Title: <u>Interaction of wandering spiders in old fields at UNDERC with notes: behavior, prey selection and distribution</u>

Abstract

In community ecology, most current models of trophic interactions are based on the assumption that groups of species can be treated as distinct functional units, such as a guild or trophic level. I determined the species richness in two old fields at UNDERC and studied the interactions between three wandering spiders that may determine their behavior and distribution. The species richness in the old field was established by surveys. The interactions were studied by manipulative experiments of intra guild interactions, prey selection and hunting behavior. I found that species richness is directly related to the complexity of the environment and to the spiders intra guild interactions. Spiders play an important role as a balancing agent for prey populations, and may prevent insect outbreaks.

Introduction

In community ecology, most current models of trophic interactions are based on the assumption that groups of species can be treated as distinct functional units, such as a guild or trophic level. This necessarily implies that species within the same functional unit have identical effects on lower levels in the food web (Schmitz, 2001). This conceptualization tends to ignore details about the effects of individual species in the food web. Predator species within the same guild may be segregated by habitat or foraging behavior. Furthermore, predator species may have differential abilities to capture and subdue prey (Schmitz, 2001). In addition, predator diversity can change how communities are structured. For example, Finke and Denno (2004) showed that increasing the diversity of arthropods in a community promoted intra-guild interactions among predators, diminished enemy impacts on herbivores, and dampened cascading effects in the time of the day spent by predators looking for resources. These changes to ecosystem function occurred because of omnivory among predators (Finke and Denno, 2004). Therefore, it may not be realistic to lump predators into a discrete trophic level.

Spiders are a good example of intra guild predators. They are diverse and have a wide variety of methods for hunting among the different species. Because spiders are omnivorous and cannibalistic, interactions among spiders are complex. Spiders compete with, and prey upon other individuals in the same guild.

Body size has been found to correlate with a wide range of physiological, ecological and behavioral traits, and is also tied to foraging strategy in spiders (Walker et all., 1999). Among spiders, active predators are more likely to be small bodied than sit-and-wait predators (Walker et all., 1999), and occupy different locations within the vegetation canopy (spatial stratification, Schmitz, 2001). The structural complexity of the vegetation determines the diversity of predators that can occupy different microhabitats at the same time. Spiders exhibit vertical stratification in vegetation based in their foraging technique. Sit-and-wait predators occupy the top part of the vegetation web building spiders are concentrated at the middle and lower litter layers, and active foragers occur in the lower litter layer and the ground (Wagner, 2003). Vertical segregation in vegetation is also believed to be a mechanism to reduce competition (resource partitioning) and predation among spiders (Wagner, 2003).

This study has four goals. First, I wish to determine the richness of spider species that occur in two old fields at UNDERC. Second, through a manipulative lab experiment, I wish to determine if the presence of different spider species {Lycosidae

(*Pardosa* sp., *Gladicosa gulosa*) and Thomisidae (*Xysticus* sp.)} can alter spider distribution in the vegetation. I hypothesize that spiders will exhibit vertical stratification to avoid the risk of predation and to reduce competition. This will lead to better understanding of intra-guild interactions among spiders. Third, I wish to study the hunting behavior of three species of spider: Lycosidae (*Pardosa* sp., *Gladicosa gulosa*) and Thomisidae (*Xysticus* sp.). Finally, I wish to determine whether the three species of spider prefer to feed on grasshopper nymphs or small spiders.

Materials and Methods

Study Organisms and Natural History

Spiders are typically omnivorous predators that prey principally on any kind of arthropod of the right size. Spiders have long generation times compared with most of their arthropod prey. They are generalist feeders which don't exhibit density-dependent tracking of their prey, but rather switch to the most common suitable prey. The wandering spiders selected for this study come from of two different families: Lycosidae (*Pardosa* sp., *Gladicosa gulosa*) that are active hunters and Thomisidae (crab spiders, *Xysticus* sp.); a sit-wait predator.

