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Natural History of Mass-action in Predator-prey Models: A Case Study from Wolf Spiders and Grasshoppers

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ABSTRACT.—Mass-action models of predator-prey interactions assume that predators encounter prey according to their relative densities as scaled by functional responses, although models seldom specify critical natural history and behavioral mechanisms that ensure that encounters actually occur. As a case study of this assumption, we assess the hypothesis that daily and seasonal activity and microhabitat use by wandering wolf spiders (Lycosidae: *Schizocosa*) searching for four common grasshopper species (Orthoptera: Acrididae) are coincident under natural conditions. There was great overlap in seasonal phenology and use of microhabitats between spiders and grasshoppers. Grasshoppers that were suitably sized (10–20 mm in length) as prey for spiders were relatively abundant from late spring through summer in this grassland. Three of the four common grasshopper species used microhabitat in a similar way, but differed from a fourth common species, *Phoetaliotes nebrascensis.* However, when they were active, spiders were about equally distributed between open microhabitats on the ground and up in the vegetation so that all grasshopper species were at risk. In response to temperature, spiders were active for only a portion of the day during which grasshoppers were also active so that the actual daily "window-of-opportunity" for capture each day was much smaller than expected. Spiders were more likely to be active during the early morning and evening, while grasshoppers were active during all daylight hours, most likely because of differences in thermal preferences. *Schizocosa* and their grasshopper prey are largely coincident in time and space except for overlap in daily activity which, presumably, reflects differences in thermal preferences. Consequently, overlap in daily time budgets that ensure actual encounter was reduced about 50%. The significance of this difference to the inclusion of simple mass-action dynamics in predator-prey models requires further consideration, but may be important.

INTRODUCTION

Predator-prey models have been very helpful for developing our understanding of the dynamics of interacting populations of predators and prey. Ecologists assess Lotka-Volterra style predator-prey models by modifying mathematical formulations of functional responses, density-dependent feedbacks in prey populations and predator mortality (Holling, 1965, 1966; Rosenzweig, 1971; Hassell, 1978; Gurney and Nisbet, 1998; Case, 1999), and then

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compare changes in the outcomes of species population dynamics or equilibrium states. Multiple prey species and other factors that alter encounter rates are sometimes included to illustrate specific factors (Hassell, 1978; Gutierrez *et al.*, 1994; Gutierrez, 1996; Murdoch *et al.*, 2003), but models are generally kept simple to make them tractable.

Most models rely on mass action dynamics between predators and prey in which the probability of encounter reflects the joint densities of the two species. In such models, mass action is depicted by multiplying prey and predator densities with the assumption that each individual of either population has the same expectation of random encounter. Yet, conceptual and empirical studies that rely on the natural history underlying predator-prey interactions are replete with anti-predator adaptations by prey and countermeasures by predators that alter the likelihood that predator and prey populations actually encounter one another in the field (Cott, 1940; Wickler, 1968; Curio, 1976; Orians, 1981; Gendron, 1983), even if they are generally in the same habitat at the same time. Moreover, arthropod predator-prey interactions are greatly affected by temperature (Logan and Hilbert, 1983; Gutierrez *et al.*, 1994; Gutierrez, 1996; Ritchie, 1996; Logan and Powell, 2001; Rochat and Gutierrez, 2001; Thomas and Blanford, 2003), conditions that can greatly alter the mass action dynamics, but are seldom included in models.

As ectotherms, temperature can critically affect ecological interactions among arthropods. Seasonal appearance and developmental rates are strongly temperature-dependent, affecting seasonal phenologies of coexisting species (Wolkind and Logan, 1978; Logan and Hilbert, 1983; Logan and Powell, 2001; Gilbert *et al.*, 2004). Daily activity is also temperature-dependent, affecting time budgets and, thus, the likelihood of encounters by predators with prey. Because preferred temperature optima can differ among species, predators and prey may be most active at different temperatures (Perring *et al.*, 1986; Thomas and Blanford, 2003). Some evidence already suggests that temperature preferences of spiders are often lower than those of grasshoppers (Li and Jackson, 1996; Schmitz, 1998), which would potentially decrease the overlap in daily activity time budgets. Because microhabitat selection is strongly temperature-dependent, changes in temperature profiles over the day and their affect on the ability of individuals to thermoregulate will potentially alter which microhabitats are actually used by different species (van Hook, 1971; Kingsolver, 1983, 1989; Kemp, 1986; Chappell and Whitman, 1990; Lactin and Johnson, 1996). Consequently, microhabitat use by predators and prey may or may not be coincident, depending on temperature, and active selection of microhabitats may vary during different times of the day for both spiders and grasshoppers.

