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# Genetically-based variation between two spider populations in foraging behavior

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**Summary.** Optimal foraging theory is based on the assumption that at least some aspects of foraging behavior are genetically determined (Pyke et al. 1977; Kamil and Sargent 1980; Pyke 1984). Nonetheless, very few studies have examined the role of genetics in foraging behavior. Here, we report on geographical differences in the foraging behavior of a spider (*Agelenopsis aperta*) and investigate whether these differences are genetically determined. Field studies were conducted on two different populations of *A. aperta*: one residing in a desert riparian habitat, and the other in a desert grassland habitat. Data from the spiders' natural encounters with prey demonstrated that grassland spiders exhibited a higher frequency of attack than riparian spiders towards 13 of 15 prey types, including crickets and ants. Grassland spiders also had shorter latencies to attack 12 of 15 prey types, including crickets and ants, than riparian spiders. Subsequently, we reared grassland and riparian spiders under controlled conditions in the laboratory and observed their interactions with prey to determine whether the populational differences we found in the field could be genetic. Again, grassland spiders showed a shorter latency to attack prey (crickets, ants) than riparian spiders. These latencies were not significantly affected by the hunger state or age of the spiders. Finally, we reared a second generation (F2) of grassland and riparian spiders in the laboratory and observed their interactions with prey to determine whether the populational differences in the previous generation were due to genetic effects or maternal effects. As before, grassland spiders exhibited a shorter latency to attack prey (crickets) than riparian spiders. We conclude that the foraging differences we observed between these two populations of *A. aperta* are genetically determined. These differences probably have resulted from either natural selection acting directly on attack frequency and the latency to attack prey, or natural selection acting on traits which are genetically correlated with these aspects of foraging behavior.

**Key words:** Population variation – Behavioral genetics – Foraging behavior – Spiders

The foraging behavior of animals has been studied intensively for the past twenty years using optimal foraging theory (Krebs et al. 1983; Pyke et al. 1977; Schoener 1987). This theory yields predictions about how animals should adjust their foraging behavior to the types and distributions of available prey, and is based on the assumption that natural selection will favor animals that forage most effectively (i.e., optimize some variable such as net energy intake per unit time; Schoener 1971; Pulliam 1974; Charnov 1976). Thus, the theory assumes that at least some aspects of foraging behavior are genetically determined (Pyke et al. 1977; Kamil and Sargent 1980; Pyke 1984). Even so, very little research has been conducted to date on the possible role of genetics in determining foraging behavior (Kamil and Sargent 1980; Schoener 1987), perhaps because the theory predicts that individuals should be opportunistic, changing their behavior frequently in response to changes in the quality and abundance of their foods (Schoener 1987).

Recently, growing interest in the genetic basis of ecologically important traits has prompted numerous studies of genetics within natural populations (Mousseau and Roff 1987), although few of these concern behavioral traits (but see e.g. Maynard Smith and Riechert 1984; Bakker 1986; Hoffmann 1988; Hedrick 1988). The genetic basis of foraging behavior has been investigated for only a few organisms: cave fish (Schemmel 1980), snakes (Arnold 1980, 1981a, b; Drummond and Burghardt 1983), mice (Gray 1980), *Drosophila* (deBelle and Sokolowski 1987; Wallin 1988), and a number of insects in which females have genetic preferences for oviposition sites containing particular kinds of food for their larvae (Futuyma 1983; Mitter and Futuyma 1983; Tauber and Tauber 1987). Here, we report on geographic differences in the foraging behavior of a spider (*Agelenopsis aperta*), and we investigate whether these differences in foraging behavior are genetically determined. Our study was conducted in two parts: first, we examined the foraging behavior of spiders in the field to determine whether populations differed in their responses to prey under natural conditions. Second, we examined the foraging behavior of spiders under controlled conditions in the laboratory, to determine whether populational differences we observed in the field were genetic.

