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Predation on lizard eggs by ants: species interactions in a variable physical environment

Abstract One explanation for long-term fluctuations in population density is that the intensity of interactions between species is variable. A population can experience variation in the intensity of a species interaction if (1) the density of species with which it directly interacts changes and/or (2) the strength of the interaction (i.e., per capita effects) changes. At Barro Colorado Island, Panama, the tropical lizard *Anolis limifrons* exhibits wide annual fluctuations in density. Previous studies have indicated that (1) the density of *A. limifrons* is negatively correlated with the amount of wet-season rainfall, (2) fluctuations in density are related more to variation in egg mortality than to variation in lizard mortality or to fecundity, and (3) most egg mortality is the result of predation by *Solenopsis* ants. We hypothesized that the amount of wet-season rainfall indirectly alters the density of *A. limifrons* by producing variation in the intensity of egg predation by *Solenopsis*. Additionally, we also wanted to determine if variation in the amount of egg mortality was influenced more by variation in the density of *Solenopsis*, or by variation in the rate of predation. We tested this hypothesis by manipulating litter moisture on experimental plots to simulate the wettest (HW) and driest (LW) wet seasons in the last 20 years, and then monitoring the density of *Solenopsis*, amount of egg mortality, and rate of predation. The amount of egg mortality was greater on the HW than on the LW treatment and all egg mortality resulted from predation by *Solenopsis*. ANCOVA indicated that the amount of egg mortality was significantly higher on plots with a greater density of *Solenopsis*. Treatment effects, however, explained more of the variation in the amount of egg mortality than did *Solenopsis* density. Our water manipulations did not change the density of *Solenopsis*, but *Solenopsis* found and attacked eggs faster on the HW than on the LW treatment. This suggests that moisture during the wet season modified the strength of the interaction between *Solenopsis* and *A. limifrons*, supporting the hypothesis that annual variation in the amount of wet-season rainfall indirectly produces parallel variation in annual density of lizard populations by modifying the rate of ant predation on eggs.

Key words Environmental heterogeneity · Indirect effect · Interaction strength · Population dynamics · Predator-prey interactions

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Introduction

For many species, population density varies both in space and time, but the mechanism(s) causing this variation is (are) seldom known. Abiotic factors are generally believed to be more important than species interactions in controlling population density over broad spatial scales, but over local scales, species interactions are considered more important (Dayton and Tegner 1984; Menge and Olson 1990; Dunson and Travis 1991; Levin 1992). Therefore, one explanation for changes in local population density is that the intensity of species interactions changes (for reviews see Chesson and Case 1986; Woolhouse and Harmsen 1987). What mechanisms, however, cause changes in the intensity of species interactions?

Variation in the biotic or abiotic environment may change the intensity of a species interaction (Power et al. 1996). Because the intensity of species interactions is a function of (1) the densities of the interacting species and (2) the strength of the interaction (i.e., per capita effects; Wootton 1997), variation in the biotic and abiotic environment could alter the intensity of species

interactions operating on a population by directly altering either the density of other species (e.g., the predator) and/or interaction strength by eliciting a physiological or behavioral response that changes how two species interact (see reviews in Dunson and Travis 1991; Strauss 1991). The biotic or abiotic environment can therefore indirectly alter the dynamics of a population by directly changing the intensity of species interactions responsible for determining population density. Traditional definitions of indirect effects (e.g., Wootton 1993, 1994a, 1994b), however, refer only to biotic factors as a cause for indirect effects, although abiotic factors may produce indirect effects through identical mechanisms. For clarity, we will define indirect effects produced by abiotic factors as environmentally contingent interactions (J.T. Wootton, personal communication) to distinguish this phenomenon from the traditional definition of indirect effects.

Ecologists have been particularly interested in documenting the occurrence and significance of indirect effects produced by variation in interaction strength (Wootton 1994a, 1994b and references therein). Significant variation in interaction strength implies that results obtained from experiments conducted under one set of conditions may not apply under another set (Billick and Case 1994; Kareiva 1994; Wootton 1994a). Very few empirical studies, however, have examined the role of environmentally contingent interactions on the long-term dynamics of populations (Kingsolver 1989; Dunson and Travis 1991). Additionally, theoretical models that consider the effect of environmental variability on population growth typically represent this variability as "white noise" and do not consider how environmental variation directly alters the intensity of a biotic interaction (e.g., May 1973). Thus, it is important to (1) determine if variation in the abiotic environment alters interaction strength predictably and (2) compare the relative amount of influence that changes in the density of species and changes in the strength of interactions between species have on the intensity of species interactions.