Given all of the factors that affect the distribution of arthropods in time and space, how appropriate is the basic assumption of mass-action for studying predator-prey interactions? Does the natural history of participants in such interactions provide critical insights that require major modifications of predator-prey models or does it provide interesting, but extraneous, ecological detail that can be largely ignored without compromising general conclusions? We present a case study of factors influencing habitat use and seasonal appearance to assess and characterize the likelihood of encounter of wandering wolf spiders (Lycosidae: genus *Schizocosa*) searching for grasshopper prey (Orthoptera: Acrididae) in grassland. We document the likelihood of local co-occurrence of *Schizocosa* and dominant grasshopper nymphs in the same habitat, patterns of daily temporal coexistence, similarities in responses to microclimatic conditions, size distributions of prey relative to predator capabilities, distribution of densities of spiders and grasshoppers over the season and behavioral interactions between spiders and grasshoppers that could affect the functional response. If mass action is an ideal representation of grasshopper-spider interactions, we hypothesize that there will be no differences in temperature-dependent activity patterns on a seasonal and daily basis, and that microhabitat use of grasshoppers and spiders will be coincident.

METHODS

STUDY SITE

Research was performed from late-April through August 2003 at Cedar Point Biological Station (University of Nebraska–Lincoln) located in Keith County, Nebraska. Structural aspects of the microhabitat are highly variable, reflecting vegetation attributes. Grasses comprise about 80% of the vegetation biomass at the site, interspersed with extensive bare areas, some forbs, small shrubs and patches of junipers. The short grasses *Bouteloua gracilis* (blue grama grass) and *Buchlöe dactyloides* (buffalo grass) predominate. Rotational grazing by cattle occurs every late-summer and fall. All studies were performed prior to grazing.

GRASSHOPPER SAMPLING

Phenological dynamics of grasshopper species was determined by sampling twice weekly using Onsager's (1977) ring method. Twenty-five 0.1 m^2 rings were randomly placed along four 100 m transects no closer than 2 m from each other at five locations each separated from the others by a kilometer. Total grasshopper density (all species) was estimated by counting the number of individuals in each ring on sunny days when wind speed was less than 0.45 $m\ s^{-1}$ and air temperature greater than 25 C. Density of each grasshopper species at the site was estimated by multiplying total density from ring samples by the relative abundance of each species, obtained with sweep samples. Abundance of grasshopper species was estimated from sweep samples along transects located about 200 m from density transects. Fifty sweeps per transect were taken twice a week. Relative abundance and developmental stage of each species was determined by multiplying relative abundance by total grasshopper density. Distribution of total body length over the growing season was measured to the nearest millimeter using digital calipers.

SPIDER SAMPLING

Spiders were sampled at weekly intervals using pitfall traps arrayed in grids located near grasshopper sampling transects. At each site, 100 pitfall traps (~10 cm diameter plastic cups) were buried flush to the ground in a grid at 3 m intervals in mid-May. Traps were opened for 24 h each week and abundance and body length of each spider was recorded. Spiders were released immediately after measurements. Sites used for grasshopper transects and spider pitfall grids were ~1 km apart, including an area of dense cedar trees. A woody barrier, distance between sites and the natural history of these spiders (Kaston and Kaston, 1953; Li and Jackson, 1996) make it unlikely that individual spiders moved between sites.

Spider densities were estimated over one week in early July during which time pitfall traps were left uncovered and checked daily and spiders marked and released at each site. A small drop of Testor's® non-toxic model paint was placed on the cephalothorax of each captured spider, using different colors on different days. Multiple captures were characterized by color combinations and different colors were used at the two sites. Capture-mark-release-recapture data were used to estimate the density of the spider predators at each site.