## Methods

*Agelenopsis aperta* (Gertsch) is a funnel-web building spider found in the western U.S. Its web is built on the ground and consists of a silken sheet with an attached funnel that extends into some feature of the habitat. Frequently, the web also includes a vertical scaffolding which extends up

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from the sheet and functions to knock prey down onto it. When foraging, *A. aperta* sits at the funnel entrance, and runs out onto the web to capture prey after they hit the web.

For this study, observations of foraging behavior were conducted on two populations of *A. aperta*. One population occurs in a desert riparian habitat in southeastern Arizona, and the other in a desert grassland habitat in south-central New Mexico.

### *Field methods*

Field observations of spider-prey interactions with 15 different prey types, including crickets (*Gryllus* spp.) and ants (*Pogonomyrmex* spp.), were conducted in the field for each population over a period of 6 years. Natural encounters with prey were observed during 30-min focal observations of individual web-sites in the two habitats. Observations were conducted only on spiders that were within 1 cm of the funnel entrance when the prey first contacted their web (i.e., they were in an active foraging mode). For each of the 15 prey types, ten to 74 spiders per population were observed during spider-prey interactions. Interactions with another 10 prey types which *A. aperta* encounters were not included in this data set because of small sample sizes ($<10$ interactions per population).

For each spider-prey interaction, we recorded whether or not the interaction resulted in an attack (the spider left the funnel entrance, ran up to the prey, and subdued it by biting and/or entangling it). Non-attacks were either rejections (the spider approached the prey, touched it, and then moved back to the funnel without biting or entangling it), or failures to respond (the spider did not leave the funnel entrance). We also recorded the latency to attack, which we defined as the time that elapsed between the prey's first contact with the web and the time at which the spider first touched the prey. Observations were continued until either the spider subdued the prey or the prey escaped from the web.

### *Laboratory methods*

*Spiders.* All laboratory observations were conducted on spiders that had been hatched and reared in the laboratory. Gravid females from each of the study sites were collected in September, 1987 and brought to the laboratory, where they laid egg-cases. Young spiders hatching from these egg-cases (the F1 generation) were reared from hatching onward at 29 degrees C, and on a L:D cycle of 12:12 h. They were fed a diet of live crickets. Each spider was given one cricket twice a week, and the size of the cricket was adjusted to the size of the growing spider. Once the spiderlings had reached their penultimate-adult molt, they were used in foraging experiments with crickets and ants as prey. Throughout these experiments, spiders from the two populations were of similar ages and weights (*cricket experiments*, $\bar{x}\pm$SE: age when testing began, grassland$=11.4\pm0.3$ wks, $n=17$; riparian$=11.0\pm0.4$ wks, $n=17$; weight when testing began, grassland$=96.1\pm3.2$ mg, $n=17$; riparian$=97.5\pm3.1$, $n=17$, $t=0.32$, $P>0.05$; weight when testing ended, grassland$=157.4\pm5.8$, $n=10$; riparian$=166.2\pm5.8$, $n=13$; $t=1.08$, $P>0.05$; *ant experiments*, $\bar{x}\pm$SE: age, grassland$=14.0\pm0.0$, riparian$=14.0\pm0.0$; weight, grassland$=263.9\pm8.6$ mg, riparian$=236.9\pm16.9$ mg, $t=1.43$, $P>0.05$). Adult males were excluded from testing because they forage only sporadically, spending most of their time searching for females (personal observation).

We also studied foraging behavior of second generation (F2) laboratory spiders to distinguish between genetic effects (which would affect F2 spiders) and maternal effects. Maternal effects would not affect F2 spiders; for example, the nutrition of field-collected mothers might influence the behavior of their F1-laboratory-reared offspring (through the yolk-sac), but would not affect that of their F2 progeny. To obtain the second laboratory (F2) generation, 25 F1 female spiders from each population were mated to an F1 male from the same population. F2 hatchlings were individually reared and maintained using our prior methods, and as with F1 spiders, were tested once they reached their penultimate molt.