If natural variation in an abiotic factor alters the intensity of biotic interactions, then such variation should also cause parallel variation in population density (Kingsolver 1989). However, empirical support for this association is limited (Kareiva et al. 1993) and the mechanisms are often unknown (Spiller and Schoener 1995). In this study we show that (1) fluctuations in the long-term dynamics of a prey population result from fluctuations in the intensity of predation produced by fluctuating abiotic conditions and (2) variation in the strength of the interaction between species accounts for more variation in the intensity of predation than does variation in predator density.

Study system

The population density of the tropical lizard, *Anolis limifrons*, has been monitored for more than two decades

at Barro Colorado Island (BCI), Panama. During this time, the density of *A. limifrons* has fluctuated as much as eightfold from one year to the next, and even more widely across decades (Andrews and Rand 1982; Andrews 1991; Andrews and Wright 1994). Several lines of evidence suggest that fluctuations in population density are related more to variation in egg mortality than to variation in either lizard mortality (hereafter lizard refers to all post-hatching individuals) or to fecundity (Andrews 1988; Andrews and Wright 1994). The population density of *A. limifrons* is negatively correlated with the amount of rainfall during the wet season (approximately mid-April to December; Andrews 1991; Andrews and Wright 1994), the time when most egg production by *A. limifrons* occurs (Andrews and Rand 1982). If population fluctuations are related to variation in egg mortality, then the amount of rainfall during the wet season and egg mortality should also be negatively correlated.

What mechanism(s) could connect moisture levels in the wet season to egg mortality? Moisture could affect egg survival directly. However, above some threshold exceeded in all wet seasons, variation in moisture is not related to egg survival (Andrews and Sexton 1981). Another possible mechanism is the effect of moisture on egg predators. Mortality of *A. limifrons* eggs in the field is largely due to predation by various species of *Solenopsis* in the subgenus *Diplorhoptrum* (Andrews 1982). These tiny (~2 mm) ants are common in the leaf litter of tropical forests (Levings 1983; Kaspari 1993) and their distribution and abundance is affected by rainfall. Ant abundance is higher in the wet than the dry season and higher in dry seasons that have relatively high rainfall than in those that have relatively low rainfall (Levings 1983; Levings and Windsor 1984, 1985). Moist microhabitats have both greater abundances of all ants and higher numbers of *Solenopsis* and other small ants foraging at baited stations (Levings 1983; Levings and Windsor 1984; Kaspari 1993).

We hypothesized that the amount of moisture during the wet season indirectly affects egg mortality of *A. limifrons* by altering predation intensity by *Solenopsis* through changing (1) the rate of predation (i.e., interaction strength) and/or (2) the abundance of *Solenopsis*. We tested these hypotheses by manipulating moisture on experimental plots and by monitoring (1) the rate of predation on *A. limifrons* eggs by *Solenopsis* and (2) the abundance of *Solenopsis*. Rejecting the null hypothesis that variation in moisture has no effect on egg mortality implies that annual variation in the amount of wet-season rainfall indirectly promotes annual variation in egg mortality and, thus, annual variation in the population density of *A. limifrons*.

Materials and methods

Study area and plot descriptions

Observations were conducted May–August 1995 in forest regrown from agricultural land abandoned 100 years ago on BCI (Foster

and Brokaw 1982). The 30 × 20 m study area had a closed canopy and an open understory dominated by the palm *Chrysophyllum panamensis* and shrubs (e.g., *Eugenia oerstedanii, Hybanthus prunifolius* and *Psychotria limonensis*). The study area was on a relatively flat area to prevent excessive water drainage either into or out of plots. Twelve plots, each measuring 2 × 5 m, were established within the study area. Plots were placed to maintain uniformity of litter depth and extent within plots, and to avoid trees, rocks, and other natural obstructions. Plots were separated by at least 2 m.

Two plots were arbitrarily selected as reference plots (RF). RF plots were marked by flagging but were otherwise unmanipulated. The 10 remaining plots were randomly assigned to one of two treatments, resulting in five plots/treatment. One simulated a wet season with low rainfall (low water treatment, LW) while the other simulated a wet season with high rainfall (high water treatment, HW). Plots were initiated sequentially during a 6-week period as eggs became available, but the sequence of events and duration of the treatment application was the same for all plots. Except for 1 week, enough eggs were produced weekly to initiate at least one or two plots of both treatments simultaneously.

