Oviposition Site Selection by the Grasshoppers Melanoplus borealis and M. sanguinipes (Orthoptera: Acrididae)

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Abstract

Female grasshoppers can affect the fitness of their offspring through their selection of oviposition sites. Successful embryological development depends on suitable temperature and moisture levels, factors which may vary greatly on a fine scale in natural environments where grasshoppers occur. Knowledge of parameters defining acceptable oviposition sites can provide guidelines for habitat manipulations that reduce the availability of such sites. This paper compares oviposition-site selection in two species of grasshopper from Alaska, *Melanoplus borealis* and *M. sanguinipes,* and a population of *M. sanguinipes* from Idaho. Laboratory experiments did not detect any differences in preferred substrate temperature among the groups of grasshoppers. In field cages containing a choice of different ground covers (bare ground, single clump of grass or turf), *M. sanguinipes* from Idaho were less selective in terms of the distribution of egg pods among the different cover types, whereas both *M. borealis* and *M. sanguinipes* from Alaska deposited the fewest egg pods under the turf. Results suggest that differences in oviposition behavior between the grasshoppers from Idaho and those from Alaska may stem more from differences in the above-ground physical structure of the vegetation, than from differences in responses to below-ground temperature.

Key words

Melanoplinae, temperature gradient, egg, vegetative cover, subarctic, Alaska

Introduction

Investment in offspring fitness takes many forms in insects, from complete care and feeding of larvae by social Hymenoptera to simply leaving eggs in a generally favorable environment. Most grasshoppers (Orthoptera: Acrididae) fall near the simpler end of the spectrum. Females provision the eggs with ample protein and fat (some of which may have been provided by males), and they select an appropriate oviposition site. Most grassland species oviposit several eggs at a time, clustered together in a pod which is placed in the soil or in plant litter on the soil surface. Stauffer & Whitman (1997) provide a detailed review of the literature and an analysis of the morphology, physiology, and behavior associated with oviposition in acridids. They break down oviposition behavior into habitat selection, microsite location and microsite acceptance. Because habitat and diet requirements of immature grasshoppers are similar to those of the adults, females are usually already in an appropriate habitat for their offspring and oviposit in the general vicinity of acceptable host plants (Stauffer & Whitman 1997).

Within heterogeneous grassland environments, the acceptability of microsites can vary greatly over small distances. Females can influence the fitness of their offspring through the selective placement of their egg pods. For instance, Kemp & Sanchez (1987) and

Fisher (1992) compared the oviposition preferences of two species of grasshopper. Eggs of the species that deposited egg pods near the soil surface in bare ground had to tolerate warmer temperatures, wider temperature extremes, and dessicating conditions, compared to the species that tended to place egg pods deeper, amongst plant roots. Branson & Vermiere (2007) showed that species that oviposited near the soil surface were more susceptible to mortality by wildfires than species that placed their eggs deeper in the soil.

The bounds of acceptable oviposition sites are largely defined by temperature and moisture (Norris 1968, Meats 1970, Sharma 1984, Beckerman 2002), which are key to survival and hatching of grasshopper eggs (Salt 1952, Moriarty 1969, Chapman & Page 1978). The successful development of embryos of many species of acridids depends on absorption of free water from the surrounding substrate (Salt 1952, Shulov & Pener 1963, Pickford 1975). Soil salinity may also affect oviposition-site selection (Ji *et al.* 2006). Acidity of the soil has not been shown to be an important factor in microsite acceptance (Stauffer & Whitman 1997). Most species avoid very dry soil and may curtail oviposition until suitable substrate is available (Stauffer & Whitman 1997). Different species exhibit different ranges of temperatures, substrates and moisture levels that are acceptable for oviposition. Stauffer & Whitman (2007) compared the suite of traits associated with oviposition in two closely related species inhabiting very different environments and concluded that oviposition behavior, including site selection, can evolve rapidly in response to changing environments.

Knowledge of oviposition requirements can have management applications. The availability of suitable oviposition sites can restrict some grasshopper populations to certain habitats (Chapman & Page 1978). Experiments reported by Beckerman (2002) provide evidence that the availability of oviposition sites was a major factor influencing the local abundance of *M. femurrubrum*.