BEHAVIORAL OBSERVATIONS: ACTIVITY PERIODS AND MICROHABITAT USE

Changes in activity and microhabitat use throughout the day for each species were determined through extensive observation on 11 d, spaced at about weekly intervals from mid-June to mid-August. Activity and microhabitat use by different individuals of the four grasshopper species and *Schizocosa* was recorded throughout the day while slowly walking along parallel transects no closer than 10 m apart. On locating an individual, species identity and developmental stage were recorded and microhabitat characterized, including the structural aspect of microhabitat (open ground or in/on vegetation) and height above ground if on vegetation. Temperature (C) was measured at reference height (2 m) and at the specific location of the grasshopper (microhabitat) using a shaded thermocouple embedded in a hypodermic needle attached to an Omega™ electronic ice reference and hand-held multimeter. Behavioral observations of grasshoppers and spiders were made during randomly scheduled 3-h periods between 0600–2100 h over several days throughout the summer. No observations were taken on days with heavy cloud cover, or on exceptionally cold or hot days.

STATISTICAL ANALYSES

Descriptive analyses of grasshopper and spider responses were performed using Base SAS or the SAS/STAT packages (Version 9.1). Analyses of spider and grasshopper behavior used R (release 2.1), a public domain statistical software package.

Observations were analyzed using contingency tables to describe relevant patterns. Ambient and microhabitat temperatures were recoded as one of three categories: microhabitat with higher or lower temperature relative to ambient air temperature or equal when temperatures differed by less than ±1.0 C. Three grasshopper species (*Ageneotettix deorum* (Scudder), *Melanoplus sanguinipes* (Fabricius) and *Amphitornus coloradus* (Thomas) selected similar microhabitats and were treated as a single group. *Phoetaliotes nebrascensis* (Thomas) behaved differently from other species and was treated separately. Categories in the analyses included: developmental stage (adult vs. nymph, I), orientation to incoming solar radiation (perpendicular vs. parallel, O), activity (active vs. quiescent, B), microhabitat temperature relative to ambient air temperature (higher vs. equal or lower, T) and habitat use (on vegetation vs. ground, U). Except for including developmental stage, the same variables were used for spiders. Log-linear models designed to evaluate cell counts in contingency tables in an interactive fashion were constructed for spiders and grasshoppers.

Poisson loglinear modeling with a log link function was used in contingency analyses. We modeled contingency table cell counts as a function of the four (spiders) or five (grasshoppers) variables using the approach of Agresti (1990, 1996). Main effects were fit first, followed by main effects and a two-way interaction, continuing to the fully saturated data set. Likelihood ratio statistics were used to determine initially which model alternative was sufficient. After choosing a starting level, forward variable selection was employed and higher-order interactions were added individually, until no terms added increased precision to the model. In this approach, the best model is one that does not differ significantly from the data. Model results were then interpreted using odds ratios of relevant two and three-way associations.

RESULTS

GRASSHOPPER DENSITIES

Between late-May and mid-August 2003, grasshopper density varied as shown in Figure 1. A maximum density of nearly $30/m^2$ was observed during the first week of July. Four species (*Ageneotettix deorum,* 37.5%; *Phoetaliotes nebrascensis,* 19.3%; *Melanoplus sanguinipes,* 4.5%;

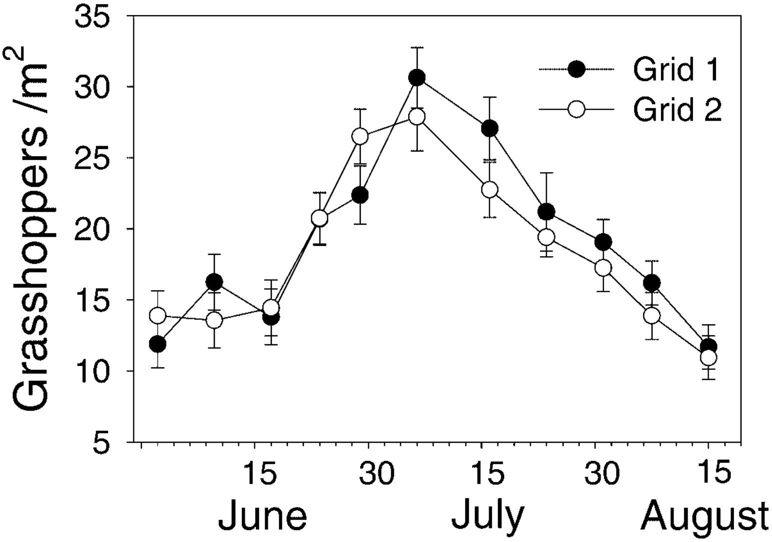


FIG. 1.—Grasshopper densities estimated at approximately weekly intervals (mean ± 1 SE) at two sites

O. and *Amphitornus coloradus,* 7.7%) were generally most abundant of 36 species that were observed at all sampling sites over the summer.

