

Climatic control of trophic interaction strength: the effect of lizards on spiders

David A. Spiller · Thomas W. Schoener

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Abstract We investigated how temporal variation in rainfall influences the impact of lizards on spiders inhabiting small islands in Abaco, Bahamas. Annual censuses of web spiders were conducted on nine lizard islands and on eight no-lizard islands 1994–2003. Repeated-measures ANOVA showed that annual variation in spider density (time) and in the lizard effect on spider density (lizard \times time) were both significant. Correlation coefficients between the lizard effect (ln ratio of no-lizard to lizard spider densities) and number of rainfall days were generally negative, and strengthened with length of the time period during which rainfall was measured prior to annual spider censuses. Spider density was also negatively correlated with rainfall days and strengthened with length of the prior time period. Longer time intervals included the hurricane season, suggesting that the strong negative correlations were linked to high rainfall years during which tropical storms impacted the region and reduced spider and lizard densities. Split-plot ANOVA showed that rainfall during the hurricane season had a significant effect on the lizard effect and on spider density. Results in this study are opposite to those found in our previous 10-year study (1981–1990) conducted in the Exuma Cays, a moderately xeric region of the Bahamas, where the relation between rainfall and the lizard effect on spider density was positive. Combined data from the Exuma and Abaco studies produce a unimodal relation between trophic interaction strength and rainfall; we suggest that the negative effect of storms associated with rain-

fall was paramount in the present study, whereas the positive bottom-up effect of rainfall prevailed in our previous study. We conclude that climatic variability has a major impact on the trophic interaction and suggest that a substantial change in precipitation in either direction may weaken the interaction significantly.

Keywords Climate change · Community processes · Lizards · Precipitation · Predation

Introduction

Understanding how climate change modifies species interactions is needed to predict the community-wide impacts of global warming (Kareiva et al. 1993; Harrington et al. 1999; Schmitz et al. 2003). Precipitation, a key factor affecting both bottom-up and top-down processes in food webs (Andrewartha and Birch 1954; Hunter and Price 1992; Stenseth et al. 2002), is now expected to change relatively quickly in many regions of the world (Huxman et al. 2004). Given that primary productivity is often positively correlated with precipitation (Webb et al. 1983; Polis et al. 1997; Chase et al. 2000; Meserve et al. 2003; Huxman et al. 2004; Baez et al. 2006), bottom-up effects caused by increased rainfall can lead to greater abundances of consumers (e.g., Lima et al. 2002; Price and Hunter 2005; Baez et al. 2006) and in theory could lead to magnification of top-down effects by predators on their prey (Oksanen et al. 1981). Other processes can also cause a positive relation between precipitation and top-down effects of predators, such as higher predator activity or efficiency with higher precipitation (Post et al. 1999; Preisser and Strong 2004; Lensing et al. 2005). However, extremely high precipitation events can cause flooding, landslides, or may be associated

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D. A. Spiller (✉) · T. W. Schoener
Section of Evolution and Ecology and Center
for Population Biology, University of California,
One Shields Avenue, Davis, CA 95616-8755, USA
e-mail: daspiller@ucdavis.edu

with high winds, thereby having negative impacts on populations in multiple trophic levels (Power et al. 1996). In accordance with the environmental stress hypothesis (Menge and Sutherland 1987), top-down effects of predators may be stronger under more benign conditions, when precipitation is not too high. Taking both the positive and negative effects of precipitation into consideration, we propose that the relationship between trophic interaction strength and precipitation may be unimodal (Fig. 1); the strength of the effect of predators on their prey increases with rainfall up to the point where disturbance associated with extremely high rainfall reduces the density and/or per capita effect of predators, causing interaction strength to decline with rainfall.

In a previous study of spider populations on small Bahamian islands (Spiller and Schoener 1995), we found that annual variability in the effect of lizards on spider density was positively correlated with rainfall over a 10-year period. The study was conducted in the Exuma Cays, a moderately xeric region in the Bahamas, during a period (1981–1990) when no hurricane impacted the region. Hence, the positive effects of rainfall on trophic interaction strength may have been prominent during the study, as in the ascending portion of Fig. 1. Since that study tropical storm activity has increased markedly in the Atlantic Basin (Goldenberg et al. 2001), and we have documented the impact of major hurricanes on island food webs in two areas in the Bahamas (Spiller et al. 1998; Schoener et al. 2001; Spiller and Agrawal 2003; Spiller and Schoener 2007). One of the areas, Abaco, was directly hit by Hurricane Floyd (category IV) in 1999, the first major hurricane to strike that area since 1965 (UNISYS.COM 2004). The storm surge completely inundated all the study islands, devastating the spider and lizard populations (Schoener et al. 2001). In 2001, the study site was impacted by Hurri-