In this paper, I examine some of the parameters involved in microsite selection by ovipositing grasshoppers in the genus *Melanoplus*. I compare two populations of *M. sanguinipes*, one originating from the subarctic region (interior of Alaska) and another from a semi-arid temperate environment (Palouse prairie of Idaho). These populations previously have been shown to differ in growth rate (Fielding & DeFoliart 2007), nutrient intake (Fielding & DeFoliart 2008a), diapause traits (Fielding & DeFoliart 2008b) and thermoregulatory efficiency (Fielding & DeFoliart 2005). Also, a population of *M. borealis*, a closely related species (Chapco & Litzenberger 2002) from the subarctic, was included in some of the experiments.

Laboratory experiments were conducted to identify the preferred temperature range for oviposition among the different grasshopper populations. Additional laboratory experiments evaluated the lower limit of substrate temperature acceptable for oviposition. Finally, results are presented of experiments with field cages to determine

the effect of different ground covers on oviposition acceptability.

Materials and methods

Laboratory colonies were initiated with > 200 individuals, collected near Lewiston, Idaho and Delta Junction, Alaska, as 4th and 5th instars in mid-July, 2003. Grasshoppers were collected about 5 km south of Lewiston, Idaho (lat 46.38 N, long 117.02 W; 450 m elevation) and about 20 km SE Delta Junction, Alaska (lat 64.00 N, long 145.73 W; 400 m elevation). All experiments were conducted on F_1 and F_2 generation offspring.

Temperature gradient.— This experiment was conducted to identify the preferred substrate temperature for oviposition. A microcosm was designed to present the grasshoppers with a gradient of substrate temperatures. The apparatus consisted of a wooden box (length 95 cm; width 30 cm; depth 30 cm). A copper plate (90 × 25 cm and 5 mm thick) was mounted 15 cm from the top of the box to form the floor of the microcosm. Four thermo-electric modules, 40 × 40 mm (model HP127-1.4-2.4-72, TE Technology, Inc., Traverse City, Michigan) were used to maintain the temperature gradient. Thermoelectric modules function as heat pumps and can be used for cooling or heating, depending on the polarity of the current flowing through them. Two modules were attached to the underside of the copper sheet near each end. These modules were sandwiched between the copper plate and aluminum-finned heat sinks. Fans at each end of the box provided airflow. Two temperature controllers (model 5C7-550(A), Oven Industries, Inc., Mechanicsburg, Pennsylvania, USA) were employed to set the temperature at each end of the microcosm. The substrate was about 5 cm deep and consisted of a mixture (95: 5 ratio by weight) of sand and cross-linked polyacrylimide crystals (Agrosoke International, Arlington, Texas, USA) to help maintain a

consistent moisture content over the three days of the experiment. Two liters of water were added to the substrate and evenly mixed. Thermocouples were buried in the substrate at a depth of 2.5 cm every 10 cm, starting 5 cm from each end. Plexiglass sides were attached to the box and a band of petroleum jelly smeared around the sides to prevent grasshoppers from climbing out. Brown paper was wrapped around the plexiglass sides to remove any outside visual stimuli that might affect oviposition-site selection. Light was provided by two compact flourescent lamps mounted at the ends of the microcosm, 70 cm above the substrate surface.

Twelve females and 12 males were placed in the microcosm for each trial, with trials repeated three times for each population of grasshoppers, using different individuals for each trial. The thermocouples were read twice a day during trials that lasted 3d. The temperature readings were averaged for each trial and linear regression used to model the temperature gradient. After 3d, the substrate was carefully searched and the location of each egg pod recorded to the nearest cm. The temperature where each egg pod was found was interpolated from the average temperature of the two nearest thermocouples. Temperature gradient was reversed after each trial.

Substrate moisture/temperature choice.—A second microcosm was designed to examine oviposition behavior when grasshoppers were constrained by less-than-optimal substrates: either too dry or too cool. Most grasshopper species that have been studied avoid ovipositing in substrates too dry or too cold (Stauffer & Whitman 1997). Grasshoppers were provided a choice of cool and moist *vs* warm and dry sand substrate for oviposition. Temperature of the cool and moist substrate was varied to determine the lower temperature limit of acceptability for oviposition.

