot. The inside surface of the rings was spray-painted with a dull red primer to eliminate gross temperature differences within the plots due to reflection of sunlight, but the effects of shading cannot be ruled out. Therefore, the data presented here are preliminary and require corroboration from further, more controlled experiments.

Expressed as percentage reduction of the available biomass in each category, the data suggest that crickets consumed ca. 11% of the arrowleaf balsamroot, 18% of the grasses and 59% of the groundsel. Thus the heaviest consumption occurred on a plant that is relatively uncommon and is not an important forage plant.

These percentage values should not be extrapolated to an area-wide estimate of potential cricket damage for at least 2 reasons: a) the data are preliminary as suggested above; and b) the consumption values were obtained in enclosures where crickets were confined for longer periods of time than a band normally spends on a gixen site. The product of cricket abundance (an average of $4/m^4$) and number of days present in the pens (ca. 25) yields a value of approximately 100 cricket-days/m , an index of feeding activity. In a natural situation, bands of crickets are often present in a given area for only 3-4 days (Swain, 1944); assuming a density of 10/m , this would represent 30-40 cricket days/m , or roughly 1/3 to 1/2 the feeding activity of the penned populations. Thus, even if the consumption values given above are a true estimate of cricket damage, they are probably 2-3 times higher than would be observed in a natural setting. Further research on forage removal at varying densities of crickets and shorter time intervals is required to describe accurately biomass losses due to crickets.

Damage to rangelands by crickets is often slight or imperceptible. Wakeland (1959) described cricket damage as varying from scalloped leaf margins, or holes in leaves, to destruction of whole plants. Currently, only the first two types are occurring, resulting in biomass losses that are difficult to measure through range survey methods which rely on vegetation weight estimates (e.g., Pechanec and Pickford 1937, Ahmed et al. 1983, Cabral and West 1986, and our procedures described above). Since records of cricket population density do not exist, it is difficult to compare the current outbreak with that of the 1930's. However, numerous photographs in the literature depict bands of migrating crickets which appear very similar in density to those found today in northwest Colorado. The total area covered by such bands is obviously much smaller at present than during past outbreaks, but the levels of herbivory in infested areas would be expected to be similar. Why then, is range damage slight at present, given that severe defoliation was occurring in the same area, and others with similar plant composition, during the 1930's ? It seems likely that at least two factors are involved: weather and grazing pressure. In contrast to conditions prevailing at that time, recent years have seen above-average precipitation in Colorado (Karl et al. 1983, Doesken et al. 1987) and stocking rates are more carefully monitored on public lands. Thus, forage availability is probably higher now than during previous outbreaks, thereby reducing the relative impact of consumption by crickets. As discussed earlier, crickets are selective feeders where an abundance of forbs and grasses exists, consuming only succulent tissues and inflorescences. If current damage levels are truly representative of an area receiving favorable precipitation and moderate grazing pressure, then the Mormon cricket's economic importance is negligible.

Part III. MANAGEMENT PROBLEMS AND OPTIONS

Currently, an understanding of pest status and the basis for management decisions suffer from at least two fundamental deficiencies: the lack of appropriate sampling methods and lack of economic injury levels. Three levels of sampling are required to determine the total cricket population in a given area: within-band density, band size and band abundance (e.g. number of bands per 100 km^2), Furthermore, the size and distribution of bands are likely to change during the season due to movement and possible coalescing of bands, such that the cricket density found at a given site over time (uicket-days) could be highly variable.

The relationship between cricket density and plant injury is little known, aside from Cowan and Shipman's (1947) laboratory consumption study. Although cricket damage to rangeland appears to be slight at present, further research is necessary to understand damage potential in relation to local plant species composition and annual productivity.

It is realistic to expect that the concerns of ranchers and government for cricket control will persist. Throughout the history of Mormon cricket control, prevention of damage to crops by timely destruction of migratory bands on rangeland has been considered essential (Wakeland 1959). However, while perhaps a valid approach for protection of farms in the 1920's, this view is inappropriate today. By virtue of the high, rapid cricket mortality produced by low concentrations of carbaryl in bran or rolled-wheat baits (Foster et al. 1979), these can be used in a reactive sense to protect agricultural areas and need not be applied further than the immediate surroundings of the crop field. More than one application may be necessary, but treatment of localized areas would result in obvious reductions in cost and pesticide loads in the environment. Biocontrol agents, such as spores of microsporidians, which can be incorporated into baits, may also provide a highly selective suppression tactic well suited for protected areas such as national park lands. While slow-acting in nature, such pathogens may persist from one generation to another and be transmitted horizontally through cannibalism. Further research is required to determine the effectiveness of these agents for use on rangeland.