### *Prey trials with crickets*

*First-generation studies.* Crickets were used as prey in laboratory observations of foraging behavior because they were readily available and are encountered naturally by *A. aperta* in both the grassland and riparian habitats. The major objective of our laboratory trials with crickets was to determine whether the two spider populations differed in their latencies to attack prey. However, we recognized that two additional factors might significantly affect latency to attack prey: hunger state and spider age. Accordingly, we observed 17 F1 spiders from each of the populations interacting with crickets in three experimental replicates, which spanned an eight-week period altogether. These replicates allowed us to examine the effects of population, hunger state and age (analyses 1 and 2 below). Replicate 1 was conducted in the first week of the study, replicate 2 in the third week, and replicate 3 in the eighth week. We carried out a single foraging trial on each of the 34 spiders on each of four consecutive days in replicate 1, and on 23 of these spiders (10 grassland, 13 riparian) on each of two consecutive days in both replicate 2 and replicate 3. Spiders were not fed for three days prior to the start of each replicate to ensure that they were all in the same hunger state when the replicate began; between replicates (during weeks 2, 4, 5, 6, and 7) they received their usual diet of one live cricket fed twice-weekly.

*Population and hunger state: analysis 1.* Because laboratory spiders were maintained on a diet of one cricket every three to four days, we reasoned that the hunger state of spiders we tested would change progressively over the days within replicates (Day 1 = hungry, Day 2 = less hungry, etc.). Thus, replicate 1 allowed us to examine whether the populations differed in their latencies to attack crickets, whether a spider's hunger state (as measured by four days of trials) influenced its latency to attack, and whether interactions between population and hunger state influenced the latency to attack.

*Population, hunger state and age: analysis 2.* Examining all three replicates together also allowed us to ask whether any difference between populations in the latency to attack crickets would persist as the spiders aged (i.e., over the three replicates) and whether population-age interactions were important.

Pilot experiments demonstrated that spiders rarely attempted to capture crickets which were greater than 25% of their own weight. Therefore, during prey trials we offered spiders crickets that were 20% of the spider's weight. Each spider was weighed at the beginning of a replicate to determine the wt of cricket it would be offered on each day of that replicate. All foraging trials were conducted at 26 degrees C, an optimum temperature for *A. aperta* (Riechert and Tracy 1975).

At the start of a foraging trial, the spider, inside a small, closed plastic box (dimensions 10 × 7 × 2.5 cm; *A. aperta*'s body length is approximately 17 mm) in which the spider had previously built a web, was placed in a larger, uncovered plastic box (dimensions 30 × 15.5 × 9 cm). Then we removed the lid from the small box, and left the spider undisturbed for 2 min. After 2 min, we dropped a cricket on the spider's web approximately 4 cm in front of the spider from a vial held 8 cm above the web. Next, we measured the time that elapsed (latency to attack) between the cricket's first movement after hitting the web and the spider's attack (first bite). This measure of latency to attack was used because in the laboratory, crickets often became immobile as soon as they contacted the silk, making their detection difficult for the spiders until they moved. In pilot experiments, 100% ($n = 12$) of attacking spiders attacked within 6 min of the cricket's first movement. Therefore, we allowed spiders 6 min after the cricket's first movement to respond. If a spider did not respond within 6 min, its latency to attack was recorded as 360.0 s.

*Second-generation studies.* Seventeen grassland and 20 riparian F2 females were each observed during a single interaction with a cricket. Trials were conducted as before, with two exceptions: (1) Spider and cricket sizes were visually assessed, and spiders from both populations were offered crickets ranging from one-third to one-half of their own body lengths. Prior prey trials had shown that crickets of this size were readily attacked by penultimate-adult spiders. (2) Spiders were tested on large webs that had been built by another spider inside an open plastic box (dimensions 30 × 15.5 × 9 cm). Test subjects were placed on these webs in the afternoon and tested the following day, after approximately 18 h of residence on the web. *A. aperta* frequently takes over used web-sites in the field (Riechert 1982), and when spiders were placed on new webs in the laboratory, they immediately engaged in activities associated with ownership (e.g., adding silk to the web and sitting at the funnel entrance; Riechert 1982).