The microcosm was constructed from a wooden box, with inner dimensions of 36 cm wide, by 55 cm long and 25 cm deep (Fig. 1). Substrate within the microcosm was washed quartz sand, 15 cm deep. The long axis of the microcosm was divided into a warm and dry end opposite a cool and moist end, these separated by two pieces of blue-foam insulation (7.5 cm thick, perpendicular to the long axis of the box) with a 4-cm air space between the two pieces of insulation. The substrate in the warm and dry half was simply air-dry sand at ambient room temperature, between 25 and 28°C for each trial. Temperature on the cool and moist side differed among trials. The cool and moist state was maintained by circulating cold fluid through four copper pipes (1.27 cm inner dia.) placed at a depth of 9 cm. Water was added to the cool/moist side through 5-cc syringe barrels, inserted to a depth of 4 cm so that the surface of the substrate remained dry. Four thermocouples were buried in the sand at a depth of 4 cm on each side of the microcosm and temperatures recorded twice each day. The two halves of the microcosm were caged above with aluminum-mesh window screen. A wire mesh partition bisected the microcosm along its long axis to allow the simultaneous testing of the two populations of *M. sanguinipes* (*M. borealis* was not available for this experiment). The surface area of the substrate available for oviposition was 18 × 18 cm for both dry and moist portions of the microcosm.

Ten female grasshoppers and a like number of males from each population were maintained in the microcosm for 14 d in each trial. Eight trials were conducted with different temperatures on the cool and moist side. Preliminary tests suggested that a temperature of 15°C or warmer was preferred for oviposition. Therefore, temperature regimes on the moist side were selected that bracketed this temperature: average temperatures on the cool and moist side varied from 11.5 to 18.7°C.
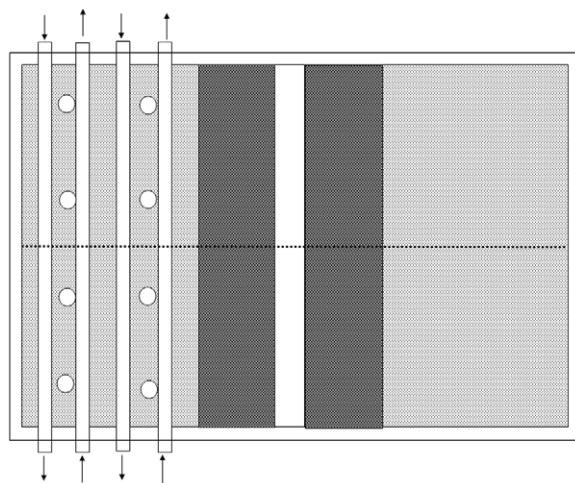

Fig. 1. Diagram of microcosm (overhead view) used to examine oviposition behavior of grasshoppers when confronted with a choice of cool/moist *vs* warm/dry substrate. The apparatus was constructed of a box (inner dimensions: 36 cm wide, by 55 cm long, and 25 cm deep) with wooden sides 1.9 cm thick. Light grey areas indicate sand substrate. Dark grey areas represent foam insulation (7.5 cm thick). White circles represent 5-cc syringe barrels used to maintain subsurface moisture. Parallel white rectangles represent 1.27-cm copper pipes through which coolant circulated to lower substrate temperature. Arrows indicate direction of flow of coolant through the pipes. Dotted line bisecting the microcosm, represents wire-mesh divider to enable simultaneous testing of two populations of grasshoppers.
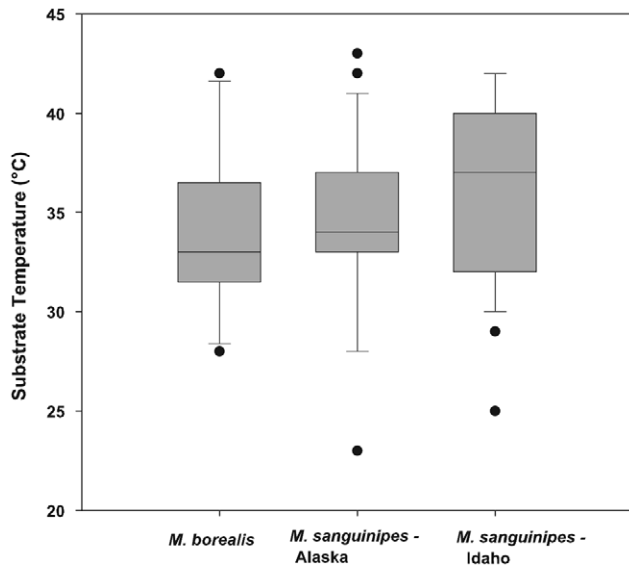
Fig. 2. Distribution of egg pods within a temperature gradient.