Spider Survey

The spider species richness was established using 1 m^2 plots and pitfall traps in two old fields (New Gravel Pit, Spider Nest-located a long the power lines between the Hank Lab. and the Wet lab.-) at UNDERC. Each 1 m^2plot was established in a place with different dominant vegetation and complexity. In the New Gravel Pit the plots were established in an area dominated by bunch berry (*Cornus canadesnsis*), Striped fern, ox-eyed daisy (*Chrysatemun leucanthenum*) and small grasses (Site NGP1). A second site

(Site NGP2) was established in an area closer to easter larch (*Larix laricina*), white spruce (*Picea glauca*), and striped fern. At Spider Nest the plots were established in an area dominated by striped fern, closer to the forest edge (Site SN1), the second was established in the center part that is dominated by striped fern, ox-eyed daisy (*Chrysatemun leucanthenum*) and small grasses (Site SN2). The final plot was established in an area of tall herbaceous plants (Site SN3). Each plot was censused once for an hour and every spider was collected.

Pitfall traps (9cm depth) were established in the two old fields during the three weeks of the study. The traps were set along a 10m transect in representative vegetation. The traps were checked once in a day in the morning before 8:00 am. At the same time the pitfall traps were used to collect the three spider species used in the lab experiments. All spiders were identified to family, and then to genus and/or species if possible.

Lab Experiments- Intra-guild interactions

As results of their physiology and their mimetic behavior wandering spiders are difficult organisms to find and study in the field. Therefore, it is necessary to study them in laboratory experiments. But my laboratory enclosures simulated the complexity of the natural environment with the use of sod from the field as substrate in the enclosures. This maintains some realism of the natural environment of spiders. The enclosures (625 cm^2 in area and 30 cm high) for the experiment of intra-guild interactions were constructed using 10 gal fish tanks and dived by the half with a screened frame to create two enclosures in each fish tank. Fiberglass window screening was used as a lid to prevent spiders from escaping. I tried to remove all the invertebrates from the sod, but I was not able to take all the invertebrates that live underground or use the underground as a diurnal refuge.

The experiment was run during a 1 week period. I used four treatments. There were three controls, one for each of the spider species {Lycosidae (*Pardosa* sp., *Gladicosa gulosa*) and Thomisidae (*Xysticus* sp.)}. The controls each had 2 spiders per cage. The fourth treatment (competition) contained 6 spiders (2 of each species) in each enclosure. The prey used for all the treatments was one small spider (Lycosidae) and one grasshopper (Acrididae) per cage. Each spider was marked and weighed at the start and weighed again at the end of the experiment to determine changes in growth. Spider observations (height and location) were taken in the last three days twice per day.

Lab Experiments- Hunting Behavior

The observations of hunting behavior were run in small plastic enclosures (228cm^2 are and 12cm high) with sod from the field as substratum. Each enclosure contained one spider and with grasshopper nymphs (Acrididae) for food. Three species of spider were observed {Lycosidae (*Pardosa* sp., *Gladicosa gulosa*) and Thomisidae (*Xysticus* sp.)}. The behavior of each spider was recorded during a 15 min period of focal observations in which the time spent moving was recorded. I observed hunting behavior and number of successful hunts was recorded in 14 replicates for *Pardosa spp*., 25 replicates for *Gladicosa gulosa* and 32 replicates for *Xysticus spp*.

Lab Experiments- Prey Selection

The prey selection experiment was run for three days in similar enclosures used in the hunting behavior experiments. Each enclosure was stocked with one spider per cage. Three prey treatments were run for each spider species {Lycosidae (*Pardosa* sp., *Gladicosa gulosa*) and Thomisidae (*Xysticus* sp.)} to test for prey selection between two types of prey: grasshopper nymphs and small spiders. The prey treatments were: control prey spider (2 prey spiders per cage), control grasshopper (2 per cage) and prey spider vs. grasshopper (one of each per cage) with four replicates per treatment. I recorded whether the spider ate, and which of the prey was selected first.

Data Analysis

The program SYSTAT 11 {SYSTAT, Software Inc, Richmond CA) was used to analyze the data. I used a two-way X^2 to analyze the observations of the prey selection experiment and compare the preference of each spider species (spider vs. grasshopper). In the behavior experiment, hunting success was also measured with a two-way $X^{2,}$ and the proportion of time spent moving was analyzed using a one-way ANOVA. In the intra-guild competition experiment, the change in weight, average height in the cage, and survivorship of the spiders in control vs. competition treatments was analyzed for each species separately using a two-sample t-test.