Given the results of this two-year study we can make certain recommendations for management of Mormon cricket in the vicinity of Dinosaur National Monument, as follows:

1) A legacy of fear of crickets compounded by problems associated with drought and overgrazing persists from the Dust Bowl era. The role of crickets as primary consumers which are critical links in the food chain of wildlife is not well appreciated. The food habits of crickets (specifically their preference for low-value plants) which reduce their damage potential considerably, is not well appreciated. Thus, a prolonged educational program in the area is needed to bring additional, positive information about crickets to local ranchers and farmers. This could be done by park staff, although it may seem self-serving and thus suspect by locals. It might be best to enlist the assistance of cooperative extension or some other neutral party. It is strongly recommended that educational material (leaflets, film strips, etc.) aimed at school children be developed to begin the educational program for future generations.

2) Recognition of the variability associated with

weather, particularly precipitation, is important. The crickets were found to have minimal impact during this study because forage growth was excellent. If the studies had been conducted during a period of prolonged drought these very same cricket populations probably would be viewed as serious pests. If ranchers lack additional pasturage or alternate feed during dry times, cattle grazing plus cricket herbivory could constitute overgrazing. Thus, awareness of the entire set of constraints facing the rancher is necessary. It would be desirable to conduct a computer simulation study to assess the effects of crickets on forage production and livestock grazing capacity under a variety of precipitation conditions.

3) Crickets will continue to breed in the area, and the monument will serve as a potential source of infestations for surrounding areas. During periods of outbreak, land outside the monument will serve as adequate breeding grounds, with crickets moving into the monument as frequently as moving out. Control of crickets over vast geographic areas may not be justified due to reduction in grazing capacity (see # 1 & 2, above), and should not be justified based on the small amount of damage to irrigated crops. The cropland is easily protected with repeated border treatments (foliar or bait), and it may be more economic to subsidize crop protection than to treat large acreages of rangeland.

4) Should it be desirable to reduce cricket densities, Nosema locustae could be recommended if applied at high rates early in cricket development. If this is not possible, insecticide-treated bait provides rapid control of small infestations. The role of Vairimorpha is not completely known, but may prove to be the key factor limiting the success of Mormon cricket. More information which would enable prediction of Vairimorpha effects, or perhaps use of Vairimorpha as a substitute for Nosema, should be obtained. Area-wide suppression of crickets on grazing land is justified only during periods of prolonged drought. Unlike the 1930's, crickets can be quickly controlled over large areas if necessary. Therefore, it is inappropriate to act prematurely to suppress cricket populations in anticipation of problems which may not materialize. Routine monitoring of the population is recommended to assure that cricket densities are known by
1111 all concerned parties.

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Bibliography

of the

Mormon cricket

(*Anabrus simplex* Haldeman; Orthoptera, Tettigoniidae)

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February, 1986

Index

Bibliography of the Mormon cricket

Wakeland (1959)[1] compiled the first comprehensive bibliography of the Mormon cricket in his excellent review article, "Mormon crickets in North America." This-included some 200 citations of published reports, and additional references to unpublished reports, correspondence, insect collections and field notes. Since 1959, only 14 papers have been published on Mormon crickets. Thus, the present bibliography, which includes all of Wakeland's references to published reports, does not present a substantially larger body of literature. However, recent papers have contributed significantly to an understanding of cricket mating behavior (Gwynne, 1981; 1984), food-plant preferences (Ueckert and Hansen, 1970; Hansen and Ueckert, 1970), and control (Foster et al., 1979; Henry and Onsager, 1982). The present bibliography aims to make access to all the literature easier and more effective by providing a simple subject index. Also, a brief introduction with references to key papers is provided to help the reader gain an overview of Mormon cricket biology and control without tedious perusal of numerous old publications, many of which are purely anecdotal and extremely repetitive in content. The subject category "Review papers" is also provided for this purpose.

Several sources were utilized to identify the literature: a) Wakeland's bibliography; b) references given by authors of papers in our files; c) the Review of Applied Entomology, 1957 to present; d) BIOSIS computerized search (covers Biological Abstracts, 1969 to present).

