THERMAL BALANCE AND PREY AVAILABILITY: BASES FOR A MODEL RELATING WEB-SITE CHARACTERISTICS TO SPIDER REPRODUCTIVE SUCCESS[1]

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Abstract. Analyses of the movements and web-site characteristics of the desert spider *Agelenopsis aperta* (Gertsch) demonstrate that web locations offering the following habitat features are actively selected: shrubs, depressions, litter, and flowering herbs. A model of the effects of the thermal environment and prey avalability on the reproductive success of spiders occupying various web-site types is developed. The estimated productivity for an excellent web site (grassland depression with attractants) is 13× that determined for a poor site (lava surface). Model results suggest that more energy is to be obtained from selection of a favorable thermal environment (eight-fold difference) than from a site offering greater numbers of prey (two-fold difference). The presence of flowers at web sites increases the probability of receiving an occasional high prey density, whereas litter and habitat features providing shade (shrubs and depressions) allow increased spider activity through limitation of body temperature.

Key words: Agelenidae; Agelenopsis aperta (*Gertsch*); *Araneae*; *energetics*; *habitat selection*.

INTRODUCTION

A definite pattern observed in the local distribution of animals can signify the underlying adaptations of individuals to their physical environment. Within a diverse group, those individuals that find suitable locations not only increase their chances of survival to maturity, but also are likely to contribute the greatest number of offspring to the next generation (i.e., exhibit greater fitness: Williams 1966, Pianka 1974). Therefore, the genotypes of individuals demonstrating greater habitat discrimination will predominate. This adaptation by the majority of the individuals to selection of favorable habitat is reflected in the local pattern of the population.

Agelenopsis aperta (Gertsch) is a member of the funnel web-building spider family, Agelenidae (Araneae). The web consists of a flat sheet with an attached funnel extending into some feature of the surrounding habitat. Occasionally a scaffolding is present. The sheet has no adhesive properties and serves merely as an extension of the spider's legs. *Agelenopsis* carries out much of its activity within a sheltered environment, coming out of the funnel only as long as required for securing prey and repairing the web. Study of the local distribution of this spider has demonstrated the presence of patterns

related to three functions: social, reproductive, and vectorial (Riechert et al. 1973, Riechert 1974*b*). A vectorial pattern is influenced by factors of the external environment (e.g., gradients of temperature and humidity, Hutchinson 1970) and in this context is observed in the association of spiders with specific habitat features. For the funnel web spider, at least, this association does not result from differential survival of randomly dispersed individuals, but rather reflects the active selection of specific web-site characteristics by the spiders (Riechert 1973). We postulate that individuals, in selecting certain habitat characteristics, are more fit than those showing less, or erroneous discrimination. In this paper, we assess the relationship between the presence of various web-site characteristics and the reproductive success of individuals at web sites offering these characteristics.

HYPOTHESIZED RELATIONSHIP

Regardless of the abundance of insects, a thermally unsuitable web location characterized by excessive thermal variability will limit the time spent by the the spider on the web sheet in prey retrieval. If the spider raises the web sheet off the substrate to avoid unfavorable thermal environments near the surface, wind damage to the sheet could be such that excess energy must be expended for web maintenance. This might offset any benefit accruing to location in an area of insect abundance. On the other hand, increasing the length of time a spider is able to spend on its sheet in prey capture is of little use if no prey are encountered.

The postulated relationship between web-site success (measured by individual fecundity) and the fac-
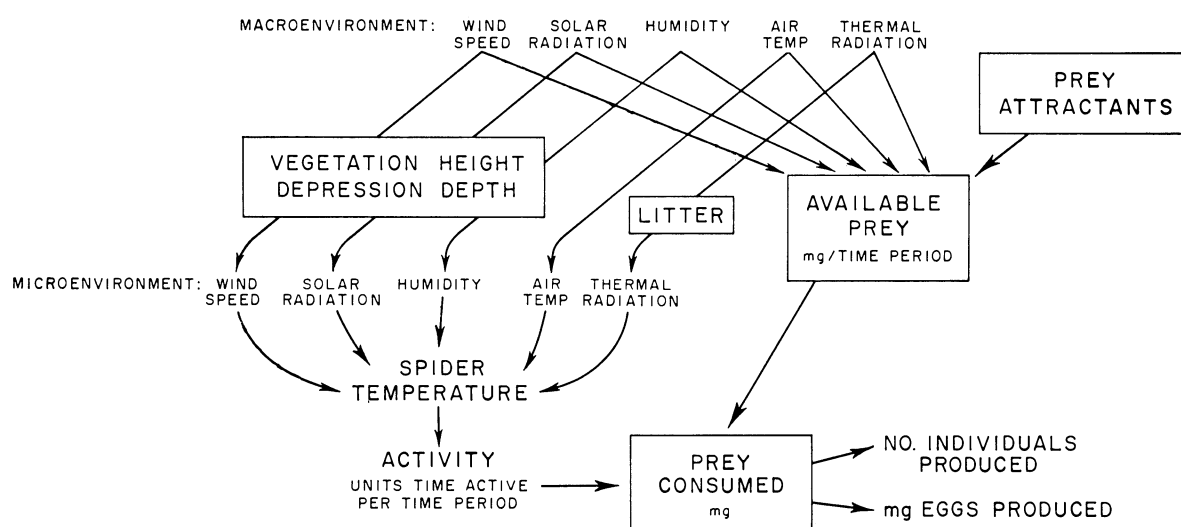
FIG. 1. Hypothesized relationship between web-site character and individual reproductive success. Solid lines indicate direct parameter effects on quantities or functions.

tors of thermal balance and prey availability are diagrammed in Fig. 1.

Parameters of the physical environment likely to affect the body temperature of an ectotherm include wind speed, humidity, air temperature, and solar and thermal radiation. Certain web-site characters modify these physical conditions of the environment. Thus, the height of the vegetation surrounding the web or the depth of the depression in which a web is situated will affect wind velocity, humidity, and the amount of solar radiation experienced by the spider at the web location. The substrate may also influence the local environment through its thermal radiative properties: if litter is present, energy input to the spider from thermal radiation may be considerably less than from a hot lava or bare ground substrate. All of these environmental parameters affect spider body temperature, their individual contributions in part being determined by physical parameters of the spider itself. Thus, lethal temperature boundaries and limits on activity are determined by the interrelationship of the spider and the microenvironment with which it is associated; this interrelationship prescribes the time period during which individuals can engage in capture of prey.

The characteristics of the web site may also influence the numbers and types of prey hitting the web. Of the total potential prey inhabiting the area, the behavior and microhabitat requirements of some are such that they may never contact an *Agelenopsis* web. Thus, at any given time the numbers and taxa of the prey actually available to *Agelenopsis* are determined largely by the characteristic behavior and habitat requirements of prey species and by general meteorological conditions. Since most of the insects likely to contact an *Agelenopsis* web are moving to the web from areas outside the immediate vicinity, prey activity may be more closely correlated to macroenvironmental conditions than to physical conditions existing precisely at the local site. However, the presence of flowers and fecal material at a web site may attract some taxa, and thus, attractiveness of the web site must be considered a factor that possibly influences the number of available prey (Fig. 1).

The amount of prey consumed at a web site is considered directly related to the number of insects available and the amount of time the individual can spend on its sheet securing prey during any given period. In turn, the total food consumption by the individual is expected to determine the number and weight of offspring produced.

THERMAL BALANCE

Chapman (1928) discussed the problems encountered by ecologists dealing with environmental effects on animal systems. Paramount is the difficulty of integrating a multitude of environmental attributes into a single measure or set of measures that reflects the effect of the attribute set. Temperatures can be used as a measure of the state of equated energy fluxes between an animal and its environment. Study of body temperature, thus, provides a means of determining the effect of thermal environments on the activity and distribution of *Agelenopsis*.

The observed distribution of *Agelenopsis* may also

reflect the influence of the hydric desert environ-ment on evaporative water loss. Initial experiments conducted on temperature and humidity relations of *Agelenopsis* indicate that water loss is not an im-portant limiting factor to individuals of this popu-lation. The present study was thus limited to inves-tigation of temperature relations of *Agelenopsis*.

Most animals have preferred (optimum) tempera-ture ranges within which their physiological effi-ciencies are maximal. These optimum ranges are often fairly restricted when compared to the range of temperatures encountered in a particular environ-ment. Adaptations for survival in extreme environ-ments, then, might involve physiological, morpho-logical, and behavioral mechanisms. Most ectotherms are unable to regulate their body temperatures through physiological means: individuals of thermally stressed invertebrate populations usually demonstrate increased temperature tolerances of only a few de-grees over those of populations occupying less stress-ful habitats (Cloudsley-Thompson 1962). Such adaptations are not sufficient to insure viability to spiders encountering diurnal extremes in many desert habitats. One must generally assume that inverte-brate species living in desert environments will have developed some form of behavioral mechanism to keep them within a tolerable temperature range.

In some cases invertebrates avoid extreme thermal environments only by selection of "home" site (Eber-hard 1971). Other behavioral adaptations involve limitation of activity periods and active shuffling from one local environment to another (Hadley 1970, Heath and Wilkin 1970). *Agelenopsis* can conceiv-ably maintain its body temperature within a favorable range through several means: (1) in the initial choice of web site, (2) in physical positioning of the web at the site, (3) in limitation of activity periods, (4) through shuttling movements along thermal gradients, or (5) through posturing.

A number of workers—Birkebak (1966), Porter (1967), Moen (1968), Gates and Porter (1969), Tracy (1972), and others—have applied heat trans-fer equations in studies of temperature relations of animals. In the present investigation, a basic heat transfer equation was used to calculate body tem-peratures of spiders under the environmental condi-tions encountered by these animals at particular web sites. Modeled temperatures were then correlated with patterns of individual activity in order to examine the temperature restrictions placed on the individuals, especially pertaining to time available for predation.