The total number of pods produced and the proportion of pods found in the moist side was analyzed by ANCOVA (Proc GLM, SAS Inst. 2003) with population as the main factor and mean temperature of the moist side as the covariable. If the two populations responded differently to temperature, I expected the interaction term between population and temperature would be significant ($P < 0.05$).

Field Cages.—Oviposition preference was compared among the grasshopper populations using field cages placed in a cultivated field that was maintained free of all vegetation. Cages (90 cm long by 30 cm wide by 30 cm high) were covered with aluminum window screening. The long axis of each cage was oriented in an east-west direction. The ground within each cage was subdivided, perpendicular to the long axis, into three areas of equal size, each with a different ground cover: a dense cover of vegetation (turf), a single clump of plants (clump) in the center of the area; and bare ground with no plants. The arrangement of ground-cover types within a cage was alternated among cages, such that for the six cages assigned to each grasshopper population, each ground-cover type was on the east, center, or west side of two cages. To rule out the possibility that the particular species of plant might affect the results, annual ryegrass was used in half the cages, and barley in the other cages. Plastic landscape edging, buried to a depth of 15 cm, separated the subplots within a cage and prevented roots from growing into the bare ground treatments.

Six cages were randomly assigned to each grasshopper population (*M. sanguinipes* – Idaho, *M. sanguinipes* - Alaska, and *M. borealis*), for a total of 18 cages. Ten male-female pairs of adult grasshoppers were placed in each cage in mid-July. Thermocouples were buried at a depth of 5 cm in each of the subplots of four cages, plus four that were buried outside the cages, to measure the effect of the cages on soil temperatures. After 4 weeks, the cages were removed and the soil sieved to recover egg pods.

Differences in the frequency of egg pods among cover types and grasshopper populations were determined by chi-square analysis of 3 by 3 (grasshopper population by ground cover type) frequency tables (Proc Freq, SAS Inst. 2003). Similarly, the effect of barley *vs* ryegrass on distribution of egg pods among the ground cover types was examined by chi-square analysis of 2 by 3 (plant species by ground cover type) frequency tables.

Differences in the mean number of pods laid in different cover types within grasshopper populations were analyzed using ANOVA (Proc GLM, SAS Inst. 2003), using square-root transformed data to stabilize variances. This experiment was repeated in each of three years (2004, 2005, 2007). The effect of position of the subdivisions within the cages (east, center, or west) on mean number of egg pods was also examined using ANOVA.