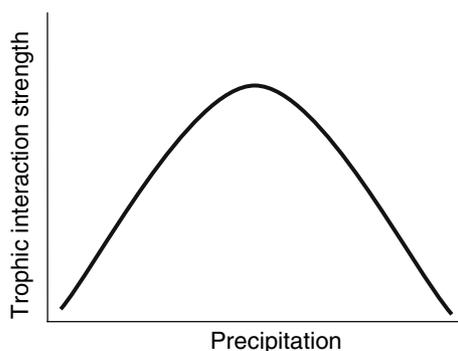


Fig. 1 Hypothesized relation between trophic interaction strength (the top-down effect of predators on their prey) and precipitation. Assuming that productivity increases with precipitation, the ascending portion of the curve is in accordance with Oksanen et al. (1981). Assuming that high precipitation is associated with physical disturbance, the descending portion is in accordance with Menge and Sutherland (1987)

cane Michelle, only a category I but having a surge that again completely or largely inundated the study islands (Schoener et al. 2004).

Below we assess the relationship between rainfall and the effect of lizards on spider density in Abaco during a 10-year period (1994–2003), which includes 6 years before Floyd and 4 years after. Previous field experiments demonstrated that lizards are major predators of spiders (Spiller and Schoener 1998). Because high tropical storm activity is caused by forces from both the Atlantic and Pacific Oceans creating climatological conditions in the Caribbean that simultaneously promote higher rainfall and greater tropical storm formation (Bove et al. 1998; Taylor et al. 2002, C. Landsea, personal communication), we predicted that the strength of the lizard–spider interaction would decrease with rainfall, as in the descending portion of the curve in Fig. 1.

Materials and methods

Study islands and species

The study islands were located in a protected “creek” waterway just south of Snake Cay, Great Abaco, Bahamas (details in Schoener et al. 2002). We selected a set of 17 islands from a larger set of 41 islands (see Schoener and Spiller 2006) using the following three criteria: (1) web spiders were censused annually from 1994 to 2003 on each island; (2) the common lizard, *Anolis sagrei*, was continuously present or absent on each island throughout the study period; and (3) the larger lizard, *Leiocephalus carinatus*, was not present naturally or experimentally introduced onto the island. This yielded a dataset consisting of 10-year time series of spider densities on nine islands with lizards present and on eight islands with lizards absent. Vegetated area of the islands ranged from 13.7 to 337.5 m²; mean (range) for no-lizard and lizard islands were 82.3 (13.7–183.8) and 158.3 (59.4–337.5), respectively.

Web spiders were censused annually (April) by carefully searching the vegetation on the entire island, as in our previous studies (details in Schoener and Spiller 1992). Vegetation on the study islands was usually sparse and rarely exceeded 2 m in height, so that we were able to inspect virtually all foliage for webs. Spider density was computed as the total number of individuals divided by vegetated area of the island. *Eustala cazieri* (Araneidae) was the most common species and comprised 80.2% of all the individuals censused during the entire study. Other species included nine araneids (*Metepeira datona*, *Metepeira* sp., *Argiope argentata*, *Argiope trifasciata*, *Argiope florida*, *Gasteracantha cancriformis*, *Eriophora ravilla*, *Cyclosa walckenaeri*, *Gea* sp.), four tetragnathids (*Plesiometa argyra*, *Nephila clavipes*, *Tetragnatha*

sp. and *Leucauge* sp.), one uloborid (*Uloborus trilineatus*) and one theridiid (*Argyrodes elevatus*).