ENERGY-EXCHANGE MODEL

The body temperature of a spider is directly de-termined by total energy exchange between the spider and its environment. If the parameters of energy exchange can be measured, it is possible to predict the temperature of the spider under any set of local conditions by applying the heat transfer equation: Energy in = energy out:

$$M + Q_{\mathrm{abs}} = \varepsilon\,\sigma T_s^4 + h_c(T_s - T_a) + E_{\mathrm{ex}} \pm C \pm W,$$

where M is the metabolic rate, Q_{abs} is the amount of radiation absorbed by the animal surface, ε is emissivity, σ is the Stefan-Boltzmann constant, T_s is the surface temperature of the spider, h_c is the convection coefficient, T_a is air temperature, E_{ex} is evaporative water loss, C is the heat conducted to and from the substrate, and W is work done. All energy fluxes are expressed in $\mathrm{cal/cm^2 \cdot min}$. For an invertebrate, heat produced by metabolism and evaporative water loss is two orders of magnitude smaller than is the energy input from external sources (Ahearn and Hadley 1969). They have, therefore, been excluded in the present analysis. Work is gen-erally a small energy term relative to heat fluxes, and its determination is to be considered in a future study. Only twice during the course of this study was *Agelenopsis* seen to position itself such that its body contacted the surface. Therefore, conductive heat exchange was assumed to be negligible. In the present study, the animal was considered to be at rest and calculated temperatures represent steady-state or equilibrium conditions.

After consideration of the above assumptions and simplifications, the reduced version of the energy budget of *Agelenopsis* may be expressed in the fol-lowing form:

$$Q_{\mathrm{abs}} = \varepsilon\,\sigma T_s^4 + h_c(T_s - T_a).$$

Energy absorbed from the environment through components of solar and thermal radiation equals the energy lost through radiation and convection. Surface temperature, the unknown, can be deter-mined by solving this polynomial equation. Because in an invertebrate so small there is little difference between surface temperature and core temperature, the calculated surface temperature is assumed equal to spider body temperature. Components of the equation are determined either through physical measurements or calculations from known relation-ships.

The solar radiation received by *Agelenopsis* in south-central New Mexico was determined using the model, SOLRAD, developed by McCullough and Porter (1971). Scattered solar radiation (skylight) was assumed to be 10% of the direct solar beam for any time of the day. *Agelenopsis* receives re-flected solar radiation from the web, surrounding plants, lava, soil, and litter substrates. Each of these varies in its contribution of reflected radiation, the

web having a much higher reflectance (0.5) than a lava substrate (0.05). Energy from reflected sources was integrated over all of the substrates and estimated to be 20% of the sum of direct and skylight radiational components. Thermal radiation from the sky was calculated using Brunt's equation, and radiation from the substrate and surrounding habitat was calculated from measured surface temperatures and the Stefan-Boltzmann equation (Gates 1969).

The actual amount of energy absorbed by the animal from each of these sources depends on the absorptivity of spider integument to solar wavelengths and on the surface area exposed to radiation sources. The spectral reflectance of *Agelenopsis* integument to solar radiation (.29–2.6 μm) was measured with a Beckman DK-2A Spectro-reflectometer in a series of experiments using intact anaesthetized adults. Percent reflectance for each wavelength was subtracted from 100 to give percent absorptivity. Absorptivity to the entire solar spectrum was calculated by integrating the spectral absorptivities of the spiders to clear day solar radiation for Carrizozo, New Mexico, during summer (McCullough and Porter 1971); *Agelenopsis aperta* from the Carrizozo area had an absorptivity of 0.85.

The direct solar beam was considered to be absorbed over the projected or silhouette area of the spider, whereas skylight was considered to be incident on the entire upper half of the body. Likewise, thermal radiation from the sky was viewed by the upper half of the body, whereas the thermal environment of the substrate was viewed by the lower half.

The convective heat transfer coefficient, which is a complex parameter that embodies the wind speed, and the size and shape and various other properties of the animal, usually must be empirically determined from each animal species. We determined convection coefficients for spider models cast in copper and plated with chrome (chrome has a low emissivity to thermal radiation). Because thermal radiation is virtually eliminated as a heat flux to or from these models, the convection coefficient can be determined from solution of the nonsteady-state
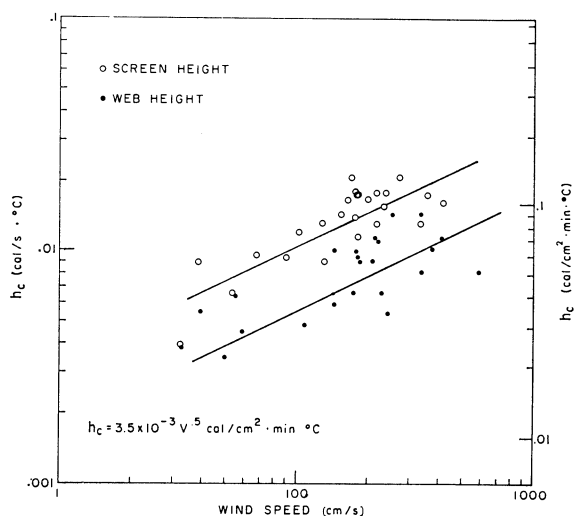

FIG. 2. Linear regression fitted to convection coefficients (h_c) plotted against wind velocities. Lower regression line represents data from experiments completed at web height. Upper regression line represents data from convection experiments completed at screen height (0.25 m).

energy balance of the model from experiments where the model has been heated to a temperature above ambient, and then allowed to cool (Kreith 1965):
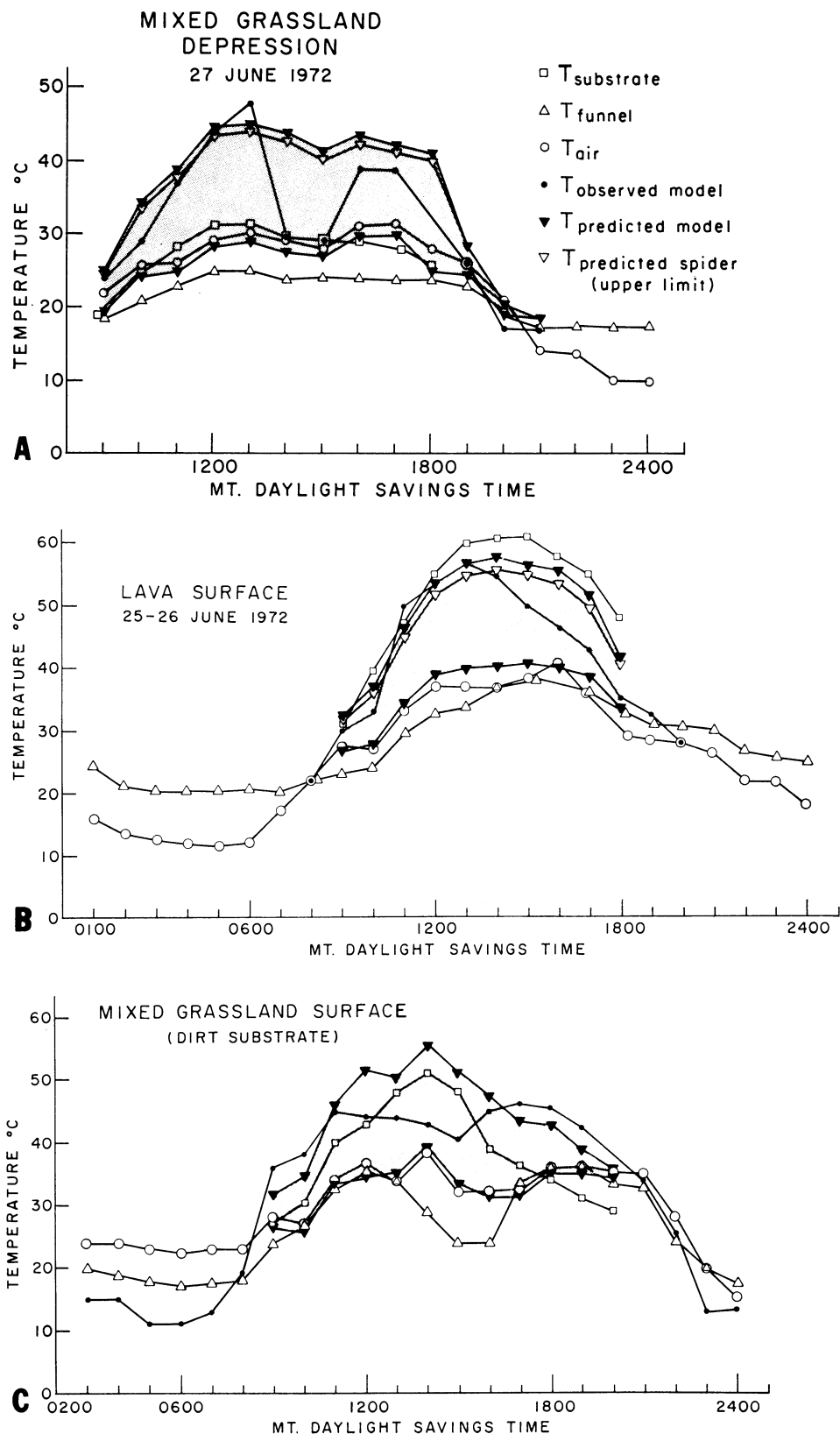
$$h_c = [\ln (T_m - T_a/T_0 - T_a)] [-mc/At],$$

where m is the mass of the model, c is the specific heat, A is the surface area, h_c is the convection coefficient, T_a is air temperature, T_m is model temperature at time t, and T_0 is the initial temperature of the model when $t = 0$.

Experiments with the model spiders were initiated by heating the models with a butane torch to 20° above ambient temperature at various web sites. The model was allowed to cool to equilibrium and time was recorded at 3° increments as cooling progressed. Simultaneously, wind speed was averaged over the cooling period using a sensitive Casella cup anemometer. Because this cup anemometer often could not measure wind speeds at web height, two cooling

FIG. 3. Temperature relations at various web sites for the course of a clear, hot day in June. Curves represent both predicted black model and spider temperatures and measured black model, substrate, funnel, and air temperatures. Curve at upper border of stippled area represents predicted black model temperature on the sheet in full sun. Curve at lower border of stippled area represents predicted black model and spider temperature on the sheet in full shade. Stippled area indicates range of the temperature of a spider while on the sheet; actual position within temperature range is dependent on degree of exposure to the direct solar beam.