Schizocosa spp. are size-selective more than species-specific predators (Oedekoven and Joern, 1998). For spiders studied in this system, grasshoppers 10–20 mm in length are most at risk (Oedekoven and Joern, 1998; Danner and Joern, 2003). The distribution of size class availability of prey over the season (Fig. 2a) indicates the likelihood that spiders will encounter prey of suitable size over the season. During June, samples were primarily dominated by grasshoppers up to 10 mm in length. The distributions of these size classes begin to shift slightly in July as grasshoppers develop and grow rapidly. However, the estimated composition of grasshopper size classes from the month of July through the middle of August remains dominated by animals between 10–20 mm in length, all acceptable size as potential prey items for wolf spiders here (Fig. 2a). Smaller individuals late in the season include grasshopper species that hatch in August.

SPIDER SIZE DISTRIBUTION AND DENSITY

Observations of adult spiders were spread out over the field season (early June through mid-August). Spider size was relatively constant across the summer, fluctuating somewhat around a mean length of approximately 11 mm (Fig. 2b); the size of spiders did not vary significantly as summer progressed ($F_{8,156} = 1.36$, $P = 0.22$). The range of spider lengths in our collections from pitfall traps was 5.0–23.2 mm.

A mark-recapture study conducted between 15–22 July collected 55 spiders in grid 1 and 50 in grid 2. At grid 1, 6 of the spiders were recaptured, and 7 were recaptured on the second grid. No spiders were re-captured more than once. Total population size at each grid was estimated using maximum likelihood to solve a series of hypergeometric distributions (Thompson, 2002). Assuming a mostly closed population, we estimate population size as 201 spiders in grid 1 and 137 spiders at grid 2, or densities of approximately 0.28 spiders/m^2 and 0.19 spiders/m^2 in grids 1 and 2, respectively.

TABLE 1.—Summary of log-linear contingency table modeling for the three models proposed here. Likelihood ratio test statistics and associated P-values presented for the single (mutual independence) and associations (2nd–4th interactions). A non-significant P-value represents models that are not significantly different from the contingency table cell counts themselves. Adding terms sequentially through forward selection (signified as ****) increased model precision, and Pearson residuals of modeled data were assessed to insure all cells were sufficiently predicted