Analyses

Monthly rainfall records were obtained from New Providence, Bahamas (Sealey 1994, 1995, 1996, 1997, 1998, 2000, 2001, 2002, 2003, 2004; Sealey et al. 1999; N. Sealey, personal communication), the nearest weather station with continuous recordings and located ~150 km from the study site. We used number of days with rain as in our previous study on rainfall effects (Spiller and Schoener 1995) and followed the general procedures in that study. First, to obtain a descriptive assessment of the relationship between rainfall and spider density, we performed a series of correlation analyses. We correlated mean spider density (ln transformed) with the number of days that had a measurable amount of rain during a specific length of time prior to our spider censuses. We calculated separate correlation coefficients for mean spider densities on lizard and no-lizard islands; we used cumulative number of days having rain during the 2, 4, 6, 8, 10 and 12 months prior to spider censuses. To measure the strength of the lizard effect on spiders in each year, we computed the natural logarithm of the ratio of mean spider density on no-lizard islands to mean spider density on lizard islands (the measurement for effect size recommended by Hedges et al. 1999; see also Osenberg et al. 1999). Then we correlated the annual lizard-effect size with number of days of rainfall. We present the correlation coefficients obtained from these analyses for descriptive purposes only, without significance levels, because the data on spider density from year to year are not independent; we did not conduct autoregressive analyses because they may be inaccurate with only ten observations in the time series (Shumway 1988; R. Shumway, personal communication).

To test for significant differences in spider density among years and between lizard and no-lizard islands we used the SAS (Freund et al. 1991) repeated-measures ANOVA program. Year was the repeated (within subjects) factor and lizard (present versus absent) was the main (between subjects) factor. The year \times lizard interaction tested whether the lizard factor varied among years. Spider densities were log transformed to stabilize variances, which tended to be proportional to means, and so that the year \times lizard interaction would test for multiplicative differences among years in the lizard factor. Note that were untransformed data used, the year \times lizard interaction would test for arithmetic differences in spider density on no-lizard and lizard islands. This difference may be expected to increase with an increase in overall mean spider density even when lizards reduce spider density by a constant factor; see Hurlbert and White (1993) for other cases in which log transformation is appropriate in analyses of

interactions. Because 14 observations (out of 170 total) were zero, 0.01 (the smallest spider density value) was added to each value before transformation. For the repeated factors, we report univariate tests with adjusted *P*-values (Huynh–Feldt method) because in this case, with ten repeated measures and only 17 subjects, the multivariate tests are too conservative (Stevens 1992).