Wind speed was measured with a Stewart cup anemometer (stall speed of 2 mph) measured at screen height. Funnel temperature and air temperature, on the web sheet, were measured with a 1-mil thermocouple and a West Pyrotest potentiometer. Substrate temperatures were measured with a 3-mil thermocouple painted white and placed in close contact with the substrate surface. A hygrothermograph at screen height provided temperature and humidity data required for the Brunt Equation. Solar radiation was calculated from Solrad (McCullough and Porter 1971). (A) a depression web site on the mixed grassland, (B) a surface web site on the lava flow, and (C) a surface web site on the mixed grassland.

MIXED GRASSLAND
DEPRESSION
27 JUNE 1972

□ $T_{substrate}$

△ T_{funnel}

○ T_{air}

● $T_{observed\ model}$

▼ $T_{predicted\ model}$

▽ $T_{predicted\ spider}$
(upper limit)

A

TEMPERATURE °C

MT. DAYLIGHT SAVINGS TIME

LAVA SURFACE
25–26 JUNE 1972

B

TEMPERATURE °C

MT. DAYLIGHT SAVINGS TIME

MIXED GRASSLAND SURFACE
(DIRT SUBSTRATE)

C

TEMPERATURE °C

MT. DAYLIGHT SAVINGS TIME

experiments were conducted for each web, one with the model on the web (web height) and another 0.25 m above the ground surface, level with the ane-mometer (screen height). The plot of convection coefficients determined for web-versus-wind height experiments is shown in Fig. 2. The slopes of the linear regressions of the two measures are identical, implying that a good correlation existed between wind measurements at screen height and convection coefficients of the spiders at web height. The least squares regression equation for spider convection co-efficients at web height as a function of wind speed at screen height is $3.5 \times 10^{-3} v^{0.5}$ (cal/cm² · min °C), where v equals wind velocity.

The area of the spider was determined by con-sidering the abdomen to be a cylinder and the cephalothorax a circle and a hemisphere. Appro-priate area measurements were made on a number of individuals from different size classes and sexes.

Results

We expected that the microenvironment provided by a particular web site would be most important to the spider during that part of the season when the macroenvironment is most severe. For *Agelenopsis*, high temperature extremes are encountered on clear days throughout June and early July (Riechert 1973, 1974*b*). During this hot, dry period just prior to the summer rains adult *Agelenopsis* requires the highest food intake of its life cycle, since, at this time, energy is being expended in production of off-spring.

Plots of predicted temperatures of a black model and *Agelenopsis* at various web sites for the course of a typical midsummer day are shown in Fig. 3A, B, C. Corresponding substrate, web, funnel, and black model temperatures actually recorded during the time period and at the locality for which pre-dictions were made are also included in the graphs. The shaded portions represent the expected range of spider temperature; the actual spider temperature within the range at any time is determined by the extent of its exposure to solar radiation. Thus, if the spider is in full view of the sun, its temperature is expected to approach the upper limit of its range, whereas if fully in the shade, it is expected to be at the lower edge of the shaded part of the graph. With no solar input (lower limit) the predicted temperatures of the black model and the spider are identical. (At equilibrium, black model temperature differs from spider temperature only in its greater absorptivity to solar radiation.)

Grassland depression web.—For a typical depres-sion web (Fig. 3A) the maximum temperature reached by the simulated spider on its sheet during the course of a clear midsummer day would be 45°C,

and if the spider remained constantly in view of the sun, it would be subjected to these temperatures from 1200 to 1800 h. When exposed to temperatures of 45°C for 4 h *Agelenopsis aperta* suffers 50% mortality. Shorter exposures to temperatures in this range probably place individuals under heat stress in which energy is inefficiently metabolized and water is lost in evaporative cooling.

If the spider remains on the shaded portion of its sheet, its temperature ranges from 20° to 29°C during daylight hours (Fig. 3A). The temperature of 30°C appears to be well within the preferred tem-perature range of *Agelenopsis aperta* as shown by the results of flushing experiments (discussed later) and temperature measurements of basking individ-uals. Observations of actual spiders showed that individuals typically moved from a basking position (exposed to direct sunlight) into shade when body temperatures (measured indirectly from black spider models) reached 30.9°C ($\pm$ 1.9; $N = 21$).

The results of the energy-balance predictions and behavioral observations indicate that spiders on grassland depression webs need only shuttle back and forth from sun into shade to maintain body temperatures at the implied optimum of ca. 30°C. In addition, the black model temperatures recorded on a depression web illustrate the importance of shade in effecting the 20° temperature difference noted between full exposure to the sun and complete shade (Fig. 3A). Between 1400 and 1500 h the model was shaded and approached the lower pre-dicted limit, whereas at other times it received more solar radiation (greatest during the morning) and consequently reached much higher temperatures. The observed temperatures of the black model that exceeded the predicted spider temperatures at 1245 h may have been based on an underestimate of con-vection when wind velocities were low, because of the insensitivity of the anemometer to low wind velocities (stall speed was 2 mph).

Of interest also are the funnel temperatures that remained fairly constant throughout the day (<24°C) and well below what are considered stressful thermal conditions (above 35°C). The depression funnel thus offers a stable environment to which the spider can escape when conditions become unfavorable on the sheet.

Lava surface web.—Results of pattern and dis-criminant analysis suggest that mixed grassland de-pressions are excellent *Agelenopsis* habitat, whereas lava surface appears to be the least favorable habitat (Riechert et al. 1973, Riechert 1973, and 1974*b*). For the most part, spiders frequent the latter habitat only during the spring, March to May, with fewer webs observed on the lava surface toward the end of spring. One would expect the lava surface web

site to afford less thermal protection than other sites. The predicted temperatures for an agelenid occupying a lava surface site in midsummer are shown in Fig. 3B. After 1000 h, temperatures become too hot for the spiders to remain in full view of the sun, and by 1200 h even full shade may become inhibitively hot. Funnel temperatures are also extreme; for 6 h of the day, lava funnel temperatures exceed 30°C (Fig. 3B).

Thus, throughout much of the adult season, lava web occupants are probably prevented from seeking prey between 1000 and 1800 h, because of prohibitively hot temperatures on the web. Funnel temperatures are also prohibitive. Temperature is clearly an important factor limiting the use of this habitat during summer months.

Grassland surface web.—Intermediate between the rather poorly suited lava web habitat and the more satisfactory grassland depression site is the grassland surface web (Fig. 3C). This web-site type appears to offer the most variable local environment of all sites, because it is the least protected from wind and sky conditions. Spiders at grassland surface sites, like lava surface spiders, are restricted in their midday activity because shade is not available (Fig. 3B, C). Of interest also is the fluctuation of funnel temperature in this web-site type. Although never reaching the stress conditions observed for funnels at lava web sites, the temperature inside the web funnel at grassland-surface sites appears to be influenced by the solar radiation hitting it.

Early in this study, spider temperatures were assumed to approximate air temperature, and behavioral observations were simply referenced to air temperature, sky cover, and position of the spider with respect to exposure to the direct solar beam. However, the model predictions reveal strong correlations between spider temperature and two environmental parameters (1) substrate temperature and (2) exposure to incident solar radiation. The effect of substrate temperature on spider temperature is obvious when comparing different web sites. Simulated temperatures, for shaded spiders over lava substrates were 15° higher in midday when thermal radiation from the substrate was very high, than at depression web sites over litter substrates (Fig. 3A, B). The bareground substrate of the grassland surface web also caused elevated temperatures; the maximum temperature for a shaded spider at such a site was 12° higher than that for a spider at a depression site with litter substrate (Fig. 3A, C). In discriminant analysis, litter was found to be a highly important web-site character in both lava and grassland habitats (Riechert 1973); the results presented here clearly show the thermal advantage of building webs over a litter substrate.
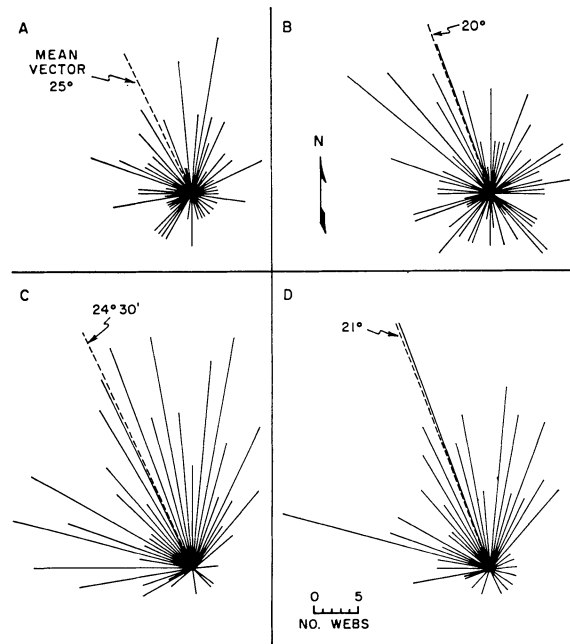

FIG. 4. Funnel orientations for various habitats and sample groups in June 1971. (A) all webs in lava study area, (B) all webs in mixed-grassland study area, (C) all unprotected surface webs from all habitats, and (D) all webs from a rangeland plot lacking depressions and shrubs. Orientations represent compass directions to which the funnels face.

A successful web site also provides accessibility to full shade, since up to a 20° difference in spider body temperature can be found depending on the degree of exposure to sunlight. The importance of depressions on the grassland, and shrubs on the lava flow, in characterizing good web sites (Riechert 1973) is obvious from the protection they afford from solar radiation. Depressions and shrubs are also of importance in that litter tends to accumulate in and under them.