Results

Spider Survey

The results from the spider survey are presented in tables 1 and 2. Spider species richness was 2.9 times higher at the Spider Nest (SN), than at the New Gravel Pit (NGP). Plots with lowest richness in SN had the same number of species as most plots at NGP. In SN, medium size spiders were more abundant. This may be related to more complex and diverse microhabitats that are not present in NGP. There is an increase in the presence of the web building spiders from two species in the NGP to nine or more species in SN (Table 2). Also, there is and increase in the number of large species and in the number of families at SN compared with NGP.

Intra-guild interactions

Change in body mass during the intra-guild interaction experiment was not significantly different between control and competition treatments for any of the species tested (Table 3). Many of the individuals used in the study lost mass over the course of the experiment. Average height of spiders in the vegetation in control and competition treatments varied significantly for Pardosa spp. (Fig 1), but not for Xysticus spp. and G. gulosa (Fig 1). Spider survivorship was significantly different results for *Xysticus* spp. but not for *Pardosa* spp. and *Gladiscosa gulosa* in the competition experiment (Fig 2).

Hunting behavior and prey selection

There was no significant difference in hunting success among the three spiders studied (P=0.626, Table 4). There was also no significant difference in the proportion of time spent moving among the three spiders studied (P=0.682).

There was no significant difference in prey choice (grasshoppers vs. small spiders) among the three spider species tested (P=1.000).

Discussion

One of the most important components that determine how species interactions in natural environments are mediated is the composition and distribution of species in different trophic levels. The natural interactions among generalist predators, such as spiders, are very complex. Spiders are omnivorous, and feed over different trophic levels. Omnivory can alter the importance of top- down effects in a food web Spiders can self-damped their own populations, by territorialism and cannibalism at higher densities (Riechert, 1999; Marshall, 1999). Territorial behavior and cannibalism determine the upper limit for population size in a given habitat (Riechert, 1999).

Spiders are a very diverse group. The composition of plant diversity determinates the number of microhabitats contained in a given habitat, and therefore the number of niches available to spiders. Different spider families occupy different niches and present different hunting behaviors. For example, Thomisidae is a sit-wait predator while Lycosidae are active hunters. Spiders, unlike many other animals, may not alter foraging patterns greatly due to hunger because they are known to have physiological adaptations to limited feeding opportunities and starvation (Persons, 1999).

The dominant vegetation at SN was taller herbaceous plants which provide cover variation in a vertical gradient, as well as providing dead organic material which creates important microhabitat for a large variety of spiders and their prey. In contrast, the NGP understory is mostly dominated by fern which creates shade and reduces the diversity of vegetation complexity. This further decreases the diversity of spiders. These results suggest that SN has a more complex environment, which increases spider diversity. If we combine the environmental complexity with the richness of species, this suggests that the interactions among spiders are very complex and there is many opportunities for intra-guild interactions.

Spider Hunting Behavior

The spider *Xysticus* spp. a sit-and–wait predator prefers to hunt in a different area than *Misumena vatia*, which occurs in the upper part of daisy flowers. *Xysticus* spp. were commonly found in the stems of herbaceous plants or just under the flower but not on top of the flower. From the behavior experiment I found that the *Xysticus spp.* starts its hunting process with the complete extension of four front legs forming an angle of at least 120^0. At the moment the prey gets close enough, the spider uses its first two legs to grab the back legs of the prey. Then, it uses its second pair of legs to grab the middle or first pair of legs of the prey. The spider then bites the prey, usually on or in the head.

The Lycosidae family is described as active hunters as adults, but are more sit and wait predators as juveniles (Persons, 1999). When hunting grasshoppers, both *Pardosa* spp. and *G. gulosa* moves closer to their target from behind, and makes a first bite to the abdomen. *Pardosa* spp. makes a short and fast drum with the first pair of legs and then runs and bites the grasshoppers in the abdomen. *G. gulosa* slowly moves closer to the back of the prey and then makes a fast movement to cover the prey with its body, then bites the prey in the abdomen. *G. gulosa* uses its body to immobilize the prey, biting it a second time, and does not release the prey until it is dead. When hunting other spiders the process is the same but *G. gulosa* turns it on its back, and bites the prey closer to the mouth parts.