Results

Temperature gradient.—In the temperature-preference experiment, the temperature gradient was linear between 10 and 85 cm, with substrate temperatures between 22 and 45°C in each of the nine trials. Regression of temperature on distance gave slopes between 0.30 and 0.34 °C per cm, with $r^2 > 0.97$ ($P < 0.001$ in each trial). No differences in the mean temperature at which pods were placed were detected ($F_{2,6} = 0.5$, $P = 0.62$) among groups of grasshoppers (mean ± SE = 36.3 ± 2.2, 33.6 ± 2.0, 33.8 ± 1.5, for *M. sanguinipes* from Idaho and Alaska and *M. borealis*, respectively). The range of temperatures where pods were placed, 28 to 42°C, was similar for all populations of grasshoppers (Fig. 2). Within this range of
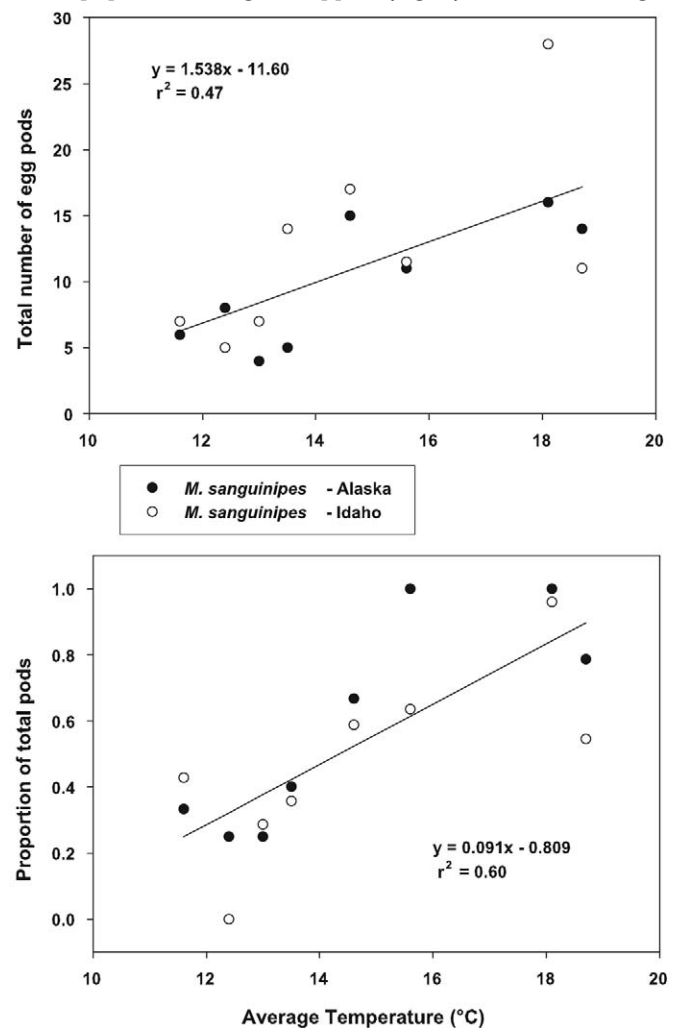

Fig. 3 Oviposition behavior by two populations of *M. sanguinipes* when given a choice between dry substrate at 25-28°C and moist substrate at a variety of temperatures (X axis). A) Total number of pods oviposited by 10 females on both moist and dry substrates (data point for the Alaska population at 15°C hidden by symbol for Idaho population). B) Proportion of total pods oviposited in the moist substrate.

Table 1. Mean (± SE) daily maximum soil temperatures (2-cm depth) under different ground covers.

	Outside of Cage	Bare ground	Clump	Turf
2004	25.1a[1] ± 1.9	25.2a ± 1.3	25.0a ± 0.5	21.5b ± 0.4
2005	22.1a ± 1.9	20.5a,b ± 1.0	20.8a,b ± 0.8	18.6b ± 0.2
2007	20.1a ± 0.4	19.1a ± 0.5	16.9b ± 0.6	15.6b ± 0.5

[1] Means within a row followed by the same letter do not differ (Tukey's test).

temperatures, however, the grasshoppers did not appear to be very selective: the egg pods were fairly evenly distributed within this range.

Substrate moisture/temperature choice.—When given a choice between warm and dry or cool and moist substrate, *M. sanguinipes* of both populations generally avoided the dry substrate. Visual inspection of the data (Fig. 3) suggested that oviposition was not affected until temperatures on the cool and moist side were below 14°C: they curtailed oviposition rather than oviposit in unfavorable conditions (Fig. 3a). The interaction term in the ANCOVA, population by temperature, was not significant for number of pods produced and the proportion of pods in the cool/moist substrate ($F_{1, 12} = 0.1$, $P = 0.78$ and $F_{1, 12} = 0.4$, $P = 0.56$, for total number and proportion of pods, respectively) indicating similar responses to temperature and moisture by both populations. Consequently, the interaction term was removed from the ANCOVA model (Engqvist 2005). The temperature of the moist side significantly affected the total number of pods produced ($F_{1, 13} = 12.6$, $P = 0.0035$) and the proportion of oviposition that occurred on the moist side ($F_{1, 13} = 21.6$, $P = 0.0005$) (Fig. 3). There was no difference between populations of *M. sanguinipes* in total number of pods produced ($F_{1, 13} = 1.1$, $P = 0.31$), or the proportion of pods placed on the moist side ($F_{1, 13} = 1.3$, $P = 0.27$).