### Prey trials with ants

To determine if populational differences in latency to attack would be exhibited for a different prey type with which laboratory spiders had no prior experience, 27 adult female F1 spiders ($n = 14$, grassland; $n = 13$, riparian) were tested in the laboratory for their foraging behavior with carpenter ants (*Camponotus* spp.). These ants closely resembled *Pogonomyrmex* spp. in their behavior on the web: they struggled vigorously and persistently. All spiders had been reared and maintained on a diet of one live cricket fed twice-weekly, and had not been fed for two days prior to the experiment. In the trials, each spider was presented a single time with an ant weighing approximately 13% of its own weight (grassland = 13.3 ± 0.6%; riparian = 13.2 ± 0.7%). Repeated observations of spider-ant interactions were not conducted for two reasons: (1) we assumed that hunger and age effects on foraging behavior would be similar for both ants and crickets, and (2) ants were more difficult to obtain than crickets for use in foraging trials.

At the beginning of each trial, we dropped an ant approximately 4 cm in front of the spider from a vial held 8 cm above the web. Ants moved continuously on the web, and spiders used two different strategies to subdue them: laying silk over them, or biting them repeatedly. Thus, we recorded the time that elapsed from the ant's first contact with the web to the spider's first bite or deposition of silk over and/or around the ant (= latency to attack). The spiders treated ants much more cautiously than crickets, and spider-ant interactions were rarely resolved in 6 min. They usually ended within 12 min. Consequently, we allowed spiders 12 min to respond. Spiders not responding in 12 min were assigned a latency to attack of 720.0 s.

### Statistical analysis of data

All latencies to attack ($y$) for both the field and laboratory trials were transformed to logarithms ($\mathrm{Log}\,(y+1)$) before analysis to stabilize variances (Weisberg 1980). Latency data from the F1 laboratory generation were analyzed using methods described below, and other latency data were analyzed using $t$-tests. Differences in attack frequencies were analyzed using Chi-square or Fisher's Exact Probability tests, depending on sample size.

*F1 spiders, analysis 1: population and hunger state.* We examined the effects of population (POP), DAY (i.e., hunger state; day 1 = hungry, day 2 = less hungry, etc.) and DAY × POP interactions on latencies from replicate 1, using a multivariate repeated-measures analysis (with DAY as the repeated measure) from the GLM procedure in SAS (Freund et al. 1986). This analysis avoids violations of the assumption that orthogonal components are uncorrelated and have equal variance (Freund et al. 1986), which occur when a traditional univariate mixed-model ANOVA is used to analyze repeated measures data (O'Brien and Kaiser 1985). Wilk's Criterion was used to calculate F-statistics (O'Brien and Kaiser 1985), and our three tests each were conducted at the 0.05 level of significance.

*F1 spiders, analysis 2: population, hunger state and age.* We conducted a second multivariate repeated-measures analysis (from the GLM procedure in SAS; Freund et al. 1986) using two repeated measures (DAY, i.e. hunger state, two levels; REP (replicate), i.e., age, 3 levels). In this analysis, we examined the effects of POP, DAY, REP, DAY × POP and REP × POP on latencies and conducted our tests at the 0.05 level of significance. Again, Wilk's Criterion was used to calculate $F$-statistics (O'Brien and Kaiser 1985).