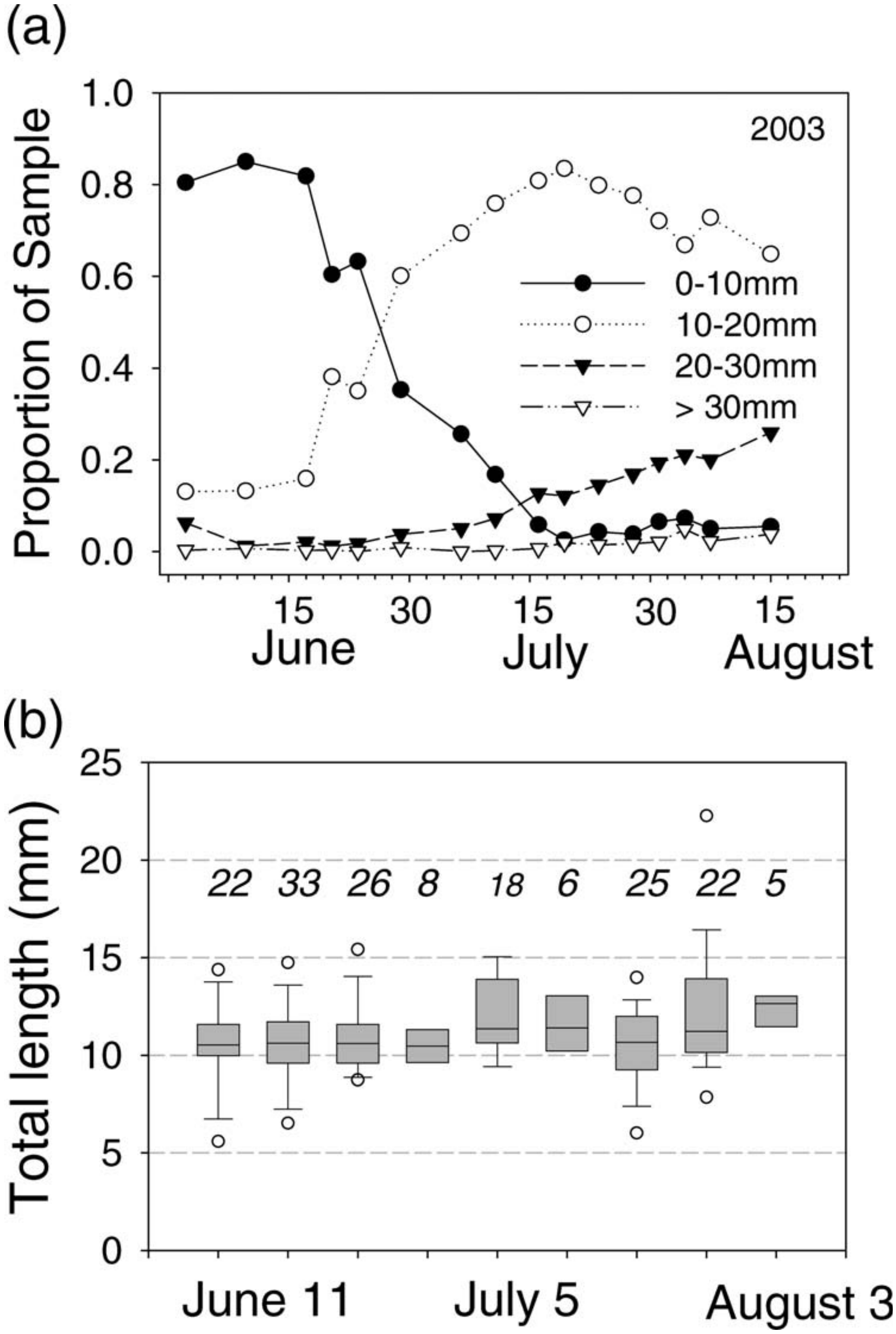
Model	G^2	df	P-value
Spiders			
(B,O,T,U)	15.3	11	0.17
(BO,BT,BU,OT,OU,TU)	6.9	5	0.23
(BOT,BOU,BTU,OUT)****	0	1	0.99
Final Model			
(BT,O,U)	11.0	10	0.36
Grasshoppers-3spp.			
(B,O,T,U,I)	119.6	26	<0.01
(All two-way associations)	13.6	16	0.63
(All three-way associations)****	5.7	6	0.45
(BI,BU,IU,IO,IT,BO,OT,BT)****	15.7	18	0.61
Final Model			
(BIU,BOT,IO,IT)	11.5	16	0.78
P. nebrascensis			
(B,O,T,U,I)	67.4	26	<0.01
(All two-way associations)	19.1	16	0.26
(All three-way associations)****	4.5	6	0.61
(BT,BU,IT,IU,OT,TU)****	21.7	20	0.36
Final Model			
(BUT,IUT,OT)	20.4	18	0.31

ACTIVITY AND MICROHABITAT USE

We observed 1439 grasshoppers and 79 lycosid spiders in their natural habitat throughout the day. Three grasshopper species (*Ageneotettix deorum,* Ad; *Amphitornus coloradus,* Ac; and *Melanoplus sanguinipes,* Ms) showed similar patterns of behavior and microhabitat use, while *Phoetaliotes nebrascensis* (Pn) exhibited different behavior. Approximately 68% of the *A. deorum, A. coloradus* and *M. sanguinipes* individuals were observed on the ground (Ad: 69%, Ac: 73%, Ms: 62%) while only 42% of *P. nebrascensis* were observed on the ground. Separate contingency models (Table 1) are developed for these two groups based on 189 observations for *P. nebrascensis* and 1250 observations for the three grasshopper species group.

Using forward variable selection, log-linear models were constructed to characterize the association between behavior (activity, orientation, habitat usage) and state variables (developmental stage and relative temperature) of the spiders and the grasshoppers. After removing independent associations between variables through forward variable selection and examining Pearson residuals, resulting contingency tables were interpreted using association graphs (Fig. 3) and odds ratios.