Intra-guild Interactions

Species abundances and dynamics in component trophic levels (food chain structure) are limited by consumers in the top trophic level (top-down control) or by nutrient inputs to the lowest trophic level (bottom-up control, Schmitz, 1993). Interactions among plants, herbivores, and natural enemies provide a variety of possible endpoints in species community composition and relative densities (Oedekoven, 2000). Predators can both reduce prey species by predation (direct effects) or may alter prey behavior (indirect effects).

Predator prey interactions in the same trophic level play an important role in shaping prey species characteristics (Oedekoven, 1998). Predator species can both reduce prey-species density and cause prey to change their behavior to avoid risk of predation. The nature of the direct effects of top predators or competitors on prey also can have a profound effects transmitted throughout community (Schmitz, 2001). Indirect effects can be classified in to two classes. The first, called density-mediated indirect effects, arise when one species (A) indirectly affects another species (B) by changing the abundance of intermediate species that interact with both species A and B (Schmitz, 2001). The second, called trait-mediated indirect effects, arise when one species (A) modifies the way two other species (B and C) interact by causing changes in the behavior or life history of the intervening species (B). Cascading effects arising from changes in prey diet or habitat selection in response to increased predation risk are examples of trait-mediated indirect effects (Schmitz, 2001).

Competitive interactions can also cause behavioral changes, such as when one species alters the space use or feeding behavior of a second species, resulting in a reduction in access to resources for the second species (Marshall, 1999). The results of the prey selection experiment show that there is no difference in the ability of the spiders to hunt either of the two organisms used as prey. Comparing their hunting success at family level, both families have ~45% success. This implies that these spiders may have similar role and effects over the prey species studied in this controlled environment. However these spiders differ in their foraging behavior and they are spatially segregated in the vegetation and their effects over prey may vary. Also they might prefer other prey species not tested here on prey in their natural environment. But Pardosa overlap spatially with

G. gulosa and they hunt each other but Pardosa developed some behavioral adaptation to avoid competition.

This change in behavior was observed in *Pardosa* spp., which altered its height from spending most of the time in cavities in the ground when alone, to spending more time higher in the vegetation when put in enclosures with other species (Fig 1). Crab spiders also slightly increased {Lycosidae (*Pardosa* sp., *Gladicosa gulosa*) and Thomisidae (*Xysticus* sp.)} height in vegetation, though the change was not significant (Fig 1). Another behavioral change observed in the *Pardosa* spp. was a reduction in the time spent moving because in all the observations *Pardosa* were observed in the same place when in enclosures with *G. gulosa*. This kind of behavior was observed in another study conducted by Persons and Rypstra (2001). They found that the spider *Pardosa milvina* displays an effective anti-predator behavior (reduced activity) in the presence of silk and excreta cues from adult *Hogna helluo*, which are the same size as *G. gulosa*). They found that this species exhibited size-structured intra-guild predation, whereby the predator and prey roles are determined by the relative mass of each spider during an encounter. This implies that *P. milvina* can hunt *H. helluo* as juveniles, but as adults, *H. helluo* are typically 20-30 times the body mass of and adult *P. milvina* which then plays the role of prey. Long periods of reduced activity greatly increase the survival probabilities of *P. milvina* in the presence of a large *H. helluo*.

Intra-guild interactions can directly affect species in the same trophic level through predation and cannibalism. Cannibalism was observed in the *G. gulosa* control cages in which two of the spiders died. This predatory behavior explains why the spider populations don’t grow exponentially in nature or reach high enough densities to set the stage for density-dependent resource limitation (Marshall, 1999). One of the key assumptions in competition theory is that one of the species in a community is better at exploiting some limiting resource, and does so to the detriment of other species (Marshall, 1999). As a result, other species can be out-competed. In this experiment, the *Xysticus* spider experienced the highest mortality in presence of the wolf spiders (100% mortality vs.100% survival in the control cages). This suggests that the spiders exhibit vertical stratification as a means to reduce competition and predation.

Vertical stratification is one mechanism used by spiders in the natural environment to reduce intra-guild interactions and to create resource partitioning. Resource partitioning is a mechanism in which the species only use a small part of all their possible resources and territories to reduce the pressure of inter specific competition. Like other generalist predators, spiders exhibit the ability to exploit temporal variability of prey without have a strong negative effect over the prey population. They operate as an assemblage of predator species feeding on an assemblage of prey species. Spiders exhibit a stable point control mechanism in which the spiders work as an assemblage of species (multiple predator species) and have a significant top down control over prey populations in the lower trophic levels(Riechert, 1999). Spider diversity and abundance plays an important role as a balancing agent for prey populations, and may help prevent insect outbreaks. Therefore, to understand how these mechanisms work, it is important to look at the effects of multiple species of spiders on a community, rather than lumping all species of spiders together as a single unit.