To test for a significant relationship between spider density and rainfall we used an explicit split-plot ANOVA model in which number of days with rain was a time-varying covariate (Winer 1971; N. Willits, personal communication). The SAS model was as follows:

```
PROC GLM;
CLASS LIZARD ISLAND YEAR;
MODEL DENSITY = LIZARD ISLAND(LIZARD)
RAIN YEAR RAIN  $\times$  LIZARD YEAR  $\times$  LIZARD/SS1;
TEST H = LIZARD E = ISLAND(LIZARD);
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This explicit model was designed to decompose year and year \times lizard into a linear response to rainfall and other unexplained sources of yearly variation. Because rain was a function of year we used type I SS; rain is not estimable by type III SS. In the model statement rain was entered before year so that the former represented yearly variation explained by rain and the latter represented unexplained (remaining) yearly variation. Data were log ($x + 0.01$) transformed as described above.

In addition to rainfall, we obtained monthly temperature records for New Providence from the Bahamian Department of Meteorology. To test for a significant relationship between spider density and temperature we performed the analogous correlation analyses and split-plot ANOVA model as described above with mean daily maximum temperature each month as the time-varying covariate.

Results

Correlation coefficients between mean spider density (ln transformed) and number of rainfall days were generally negative, larger for no-lizard than for lizards islands and tended to strengthen with the length of the time period during which rainfall was measured prior to the annual spider censuses (Table 1). The lizard effect was also negatively correlated with rainfall days and the relation tended to strengthen with length of the prior time period.

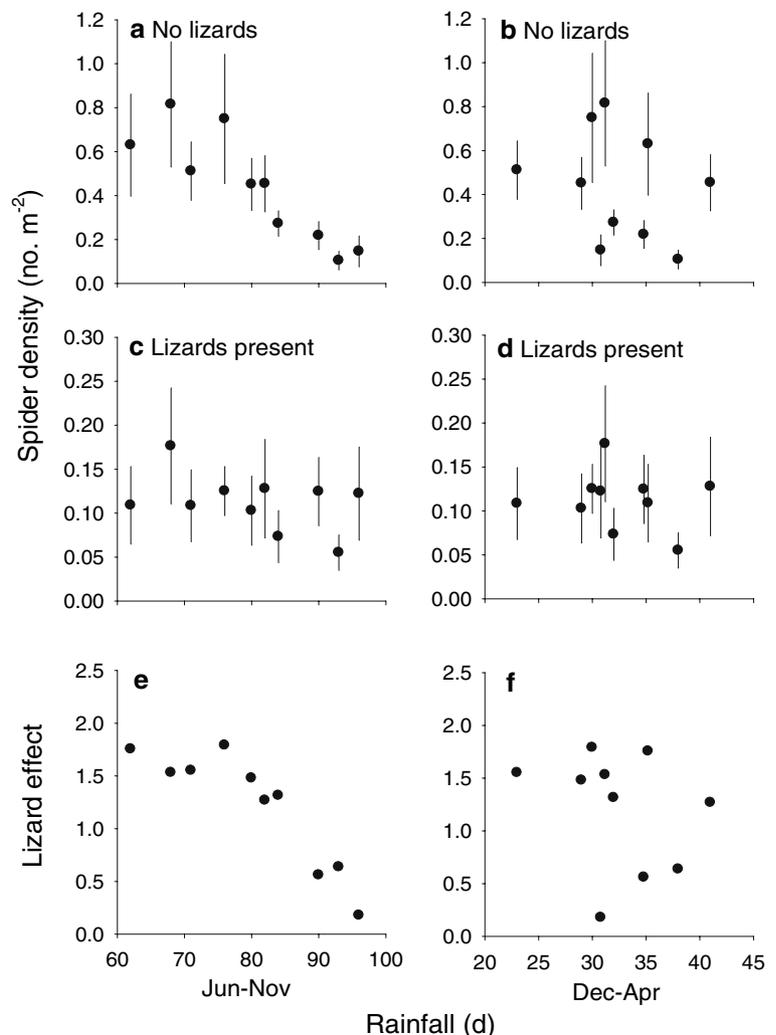
Longer time intervals include the hurricane season (June–November), suggesting that the strong negative correlations were linked to high rainfall years in which tropical storms impacted the region and reduced spider density. Indeed, the negative effect of rainfall on spider density was more apparent in analyses of number of rainfall days during the hurricane season (June–November) than after (Decem-

ber–April) (Fig. 2). Note that rainfall in May is excluded from the presentation of hurricane versus non-hurricane rainfall because: (1) May is not part of the official hurricane season, and (2) it occurs after the annual April spider cen-

Table 1 Pearson correlation coefficients of mean web-spider density (ln transformed) on islands with lizards absent (*No lizards*) and present (*Lizards*), and the lizard effect on web-spider density (*Lizard effect*; measured by the ln ratio of mean spider density on no-lizard to lizard islands), versus cumulative number of days of rain within different time periods prior to the annual spider census ($n = 10$; 1994–2003)

Rainfall (days)	ln (mean number of spiders m^{-2})		
	No lizards	Lizards	Lizard effect
2 Months	-0.383	-0.005	-0.482
4 Months	-0.241	-0.255	-0.157
6 Months	-0.393	-0.201	-0.381
8 Months	-0.849	-0.564	-0.749
10 Months	-0.843	-0.429	-0.820
12 Months	-0.873	-0.458	-0.840

Fig. 2a–f Correlations between annual web-spider population properties and cumulative rainfall during the hurricane season, June–November (*Jun–Nov*) (*left-hand panels*) and the non-hurricane season, December–April (*Dec–Apr*) (*right-hand panels*) during 1994–2003 at Abaco, Bahamas. Annual spider density (mean \pm SE) in April for islands with lizards **a**, **b** absent and **c**, **d** present. **e**, **f** Effect of lizards on spider density (measured as natural logarithm of the ratio of mean spider density in April on no-lizard islands to mean spider density in April on lizard-present islands). Pearson correlation coefficients (r) are **a** -0.876, **b** -0.297, **c** -0.402, **d** -0.141, **e** -0.886 and **f** -0.300 ($n = 10$ in each)



sus and is thereby discontinuous with the non-hurricane rainfall interval prior to the census.

The strong negative relationship between mean spider density on no-lizard islands and rainfall during the hurricane season (June–November) prior to the spider census (April) can be seen in time-series plots (Fig. 3). Rainfall was highest in 1999, and in the following year (2000) spider density on no-lizard islands declined, whereas in 1996 rainfall was lowest and in the following year (1997) spider density increased. Rainfall was also high in 2000–2001 and spider density was low in 2001–2002; this was followed by lower rainfall in 2002 and higher spider density in 2003. The lizard effect followed the same pattern.