Active avoidance of direct sunlight at the web site is also indicated by the funnel orientations of unprotected webs during the hot season, June–July (Fig. 4): directionality is significantly different from a uniform circular distribution (Kolmogorov-Smirnov test) in webs on a rangeland plot lacking depressions and shrubs ($P < 0.01$) and in a sample representing unprotected surface webs from lava, rangeland, and mixed grassland habitats ($P < 0.01$). A Rayleigh test computed on mean direction indicated the concentration of webs facing the NW to be significant for all four samples ($P < 0.01$ in all cases). For a latitude of 32° and the month of June, funnels facing between 20° and 25° west of north will receive direct sunlight over the smallest period of time during the day (just prior to sunset), than any other
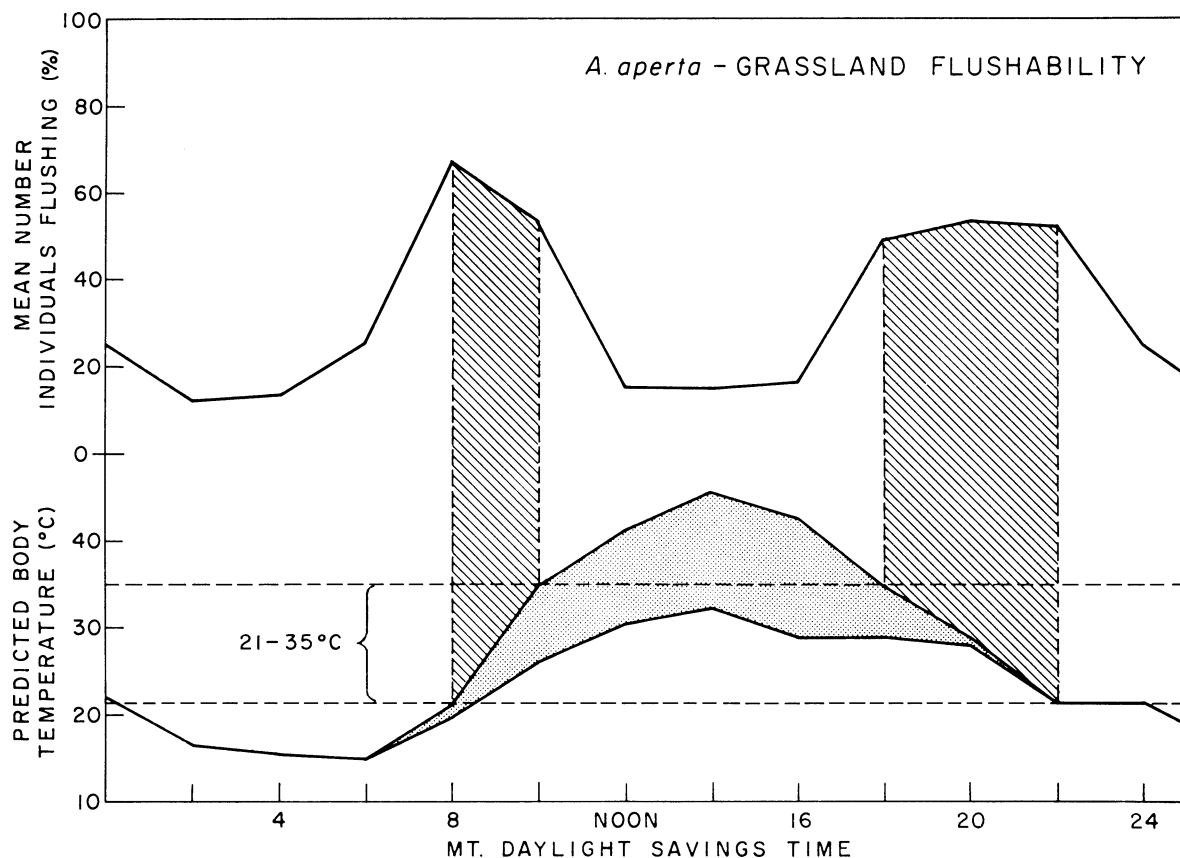
FIG. 5. Graph of percent of spiders active on the sheet with time of day on the mixed-grassland study area in midsummer (July and August) imposed on predicted spider temperature under these conditions and assuming a web-over-litter substrate. Barred area under flushability curve represents time periods during which over 50% of the individuals were active. Stippled area represents range of spider temperatures, exact temperature dependent upon amount of exposure to solar radiation. Upper boundary of predicted temperature curve signifies spider temperature if in full sunlight. Lower boundary signifies spider temperature if in full shade. Area enclosed by dashed lines represents body temperature range within which over 50% of the spiders are active.

orientation (List 1966). The orientations observed for funnels of this spider may also be a response to prevailing winds (from the SE). However, since funnel orientations were not significantly different from random except during the hot-dry season, directionality probably reflects efforts to escape thermal stress.

SPIDER ACTIVITY

The ranges of body temperature under local web-site conditions can often limit spider activity. Our discussion so far has been primarily concerned with the relationship between body temperature and the environment, with little regard to possible modifications of body temperature by behavioral thermoregulation.

Various studies have produced inconclusive evidence of spiders' abilities to select favorable thermal environments within laboratory gradients (Palmgren 1936, Lagerspetz and Jäynäs 1959, Nemenz 1965,

and Kraft 1967). Thermal preferences are especially difficult to determine among agelenids because they often select corners or ends of the experimental chambers instead of exhibiting any temperature preference (Kraft 1967).

Because of the difficulty in obtaining meaningful temperature preference results under laboratory conditions, an attempt was made to deduce them for *Agelenopsis* under field conditions. In July and August 1973 between 15 and 20 mixed grassland spiders were flushed at 2-h intervals for a total of 3,455 observations. Individuals were scored as flushed (active) if they appeared at the funnel entrance when their webs were approached. Environmental conditions existing at the time of flushings were recorded. A plot of predicted spider temperature for average conditions at this time of year and grassland litter webs was imposed on a graph of mean percent spiders flushing at 2-h intervals (Fig. 5). Periods during which over 50% of the indi-

viduals are active (on the basis of flushing) occur between 0800 and 1000 h and between 1800 and 2200 h. The predicted spider body temperature at which the early peak in activity begins is 21°C. This peak drops off at 1000 h when body temperature reaches 35°C. Peak activity starts in the afternoon when body temperature again is at 35°C and activity levels decrease when the temperature falls below 21°C in the evening. A percentage of the spiders remain active throughout the day. (Most individuals are probably unable to be active throughout the entire course of the day, but rather various individuals are out for periods when their webs are shaded.)

Our results show that *Agelenopsis* activity in the New Mexican study area is bimodal and dependent on spider temperature. These data provide empirical proof of the model proposed by G. Williams (1966) for invertebrate activity, in which periodicity is largely determined by environmental parameters. The buffering of the environment (e.g., overcast days), then, would serve to reduce the separation of bimodal peaks in activity. Figure 6 shows the temporal pattern of certain activities for both clear and cloudy days. The bimodality in activity for clear days does not hold for activities associated with prey capture on cloudy days. These results are consistent with Williams' model (1966).

Included in Fig. 6 are all activities occurring on the web sheet. Basking, by definition exposure of part or all of the body to solar radiation, functions to raise body temperature to within a preferred range. Spiders stop basking at approximately 31°C and seek shade, though individuals forced to remain on the web sheet in order to secure prey (actual observations) will remain with the prey until their body temperatures reach 35°C. Basking occurs between 0800 and 1000 h, coinciding with the initial peak in 50% flushing activity for *Agelenopsis* (Fig. 5, 6).

The oscillatory movements between shade and exposure to sunlight, shuttling, may initially serve to maintain the preferred body temperature obtained by basking, and later in the morning may represent a means for remaining on the sheet after a favorable microenvironment is no longer available over the entire catching area. The median time for shuttling occurs latest of all medians for morning activity (Fig. 6).

Searching and prey attack are related behaviors. Searching is characterized by short jerky movements around the periphery of the web or over some portion of it. Particles on the web are picked up during this activity and portions of the sheet are pulled or tugged. Through these motions, small prey items are collected, including leafhoppers (Cicadellidae) and small dipterans and hymenopterans which,
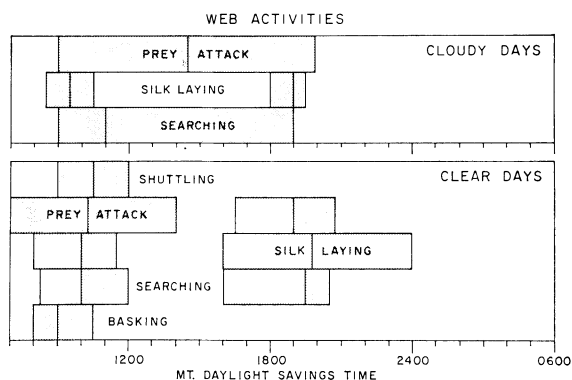

FIG. 6. Periodicity of various web activities for clear and cloudy days. Bars represent time periods in which 90% of each of the designated activities were observed. Vertical lines represent the medians of these activities.

though ensnared, would escape notice. Although searching is a type of prey capture, spiders can obtain prey over a much longer time span than through searching (Fig. 6). Prey capture can take place whenever the spider sits at the funnel entrance with front legs extending onto the sheet. Upon sensing the vibrations the spider can locate the source and assume an attack posture. Subsequent behavior depends on the type of insect encountered.

Apparently then, all activity on the sheet is coupled with body temperature and little activity occurs outside of the 21°–35°C optimal range. Prey capture and the activities related to it (searching, silk laying, basking, and shuttling) are limited to periods when the spider can stay within this temperature range. Certainly a spider that is capable through basking, shuttling, and choice of web site, to engage in these activities for a greater portion of the day will increase its chances for taking prey.