## Results

### Field

Grassland spiders exhibited a significantly higher frequency of attack than riparian spiders for 13 of 15 prey categories (Table 1), including both crickets and ants. For the remaining two prey categories (treehoppers and plant bugs), differences between the grassland and riparian spiders in frequency of attack were not significant. Thus, riparian spiders

**Table 1.** Attack frequencies for grassland and riparian spiders towards different prey types occurring in both habitats

| Prey type | Grassland Attacks | Grassland Non-attacks | Riparian Attacks | Riparian Non-attacks | $P$ |
|---|---|---|---|---|---|
| Ants | 23 | 1 | 30 | 21 | <0.001 |
| Crickets | 18 | 3 | 4 | 11 | <0.001 |
| Small beetles | 32 | 13 | 4 | 10 | <0.01 |
| Plant beetles | 40 | 14 | 1 | 23 | <0.00001 |
| Soft-bodied beetles | 23 | 7 | 15 | 27 | <0.001 |
| Predaceous beetles | 20 | 2 | 2 | 14 | <0.001 |
| Leafhoppers | 11 | 7 | 3 | 11 | <0.05 |
| Treehoppers | 16 | 1 | 13 | 5 | >0.05 |
| Gnats | 9 | 4 | 5 | 17 | <0.01 |
| Flies | 49 | 3 | 26 | 19 | <0.00001 |
| Moths | 27 | 4 | 13 | 11 | <0.01 |
| Grasshoppers | 25 | 1 | 12 | 18 | <0.001 |
| Damselflies | 23 | 1 | 9 | 10 | <0.001 |
| Spiders | 9 | 1 | 27 | 39 | <0.01 |
| Plant bugs | 18 | 7 | 37 | 37 | >0.05 |

**Table 2.** Mean attack latencies for grassland and riparian spiders towards different prey types occurring in both habitats. Sample sizes are given in parentheses

| Prey type | Grassland latency (s) | Riparian latency (s) | $t$ | $P$ |
|---|---|---|---|---|
| Ants | 1.3± 0.2 (28) | 25.3± 0.3 (27) | 7.40 | <0.001 |
| Crickets | 2.6± 0.3 (22) | 55.0± 0.3 (12) | 7.41 | <0.001 |
| Small beetles | 5.8± 1.8 (32) | 9.5± 3.5 (4) | 1.19 | >0.05 |
| Plant beetles | 13.7± 2.4 (40) | 83.5 (1) | – | – |
| Soft-bodied beetles | 7.6± 2.0 (23) | 85.1±19.6 (15) | 6.28 | <0.00001 |
| Predaceous beetles | 24.0±10.5 (20) | 71.5±31.1 (2) | 2.41 | <0.05 |
| Leafhoppers | 46.3±12.2 (11) | 107.3±38.1 (3) | 1.72 | >0.05 |
| Treehoppers | 11.0± 4.7 (16) | 82.4±25.7 (13) | 2.62 | <0.05 |
| Gnats | 14.0±13.0 (9) | 157.1±63.9 (5) | 2.50 | <0.05 |
| Flies | 8.6± 2.6 (49) | 81.8±17.8 (26) | 7.74 | <0.00001 |
| Moths | 4.8± 1.7 (27) | 143.1±59.3 (13) | 6.24 | <0.00001 |
| Grasshoppers | 35.9± 9.1 (25) | 123.7±40.7 (12) | 2.07 | <0.05 |
| Damselflies | 40.3±12.1 (23) | 261.1±62.8 (9) | 5.67 | <0.00001 |
| Spiders | 27.9±16.8 (9) | 146.1±43.6 (27) | 3.38 | <0.005 |
| Plant bugs | 12.8± 4.3 (18) | 50.8±11.3 (37) | 3.82 | <0.0005 |

did not exhibit a significantly higher frequency of attack than grassland spiders for *any* of the 15 prey categories. In addition, latencies to attack prey were shorter for grassland spiders than riparian spiders in every prey category, and significantly shorter for 12 of the 15 categories (Table 2), including crickets ($\bar{x}\pm$SE: grassland$=2.6\pm0.3$ s, $n=22$; riparian$=55.0\pm0.3$ s, $n=12$; $t=7.41$, $P<0.001$) and ants ($\bar{x}\pm$SE: grassland$=1.3\pm0.2$ s, $n=28$; riparian$=25.3\pm0.3$ s, $n=27$; $t=7.40$, $P<0.001$).