Repeated-measures ANOVA showed that the overall effect of lizards on spider density was significant (Lizard effect, $F_{1,15} = 11.31$ and $P = 0.0043$) as well as annual variation in spider density (Year effect, $F_{9,135} = 5.52$ and $P = 0.0001$) and annual variation in the lizard effect (Year \times Lizard effect, $F_{9,135} = 2.70$ and $P = 0.0130$). Split-plot analysis with cumulative rainfall 12 months prior to

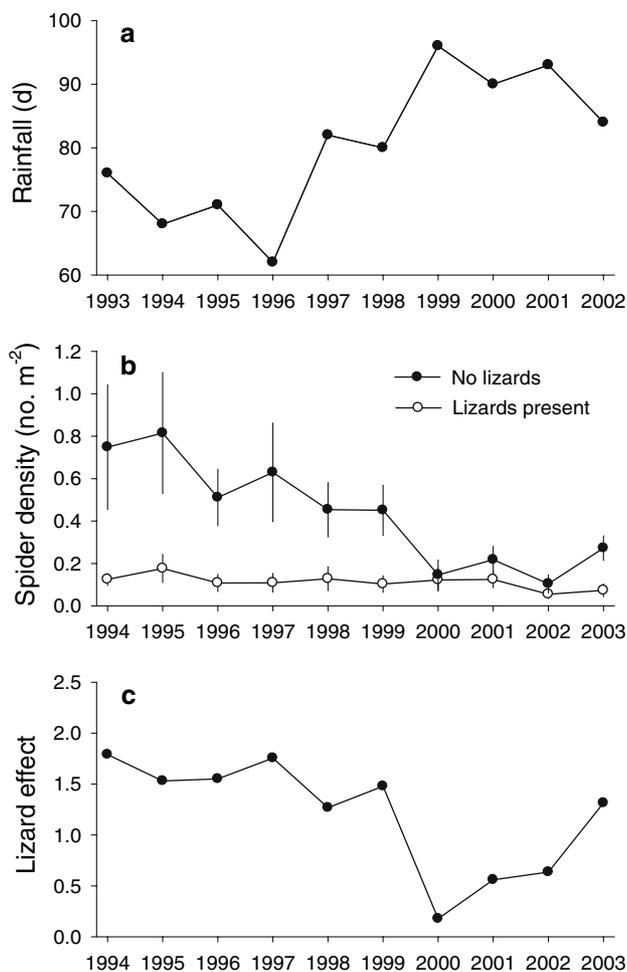


Fig. 3 **a** Rainfall (number of days with rain) during the hurricane season (June–November) prior to the annual spider censuses in April. **b** Density of web spiders at Abaco, Bahamas in April 1994–2003 on islands with lizards absent and present (mean \pm SE). **c** Lizard effect measured as the natural logarithm of the ratio of mean spider density in April on no-lizard islands to mean spider density in April on lizard-present islands, 1994–2003

the spider censuses as the time-varying covariate showed that rain had a significant effect on spider density (Rain effect, Table 2) and the lizard effect (Rain \times Lizard effect, Table 2). To separate the effects of rain during the hurricane season and non-hurricane season we conducted another split-plot analysis with two time-varying covariates: rainfall during and rainfall after the hurricane season; this analysis showed that rainfall during the hurricane season had a significant effect on spider density and on the lizard effect, whereas effects of rainfall from December to April were not significant (Table 3).

We were concerned that the difference in mean island area between lizard and no-lizard islands may have biased the results. For example, the negative impact of rainfall could have been stronger on the smaller no-lizard islands than on the larger lizard islands. Therefore, we conducted

Table 2 Split-plot ANOVA of spider densities 1994–2003, with cumulative number of rain days 12 months prior to each annual spider census (in April) as a time-varying covariate, on islands with lizards absent and present^a

Source	df	SS	F	P
Lizard (present vs. absent) ^b	1	12.88	11.31	0.0043
Island	15	17.08	8.06	0.0001
Rain	1	4.81	34.07	0.0001
Year (unexplained)	8	1.78	1.57	0.1389
Rain \times Lizard	1	2.22	15.73	0.0001
Year \times Lizard (unexplained)	8	1.21	1.07	0.3897
Error	135	19.06		

^a See Materials and methods for the SAS GLM program

^b Variation among islands was used as the error term

Table 3 Split-plot ANOVA of spider densities 1994–2003, with the number of rain days from June to November (*Rain 1* hurricane season) and from December to April (*Rain 2*) each year prior to each annual census (in April) as time-varying covariates, on islands with lizards absent and present^a

Source	df	SS	F	P
Lizard (present vs. absent) ^b	1	12.88	11.31	0.0043
Island	15	17.08	8.06	0.0001
Rain 1 (hurricane season)	1	3.40	24.09	0.0001
Rain 2	1	9.133	0.05	0.3326
Year (unexplained)	7	2.21	2.24	0.0347
Rain 1 \times Lizard	1	2.14	15.13	0.0002
Rain 2 \times Lizard	1	0.029	0.21	0.6498
Year \times Lizard (unexplained)	7	0.86	0.87	0.5324
Error	135	19.06		

^a The statistics for Rain 1 and Rain 2 and their interactions with Lizard were derived by running two different versions of the SAS GLM program given in Materials and methods. Rain 2 was entered before Rain 1 in the model statement of the first analysis, whereas Rain 1 was entered before Rain 2 in the second. The statistics for Rain 1 are taken from the first analysis, representing the amount of variation due to Rain 1 after accounting for the variation due to Rain 2. The statistics for Rain 2 are taken from the second analysis

^b Variation among islands was used as the error term

the same analysis on a restricted dataset; we deleted the smallest no-lizard island and all lizard islands larger than the largest no-lizard island, yielding sets of islands in which the mean areas with and without lizards were nearly identical (lizards islands, $n = 5$, mean = 91 m² and range = 59–144; no-lizard islands, $n = 7$, mean = 92 m² and range = 52–184). A split-plot analysis with two covariates (as in Table 3) on the reduced dataset showed that rainfall during the hurricane season had a significant effect on spider density ($P = 0.0008$) and the lizard effect on spider density ($P = 0.0002$), whereas the effects of rainfall from December to April were not significant. Thus, this analysis