Water manipulation

Treatments were applied to experimental plots for 5 weeks. Each LW and HW plot received 440 and 880 l of water per week, respectively. The volume of water applied to LW plots each week approximated the mean weekly rainfall for the months of June, July, and August 1976, the year with the lowest amount of rainfall (57.8 cm) during these months in the last 20 years (Windsor 1990). The volume of water applied to HW plots each week corresponded, similarly, to 1979, the year with the highest amount of rainfall (101.8 cm) during these months in the last 20 years (Windsor 1990). The normal frequency of rainfall during the wet season is approximately three to four times a week. Therefore, each plot received 25% of its weekly volume of water on 4 days during each week of the experiment. To ensure that water availability was at prescribed levels, a clear plastic tarp was placed above each LW and HW plot to intercept and divert normal rainfall. The lowest portion of the tarp was at least 1 m above the ground so that air movement was not impeded. Three 110-l barrels placed outside each plot along the lowest edge of the tarp collected runoff. Litter that fell on the tarps was scattered evenly on their respective plots weekly.

Water for plots was collected in barrels and supplemented with untreated lake water as necessary. Water was sprayed evenly over each plot with a garden hose connected to an electric sump pump. Delivery of the daily allotment of water to each plot took 30–60 min.

Ant density and number of foraging ants

To determine if differences in the amount of egg mortality between treatments was the result of a change in the rate of predation rather than a change in the density of *Solenopsis*, we attempted to minimize the likelihood of a change in the density of *Solenopsis* by (1) conducting the experiment over a short time period and (2) by surrounding each LW and HW plot with a terrestrial-arthropod-proof enclosure. The enclosure ensured that predation intensity on eggs was a result of experimental manipulations altering the abundance and/or rate of predation of *Solenopsis* that were on the plot initially, and not the result of their migration into or out of the plots in response to experimental manipulations. RF plots were not enclosed. The density of *Solenopsis* on plots was not manipulated and therefore variation in the density of *Solenopsis* among plots reflected natural variation.

Enclosures consisted of 34-cm-high corrugated fibreglass sheets buried in the ground to a depth of 5–10 cm. Sheets were cut to fit over large roots and any gaps were sealed with duct

tape. The top 5 cm on both sides of each enclosure was painted with Fluon AD1 (Northeast Chemical Co., Woonsocket, R.I.), a teflon-based paint that creates a frictionless surface, preventing ants and other arthropods from crawling on it (Hölldobler and Wilson 1990). After 2.5 weeks, Fluon strips were wiped clean and Fluon reapplied. Enclosure integrity was checked daily. The day prior to beginning the experiment, all litter within a 1-m-wide strip around the outside of each plot was raked away (after ant density was sampled, see below) to remove any nearby colonies or individuals and to serve as a further barrier for ant movement.

The density of *Solenopsis* (number of ants/0.25 m²) was estimated at the start and end of the experiment after collecting six 0.25-m² litter samples from each plot using a stratified sampling scheme (at least one haphazardly located sample from each side of the plot). To minimize disturbance, initial litter collections were made from the 1-m-wide strip surrounding each plot, but after the experiment was terminated, litter was collected from within the plots themselves. Litter samples were placed in Berlese funnels heated with a 60-W light bulb for 48 h, and invertebrates were collected in small cups containing 70% ethanol. To prevent other arthropods from entering the funnel, the tops were covered with plastic bags. Dry litter was weighed (±0.1 g) and used as an index of litter quantity at the start and end of the experiment. In six of the 120 Berlese samples, the funnels became plugged and no arthropods were extracted. To avoid missing values for data analyses, the mean number of *Solenopsis* collected from other samples on the same plot during the same time period was substituted for the missing value. No more than one sample was missing for any plot for a given time period.

Our measure of foraging activity by *Solenopsis* on each plot is the total number of *Solenopsis* captured in pitfall traps during a 24-h period. We assumed the traps captured only those ants foraging in the leaf litter. Pitfall traps consisted of a film canister (opening width 32 mm) containing 70% ethanol. Traps were inserted into plastic tubes that had been sunk into the ground 3 weeks prior to the start of the experiment to avoid the "digging-in" effect (Greenslade 1973). Two rows of five evenly spaced pitfall traps were placed on each plot. Traps were open for 24 h 1 day per week throughout the experiment to minimize negative effects on ant density.