Discussion: temperature relations

The evidence of a well defined preferred temperature range for *Agelenopsis*, and inspection of the local environments offered by various web sites in the habitats studied, suggest that temperature strongly influences the activity of *Agelenopsis* and its choice of web location. *Agelenopsis* appears to conduct most of its prey capturing and associated behaviors between temperatures of 21°C and 35°C with a preferred maximum of only 31°C. The results of body temperature predictions for various web sites indicate that the local physical conditions offered by depressions in the mixed grassland allow activity within the preferred range for a greater portion of the day than do the microenvironments of other web sites. This is largely the result of two factors: (1) depressions afford protection from incident solar radiation, and (2) the litter accumulated in them

offers less radiant heat than the lava and bare ground substrates characteristic of other web sites. Since incident solar and substrate thermal radiation were shown to influence spider temperature, one would expect a web site that modifies the heat input from these two sources to be favored. The results of both pattern (Riechert et al. 1973, Riechert 1974b) and discriminant analyses (Riechert 1973) indicate that web distribution is highly correlated with depression location in this population of *Agelenopsis*. Other web sites provide less favorable local environments. The spiders inhabiting grassland surface webs are subjected to highly variable thermal environments both on the sheet and in the funnel. The surface web on the lava flow, though less variable than its grassland counterpart, often provides stressfully high thermal environments during the summer months. Even funnel temperatures at the lava site can be stressful.

Temperature relations at the lava site probably explain the marked decrease in *Agelenopsis* numbers noted on the lava beds in summer (Riechert 1974b). Given that each year a few individuals move on to the lava beds with the advent of the summer rains, the numbers of offspring produced by these few adults could account for the high density of imma- tures noted on the flow the following spring. In the spring, the warmer conditions offered by the lava substrate may be advantageous to feeding, so sur- vival on the lava bed during this period may be high. However, as summer approaches the majority seem to either suffer thermal mortality or migrate to more favorable habitats (usually on the grassland: Riechert 1973, 1974b). Under these conditions, we must conclude that the lava bed is a marginal habitat, at least for a portion of the year.

However, if *Agelenopsis* were truly an opportunist, it would take advantage of the temporal and spatial thermal environments available on and around the lava flow. Thus, the spiders might occupy lava sites early in the season, when activity is possibly aug- mented by warmer microclimates at lava sites. With progessing spring and rising temperatures, spiders could move to the more equitable grassland depres- sion sites. Finally, adults caught in heavy July rains might move onto the lava flow to escape drowning and subsequently produce additional egg sacs. Such a pattern of movement is certainly feasible consider- ing the number of moves made by *Agelenopsis*, and also by the fact that some marked individuals were observed to have escaped drowning by moving onto the lava flow when the grassland became flooded (Riechert 1973). At any rate, during the hottest period of the year and when *Agelenopsis* requires its greatest food intake for reproduction, spiders oc- cupying depression sites on the mixed grassland can achieve optimal body temperatures for a longer in- terval of the day and, hence, they can feed longer than spiders at other types of web-site habitats. From a thermal standpoint, therefore, the grassland de- pressions should be regarded as optimal web-site locations.

PREY AVAILABILITY

Except for direct selection of the web site and possibly construction of a scaffolding, *Agelenopsis* cannot influence the types or numbers of available prey, and the type of prey hitting an *Agelenopsis* web largely depends on the locomotory patterns evidenced by various groups; flying and hopping in- sects by nature of their movements will more fre- quently encounter an *Agelenopsis* web than will crawling prey.

Spiders generally are known to consume a wide range of taxa (Turnbull 1966), and, therefore, most of the invertebrates of suitable size in the lava flow area could be considered "potential" prey to *Agele- nopsis*. Of the set of potential prey species, some are likely to contact an *Agelenopsis* web more frequently than others. This subset represents the "available" prey. At the web, *Agelenopsis* might consume only a more restricted subset of "acceptable" (vulnerable: Craighead and Craighead 1956) prey, actively dis- carding others or passively allowing their escape. Spiders are known to reject prey because of foul taste, odors, or unfamiliarity (Bristowe 1941, Turn- bull 1960). In addition, some prey may escape cap- ture through strength or agility upon contact with the sheet. In such cases method of capture rather than behavioral rejection becomes a factor.

In the present study we have attempted to assess the proportion of the potential prey community available to *Agelenopsis* and determine the influence of various web-site characteristics on prey availability. The discrimination among encountered prey by *Agelenopsis* and its effect on the quality and num- bers of prey consumed are also considered.

Methods

Potential prey.—A suction apparatus, modified from units described by Dietrick et al. (1959) and Turnbull (1966) was used to sample the inverte- brate community. The vacuum sampler had an in- take opening of 0.30 m² and was powered by a model 2B-13 Homelite Blower with 3½ hp capacity.

Bimonthly samples were collected in grassland, interface, and lava habitats. A sample consisted of invertebrates collected from 40 "setdowns" (12 m² = total area) of the sampling orifice along a 300-m transect of a given habitat type. The se- quence of distances moved along the transect was previously determined from a randomization tech-

nique. Two sample transects were completed for each of the following habitat features: grassland depressions, grassland surface, lava shrubs, lava surface, and lava crevices. Samples were refrigerated prior to handsorting to help inhibit escape of the more mobile prey.

Johnson et al. (1957) have assessed suction sampling efficiency in grassland vegetation at 95%–100% for all Hemiptera, Diptera, and Hymenoptera, and at 70%–75% for Coleoptera and larval Diptera. Whittaker (1965) found suction sampling, though demonstrating 96.2% overall efficiency, to show some serious group deficiencies: Homoptera 12.1%, hemipterous larvae 12.5%, Coleoptera 6.9% (Carabidae 40%) missed. Even assuming maximum suction efficiency this sampling method still suffers two other disadvantages. First, flying forms are probably underestimated since the noise of the blower frightens them off before collection is made. Sampling was restricted to between 0600 and 0800 h to overcome this difficulty; most diurnal dipterans and hymenopterans were sedentary then. Another disadvantage of suction sampling reflects the difficulty of absolute sampling in any patchy habitat. The small unit collecting area results in a very high sample variance (Southwood 1966). This deficiency of method was ameliorated by grouping the individual sample units along each transect into a single sample set.

Available prey.—Artificial sticky webs were used to estimate available prey at various web sites. Adhesives have been widely used in general invertebrate collections (Kaloostian 1961) and artificial sticky webs have been applied in studies of the food relations of orb-weaving spiders (Cherret 1964, Kajak 1965). Ten embroidery hoops measuring 20.54 cm in diameter (roughly the diameter of an adult *Agelenopsis* sheet) were covered with cheese cloth and sprayed with a sticky banding compound (Tree Tanglefoot, Tanglefoot Company, Michigan). These artificial webs were placed at what appeared to be adequate web-site locations: depressions, surface, and shrubs. The occurrence of arthropod attractants (i.e., flowers and scats) at these sites was noted. The artificial webs were sampled at 0700, 1300, and 1800 h for 4 days on each major habitat type (i.e., lava and grassland). A 7-day break followed each 8-day sampling period. Additional adhesive was applied to the webs every 2 days. These Tanglefoot webs provided an estimate of the catch per unit time, assuming the spider and Tanglefoot captures everything hitting the web.

Tanglefoot web sampling is considered an absolute sampling method since ideally the animals collected represent all invertebrates available to *Agelenopsis* at a particular web site per unit time. It is unlikely,

however, that adhesives are totally effective in restraining all individuals that make contact (Kaloostian 1961). Experiments completed on Tanglefoot (Assay Report WARF 1963) show retention of stickiness between temperatures of −30°C and 76°C. In this study, we tried to determine the efficiency of collection for various invertebrate groups. Arthropods, 30 of each of 14 families and nine orders, were caught and dropped on freshly sprayed Tanglefoot webs at midday in full sunlight (air temperature between 30° and 32°C). No more than 10 insects were placed on a web. After 30 min the webs were checked and the number and type of prey having escaped during that time recorded. The results of these experiments indicate that absolute efficiency for all taxa was 86.7%. Poorest collection efficiency occurred in the Formicidae (10%) and larger coleopterans (45%). Strong crawling movements of these insects account for their ability to escape. (Tanglefoot catch values used in this analysis have not been corrected for the percent of escape of various prey types.)

Actual prey capture and consumption depend on spider temperature, time required to capture the particular prey, active selection or rejection of the prey, and the ability of the prey to escape. Information on preferences exhibited for particular prey was collected from observations in the field and on captive individuals. Estimates of escape frequencies for various prey types were also obtained through field observations.

Method of analysis.—A least squares multiple linear regression (Draper and Smith 1966) was used to predict prey weight and density/h on characteristic web sites at different times and under varying environmental conditions. A two-sided t-test was used to determine the significance of independent variables in the regression. Variables tested for predictive value in influencing dry weight and density of prey included presence-absence of the lava study area, of the mixed grassland study area, of depressions, shrubs, and surface sites, of flowers, of scats, and of the separate sampling periods of morning, afternoon, and night, and the cross products of all these. Continuous variates tested included wind velocity, percent cloud cover, temperature, and cross products of these.