provides no evidence that the larger lizard islands in the full dataset biased the results.

Correlation coefficients between spider density and temperature during 2-, 4-, 6-, 8-, 10- and 12-month intervals before the annual censuses were generally weak, ranging from -0.087 to 0.126 on no-lizard islands, -0.483 to -0.576 on lizard islands, and 0.171 to 0.453 for the lizard effect. Split-plot analysis with mean daily maximum temperature 12 months prior to the spider censuses as the time-varying covariate showed that the Temperature effect was not significant ($P = 0.935$), but the Temperature \times Lizard effect was marginally significant ($P = 0.0731$). The correlation between temperature and rainfall was weak ($r = -0.154$). Split plot analysis with both rainfall and mean daily maximum temperature 12 months prior to the spider census showed that the Rain and Rain \times Lizard effects were both highly significant ($P < 0.0001$ and 0.0003) and the Temperature and Temperature \times Lizard effects were not significant ($P = 0.410$ and 0.229). Thus, after accounting for temperature, the rain effect was still highly significant, whereas after accounting for rain, the temperature effect was not significant.

Discussion

The strength of the lizard effect on spider density varied significantly from year to year and was negatively correlated with annual rainfall. Because the negative relation was significant with rainfall during the hurricane season (June–November), but not with rainfall during the non-hurricane season, we suggest that it was linked to higher lizard mortality in years with both high rainfall and high tropical storm activity. In 1999, the year with highest June–November rainfall, Floyd (a category IV hurricane) passed directly over the study site in September and the storm surge completely inundated all the study islands; all free-living lizards apparently died or were washed away (Schoener et al. 2001). The islands were “repopulated” by hatchlings emerging from eggs that survived the storm surge, but lizard densities in the following spring were still much lower than before the hurricane (Spiller and Schoener 2007). In 2001, the second highest rainfall year, the surge from Michelle again completely or largely inundated the study islands and lizard densities declined (Schoener et al. 2004; Spiller and Schoener 2007). The link between years with high rainfall and high tropical storm activity is caused by forces from both the Atlantic and Pacific Oceans that create climatological conditions in the Caribbean simultaneously promoting higher rainfall and greater tropical storm formation (Bove et al. 1998; Taylor et al. 2002; C. Landsea, personal communication). Hence, the negative relation between trophic interaction strength and rainfall is gener-

ally consistent with the environmental stress hypothesis (Menge and Sutherland 1987) in which the top-down effect of predators is weaker under harsh conditions.

Spider density was also negatively correlated with rainfall during the hurricane season. We suggest that this negative relation was linked to higher spider mortality in years with both high rainfall and high tropical storm activity. This was most evident in 1999 (Fig. 3), when Floyd devastated spider populations (Schoener and Spiller 2006). We surveyed the site 6 weeks after Floyd and found no web spider on half the islands; mean density was 3% the level of the previous census. Although spider populations had partially recovered the following spring (the time of our annual census), densities on no-lizard islands were still much lower than in previous years. In 2001, Hurricane Michelle impacted the study site, devastating spider populations again; the following spring spider densities on both lizard and no-lizard islands were at their lowest level in the 10-year time series.