### *Laboratory: F1 generation*

Analyses on the F1 generation demonstrated that POP (population) was the only variable to significantly affect latency to attack crickets. Neither hunger state (DAY, analysis 1; Table 3) nor age (REP, analysis 2; Table 4) produced a significant effect.

*Analysis 1: population and hunger state.* Within replicate 1, latency to attack crickets was shorter for grassland spiders than for riparian spiders ($\bar{x}\pm$SE: grassland$=14.1\pm6.6$ s; riparian$=70.0\pm15.2$ s; $F(1, 32)=15.80$, $P=0.0004$). DAY and DAY × POP effects were not statistically significant (Table 3).

**Table 3.** Analysis 1 results (repeated measures analysis of variance)

| Source | df | $F$ | $P$ |
|---|---|---|---|
| POP | 1, 32 | 15.80 | 0.0004 |
| DAY | 3, 30 | 0.19 | 0.901 |
| DAY × POP | 3, 30 | 0.60 | 0.623 |

**Table 4.** Analysis 2 results (repeated measures analysis of variance)

| Source | df | $F$ | $P$ |
|---|---|---|---|
| POP | 1, 21 | 21.06 | 0.0002 |
| REP | 2, 20 | 0.02 | 0.979 |
| DAY | 1, 21 | 0.45 | 0.512 |
| DAY × POP | 1, 21 | 0.01 | 0.904 |
| REP × POP | 2, 20 | 0.82 | 0.456 |

*Analysis 2: population, hunger state and age.* Similarly, over all replicates, latency to attack crickets was shorter for grassland spiders than for riparian spiders ($\bar{x}\pm$SE: grassland$=3.9\pm0.1$ s; riparian$=56.3\pm12.0$; F(1, 21)$=21.06$, $P=0.0002$). REP, DAY, DAY × POP, and REP × POP effects were not statistically significant (Table 4).

One complication of the two analyses discussed above is that in our laboratory data, failures to attack prey were represented by maximum latencies. Thus, populational differences in latency might have been solely due to differences in the frequency of attack. To rule out this possibility, we conducted analysis 2 again, after excluding all maximum values. Its results were unchanged. Latencies to attack crickets were significantly shorter for grassland spiders than for riparian spiders ($\bar{x} \pm$ SE: grassland $= 3.9 \pm 1.0$ s, riparian $= 34.5 \pm 12.3$ s, $F(1, 16) = 10.5$, $P < 0.005$), and other effects were not statistically significant.

Finally, latency to attack ants in the F1 generation was shorter for grassland spiders than riparian spiders ($\bar{x} \pm$ SE: grassland $= 190.2 \pm 78.1$, $n = 14$; riparian $= 486.5 \pm 89.4$ s, $n = 13$; $t = 1.89$, $P < 0.05$, one-tailed).

### *Laboratory: F2 generation*

A difference between populations in latency to attack crickets also was found in the second generation of laboratory spiders. F2 grassland spiders had significantly shorter latencies than F2 riparian spiders ($\bar{x} \pm$ SE: grassland $= 1.1 \pm 0.3$ s, $n = 17$; riparian $= 30.7 \pm 11.1$ s, $n = 20$; one-tailed $t = 3.83$, $P < 0.0005$).