RESULTS AND DISCUSSION

The abundance of prey taxa contacting funnel webs relative to their numerical importance in the total invertebrate community is given in Table 1. Of the 85 invertebrate families represented from the lava study area, individuals from 66 of these families encountered *Agelenopsis* webs, and 15 families occur on these webs with a relative density > 1%. Some of

TABLE 1. Relative importance of invertebrate families in suction (potential prey) and Tanglefoot (available prey) samples and in the diet of *Agelenopsis* occupying mixed-grassland and lava-bed habitats. Percent importance based on data from field observation on feeding and collections of discarded remains. Only families exhibiting a relative importance in the diet for one of the habitats of 3% or greater have been included. Complete tables are available from the authors

Taxon	Lava bed			Mixed grassland		
	Relative % density (Potential prey)	Relative % density (Available prey)	Relative % importance in diet	Relative % density (Potential prey)	Relative % density (Available prey)	Relative % importance in diet
Orthoptera						
Locustidae	4.39	2.28	3.11	1.26	3.32	14.48
Coleoptera						
Carabidae	4.22	0.43	9.10	1.14	0.31	1.01
Chrysomellidae	8.62	4.21	2.81	2.19	2.10	3.32
Scarabaeidae	0.02	0.12	5.88	0.23	0.10	0.56
Hemiptera						
Miridae	4.29	0.23	3.00	22.47	0.83	0.99
Homoptera						
Cicadellidae	5.21	9.80	3.03	29.95	26.99	16.00
Lepidoptera						
Larvae	1.72	0.25	3.61	0.92	0.14	1.08
Noctuidae	3.53	2.29	11.30	1.14	1.52	7.15
Diptera						
Anthomyidae	0.18	0.83	3.80	0.03	0.42	0.00
Asilidae	4.83	1.48	3.44	1.90	0.99	3.00
Muscidae	1.56	2.01	0.81	0.20	2.00	6.18
Sarcophagidae	3.19	26.42	6.00	0.09	31.40	12.38
Tipullidae	0.33	2.04	6.82	1.70	3.90	6.81
Hymenoptera						
Formicidae	5.10	0.11	9.96	0.02	0.31	3.37

the more important families (e.g., Locustidae and Noctuidae) were caught in densities similar to their densities in the suction samples. Others were more important in the Tanglefoot samples than in the suction samples, an indication that they encounter webs more frequently than would be expected from random movements and positioning. For example, the Sarcophagidae (flesh flies) represent only 3% of the potential lava prey but account for 26% of the available prey. Other families in this category include: the Cicadellidae (leafhoppers); various Dipterans, Asilidae (robber flies), Ephydridae (shore-flies), Dolichopidae (long-legged flies), Chloropidae (fruit flies); and the hymenopteran family Halictidae. Both the Carabidae (ground beetles) and Formicidae (ants) are important in the lava-bed invertebrate community but unimportant in the available prey group (Table 1). This result, not necessarily due to differences in behavior, possibly reflects the inefficiency of Tanglefoot in ensnaring members of these groups.

Mixed-grassland study area results are similar to those noted for the laval flow (Table 1). Of 86 families 64 were represented in the Tanglefoot samples. Twelve of these represented over 1% of the total catch. Sarcophagids again ranked very high among available prey. Other Dipterans were also important. These included the Muscidae (house flies and other pest species), Ephydridae, Lonchaeidae, Dolichopidae, and Asilidae. Cicadellidae were also prominent in the web catches, though in lesser numbers than would be expected on the basis of their relative abundance in the habitat, whereas chrysomellids, also important available prey in the grassland study area, are present on the webs in numbers equivalent to their density in this habitat.

Of interest is the abundance of the hemipteran families Miridae (plant bugs), Lygaeidae (chinch bugs), Tingidae (lace bugs) and Reduviidae (assasin bugs) in the grassland habitat and their infrequent occurrence on the Tanglefoot webs. Their habits must be such that they rarely become prey of *Agelenopsis*. The Gryllidae (crickets) also appear under represented; they generally crawl under the webs rather than land on them.

Total density and biomass of prey were hypothesized to differ at web sites depending upon site characteristics, time of day and environmental conditions (Fig. 1). In actuality, the variates found useful in predicting biomass differed from those best predicting density of available prey. In both predictions it was necessary to perform the regression on the log of the dependent variable because of long tails in the sample distributions. Both prey density

and dry weight/h, when capture was averaged over the time intervals sampled, were fairly constant; web site characteristics accounted for the occasional high values observed.

T-tests performed on regression results indicated percent cloud cover ($P < 0.07$), temperature ($P < 0.01$), and a crossproduct of these two environmental parameters ($P < 0.09$) to be the only important determinants of available dry weight of prey. The predictive equation for dry weight per hour of available prey is

$$W = 1.17\, e^{[-1.78 + .03C + .071T - .001CT]},$$

where W is dry weight/h, C is percent cloud cover, T is temperature (°C), and e is the base of the natural log. A 17% correction is added to the dry weight estimate, accounting for weight loss through preservation of the samples in alcohol prior to drying (Breymeyer 1967).

Although absolute dry weight available to *Agelenopsis* provides an indication of total available energy, it is hard to determine on the basis of weight alone what portion of the available dry weight is actually consumed. *Agelenopsis* observed during the course of the study missed 29% of the individuals encountered on the sheet, ignored another 10%, and rejected 1% ($N = 718$). In addition, observations showed the first individuals encountered were more likely to be missed than those hitting the web later during a feeding period. In light of these observations, one would expect *Agelenopsis* to consume an increased amount of the available biomass when that biomass is distributed among a larger number of prey encountered during a given time. Five variates were important in predicting available prey density per hour in the regression. These included the presence of attractants ($P < 0.04$), a crossproduct of attractants and depressions ($P < 0.01$) and the continuous environmental parameters found important in the dry weight predictions, temperature ($P < 0.002$), percent cloud cover ($P < 0.06$), and the crossproduct of these two ($P < 0.03$). Attractants are significant in increasing prey density; flowering plants are important in discriminating good web sites from poorer ones (Riechert 1973).

The regression equation best predicting prey density is

$$N = e^{[-1.97 + .1A + .63DA - .01C + .06T + .0004CT]},$$

where N is prey density, A is attractant, D is depression, C is percent cloud cover, and T is temperature (°C). Available dry weight based on the density of available prey, then equals

$$W = 2.9N,$$

where 2.9 is the product of the mean dry weight per individual (2.48 mg) times the correction for preservation in alcohol (1.17).

Prey density depends on web-site characteristics, whereas absolute prey biomass depends more significantly on climatic conditions existing at the time of collection. The presence of attractants at a web site appears to affect the number of pollinators and scavengers frequenting the location. The dipterans and hymenopterans primarily making up this group are small compared with Locustidae and other larger forms not influenced by these habitat features. Despite their lighter weight, these flying forms represent a very large portion of *Agelenopsis*' available diet (Riechert 1973). Because the presence of attractant flowers and feces are highly important determinants of good web sites (Riechert 1973), clearly the pollinating and winged forms are significant in *Agelenopsis* prey relations. For the reasons discussed here and for those mentioned earlier, their numbers are important when considering available prey.

Prey captured.—No animal captures all of the prey available to it. Wolves capture about 7.8% (Mech 1966); wild dogs capture 86% of the prey attacked (Estes and Goddard 1967). The capture rates of mantids vary with density of prey, from 26% at high prey densities to 58% when prey is scarce (Holling 1965). In part, the rate of capture is indicative of capture attempts and misses, but in *Agelenopsis* it is related to available prey ignored or rejected. From 718 feeding observations of individual *Agelenopsis* either on the sheet or visible in the funnel, 60% of the prey hitting the web was captured. (This does not include those prey types missed while the spider was inactive.) Table 1 illustrates the relative availability and importance of various prey families to the diet of *Agelenopsis*. Several factors appear to be important in determining feeding success: relative size of predator and prey (Schoener 1971), relative mobility of both (Pritchard 1965), prey density (Goss-Custard 1970), and predator experience (Dixon 1959). Prey size seems to be of some importance in limiting *Agelenopsis* capture, but other factors seem also significant. Vibrations of small insects are often not sensed or at least appear to be ignored by adult *Agelenopsis*. Likewise, some larger prey, for example heavy locustids and coleopterans (Scarabaeidae), are cut from the web when prey are abundant. Spiders inhabiting the lava flow eat more of the larger prey than do the grassland spiders, perhaps because of the restrictions placed on their activity by temperature and the need to replace water lost by evaporation during the heat of the day. Such factors may inhibit their selectivity in what they eat. Certainly much energy is expended in capture of these larger individuals, though it is

not clear that more energy per gram of obtained biomass is expended.

The mobility of the prey accounts for the largest number of misses by *Agelenopsis*. Because the sheet of an *Agelenopsis* web is non-sticky, insects momentarily ensnared will escape if not attacked immediately. Capture of strong fliers depends on a complex of factors including the spider's temperature (which seems to affect its speed of pursuit), the wind at the web (apparently affecting the spider's ability to detect the presence of the prey), and experience of the spider in handling the particular prey (Riechert 1974*a*).

Agelenopsis' capture rate also differs for certain prey types with time of day. In part, this varies with the specific activity periods of the prey themselves, but it also reflects variation in spider behavior toward the particular prey. The kind of prey captured during the heat of the day may be influenced by spider temperature, especially if the prey lands on a portion of the sheet exposed to the sun. Prey requiring wrapping on the sheet (e.g., Formicidae, Locustidae, Asilidae, and larger coleopterans) cannot be handled, because the temperature of the spider will often increase above tolerance levels within about 20 s of exposure to direct noontime radiation. *Agelenopsis* at midday is thus limited to capturing those insects requiring only a few seconds of activity on the sheet (e.g., small dipterans, hymenopterans, and cicadellids).

Under natural conditions *Agelenopsis* rejects very little of the prey available to it (15 of 718 observations). These were beetles of the families Chrysomelidae (five occasions), a scarabid and a clerid; a locustid; a formicid; a lepidopteran caterpillar; and a sarcophagid (three occasions). The caterpillar was large and was repelled by the spider as it attempted to descend the funnel; it was subsequently allowed to escape. Locustids are difficult prey to handle, requiring wrapping on the sheet, since within the confines of the funnel their kicks can perforate the spider's soft integument (Riechert 1973). Scarabid beetles and ants, like grasshoppers, require wrapping on the sheet. This activity both expends considerable energy and often exposes the spider to thermal stress. The chrysomelids, most frequently rejected, were eaten by some individuals. They might have been rejected because of their morphological similarity to the foul-tasting lady bug beetles, Coccinellidae, which were always rejected by captive individuals.