Predation on eggs

Following Andrews (1988), newly laid eggs were collected weekly from 43 female *A. limifrons*. All eggs were placed in small nylon mesh bags before being placed on the plots to contain hatchlings. The mesh (diameter 5 mm) allowed predators access to eggs but prevented hatchlings from escaping.

Ten newly laid eggs were uniformly distributed (at 1 egg/m²) on each plot under the litter, the typical nest site of *A. limifrons* (Andrews 1988). Most, if not all eggs on a plot were produced by different females because they lay approximately one egg per week. Eggs were marked by flags and checked every 2 days during the 5-week experiment. The incubation time of *A. limifrons* eggs is 6 weeks (Andrews and Sexton 1981), and eggs were at most 1 week old when they were placed into the field. At each check, eggs were recorded as present, hatched, or predated. Date of death for predated eggs was the day the egg was found eaten. The interval between the date when eggs were placed in the field and date of predation is the survival time, an estimate of how long it took *Solenopsis* to find and attack eggs. Four eggs hatched before day 35 (on day 32); these were classified as having survived to day 35 for subsequent analyses.

To determine egg mortality without arthropod predators, 20 eggs were placed in arthropod-proof containers in one HW (*n* = 10) and one LW (*n* = 10) plot for the duration of the experiment. The number of replicates for this experiment was restricted by the number of eggs available. Each egg was placed under the litter and surrounded by a bottomless plastic cup that was painted with Fluon and partially buried to prevent invertebrates

from crawling into the cup. The status of these eggs was checked as above. These eggs were left in the field until they hatched.

Litter and soil moisture

Litter moisture was monitored weekly during the experiment. Approximately 15–20 g of litter (all organic material down to the mineral horizon) per plot per week was collected from an area of about 25 cm^2 after collecting pitfall traps. Litter was weighed wet, and after drying at 60°C to a constant weight (± 0.001 g). Litter moisture was calculated as percent moisture lost [(wet mass–dry mass)/(wet mass)].

Soil moisture was also monitored, but did not vary between treatments and will not be discussed further. Lack of a treatment effect on soil moisture was not surprising as soil moisture at BCI ranges from 40–45% during the wet season and is independent of the amount of rainfall (Dietrich et al. 1982).

Data analysis

Data from RF plots are presented for comparative purposes and are not part of the experiment; assuming that 1995 was an average year, we expected values intermediate to those obtained from HW and LW plots. RF plots were not included in statistical analyses for two reasons. First, statistical comparisons with RF plots are not warranted because our experiment was designed to differentiate mortality between a relatively wet and a relatively dry wet season. Second, valid statistical comparisons cannot be made between RF plots and treated plots because RF plots differed from treatment plots in more than one way (i.e., they received a different amount of water at different intervals and were not covered with tarps or surrounded by arthropod-proof enclosures).

Our experimental design allowed us to test six main hypotheses: (1) treatments did not differ in the amount of litter moisture, (2) the amount of foraging activity by *Solenopsis* did not differ between treatments, (3) the density of *Solenopsis* on each plot did not change during the experiment, (4) the amount of litter mass did not change during the experiment, (5) the survival time (i.e., the rate of predation) of eggs did not differ between treatments and (6) the amount of egg mortality (i.e., predation intensity) did not differ between treatments.

We tested null hypotheses 1 and 2 with repeated-measures analysis of variance. The data matrices we analysed consisted of the five weekly measurements of (1) litter moisture and (2) foraging activity on each of the five replicates (plots) for the two treatments. We rejected the null hypotheses if we detected a significant treatment effect, indicating that our manipulations were successful in producing different moisture conditions and different levels of foraging activity by *Solenopsis*.

We also tested null hypotheses 3 and 4 with a repeated-measures ANOVA. The data matrices we analysed consisted of the mean values (based upon six subsamples) for (1) the density of *Solenopsis* and (2) the amount of litter mass on each of the five replicates (plots) for the two treatments at the start and end of the experiment. We rejected the null hypotheses if we detected a significant time effect. Failure to reject the null hypothesis that the density of *Solenopsis* did not change during the experiment would indicate that egg mortality during the 5-week period would not have been associated with changes in the density of *Solenopsis*. A significant interaction between time and treatment would indicate a numerical response by *Solenopsis* to moisture availability.