Table 1 Results of species richness in plots (1 m^2)

Spider	*Site*					
	NGP1	NPG2	NPG3	SN1	SN2	SN3
Family: Lycosidae						
Pardosa spp. 1	1					
Pardosa spp. 2				1		1
Gladicosa golosa		1	1			
Family: Thomisidae						
Unknown species 1				1		
Misumena vatia				1		
Xysticus tranversatus	1			1	3	
Family: Philodromidae						
Thanatus formicinus				1	3	1
Tibellus oblongus	1			2	2	
Family: Pisauridae						
Pisaurina mira		1				
Family: Gnaphosidae						
Gnaphosa muscorum				1	4	
Family: Linyphiidae						
Hypselistes florens			1		1	
Family: Tetragnathidae						
Unknown species 2				1	1	
Family: Araneidae						
Araniella displicata						1
Family: Salticidae						
Pelegrina proterva					1	
Unknown species 3					2	
Total Species	3	2	2	9	8	3
Total Individuals	3	2	2	10	15	3

Table 2 Species richness by site

Spider	NGP	SN
Family: Lycosidae		
Pardosa spp. 1	X	X
Pardosa spp. 2		X
Pardosa spp. 3		X
Pardosa spp. 4		X
Gladicosa golosa	X	X
Alopecosa aculatea	X	X
Hogna frondicula		X
Family: Thomisidae		
Unknown species 1		X
Misumena vatia		X
Xysticus tranversatus	X	X
Xystycus spp.		X
Family: Philodromidae		
Thanatus formicinus		X
Tibellus oblongus	X	X
Family: Pisauridae		
Pisaurina mira	X	X
Family: Gnaphosidae		
Gnaphosa muscorum		X
Family: Linyphiidae		
Hypselistes florens	X	X
Pityohyphantes costatus		X
Family: Tetragnathidae		
Tetragnatha spp.		X
Unknown species 2		X
Family: Araneidae		
Araniella displicata	X	X
Araneus spp.		X
Family: Salticidae		
Pelegrina proterva		X
Phidippus audax		X
Evarcha hoyi	X	

Unknown species 3		X
Family: Clubionidae		
Clubiona spp.		X
Family:Agelenidae		X
Total Species	9	26

Table 3 Change in weight

Species	N	df	Mean	t	SE	P
Xysticus	6	-	-0.43	-	0.27	-
Gladicosa	10	8	0.20	-0.264	0.21	0.799
Pardosa	7	5	-0.009	0.956	0.025	0.383

Table 4 Hunting successful

Species	Total	Completed	Succesfull
Xysticus	17	7	.41
Gladicosa	6	2	.33
Pardosa	3	2	.66