These observations indicate that *Agelenopsis*, like other spiders, is not very selective in its feeding. Turnbull (1960) found the sheet weaver *Linyphia triangularia* (Clerck) to reject prey regularly, though it was not consistent in the type of prey rejected (150 of the 153 prey species encountered were ac-

TABLE 2. Rejection of prey by captive spiders

	Offered (N)	Rejected (N)	Rejected (%)
Orthoptera			
Blattidae	7	0	0.00
Locustidae	144	31	21.53
Gryllidae	7	2	28.57
Coleoptera			
Carabidae	19	6	31.58
Cantharidae	4	0	0.00
Mordellidae	1	0	0.00
Elateridae	2	2	100.00
Coccinellidae	4	4	100.00
Scarabaeidae	9	9	100.00
Chrysomelidae	40	12	30.00
Dermestidae	8	6	75.00
Hemiptera			
Pentatomidae	2	0	0.00
Lygaeidae	9	5	55.56
Reduviidae	3	2	66.67
Nabidae	3	0	0.00
Neuroptera			
Chrysopidae	7	0	0.00
Myrmeleontidae	73	10	13.70
Lepidoptera			
Noctuidae	486	30	6.17
Nymphalidae	2	1	50.00
Larvae	6	3	50.00
Diptera	338	26	7.69
Tipullidae	5	0	0.00
Asilidae	2	1	50.00
Sarcophagidae	176	14	7.95
Calliphoridae	141	7	4.96
Tachinidae	18	3	16.60
Hymenoptera			
Mutillidae	6	0	0.00
Formicidae	14	6	42.86
Sphecidae	3	0	0.00
Total	1539	183	11.89

cepted on some occasions). Such indiscrimination is generally assumed to occur when food. is in short supply (Ivlev 1961, Emlen 1966).

If the suggestions are true, it follows that spiders assured of adequate daily food would probably discriminate more strongly than others in what is eaten. Table 2 lists the percent of prey types rejected by captive spiders under laboratory conditions that were offered between 6.7 and 17.3 mg of food per day, the relative abundances of each prey type being similar to that available in the field. The overall acceptance rate was great, 88.3%, though these spiders did demonstrate more discrimination than did their field counterparts. Species most frequently rejected by *Agelenopsis* in the food study were also rejected by spiders in the field. Ants and beetles were rejected approximately 50% of the time. Rejection of these two types by captive spiders, half of which were collected from the lava study area, and spiders in the field is indicative of the difficulty

TABLE 3. Probability of falling prey to *Agelenopsis*

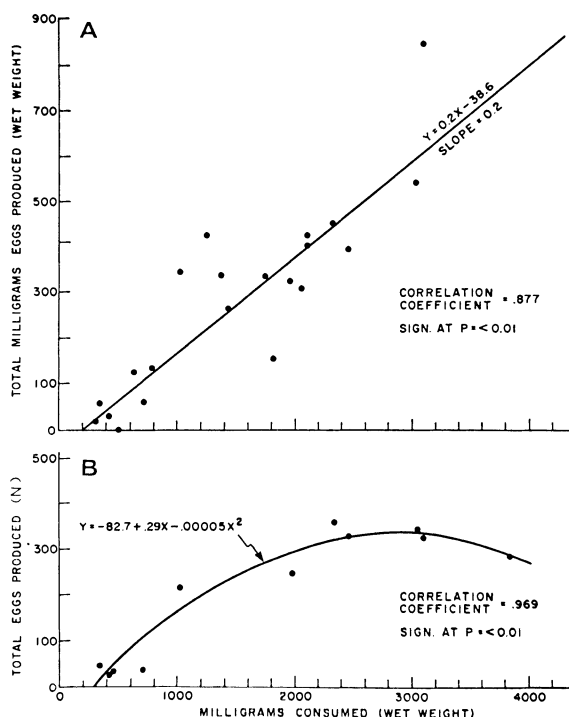|	Lava	Mixed grassland
Orthoptera		
Locustidae	.020	.059
Gryllidae	.0020	.0007
Coleoptera		
Carabidae	.0300	.0006
Cantharidae	.0010	.0004
Scarabaeidae	.0009	.00002
Cerambycidae		.000007
Chrysomelidae	.040	.0076
Curculionidae	.0015	.0002
Hempitera		
Lygaeidae		.0007
Coreidae	.0003	
Reduviidae		.00006
Miridae	.004	.0006
Nabidae		.00004
Homoptera		
Cicadellidae	.10	.4662
Fulgoridae	.004	.00023
Neuroptera		
Chrysopidae	.002	.0050
Lepidoptera		
Noctuidae	.08	.0082
Larvae	.005	.00020
Diptera		
Tipullidae	.05	
Dolichopidae	.06	.0011
Syrphidae	.005	.0001
Lauxaniidae	.005	.0004
Muscidae	.004	.0047
Sarcophagidae	.56	.4280
Calliphoridae		.0004
Anthomyidae	.008	
Tephritidae	.002	
Hymenoptera		
Pamphiliidae		.00031
Chrysidae	.0006	
Argidae		.0001
Multillidae	.001	
Pteromalidae		.0003
Formicidae	.004	.0009
Sphecidae	.01	.0011
Halictidae		.0011
Arachnidae		
Araneae		
Salticidae	.002	
Lycosidae		.00001

FIG. 7. Linear regressions fitted to milligrams (A) and number (B) of eggs produced as a function of total prey consumed by *Agelenopsis* from subadulthood to death.

with which these prey are secured. Their importance as food to lava spiders (Table 1) suggests that existence of *Agelenopsis* on the flow is marginal and that these prey types are required for maintenance despite what appears to be an increased energy expenditure necessary to obtain them.

Prey most frequently rejected by the sheet weaver, *Linyphia*, were those groups with which it was least familiar (Turnbull 1960). *Agelenopsis* also was hesitant toward unfamiliar prey; captive individuals almost always rejected insect types with which they were unlikely to have had previous experience (Dermestidae and Reduviidae; Table 2). Although members of the family Asilidae were important prey to field individuals, an asilid was rejected by a captive individual on one occasion. The asilid is a voracious predator in its own right and difficult for a spider to handle in the confines of a cage. (The spider was eaten by the prey in this instance; subsequently, asilids were not offered to captive individuals.)

Though *Agelenopsis* consumes a wide variety of prey, the main portion of its diet is largely contributed by a few families. The probability of a particular invertebrate becoming *Agelenopsis* prey may be assumed equal to a product of its relative abundance in the Tanglefoot collections and its relative percent acceptance (Table 1). Table 3 shows on the above basis, the importance of various invertebrate types as possible prey to *Agelenopsis* in both lava and grassland habitats. The sarcophagids and cicadellids are extremely abundant in the habitat and encounter *Agelenopsis* webs in similar numbers. Sarcophagids, as mentioned earlier, encounter *Agelenopsis* webs in greater numbers than expected by their abundance in the habitat. Thus, even though *Agelenopsis* accepts a diverse group of prey, its diet is dominated by prey that are numerically abundant. These are prey types with which the predator is likely to have become most familiar and thus probably will require the least energy to obtain.
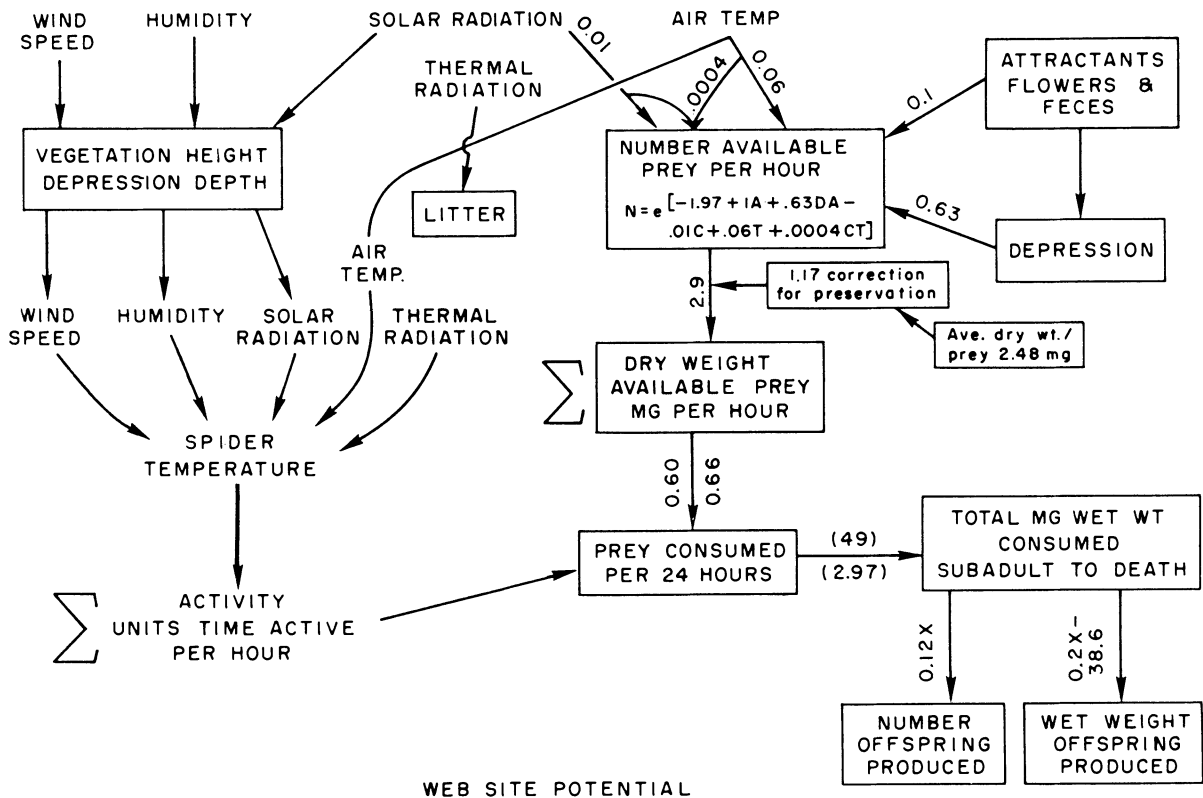
FIG. 8. Diagram of the numerical relationship between web-site character and reproductive success. The notation is explained in the text.

FOOD CONSUMPTION AND PRODUCTIVITY

That spider fecundity is related to food consumption has been demonstrated (Turnbull 1962). A linear relationship was found between total food consumption and weight but not number of eggs produced by *Linyphia triangularis* (Clerck) in laboratory experiments. This direct association between food consumption and egg weight reflected differences in the quantity of yolk contained in the eggs, which could be very important to the success of the spiderlings.