Field cages.—Grasshoppers in the field cages produced 211, 279, and 250 pods in 2004, 2005 and 2007, respectively. The relative number of egg pods produced by each population did not change between years ($\chi^2 = 5.84$, d.f. = 4, $P = 0.21$), with *M. borealis* producing a total of 241 pods over the three years, and *M. sanguinipes* from Alaska and Idaho producing 295 and 205 pods respectively.

The distribution of egg pods among the three ground-cover types (turf, clump, and bare ground) by all populations of grasshoppers combined, differed between years ($\chi^2 = 44.5$, d.f. = 4, $P < 0.001$). In 2004 greatest numbers of egg pods were found in the bare ground, but in 2005 and 2007 similar numbers of egg pods were found in the clump as in the bare ground (Fig. 4). Turf ground cover had the fewest egg pods in all years (Fig. 4) and had the lowest mean daily maximum soil temperatures (Table 1).

Plant species (barley *vs* ryegrass) had no effect on the distribution of egg pods among ground-cover types ($\chi^2 < 4.2$, d.f. = 2, $P > 0.1$ in all years), although *M. sanguinipes* from Idaho showed a tendency to lay more eggs than expected in turf ground cover when barley was grown, and less than expected in ryegrass turf ($\chi^2 = 5.6$, d.f. = 2, $P = 0.062$). Analysis of variance showed that position of subplots (east, center, west) within a cage had a significant effect on placement of egg pods ($F_{2, 158} = 5.8$, $P = 0.004$). The subplots on the east and west ends of the cages had more pods than did the center subplot (mean of 4.4, 3.1, and 1.6 pods in east, west, and center subplots, respectively). There were no significant interactions of year, grasshopper population, or cover type with position ($F_{4, 152} < 1.5$, $P > 0.25$).

There were significant differences among grasshopper populations in the distribution of egg pods among cover types (all years combined: $\chi^2 = 34.3$, d.f. = 4, $P < 0.001$). *M. sanguinipes* from Idaho was less selective in terms of ground cover than the Alaskan grass-

hoppers. Both species of Alaskan grasshoppers laid significantly more pods in the bare ground and clumped vegetation than in turf (Fig. 4) in each year (*M. borealis*: $F_{2, 15} = 11.6$, $P < 0.001$; $F_{2, 15} = 5.6$, $P = 0.015$; $F_{2, 15} = 7.8$, $P = 0.004$ in 2004, 2005, 2007 respectively; *M. sanguinipes* - Alaska: $F_{2, 15} = 15.5$, $P < 0.001$; $F_{2, 15} = 4.3$, $P = 0.033$; $F_{2, 15} = 31.4$, $P < 0.001$ in 2004, 2005, 2007 respectively), whereas, *M. sanguinipes* from Idaho laid similar numbers of egg pods in all ground cover types (Fig. 4) in all years ($F_{2, 15} = 0.2$, $P = 0.82$; $F_{2, 15} = 1.1$, $P = 0.37$; $F_{2, 15} = 1.4$, $P = 0.29$ in 2004, 2005, and 2007 respectively). Although it appeared that *M. sanguinipes* from Idaho laid fewer eggs in the turf than other ground-cover types in 2007 (Fig. 4), the high variance did not allow for statistically significant separation of means.