Although the negative correlation was obviously influenced by the continuously high rainfall and low spider density each year following Hurricane Floyd, it was also apparent during the 6 years before Floyd (Fig. 3). A separate analysis on the data from 1994 to 1999 showed that the correlation between spider density and rainfall 12 months prior to the spider census was negative, and the split-plot analysis showed that the rainfall effect was significant ($P = 0.042$); no major hurricane directly hit the study site during this time period, suggesting that rainfall does not have to be associated with catastrophic storms to impact spiders negatively. Local thunderstorms producing high wind and hard rain, which are common in the study region, may also cause some spider mortality. Assuming that such storms occur in approximately the same fraction of the total number of rainfall days each year, the frequency of such moderate disturbance events should increase with number of rainfall days. However, analysis from 1994 to 1999 showed that the Rain \times Lizard effect was not significant ($P = 0.96$), implying that the impact of moderate disturbance on lizards is minimal and thereby does not affect the lizard effect on spiders. This is consistent with findings in Spiller et al. (1998) showing that the effect of moderate disturbance was stronger for spiders than for lizards.

The relation between trophic interaction strength and rainfall found in this 10-year study (1994–2003) is opposite to the positive relation found in our previous 10-year study (1981–1990) conducted in the Exuma Cays, located ~ 250 km south of the present study site (Spiller and Schoener 1995). Temporal variation in the lizard effect on spiders found in our field experiments conducted in the Exuma Cays during the same time period is also consistent with this pattern (Spiller and Schoener 1994, 1996). We hypoth-

esize that the positive relation may have been caused by higher lizard density or higher per capita effect of lizards on spiders in wet years than in dry years and offer the following mechanistic explanations (see Spiller and Schoener 1995 for further discussion). In wet years lizards may respond numerically to higher insect abundance and subsequently have a stronger impact on spiders (as in Holt 1977). In addition, water availability per se may affect growth rate of individual lizards (Stamps and Tanaka 1981), leading to higher lizard density or biomass in wet years. In dry years lizards may respond to desiccation by spending more time in unexposed microhabitats and less time foraging. Consequently, the per capita effect of lizards on spiders is stronger in wet years.

We suggest that the opposing results of our two studies were caused by two factors. First, because the location of our previous study (the Exuma Cays) is on average drier than the location of the present study (Abaco), the bottom-up effect of increased rainfall on consumers, stemming from increased primary productivity, is stronger in the Exuma Cays than in Abaco. This explanation is consistent with the findings in Huxman et al. (2004) showing that the sensitivity of annual net primary productivity to annual variation in precipitation is higher at xeric sites than at mesic sites. Second, no hurricane impacted the Exuma Cays during 1981–1990, a period when tropical storm activity throughout the Atlantic Basin was much lower than during the present study (Goldenberg et al. 2001; Emanuel 2005). Hence, the positive effect of rainfall via increased productivity on trophic interaction strength occurred during the Exuma study, whereas the negative effect of rainfall via disturbance occurred during the Abaco study.

In addition, the relation between rainfall and spider density was positive in the Exuma Cay study, not negative as in this study. We suggest that in the Exuma Cays, bottom-up effects of high rainfall via increased primary productivity led to more spider prey and consequently larger spider populations, as found by Frampton et al. (2000) and Langlands et al. (2006). However, Carrel (2001) found no evidence that rainfall influenced abundance of the red widow spider, possibly because the overriding controlling factor of the spider population was predation by birds and wasps. Moreover, two studies found evidence for negative effects of rainfall on spiders. Polis et al. (1998) discovered that spider densities declined dramatically during wet El Niño years and suggested that this was caused by increased abundance of major spider predators (pompilid wasps) that were limited during previous years by lower nectar resources. In this case, the top-down effect of wasps on spiders appeared to increase during wet years. Lensing et al. (2005) showed that experimentally increasing precipitation caused a reduction in gnathosid spiders and suggested that this may have been caused by increased abundance of

predatory centipedes, making the top-down effect of centipedes on gnathosids positively related to rainfall. Thus, in both these studies the negative effects of rainfall on spiders may have been indirect via increased predation with rainfall.