For the three grasshopper species combination, the best model to explain associations in the contingency table following the notation of Agresti (1990, 1996) is (Table 1):


(a)
Proportion of Sample
1.0
0.8
0.6
0.4
0.2
0.0
2003
0-10mm
10-20mm
20-30mm
> 30mm
15
30
15
30
15
June
July
August
(b)
Total length (mm)
25
20
15
10
5
0
22
33
26
8
18
6
25
22
5
June 11
July 5
August 3

$$B*I*U + B*O*T + I*O + I*T,$$

where 2 significant three-way interactions (including the 3 hierarchically nested two-way effects in each) and 2 two-way interactions satisfactorily explain the data, in contingency table format ($\chi^2 = 12.0$, $P = 0.74$, LRT $G^2 = 11.5$, $P = 0.78$). Using odds ratios to interpret the results of this model (Fig. 3), the odds of a grasshopper utilizing microhabitat with a higher temperature than ambient air was 1.5 times higher as an adult (the I*T interaction), the odds of orienting to the sun in a perpendicular posture 1.4 times higher as a nymph (I*O), the odds of exhibiting active behaviors on the ground 1.4 times higher as adults (B*I*U) and the odds of exhibiting active behavior while holding a perpendicular orientation to the sun 1.4 times higher when microhabitat temperature exceeded ambient air temperature (B*O*T) (Fig. 3a). Alternatively, three-way interactions indicate the odds an adult exhibits quiescent behavior is 2.2 times higher on the ground (B*I*U) and the odds of exhibiting quiescent behavior while holding a perpendicular orientation to the sun 1.8 times higher when microhabitat temperature exceeded ambient air temperature (B*O*T).

The association of contingency variables was slightly different for *Phoetaliotes nebrascensis* (Table 1, Fig. 3b). The final model after forward variable selection is:

$$I*U*T + B*U*T + O*T.$$

Two significant three-way associations (including the 3 hierarchically nested two-way effects in each), and 1 two-way association explain the data in contingency table format ($\chi^2 = 14.8$, $P = 0.67$, LRT $G^2 = 14.6$, $P = 0.31$). For *P. nebrascensis*, the odds of an observed grasshopper orienting perpendicularly to the sun were 3.1 times higher when microhabitat temperature was less than or equal to ambient air temperature (O*T), the odds an adult would utilize vegetation were 1.4 times higher when microhabitat temperature exceeded ambient air temperatures (I*U*T), and when found on the ground, the odds of engaging in active behavior were 2.5 times higher when microhabitat temperature exceeded ambient air temperature.

The best model to characterize the wolf spider activity contingency tables is:

$$B*T + O + U,$$

where one significant two-way association (between behavior and relative temperature difference), along with orientation and habitat use independent of other factors, was satisfactory to explain the contingency table cells ($\chi^2 = 8.7$, $P = 0.56$, LRT $G^2 = 11.0$, $P = 0.36$). Here, orientation to incoming solar radiation and habitat use is independent of the

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FIG. 2.—Distribution of grasshopper size over the season. (a) All grasshoppers captured during relative abundance sweep sampling were identified and length determined. Lengths were recorded to the nearest millimeter, but are presented here using three size classes, corresponding to risk to predation by *Schizocosa*. Furthermore, the 30–45 mm size class is not presented; it never composed greater than 5% of the sample composition (but towards the end of the summer reached nearly 4%), and this size class has been determined to be a highly unlikely prey class available for spider consumption. (b) Box-plot graph displaying lengths of spiders caught using pitfall trapping grids. Weekly sample sizes are presented in *italics* and outliers are represented with open circles. Lines within the bars represent the median length for that week of the study. One-hundred-sixty-five spiders were measured over the entirety of the summer in this study, and we found that although there was a slight increase in size across the summer, the differences were not statistically significant