There was no difference in the distribution of egg pods among the cover types between *M. sanguinipes* from Alaska and *M. borealis* in any year ($\chi^2 = 1.3$, d.f. = 2, $P = 0.52$ in 2004; $\chi^2 = 1.8$, d.f. = 2, $P = 0.40$ in 2005; and $\chi^2 = 2.5$, d.f. = 2, $P = 0.12$ in 2007). Distribution of egg pods differed between *M. sanguinipes* from Alaska and from Idaho in 2004 ($\chi^2 = 26.1$, d.f. = 2, $P < 0.001$) and in 2007 ($\chi^2 = 7.1$, d.f. = 2, $P = 0.029$), but not in 2005 ($\chi^2 = 4.8$, d.f. = 2, $P = 0.089$). Distribution of egg pods differed between *M. borealis* and *M. sanguinipes* from Idaho in 2004 ($\chi^2 = 15.6$, d.f. = 2, $P < 0.001$) and in 2005 ($\chi^2 = 6.5$, d.f. = 2, $P = 0.045$), but not in 2007 ($\chi^2 = 0.2$, d.f. = 2, $P = 0.88$).

Discussion

All grasshoppers preferred substrate temperatures above 26°C. This is similar to the range of temperatures reported previously for *Locusta migratoria* (26-45°C) (Choudhuri 1956, Popov 1959) and *Nomadacris septemfasciata* (Woodrow 1965), suggesting this range of temperatures is widely applicable to many acridids. Examination of soil-temperature records from the interior of Alaska (Fielding & DeFoliart 2008) however, reveals that soil temperature, even at a shallow depth of 2 cm, rarely reaches this threshold. Results of the second experiment, which confronted grasshoppers with a choice between less than optimal temperature/moisture conditions, showed that oviposition was not affected until substrate temperature dropped below 14°C. Edwards and Epp (1965) also found that *M. sanguinipes* would refrain from oviposition, at least temporarily, if suitable substrate was not available. These results provide a guideline for habitat management practices that seek to reduce the availability of suitable oviposition microsites by manipulating ground cover and hence, soil temperature.

Both populations of *M. sanguinipes* responded similarly in the laboratory experiments. Stauffer and Whitman (2007) found that two closely related species, adapted to very different environments, differed in oviposition preferences. Many other traits differ between these two populations of *M. sanguinipes* from Idaho and Alaska, suggesting extensive adaptation to local environments. Therefore, it seems somewhat surprising that more differences were not detected in the laboratory experiments. In the field cages, *M. sanguinipes* from Idaho were less selective than either species from Alaska. These results suggest that differences in oviposition behavior in the field cages between the grasshoppers from Idaho and those from Alaska,
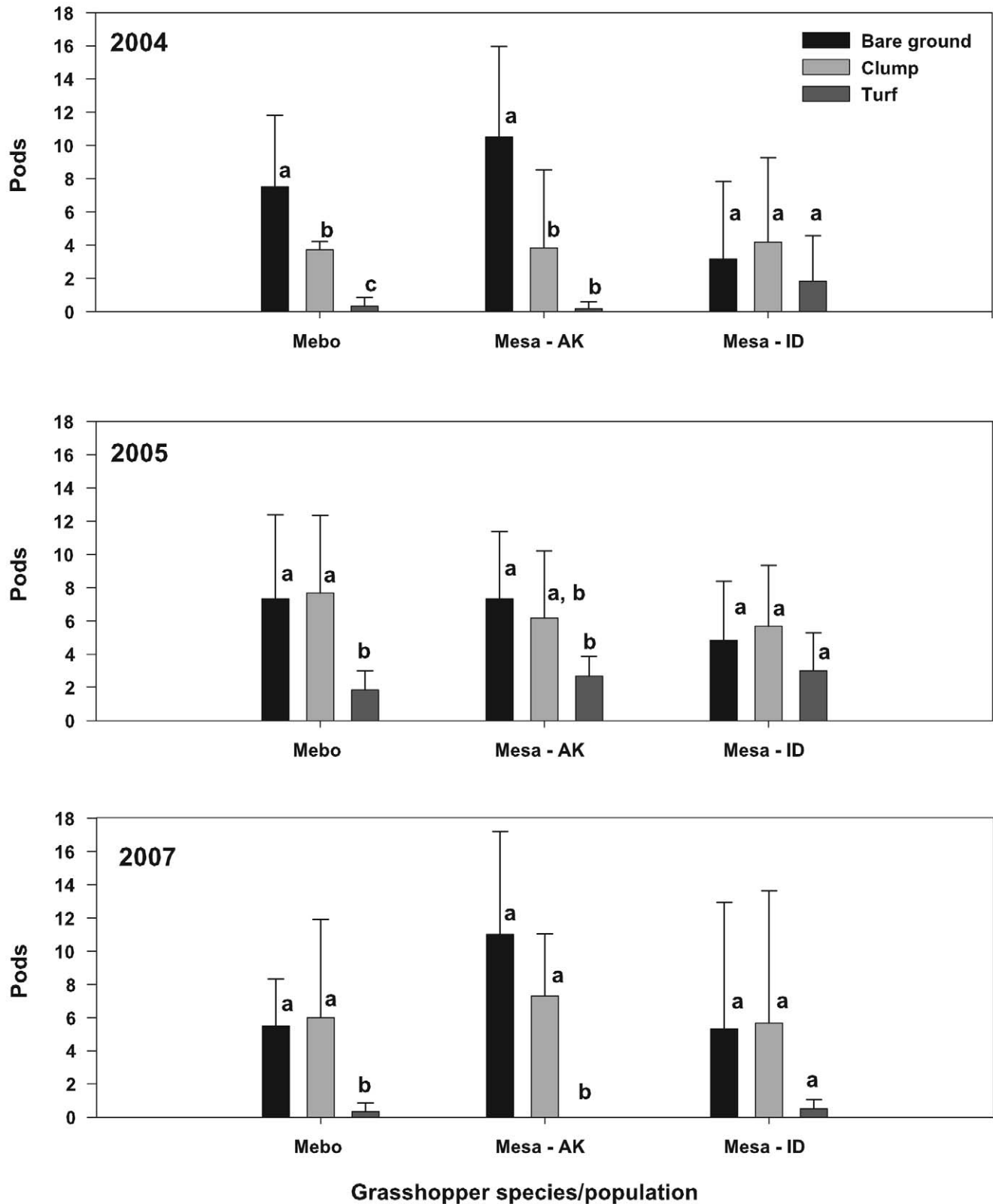
Fig. 4. Mean number of egg pods found under different ground-cover types. Error bars indicate one standard deviation. Bars with the same letter within a grasshopper population do not differ significantly (Tukey's test, $P < 0.05$).