We tested null hypotheses 5 and 6 with ANCOVA. The data matrices we analysed consisted of (1) the mean survival time of an egg and (2) the amount of egg mortality on each of the five replicates (plots) for the two treatments. Covariates included the density of *Solenopsis* and the amount of litter mass on a plot. Because the number of replicates per treatment is relatively small, we performed a separate ANCOVA for each covariate and response variable combination. In each case, there was no significant interaction between the covariate and treatment. Additionally, because we did not detect a significant change in the density of *Solenopsis* or the amount of litter mass on a plot (see Results), data collected at the start and end of the experiment were pooled to derive estimates for the mean density of *Solenopsis* and mean litter mass.

We determined the relative importance of *Solenopsis* density and treatment effects on egg mortality by extending the underlying logic of ANCOVA to partition the amount of variance explained by each in the ANCOVA model. The basic idea of ANCOVA is to determine if there is a difference between treatments after the effects of the covariate are removed. By extension, we determined the amount of variation explained by treatment effects after we removed the amount of variation explained by the covariate. This was done by subtracting the coefficient of determination for a model specifying only the effect of the covariate (i.e., the amount of variance explained by the covariate alone) from the coefficient of determination for the ANCOVA model (i.e., the total amount of variance explained). The result is the amount of variance explained by treatment effects after the amount of variance explained by the covariate is removed. This differs from the standard procedure used by others for factorial ANOVA (e.g., Wilbur et al. 1983; Morin 1984; Welden and Slauson 1986) because the density of *Solenopsis* is not orthogonal to treatment levels and therefore the *F*-ratios for each effect are not independent of each other.

Data were checked for skewness, kurtosis, and homogeneity of variances, and logarithmic transformations [$\ln(x + 1)$] were applied as required (Sokal and Rohlf 1981). All means are reported $\pm$SE. The null hypothesis for statistical analysis was rejected when $\alpha < 0.05$. All statistical analyses were performed with SYSTAT statistical software (Wilkinson 1989).

Results

Litter mass did not differ between treatments (repeated-measures ANOVA: treatment effect, $F_{1,8} = 0.08$, $P = 0.79$) or between the start and end of the experiment (time effect, $F_{1,8} = 0.00$, $P = 0.99$; interaction effect, $F_{1,8} = 0.23$, $P = 0.65$). Litter moisture was higher on the HW than on the LW treatment and did not vary as a function of time in either treatment (Table 1, Fig. 1). Litter moisture on the RF plots, which experienced natural variation in rainfall, was intermediate to that on HW and LW plots (Fig. 1).

The density of *Solenopsis* did not differ between treatments (repeated-measures ANOVA: treatment effect, $F_{1,8} = 0.05$, $P = 0.83$) or between the start and end of the experiment (time effect, $F_{1,8} = 0.01$, $P = 0.95$; interaction effect, $F_{1,8} = 0.40$, $P = 0.55$). Similarly, the foraging activity of *Solenopsis* did not differ between treatments (repeated-measures ANOVA: treatment effect, $F_{1,8} = 3.66$, $P = 0.09$) and did not change during the course of the experiment (time effect,

Table 1 Repeated-measures ANOVA of weekly values for litter moisture on HW and LW treatments

Source	df	SS	F	P
Between subjects				
Treatment	1	934.59	22.69	0.001
Error	8	329.56		
Within subjects				
Time	4	88.26	1.64	0.19
Time × treatment	4	60.97	1.13	0.36
Error	32	431.57		

$F_{4,32} = 0.67$, $P = 0.62$; interaction effect, $F_{4,32} = 1.10$, $P = 0.37$). Litter mass was not correlated with either the density of *Solenopsis* ($r = 0.07$, $n = 10$, $P > 0.05$) or foraging activity of *Solenopsis* ($r = 0.37$, $n = 10$, $P > 0.05$).

Egg survival time was shorter on the HW than on the LW treatment (Table 2, Fig. 2). The density of *Solenopsis* had no affect on egg survival time (Table 2, Fig. 2A), but there was a significant negative effect of litter mass (Table 2, Fig. 2B). Egg mortality was significantly higher on the HW than on the LW treatment (Table 3, Fig. 3). In contrast to egg survival time, the density of *Solenopsis* had a significant positive effect on egg mortality (Table 3, Fig. 3A), but litter mass was not related to egg mortality (Table 3, Fig. 3B). The coefficient of determination for the regression of the amount of egg mortality on the density of *Solenopsis* indicates that *Solenopsis* density accounted for 20.1% of the variation in egg mortality. By subtracting the coefficient of determination for the regression model from the coefficient of determination for the ANCOVA model with *Solenopsis* density as a covariate (65.4%), we determined that treatment effects accounted for 45.3% of the variation in egg mortality. The date on which a manipulation began was not correlated with either egg survival time ($r = 0.17$, $n = 10$, $P > 0.05$) or egg mortality ($r = -0.40$, $n = 10$, $P > 0.05$).