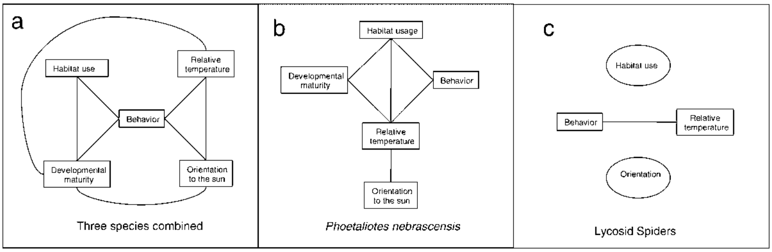

FIG. 3.—Association graphs representing the relationship between the various discrete observations recorded for spiders and grasshoppers in their natural environment. Lines connecting variables signify that there is statistically significant dependence between these variables of interest, and that the magnitude of the response may be assessed by 'collapsing' over the levels of the other variables in the scheme, or contingency table. In 3c, ovals represent factors in the model that were found to be independent of all other variables

other two factors (Table 1, Fig. 3c). Specifically, 87% of observed spiders were located on the ground rather than on vegetation, and orientation to the sun did not differ between a perpendicular (44%) vs. parallel or oblique orientation (56%). The odds of observing a spider exhibiting active behavior was 2.7 times higher when microhabitat temperature was less than or equal to ambient air temperature.

Of the 79 observed spider encounters, only 16% occurred between 1100–1700 h, typically the hottest portion of the day. Of the remaining 66 encounters, 48 (61%) occurred between 0600–1100 h, and the rest (23%) occurred in the evening when temperatures drop rapidly. In a complementary sample to these data where spiders were tracked over a period of one day, similar results were obtained: 18 of 33 (55%) encounters occurred during the early morning window, and 9 of 33 (27%) occurred during the evening when temperatures were dropping. Of the more than 1400 grasshoppers observed, grasshoppers were active throughout the day once microhabitat temperatures were above about 22 C.

DISCUSSION

Experiments document that spiders can effectively limit prey populations under many conditions (Schmitz, 1993; Wise, 1993; Chase, 1996; Beckerman *et al.*, 1997; Schmitz, 1997; Schmitz *et al.*, 1997; Oedekoven and Joern, 1998, 2000; Danner and Joern, 2003, 2004), indicating that predator-prey interactions and models based on these responses are important. Many of these same studies also indicate that interactions can be complicated by a variety of external conditions such as vegetation structure or temperature (Riechert and Tracy, 1975; Chase, 1996), and the effect of predators on prey may reflect shifts in microhabitat and reduced feeding rather than direct feeding by spiders on prey (Beckerman *et al.*, 1997; Schmitz *et al.*, 1997; Abrams and Schmitz, 1999; Danner and Joern, 2003). Clearly many factors mold the interactions between predators and prey. Delineating natural history of participants will provide important insights regarding the use of mass action interactions in predator-prey models. If seasonal and daily activity periods and patterns of microhabitat use by grasshoppers match that of the spiders, and if grasshopper sizes that can be readily handled by spiders are available throughout the growing season, mass-action seems to be justified in a modeling context. And of course, a sufficient density of grasshoppers throughout the season is expected. What do our results suggest in this regard?

Grasshoppers of an appropriate size to be prey were available and abundant throughout the field season. Recorded density of grasshopper prey during the summer of 2003 was typical for this site (Joern, pers. obs.), culminating at the time when most late-season species were fully completing the hatching period (Fig. 1). Encounters and captures of spiders in pitfall traps occurred consistently across the summer, and the estimate of one *Schizocosa* every 4–5 m^2 is a reasonable density projection of the spider population size that is capable of limiting grasshopper prey in grasslands (Logan *et al.*, 2006a). The composition of grasshopper size classes across the summer (Fig. 2) further demonstrates a nearly constant pool from which spiders draw their prey; this pool is made up of different species over the summer. There is no evidence from this study that spider and grasshopper phenologies are offset in such a way to reduce encounter rates at critical portions of the growing season. While phenologies of grasshoppers and spiders are temperature-dependent (Kemp and Onsager, 1986; Kemp and Dennis, 1991; Li and Jackson, 1996) suggesting the opportunity for seasonal phase shifts between species, responses by grasshopper (and presumably spider) life histories to temperature differences are evolutionarily malleable (Atkinson and Begon, 1988). There should be strong selection pressure on spiders to remain in synchrony with prey dynamics, including the grasshopper populations here which are the most common prey available. Our data indicate that phenologies of spiders and grasshoppers were coincident.