Figure 4 shows on the same graph the relation between trophic interaction strength and rainfall for both our studies. A polynomial regression on all 20 points explains 63% of the variation (adjusted R^2) and both the positive (linear) and negative (quadratic) coefficients are highly “significant” ($P < 0.001$); the statistical analysis is only given for descriptive purposes, not formal hypothesis testing, because the data are not independent. The unimodal curve supports the predictions in Fig. 1. Although a longer continuous time series from the same locality showing the unimodal relation would be desirable, such data are not now available. We suggest that an overall increase in rainfall in the Exuma Cays would be associated with high tropical storm activity and the lizard effect on spiders would decline. No major drought occurred during either study, but if one occurs in the future, we predict that the lizard effect will be less than values of the points on the left end of the graph. Therefore, any substantial change in precipitation— increase, decrease or extreme annual fluctuations—may weaken the trophic interaction significantly. Although the unimodal relation may occur in other systems when disturbance is associated with high precipitation, we recognize that effects of precipitation on species interactions can be complex (Post et al. 1999; Ovadia and Schmitz 2004;

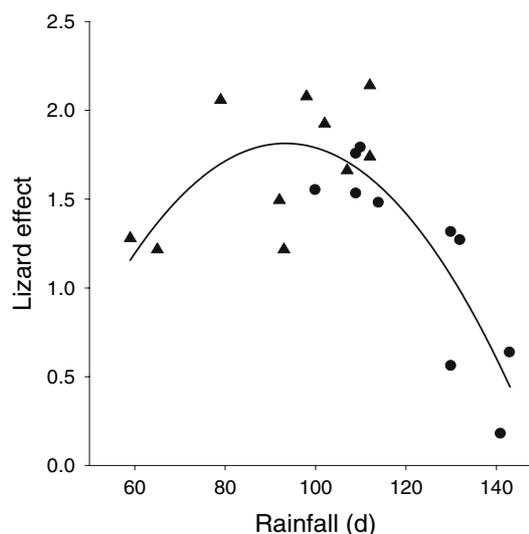


Fig. 4 Relationship between the lizard effect and cumulative number of days with rain in the 12 months prior to the annual spider censuses taken in May 1981–1990 at the Exuma Cays site (filled triangle) and in April 1994–2203 at the Abaco site (filled circle). Polynomial regression: Lizard effect = $-3.0413 + 0.1040(\text{Rain}) - 0.0006(\text{Rain}^2)$; adjusted $R^2 = 0.63$

Martin 2007). Further long-term research is needed to evaluate the generality of our findings.

Following a catastrophic event, differences in recovery rates between species in different trophic levels can be important (Holt 1996). In 1996 Hurricane Lili exterminated all populations of both lizards and spiders on exposed islands off the coast of Great Exuma, but only spiders recolonized the islands during the following year (Spiller et al. 1998); thus the lizard effect was virtually zero the year after the hurricane and remained low for several years. In this study, lizards partially recovered the years following Floyd and Michelle because their eggs survived the storms. Hence, the negative impact of disturbance on trophic interaction strength is more pronounced and lasts longer when species are exterminated and must recolonize the community.

In conclusion, the results of our two 10-year studies show that climatic variability can have a major impact on a trophic interaction. Previously, we showed that herbivory increased markedly in Abaco following hurricane disturbance and suggested that this was caused by a reduction of many predatory species, including lizards, spiders and parasitoids (Spiller and Schoener 2007). Hence, hurricane disturbance associated with extremely high rainfall may devastate predators in multiple trophic levels simultaneously and thereby decrease the overall trophic interaction strength of predators on herbivores, as in the descending portion of Fig. 1. Because such major disturbance is continuing as part of the recent upsurge in Atlantic hurricane activity (Goldenberg et al. 2001), possibly caused by global warming (Emanuel 2005; but see Landsea 2005), we predict that top-down effects of predators on herbivores will continue to weaken and herbivory will become more severe. Similarly, Stireman et al. (2005), suggested that climatic variability disrupts top-down control by parasitoids on host populations and predicted that herbivore outbreaks will increase as climate becomes more variable due to global warming. Schmitz et al. (2003) suggested that an overall reduction in precipitation will weaken the impact of wolves on moose which will indirectly have a devastating impact on fir trees. Thus, in addition to the profound effects of climate change on species' distributions, major indirect effects caused by modified species interactions need to be considered when evaluating the ecological impacts of climate change (Bertness and Ewanchuk 2002; Walther 2002; Parmesan 2006; Suttle et al. 2007).

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