All mortality of experimental eggs was the result of predation by *Solenopsis*. When eggs were recorded as predated either (1) *Solenopsis* was observed consuming them or (2) the remaining egg shells had distinctive holes
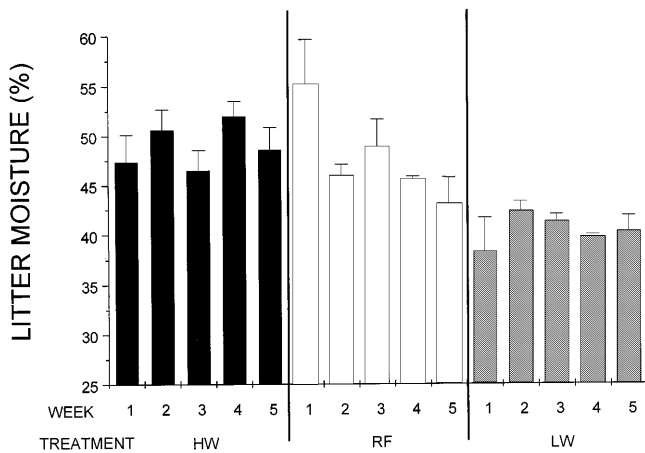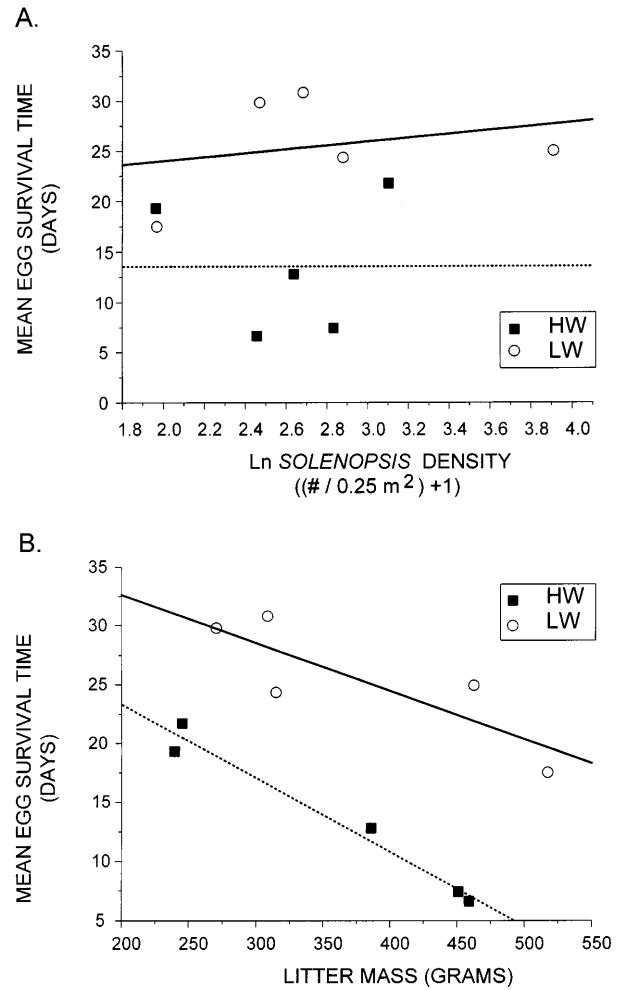

Fig. 2 Regression of mean egg survival time (days) on HW and LW plots with the density of *Solenopsis* {ln[(number/0.25 m²) + 1]} (**A**) and litter mass (g/0.25 m²) (**B**) as a covariate. The *dashed line* represents the least-squares regression line for the HW treatment and the *solid line* represents the least-squares regression line for the LW treatment

Fig. 1 Mean (±SE) litter moisture on HW, RF, and LW treatments. Litter moisture was significantly higher on the HW than on the LW treatment during the experiment

Table 2 ANCOVA for the effects of treatments on time to predation with the density of *Solenopsis*, and the amount of litter mass as covariates

Source	df	SS	F	P
Solenopsis density				
Treatment	1	329.05	7.86	0.03
Density of *Solenopsis*	1	5.34	0.13	0.73
Error	7	293.20		
Litter mass				
Treatment	1	409.84	57.61	0.000
Litter mass	1	248.75	34.97	0.001
Error	7	0.35		

Table 3 ANCOVA for the effects of treatments on the amount of egg mortality with the density of *Solenopsis* and the amount of litter mass as covariates

Source	df	SS	F	P
Solenopsis density				
Treatment	1	0.38	9.16	0.02
Density of *Solenopsis*	1	0.26	6.28	0.04
Error	7	0.29		
Litter mass				
Treatment	1	0.34	6.72	0.04
Litter mass	1	0.20	4.08	0.08
Error	7	0.35		

A.