Intra-guild interactions height

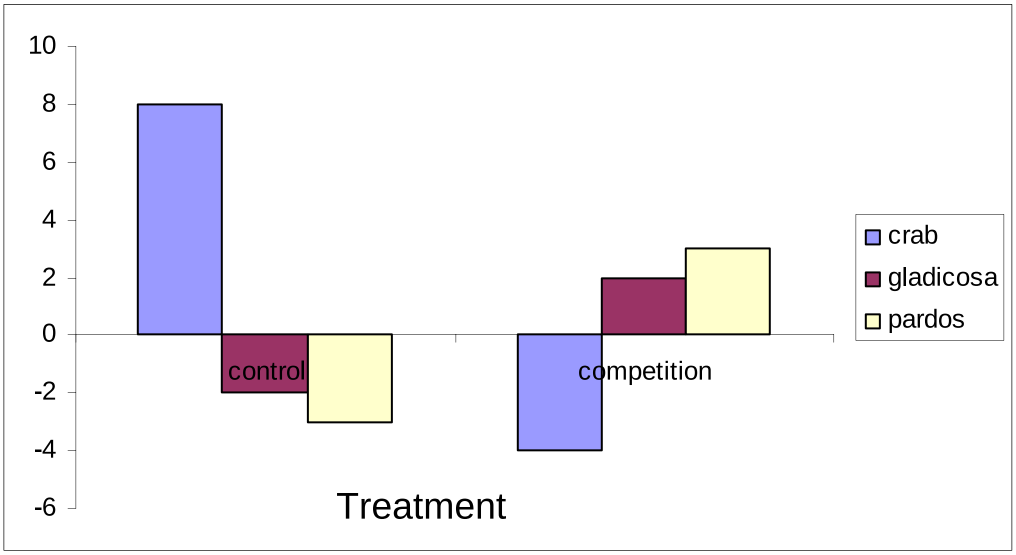

Fig. 1 In this figure is possible to observe how the Pardosa spp. is changing its behavior has results of the intra guild interactions with Gladicosa gulosa presence and also the crab spider is a little bit higher in the vegetation

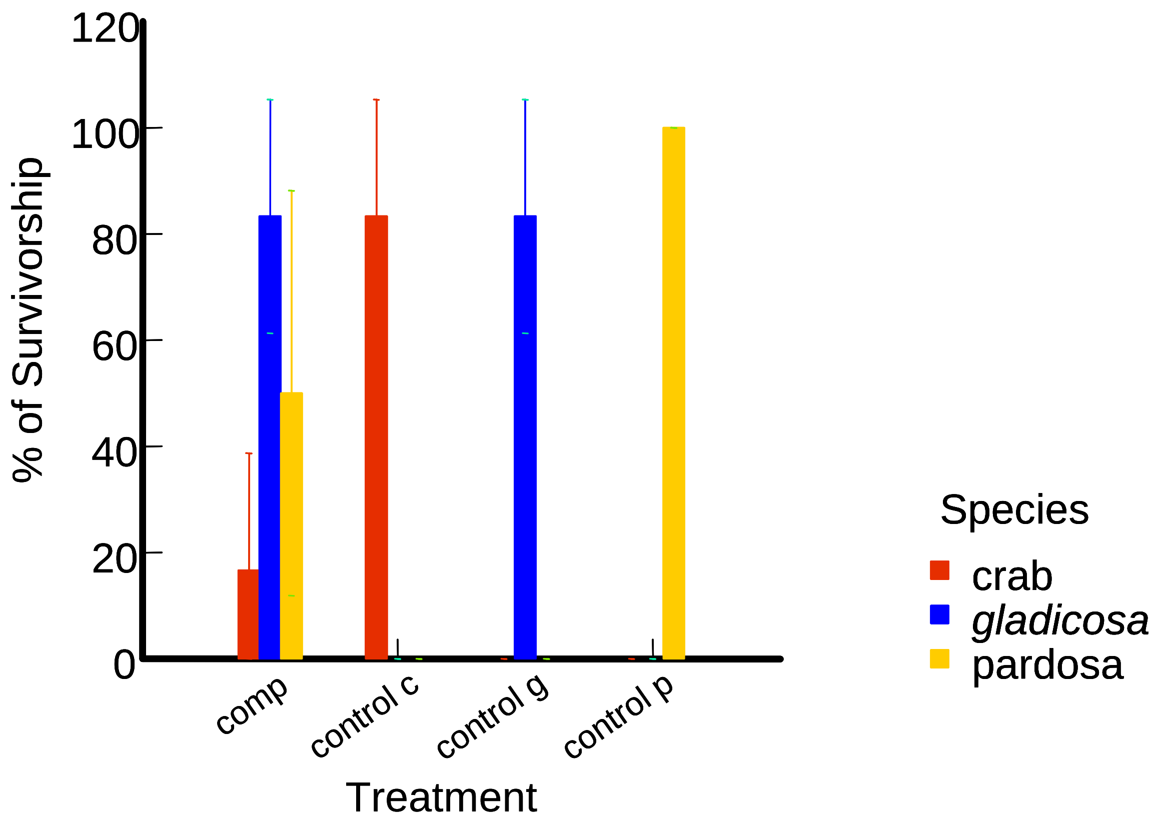

Fig. 2 Show how the Xysticus spp. its out competed by the other two Lycosidae in a confined environment and the Xysticus spp. don’t have the opportunity to go to the tallest vegetation. Lycosidae species show to have a more aggressive behavior and also predate on his own species during the experiment.

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The Bernard J. Hank Family Endowment.

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