Methods

In this study, 30 subadult *Agelenopsis* individuals were collected (15 each from lava bed and grassland habitats) in April 1972 and kept individually in plastic containers (10.8 × 13.3 × 7.0 cm). These containers were kept shaded in Styrofoam boxes to provide as stable a thermal environment as possible under field conditions (temperature range equals 20°–23°C). Individuals were fed (between 0800 and 0900 h daily), prey species ranging between 10 mg and 200 mg wet weight. Both eaten and uneaten prey were removed prior to the next feeding on the following day and were weighed once again.

Feeding was scheduled so that over the course of the season certain individuals would be offered larger quantities of prey than others. Thus, three groups were separated on the basis of average food offered per day (10 mg, 30 mg, and 50 mg) wet weight. Adequate water was sprayed on the webs daily.

Spiders were allowed to live out the remainder of their lives and record was kept of (1) prey rejected, (2) secured but not eaten, and (3) ingested. Adults were bred within a week after the final molt, and the eggs produced were weighed (Fig. 7A). Egg sacs from 11 individuals were opened after weighing to determine numbers of individuals produced; others were allowed to mature, whereupon an accurate count of the numbers became impossible (Fig. 7B).

Results and discussion

The relationships between total food intake and weight and number of individuals produced is illustrated in Fig. 7A and B. A significant ($P < 0.01$) linear relationship was found to exist between food eaten by *Agelenopsis aperta* and weight of eggs produced. A significant ($P < 0.01$) curvilinear relationship existed between food eaten and number of offspring produced. In this experiment the increase in weight of eggs produced associated with greater

TABLE 4. Sample calculations of reproductive success

Time (MDST)	$\bar{x}$ air temp (°C)	Excellent site Mixed grassland depression with attractants: full shade		Average site Mixed grassland depression with attractants: partial shade		Poor site Lave bed surface no attractants: no shade	
		Active (Min)	Dry wt avail. prey	Active (Min)	Dry wt avail. prey	Active (Min)	Dry wt avail. prey
0800–0900	24.0	60	3.54	60	3.54	60	1.71
0900–1000	26.5	60	3.99	60	3.99	30	0.99
1000–1100	28.5	60	4.64	60	4.64	0	
1100–1200	30.0	60	5.08	0		0	
1200–1300	31.5	60	5.56	0		0	
1300–1400	32.0	60	5.72	60	5.72	0	
1400–1500	31.5	60	5.56	60	5.56	0	
1500–1600	31.0	60	5.39	30	2.71	0	
1600–1700	30.0	60	5.08	0		0	
1700–1800	28.5	60	4.64	30	2.32	0	
1800–1900	27.0	60	4.24	60	4.24	60	2.04
1900–2000	26.0	60	3.99	60	3.99	60	1.92
2000–2100	25.0	45	3.76	45	2.82	45	1.36
Available dry wt/day		60.03		39.53		8.02	
Capture dry wt/day		36.02		23.72		4.81	
Dry wt consumed/day		23.77		15.65		3.18	
Total wet wt consumed		3459.25		2278.11		451.30	
Total wt egg sacs produced		653.25		417.02		51.66	
Total no. offspring produced		415.11		273.37		54.16	

food intake appears boundless (Fig. 7A). However, the number of eggs produced seems to have an upper limit (Fig. 7B). The presence of an upper limit suggests that the total number of offspring produced per adult may be genetically determined.

It appears that the increased productivity noted under these artificial conditions can be realized in field populations. For *Agelenopsis aperta* in New Mexico, size of individuals of the same age class varied and, in several cases, small individuals were noted for web sites demonstrating a paucity of prey and vice versa. Because egg sacs are difficult to obtain in the field, no direct measure of variation in production of the next generation was available, though it can be assumed that individuals able to put more energy into biomass have a greater reproductive potential as well. Similar indirect evidence for increased productivity with greater food supply is available from Kajak (1967). She attributed yearly differences in the size of field populations of araneids to amounts of available prey; her finding that food consumption of a population was also much more uniform throughout a season than individual rates suggested that the prey-catching frequencies varied with different web sites.

THE MODEL: SPIDER REPRODUCTIVE SUCCESS

A model can be useful for its predictive capabilities or for the understanding it provides of complex interactions within a system. The model (Fig. 8) de-

veloped in this study proved useful in both respects, though the understanding it provides of the relations between web location and reproductive success of *Agelenopsis* has been constrained to fit the two factors studied, thermal balance and prey availability: intra- and interspecific relations and other such factors influencing individual productivity were excluded.

Table 4 demonstrates the values obtained for various relationships in the model (Fig. 8) given an excellent web site, an average web site and a poor web site, still allowing survival to reproductive age. Production (wet weight of offspring) was calculated both for an excellent web site (i.e., depression on the mixed grassland with attractants and available shade throughout the day) and a poor web site (lava surface with no attractants and no available shade during the day). Air temperatures were assumed similar on both the lava flow and grassland and represent mean temperatures for the time intervals indicated on a typical clear mid-June day. Available prey was calculated only for the duration of prey feeding activity determined earlier (Fig. 5, 6). On the basis of the calculated temperatures (Fig. 3A, 8) a grassland-depression spider, if provided shade, could remain active throughout the course of its feeding period (0800–2045 h). On the other hand, temperature extremes greatly limit the feeding period of the lava web-site spider (Fig. 3B); it was assumed able to be active for a period of only 1½ h/day.

In addition, twice as much prey was available at the grassland-depression web per time interval than at the lava web. The prey captured by spiders from both habitats while active was estimated at 60% of the available prey (Fig. 8); the 60% estimate was obtained from the percent capture rate noted for active *Agelenopsis*. Ingestion efficiencies determined for captive spiders showed that an average of 66% of the prey weight was consumed by the spider. Field individuals were, thus, assumed to consume 66% of the biomass of captured prey.

Total prey biomass consumption for the 7-wk period during which most *Agelenopsis* in the study area matured and produced eggs (ca. mid-May to early July) was determined and converted to wet weight, assuming dry weight equivalent to 33.7% of wet weight. This percent equivalence reflects the average relationship determined from measurements of weight loss in typical prey after oven drying: Diptera, $\bar{x} = 31.21\%$; Orthoptera, $\bar{x} = 34.15$; Lepidoptera, $\bar{x} = 35.83\%$. Total weight of eggs and number of offspring produced were estimated using the food-egg production regression relationship determined under laboratory conditions for captive individuals, assuming metabolic energy loss equivalent in both groups (Breymeyer 1967, Kajak 1967, Van Hook et al. 1970).

The estimated wet weight of eggs produced at the excellent grassland site (653.3 mg) was 13× that determined for the poor lava site (51.7) (Table 4). These results closely approximate the extremes of the values measured in the laboratory experiment. The prediction for the excellent site, however, is probably unrealistic, since no depression spider will be afforded complete shade throughout the day on clear days. In addition, the spiders were assumed to have engaged actively in prey capture for the entire period allowed by energy balance considerations. Individuals, especially those with an adequate food supply, may not spend 100% of the allowed time at the funnel entrance. However, even a daily capture rate of 36.03 mg dry weight is reasonable in light of the observations made by Robinson and Robinson (1972) on *Argiope argentata*, a spider similar to *Agelenopsis* in size and weight. This tropical orb weaver captured an average of 54 mg dry weight/day. The daily food consumption estimate for the average web site providing shade for limited periods of the day (Fig. 3A) equals 15.65 mg dry weight (Table 4). This average daily consumption is still 5× the estimate for the poorest web site. The range of prey captured between the poor lava site and the average site approximates the range of prey capture rates noted by Kajak (1967) for *Araneus quadratus* Clerck (Araneidae) in a meadow habitat. We can compare daily food intake and resultant

egg production of captive and field individuals. Three groups of captive spiders were offered varying weights of prey (6.8, 10.2, 17 mg dry weight/day). The individuals continued feeding up to 80 days after capture in May and, following maturity, produced 1–6 egg sacs/individual. Field individuals, however, received varying amounts of prey per day depending on the character of web sites and environmental conditions, at least some individuals receiving more prey than the captive spiders. These spiders completed development and subsequent production of eggs within the 7-wk period between mid-May and early July. If offspring production was not completed within this period, chances of survival to reproduce were greatly reduced by the onslaught of summer rains and consequent flooding. Of 99 individuals marked in the grassland study area, only three were recovered following the first rain in early July.

The results demonstrate one aspect of spider biology that contributes to their success in most habitats, the capacity for maximization of food intake. Production of offspring clearly appears to be more dependent on total food consumption than on the time required for development. Within limits, individuals receiving less food will still mature, but more slowly than those with greater food intake. Presumably, after a certain threshold of food is consumed, the first egg sac will be laid; with further food consumption, additional eggs are produced. Turnbull's (1965) laboratory studies of *Agelenopsis potteri* substantiate the slower development with lesser food intake noted for *A. aperta*. In addition, in its capacity as an opportunist feeder, this spider can consume large quantities of prey whenever it is available (Riechert 1974a). With this capability, those individuals receiving larger quantities of food can complete the life cycle prior to the advent of summer rains (Riechert 1974b). Under these local catastrophic conditions, production of the next generation is, then, dependent on some individuals' receiving large quantities of food early in the season.

The model demonstrates the differing roles of thermal balance and prey availability in influencing individual productivity and web-site success. Apparently, regardless of prey numbers hitting the web-site, the predator's temperature must lie between 21° and 35°C for it to make use of available prey (Fig. 5). And yet, the ability to stay within bounds of this optimum temperature range is of little use if no prey are available for capture. The two factors are closely coupled. However, the model shows that the greatest amount of energy is to be gained from an increased activity period, since there is only a two-fold difference in prey availability from the

poorest to the best web site at most time intervals, whereas there is an eight-fold difference between maximum available actvity and minimum activity (Table 4). This result is related to the fairly constant densities of available prey in the study areas augmented at local sites only by the presence of flowers and, to some extent, flowers in conjunction with depressions. The presence of flowers does not necessarily increase overall density of available prey at a web site but rather increases the probability of receiving an occasional high density (i.e., increases the variance). On the other hand, presence of litter and habitat features providing shade remove limits on spider activity through their influence on body temperature.

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