## Discussion

Field results from this study indicated that grassland spiders exhibit a higher frequency of attacking most prey types, including crickets and ants, and a shorter latency to attack than riparian spiders. These populational differences in foraging behavior could result from several possible causes. First, grassland spiders might have shown higher attack frequencies and shorter latencies because they were more familiar than riparian spiders (either individually or on an evolutionary time scale) with most of the prey types (i.e., if most of the prey types hit grassland spider webs more frequently than riparian webs). However, data collected over a period of nine years do not support this explanation: only three prey types (ants, gnats and grasshoppers) contact grassland webs more frequently, whereas the remaining 12 prey types contact riparian webs just as frequently or more frequently (Riechert, unpublished).

Second, riparian spiders might have been satiated and grassland spiders hungry at the time of testing, because food resources are more abundant in the riparian habitat (Riechert 1978). However, laboratory results from this study showed that populational differences in foraging behavior are not due to either hunger levels or experience, because foraging differences persisted when members of both populations were reared, maintained, and tested in the laboratory under identical conditions. Additionally, foraging differences were not changed significantly by either hunger levels or ages of spiders.

Finally, the populational differences in foraging behavior could have been genetic, or could have resulted from maternal effects. Both of these explanations might have accounted for the correspondence between field and first-generation laboratory observations of foraging behavior. However, the results of our foraging trials on second-generation laboratory spiders indicate that maternal effects are not the major cause of population differences: foraging differences appeared between the offspring of grassland and riparian mothers, even when the *mothers* (as well as the offspring) from the two populations were reared and maintained in the laboratory under identical conditions. Thus, differences in foraging behavior between the grassland and riparian populations of *A. aperta* probably have a genetic basis.

### *Possible explanations for population differences*

Populational differences in the foraging behavior of *A. aperta* may have resulted from a non-adaptive evolutionary process such as genetic drift. Alternatively, they may have resulted from either natural selection acting directly on attack frequencies and latencies to attack, or selection acting on traits which are genetically correlated with these two aspects of foraging behavior. Electrophoretic studies of genetic variation in the grassland and riparian populations have indicated that neither population is inbred (Riechert 1986), and gene flow is extensive (Riechert, unpublished); thus, genetic drift is probably not responsible for foraging differences. Below, we consider each of the two remaining explanations in turn.

*1 Natural selection acting on attack frequencies and latencies.* Most of the previous studies on the genetic basis of foraging behavior have focused on feeding preferences which correspond to differences in the availability of certain food types. For example, Arnold (1980, 1981a, b) demonstrated that in the garter snake (*Thamnophis elegans*), one population which lives in a predominantly aquatic environment has a genetically-based preference for fish, whereas another which lives in a terrestrial environment prefers slugs.

In our study, genetic differences in foraging behavior were exhibited for a wide variety of prey types. We suggest that these differences may correspond to differences in the *overall* availability of food in the two habitats. In the desert grassland, where the dominant vegetation is dropseed grass (*Sporobolus flexuosus*), prey availability is relatively low, averaging $27.2 \pm 7.3$ mg of live wt/day (Riechert 1986), and temperature extremes restrict foraging activity by adult *A. aperta* to a mean of 525 min/day (Riechert and Tracy 1975; Riechert 1978). In the riparian habitat, which is bisected by a permanent stream and contains a tree canopy of box elder (*Acer negundo*), juniper (*Juniperus osteosperma*) and sycamore (*Plantanus wrightii*), prey availability is higher, averaging $79.6 \pm 9.8$ mg live wt/day, and thermal conditions allow foraging for a mean of 660 min/day (Riechert 1978). Thus, grassland spiders encounter prey at a relatively low rate, and attack prey more frequently and more quickly than riparian spiders, which encounter prey at a much higher rate.

Why might lower attack frequencies be selectively favored in the riparian population? One reason might be that the riparian spiders have responded to their higher encounter rates with prey by becoming more selective in their diet choices. Short-term increases in selectivity with increases in the availability of preferred food types have been documented in other species (Werner and Hall 1974, also see Li et al. 1985; Krebs et al. 1977; Davies 1977; Goss-Custard 1977; Davidson 1978), and are predicted by models of optimal foraging (Schoener 1971; Charnov 1976). However, genetic changes in selectivity within species have not been identified previously.