may stem more from differences in the above-ground physical structure of the vegetation than from differences in below-ground temperatures, because no differences in temperature preferences among populations were observed under laboratory conditions.

The fact that oviposition is curtailed by a lack of suitable substrate suggests that habitat manipulations are a potentially effective tactic to limit populations in cool climates. Beckerman (2002) reported that populations of *M. femurrubrum* were lowest in fields with a high percentage cover by grasses, even though grasses were the preferred food for this species. Beckerman (2002) concluded that shading by grasses and the thick litter covering the ground, resulted in cooler soil temperatures that were not acceptable for oviposition. By promoting or establishing dense grass cover, or increased shading by shrubs, soil temperatures may be reduced to minimize the availability of acceptable oviposition microsites. The presence of predators (lycosid spiders) has been shown to impede the ability of grasshoppers to forage for food (Schmitz 1998, Danner & Joern 2004). Even if some microsites suitable for oviposition are available, making them more scarce could have the effect of causing the females to move about more as they search for oviposition sites, and thus make them more vulnerable to predation.

Establishment of dense vegetation may also induce grasshoppers to oviposit in a relatively small area, such as a field margin, where hatchlings may be more easily controlled. By concentrating oviposition in small areas of favorable habitat, less area would need to be treated to effectively control outbreak populations. In the field cages, the daily maximum temperature of the soil under the turf was 2 to 3 °C lower than that of the bare ground. These were small areas (30 × 30 cm) however, and larger areas may result in greater differences between cover types.

Knowing the physical parameters of preferred oviposition sites can provide guidelines for methods of habitat management that reduce the availability of suitable oviposition sites. Further research is planned to determine the effect of various ground and canopy covers on soil temperatures, to provide more reliable recommendations for the management of grasshopper populations.

Acknowledgments

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