Are spiders and grasshoppers active at the same time of day? Active grasshoppers were observed throughout the day throughout the summer. Spiders were not actively hunting during the hottest portions of the day even though grasshoppers are active, reducing the total time they have to forage, as also discussed by Li and Jackson (1996). Discounting the possibility for spider foraging at night when grasshoppers are not active, spiders in this study rely on about a 6–8 h window of opportunity to actively seek and consume their prey. This corresponds to about half of the time over which grasshoppers may be active each day in summer, although there may be better correspondence in daily activity in spring and fall. As temperatures increase throughout the season or in overall response to global climate change, the overlap of activity times and the likelihood of successful predator-prey encounters will be reduced. Regression models describing activity differ between spiders and grasshoppers, supporting the conclusion that daily activity patterns are not those predicted in a simple mass action scenario. We do not have data to assess the likelihood of spider predation on grasshoppers at night, but believe it to be minimal. The spiders are visually hunting spiders, making nighttime foraging difficult, and grasshoppers often move to inaccessible parts of the vegetation at night, presumably to minimize encounters with predators.

What is the impact of spider predation on grasshoppers if joint activity of spiders and prey on a daily basis is reduced in response to temperature, even though they are otherwise coincident in seasonal appearance and microhabitat use? In a modeling framework, one can modify functional responses to account for such reduced probability of encounter rate (Logan *et al.*, 2006a). Our model simulations indicate that the quantitative details of temperature effects on both phenologies (especially those that reduce the development time during vulnerable stages and exposure to spider predation) and the actual encounter window on a daily basis determine the ability of spiders to limit grasshopper abundances. These influences are temperature-based, and their importance further supports the quest for physiologically-based modeling (Metz and Diekmann, 1986; Gutierrez, 1996; Ritchie, 1996; Pitt, 1999). In arthropod predator-prey interactions such as the *Schizocosa*-grasshopper nymph system studied here, temperature-dependence and joint activity as they influence encounter rates are critical components to be incorporated into the mass-action term, but for non-obvious reasons.

Given the complexity inherent in this system, future consideration of the interactions between spider predators and grasshopper prey should include or at least be aware of behaviorally mediated pathways, and how these are related to microhabitat temperatures. Any extrapolation to predict grasshopper densities and subsequent impacts on grassland functioning must consider a similar approach. Although grasshoppers were available for spider consumption on a nearly continuous basis throughout the summer, slight shifts in the development and growth of prey could have the potential to have significant consequences (Logan *et al.*, 2006a).

Spider-grasshopper interactions can be viewed at seasonal and daily temporal scales; mass action is an appropriate representation at the longer temporal scale given the high degree of overlap in time, space and appropriate sizes. What about the differences observed at short time scales? One cannot reject the use of mass action between predators and prey merely by showing that daily activity patterns are not concordant. For example, if spiders are normally satiated in the short period of the day in which their activity overlaps with grasshoppers, then additional time is not needed to find prey to satisfy nutritional needs until food is digested – perhaps the next day. If this is the case, then mass action is an appropriate representation of the interaction, at least qualitatively.

We explored these issues using discrete dynamical models of this predator-prey interaction, which incorporated the effects of temperature and joint activity distributions of grasshoppers and spiders (Logan *et al.*, 2006a, b). Increasing the average daily temperature resulted in increased numbers of adults, primarily because of the effects of temperature on nymphal developmental rate and survival independent of spider predation (Logan *et al.*, 2006a). Reductions in joint activity also can be important to grasshopper survival. However, this was not because of lower direct mortality from spider predation, however. Rather, the presence of spiders alters grasshopper activity, leading to increased vigilance and reduced feeding, which then lowers survivorship (Schmitz *et al.*, 1997; Schmitz, 1998; Danner and Joern, 2003, 2004). Such behaviorally mediated shifts in activity by prey after exposure to predators are not uncommon for many species (Lima, 1998). After the direct effects of temperature on grasshoppers are accounted for in dynamic models of the grasshopper-spider interaction, vigilance influences greatly the survival of grasshoppers (Logan *et al.*, 2006b). Obviously, vigilance will only be important during the periods of the day when spider activity corresponds to grasshopper activity. Thus, mass action as a description of predator-prey interactions is incomplete insofar as the behavioral effects of predators on prey are ignored. The degree of joint activity between spiders and grasshoppers then becomes important. Under the assumptions of this model, mass action is appropriate when prey do not respond behaviorally to the presence of predators, but probably not when behavioral shifts by prey from foraging to vigilance are common. Clearly, the natural history of a predator-prey interaction can determine the legitimacy of mass action models.

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