Omissions have undoubtedly occurred in compiling this bibliography. Brief reports in weekly or monthly government bulletins, such as "Canadian Insect Pest Review," or "Insect Pest Survey Bulletin" are particularly easy to overlook since they are rarely cited in other publications or abstracting journals. However, we believe the bibliography to be complete with respect to major publications.

[1] papers mentioned by author and date are fully referenced in the body of the bibliography.

References to published reports are presented in two independent listings: a) grouped by subject matter, with abbreviated author and date entries (a given paper may appear in several subject categories); and b) alphabetically by author, with the full reference. Abstracts are provided for key papers. In the alphabetical section, numbers following each reference indicate the subject categories (below) addressed in the paper. Subject categories are meant to fit the existing literature and the peculiarities of the insect. Categories such as "Migration, banding behavior" and "Mating behavior" have been used in addition to "Life History" because they contain studies on unique aspects of Mormon cricket biology which might be overlooked if lumped together under "Life history." A listing for the Coulee cricket (Peranabrus scabricollis) is included because of its great similarity in habits to Anabrus simplex.

The subject categories are:

1. Review papers -- though quite old, these introduce most of the available literature and information on Mormon crickets.

2. Anatomy, physiology

3. Banding, migration

4. Control, pest status

5. Feeding habits -- including assessment of damage.

6. Fossils

7. Genetics

8. Historical importance -- description of cricket infestations and their impact on early settlement of the western U.S.

9. Life history

10. Mating behavior

11. Natural enemies

12. Nutritional value -- use of crickets as food.

13. Taxonomy, geographic distribution -- including collection records, reports of occurrence.

14. Coulee cricket -- all aspects.

Introduction to the Mormon cricket

(*Anabrus simplex* Haldeman, Orthoptera: Tettigoniidae)

Mormon crickets are flightless, shield-backed grasshoppers which occur primarily in the high plains and sagebrush-dominated regions of western United States and Canada. In the U.S. they are distributed from Minnesota south to Kansas and New Mexico, and west to California, Washington and Oregon. They are gregarious insects and are probably best known for their huge migratory aggregations, or bands, which have periodically inflicted severe damage to range and crops. The name "Mormon cricket" stems from the early encounter in 1848 between Mormon settlers in Utah and this grasshopper, which somewhat resembles a large cricket, and which did considerable damage to the settlers' first crops. Although "cricket" is a misnomer, the name has gained extensive use and acceptance (Wakeland, 1959).

Anabrus is one of 22 genera in the subfamily Decticinae. The name "Mormon cricket" applies strictly only to *Anabrus simplex* Hald., though it has also been used for congeners, due to their great similarity in appearance and biology. Other common names for A. *simplex* found in the literature include "western cricket," "Idaho cricket," "great plains cricket," and "mountain cricket." Other species names found in the literature which are synonymous with *simplex* are: *purpurascens, coloradus, similis,* and the "varieties" *nigra* and *maculatus* (Rentz and Birchim, 1968). Currently, 4 species of *Anabrus* are recognized: *simplex, cerciata, longipes,* and *spokan.* These can be separated with keys given by Rentz and Birchim (1968) and Gurney (1939). While all are potential pests, *simplex* is the most widespread and has caused the most damage. Only A. *simplex* occurs in Colorado, the other species being confined to the northwestern regions of the U.S. The related genus *Peranabrus* contains only one species, P. *scabricollis,* the "coulee cricket" of Washington, which is extremely similar to A. *simplex* in appearance and habits, and has periodically achieved pest status.

A. *simplex* is an omnivorous, cannibalistic insect and is known to prefer succulent, weedy species to grasses in its native habitat (Corkins, 1923; Cowan, 1929; Mills, 1939; Swain, 1944). It also appears to feed heavily on fungi (Ueckert and Hansen, 1970). Most crops, especially wheat and alfalfa, are readily eaten and have historically suffered much more economic damage than rangeland. However, during periods of unusually high population densities, crickets have caused serious injury to forage species on rangeland (Wakeland, 1959; Swain, 1944).