% MORTALITY

Ln SOLENOPSIS DENSITY
((# / 0.25 m²) +1))

HW
LW
BOTH

B.

% MORTALITY

LITTER MASS
(GRAMS)

HW
LW

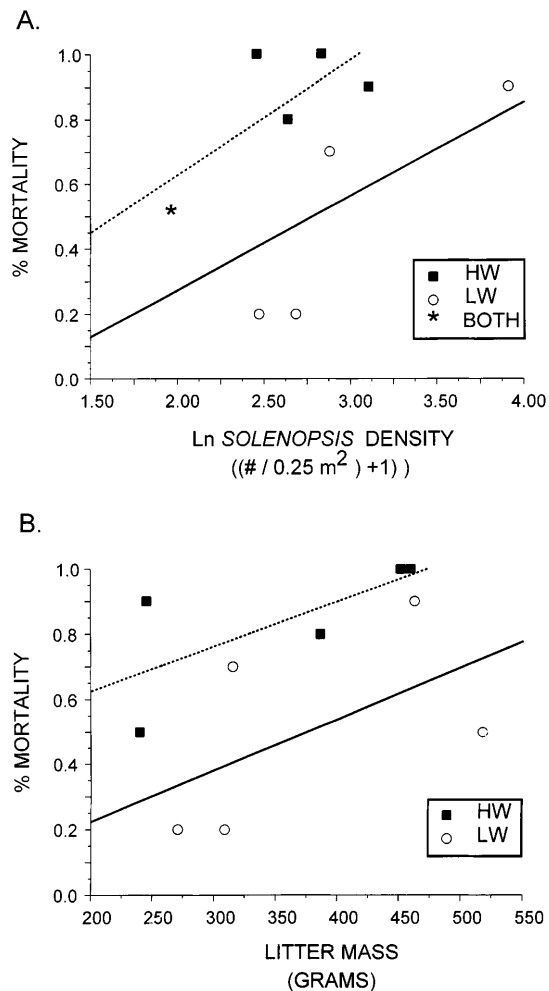**Fig. 3** Regression of percent egg mortality on HW and LW plots with the density of *Solenopsis* {ln[(number/0.25 m²) + 1]} (**A**) and litter mass (g/0.25 m²) (**B**) as a covariate. The *asterisk* indicates where a data point for a HW and LW plot overlap. The *dashed line* represents the least-squares regression line for the HW treatment and the *solid line* represents the least-squares regression line for the LW treatment

that are characteristic of predation by *Solenopsis* (Andrews 1982; D. Chalcraft, personal observation). In contrast, all eggs (ten/treatment) enclosed by arthropod-proof plastic cups hatched. Mean time to hatching for protected eggs was 37.2 ± 0.6 and 38.2 ± 0.6 days on the HW and LW plots, respectively (*t*-test, $P = 0.27$). Note that the experiment ended 2–3 days short of the mean time that eggs hatched in arthropod-proof cups, indicating that the experiment was long enough to cover most of the incubation period.

Discussion

Our results demonstrate that mortality of *A. limifrons* eggs was caused by *Solenopsis* and that mortality was higher under relatively wet than relatively dry conditions. Experimental eggs that were not killed by ants

survived to the end of the experiment, and all eggs that were protected from ants in arthropod-proof cups hatched. Although we found evidence for density-dependent mortality, treatment effects explained more of the variation in the amount of egg mortality than did the density of *Solenopsis*. This suggests that environmentally contingent interactions play an important role in influencing the dynamics of a population by changing the amount of egg mortality.