Another reason that both differences in attack frequencies and latencies to attack prey might be favored by natural selection is that these behaviors could be shaped by differential predation risk. Foraging behavior is affected by predation risk in a number of species (Milinski and Heller 1978; Sih 1980; Dill and Fraser 1984; Lima and Valone 1986; Metcalfe et al. 1987). For example, backswimmers decrease their feeding rates when predators are present, as a result of moving into safer habitats (Sih 1980). In *A. aperta*, prey capture requires that the spider emerge onto the web from the protection of its funnel. Exclosure experiments have shown that riparian spiders experience much higher predation (from avian predators) than grassland spiders when exposed on their webs (Hammerstein and Riechert 1988). Thus, the riparian spiders' low rates of attack may be due to their higher risk of mortality when exposed on the web. Similarly, their long latencies to attack may be related to mortality risk: by waiting to attack prey until its persistent struggling indicates that it is unlikely to escape from the web, riparian spiders possibly can minimize the time they spend on the web in pursuit of prey. In contrast, the grassland spiders, which experience much lower predation and lower prey availability, may attack prey swiftly because this minimizes the probability that the prey will escape from the web before it is captured.

2 *Natural selection acting on correlated traits*. The explanations above assume that frequency of attack and latency to attack have been direct targets of selection. However, populational differences in these behaviors may be by-products of selection acting on some other trait(s) which are genetically correlated with them. Previous work on territorial behavior of *A. aperta* (Riechert 1982) has demonstrated that the grassland and riparian populations differ in their levels of intraspecific aggression. Grassland spiders fight more intensely with one another than riparian spiders do for access to suitable territories. This difference in territorial behavior is genetically based (Maynard Smith and Riechert 1984), and appears to be adaptive: grassland spiders must compete heavily to gain and defend a territory affording adequate food and thermal protection, whereas riparian spiders do not (Riechert 1979). Moreover, population differences in agonistic behavior are associated with differences in territory size, and territory size seems to be determined by the same genes that affect agonistic behavior (Riechert and Maynard Smith 1989).

Thus, at the population level, both the frequency of attacks toward prey and the latency to attack prey are phenotypically correlated with intraspecific aggression and territory size. Furthermore, both intra- and interspecific aggression have a genetic basis. We do not know if these two kinds of behavior are correlated on an individual level, or whether they are genetically correlated as well, such that selection on one type of aggression could cause evolution in both types (for example, selection for increased aggression with conspecifics might produce increased aggression with prey). However, these two kinds of aggression could stem from a common cause; in sticklebacks, in which intraspecific aggression co-varies with aggression (boldness) towards nest predators, the covariance is thought to arise from hormonal levels which affect both types of behavior (Huntingford 1976; Tulley and Huntingford 1988).

### *The genetics of foraging behavior*

The results of this study demonstrate that within an animal species, populational differences in foraging behavior may be exhibited over a wide variety of food types, and these differences can be genetic. Along with previous studies on the genetics of food preferences and foraging behavior (e.g., Arnold 1981b; Wallin 1988; Tauber and Tauber 1987), our work supports one of the assumptions underlying optimal foraging theory: that genetic factors can play a role in at least some aspects of foraging behavior.

Nonetheless, some important questions remain for future research. First, because genetically based differences in foraging behavior have been identified within only a few species, we do not know the extent to which they occur; they may be rare in animal groups (e.g. birds) that are capable of extensive migration between different foraging areas, where widely differing prey availabilities are encountered. Second, whereas genetic variation in foraging behavior has been shown *among* populations of single species, little is known about genetic variation *within* populations (but see Ehlinger and Wilson 1988). Finally, no studies of foraging behavior have investigated whether or not specific variables in optimal foraging models, such as handling time, are influenced by genetic factors.

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