Mormon crickets are univoltine, early-season insects, hatching in March to May (in Colorado) from eggs laid in the ground during the preceding summer. The nymphs develop through 7 stadia before the final molt to adults (Cowan, 1929; Cowan and Shipman, 1947). They are gregarious throughout their lifetime, and after the first 2-3 molts aggregate into dense migratory bands which may cover many square kilometers. During daylight hours, these large groups of crickets walk in fixed directions, pausing occasionally to feed or to seek shelter from adverse weather. At night, the army-like migrations stop and crickets form tight clusters around the base of sage bushes, rocks, etc.

Mating occurs in June to July. Gwynne (1981, 1984) has found that males are selective in their choice of mates and often reject the smaller females in the band. This is apparently related to the unusual energy investment males make in the form of a proteinaceous spermatophore which the females eat after copulating and utilize, in part, for egg production.

Control measures for Mormon crickets have evolved from the use of crude poisoned mashes and mechanical barriers to aerial sprays (Wakeland, 1951; 1959). Recently, use of reduced amounts of pesticide (Foster et al., 1979) and natural parasites (Henry and Onsager, 1982) in a bran bait formulation have received renewed attention.

Part I. Subject listing

1. Review papers

La Rivers, I. 1944.

Wakeland, C. 1951.

1959.

Wakeland, C. and J. R. Parker. 1952.

2. Anatomy, physiology

Jackson, L. L. and G. L. Blomquist. 1976.

Kellogg, V. L. and R. G. Bell. 1904.

La Rivers, I. 1941.

Packard, A. S. 1880 b.

Banding, migration

Aldrich, J. M. 1904.

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Doten, S. B. 1904.

Howard, L. O. 1895.

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Corkins, C. L. 1922.

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Cowan, F. T. 1928.

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6. Fossils

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Corkins, C. L. 1922.

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Cowan, F. T. 1929.

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ABSTRACT: Brief history of early outbreaks, as of 1848 in Great Salt Lake Basin, UT. Habitat: broken mountainous country with sagebrush and native grasses. Outbreaks last from 2-6 years. Bands of crickets may cover 1 city block to 1 sq. mile or more. In early stages, crickets may have a density of 100-500/sq. ft. Damage is done primarily by adults, when grain is headed, as they eat kernels. Garden crops are a "delicacy" and small fruits are readily eaten; alfalfa is also damaged. Food plants: bitterroot and mustards are favored; seeds and pods of mustards eaten (Montana). Life history: completes development to adult by June 15-July 15, and 10-14 days later oviposition begins. Mating occurs very shortly before egg laying. Eggs are embryonated before frost sets in. Rearing: gives techniques; descriptions of egg, each of the 7 instars and adult, illus. Developmental time, hatch to maturity, 40-58 days, longer in nature, 75-90 days. Habits: soil temps. of ca. 100 °F drive crickets up on weeds, fences, etc. Cannibalism is present throughout life span. Describes mating [contrast with Gwynne, 1981]. Migration occurs in any direction for a given band, but is constant once chosen; occurs throughout season and life cycle, especially after 4th instar. Oviposition occurs almost anywhere,

except north-facing slopes; bare ground is preferred. Females lay eggs about once every 7-8 days after the 1st oviposition. Up to 35 eggs/day for a total/female of up to 160 eggs, in the lab. Natural enemies: birds, mammals; Sparaison pilosum (Hymenop.) is an egg parasite; Palmodes laeviventris (Hymenop.) preys on adult crickets. Control: results with poisoned-bran mash erratic; feeding erratic. Barriers made of 10-inch strips of galvanized iron are effective; other barriers are discussed.

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ABSTRACT: Determined daily consumption by nymphal and adult stages. Held crickets individually in glass vials and fed them disks of lettuce in 1st study (lab reared crickets, 77 °F): consumption (expressed as dry weight) increased linearly from about 1 mg/day to 34 mg/day between 1st and 7th instars (except for ca. 3-day non-feeding periods at each molt); 100 mg/day for adults. Average duration of stages was 7-8 days for instars 1-4, 10 for 5th, 13-14 for 6-7th, 20 for adult. Second study (field-collected crickets at each stage, held outdoors, fed alfalfa): feeding increased exponentially from about 0.74 mg/day by 1st instar to 44 mg/day by 7th, and 88 mg/day by adults (dry weight). Stage durations were longer than in 1st study due to lower temps., but total consumption was less over whole life span, 1760 vs. 2017 mg. Found high mortality in caged insects, especially lab-reared ones. Total food required to take insects through 20 days of adult life was 3518 mg/insect. Compares extrapolations of above feeding rates to amounts consumed by cattle in Nevada; a band of crickets covering 1 section of land at 10/sq. yd would consume 120 tons of forage in 4 months, about 4.4 times as much as cattle would remove in 9 months. Ten head of cattle can be grazed on 1 section for 9 months. In Montana and Wyoming damage is less due to plant composition--crickets don't eat main forage plants.

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ABSTRACT: Field tests with small cages were used to determine if a reduced concentration of carbaryl (Sevin 4 Oil) in a flaky wheat bran bait and a reduced rate of application of the bait could still yield satisfactory control of Anabrus simplex Haldeman on rangeland. A reduction from 5% AI to 2% AI in concentration yielded no statistical difference in mortality. The tests indicate that control with bait may be achieved with 60% less carbaryl and a reduction in rate of application as great as 75% when compared with present carbaryl bait labels.

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ABSTRACT: Gives key to genera: Steiroxys, Anabrus, Apote, Pediodectes, Peranabrus, Eremopedes. Key to species of Anabrus: cerciata, simplex and longipes. Distribution data and maps, indicating that probably only simplex occurs in Colorado. Pediodectes and Eremopedes also occur in Colorado but are easily distinguished from Anabrus.

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<u>NOTE:</u> This paper provides a good overview of distribution, life history, foods, mating habits, oviposition, and control of the coulee cricket, which is very similar to the Mormon cricket in all respects.

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ABSTRACT: Provides keys to subfamilies of Tettigoniidae, genera and species of Decticinae, with revision. Recognizes 4 spp. of Anabrus: cerciata, simplex, longipes and spokan. Gives summaries of biology, zoogeography of Decticinae; collection and preservation techniques.

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ABSTRACT: Evaluatesfood preferences and damage potential of crickets in several states based on a) visual estimates of consumption in 1/10 acre plots and in transect point samples; b) dry weight approximations of plant material present before and after cricket feeding in plots. Almost no plant is totally avoided. Succulent forbes are preferred, inflorescences preferred over vegetative tissue, crops preferred to range vegetation. Downy chess *(Bromus tectorum)* is possibly most preferred grass. Weeds, especially mustards, are most preferred "class" of plants, compared with grasses and grasslike plants. Consumption data, by plant species, are presented as % of available forage for livestock, and as dry wt., removed by crickets. In some areas of Nevada and Oregon consumption neared 100% of seasonal forage production, but this was unusual; most areas suffered very slight damage (less than 10%).

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ABSTRACT: The dry-weight composition of the diet and the food preferences were determined for Anabrus simplex Haldeman, inhabiting an arid ponderosa pine-bunchgrass community in northern Colorado. Thirty-five plant species were microscopically identified from the crops of this insect. Only 2-4 staple foods occurred in the diet during any period. Although primarily herbivorous, Mormon crickets were found to be carnivorous and fungivorous. Forbs contributed an average of about 50% of the diet, while arthropods and fungi contributed about 21 and 16%, respectively. Grasses, clubmoss, and grasslike plants comprised about 6, 5, and 2% of the diet, respectively. Diet and food preference changed as the season progressed.

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Year	Vol	pp.	Subject
1952	2	162, 189, 220, 234	4,14
1953	3	50, 251, 387, 429, 696	4
1954	4	48, 1046	4
1955	5	454, 735	4
1956	6	541, 604, 749	4
1962	12	682	4

USDA Bur. Ent. and Plant Quar. Insect Pest Survey Bull.:

Year	Vol	pp.	Subject
1921	1	185, 188	4
1922	2	193, 197	4
1924	4	114	4
1925	5	97, 154, 231	4
1926	6	88, 131, 132	4
1932	12	299	4
1933	13	226,227	4
1934	14	214	4
1935	15	218, 219, 398	4,11
1936	16	357	4
1937	17	155, 272, 598-599	4
1938	18	147, 151, 320, 324, 325	4,11
1939	19	547	4
1940	20	297, 298	4
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<u>NOTE:</u> This paper provides an excellent review of all aspects of the Mormon cricket: taxonomy and common names, crickets as food, distribution in U.S. and Canada, habitat, biology, food plants, nature and amount of damage, outbreaks, control methods, natural enemies, development of cooperative control, and a comprehensive bibliography up to 1959.

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