What is the mechanism by which rainfall alters the intensity of predation on eggs? Our experiment supports the hypothesis that variation in rainfall alters predation intensity by changing the rate of predation by *Solenopsis* rather than by changing the density of *Solenopsis*. This conclusion is supported by four pieces of evidence. First, treatment effects accounted for more of the variation in egg mortality than did *Solenopsis* density. Second, treatments did not promote a change in the density of *Solenopsis* during the experiment. Third, treatments did not differ in the number of *Solenopsis* captured in pitfall traps during the experiment. Fourth, the mean survival time of an egg was shorter on the HW treatment than on the LW treatment and was independent of the density of *Solenopsis*. These results suggest that eggs became more attractive to, are more easily found by, or more susceptible to predation by *Solenopsis* under conditions of high litter moisture. Therefore, the indirect effect of litter moisture on egg mortality is a result of the abiotic environment changing the strength of the interaction (i.e., an interaction modification) between *Solenopsis* and *A. limifrons*.

This study provides a conservative estimate of the total impact that rainfall has on the intensity of egg predation because the relationship between annual variation in wet-season rainfall and the number of *Solenopsis* is still unclear. Although we did not find a numerical response by *Solenopsis* to altered moisture conditions, others (Levings 1983; Levings and Windsor 1984) have found that the number of ants increased when water was added to 0.25-m² litter plots. However, their manipulations were conducted in the dry season, and their small plots were not enclosed. Thus, the increase they observed may have resulted from ants migrating from surrounding dry areas onto their plots. In our study, movements in or out of the plots were precluded by ant-proof barriers. Therefore, changes in mortality were due to changes in the response of in situ ants to eggs, not to ant immigration or emigration in response to the local variation in moisture that was created experimentally. However, 5 weeks may not have been long enough to detect a numerical response by *Solenopsis*; eggs of *Solenopsis invicta* develop into workers in 3–6.5 weeks, depending on temperature (Hölldobler and Wilson 1990). Had this experiment been conducted for a longer period, differences in moisture may have produced greater differences in the amount of mortality between treatments by eliciting a numerical response by *Solenopsis*. This would have obscured our ability to determine the role of variation in the amount

of rainfall on the intensity of predation by changing the rate of predation.

What is the relative importance of the mechanisms producing variation in the intensity of predation? In this study, differences in the rate of predation produced by treatment effects accounted for more of the variation in egg mortality than did differences in density. This would indicate that variation in the rate of predation is more important than variation in the density of *Solenopsis*. A longer-term study would have to be conducted to determine if variation in rainfall produces long-term changes in the density of *Solenopsis* that span a greater range of densities than we observed among our plots (6.17–49.00 *Solenopsis*/0.25 m^2).

The exact mechanism through which rainfall alters the rate of predation remains unclear. The negative relationship between litter mass and time to predation suggests that moisture per se affected the ability of *Solenopsis* to find and attack eggs; litter mass may influence time to predation by maintaining moisture in the litter. Eggs with parchment-type shells (like those of *A. limifrons*) readily absorb water from nest sites (Tracy 1980; Andrews and Sexton 1981), and water uptake is associated with expansion of eggs and thinning of their shells. Moreover, at least for crocodilian eggs, eggshell thickness decreases and porosity increases as the result of the biochemical activities of soil microbes under moist conditions (Ferguson 1981). Thus, *Solenopsis* ants may have been more successful in finding and attacking eggs on the HW than on the LW treatment if increased levels of moisture caused eggshells to become thinner or more porous and promoted the release of chemicals from eggs.

Alternatively, changes in litter moisture may affect the abundance or activity patterns of prey other than eggs. For example, the number of non-ant arthropods is often higher on unwatered than watered plots (Levings and Windsor 1984). Thus, under relatively dry conditions, *Solenopsis* may prey upon non-ant arthropods rather than lizard eggs because (1) the non-ant arthropods are more abundant than lizard eggs, or (2) non-ant arthropods are more attractive to ants than eggs. However, little is known about the interactions among *Solenopsis*, other litter invertebrates, lizard eggs, and litter moisture.

This study supports the idea that interactions between abiotic factors and biotic processes can play an important role in the dynamics of species interactions (Chesson and Huntley 1989; Kingsolver 1989; Dunson and Travis 1991; Werner and McPeek 1994; Power et al. 1996; Wootton et al. 1996). However, actual mechanisms through which environmental variation affects population dynamics are poorly understood. In our study, rainfall affected long-term dynamics of a population through an environmentally contingent interaction. Annual variation in the amount of rainfall produces parallel annual variation in population density of *A. limifrons* by altering the rate of predation by *Solenopsis* on *A. limifrons* eggs. This does not mean that abiotic factors are more important than biotic factors in determining population size, but rather that abiotic factors significantly affect the strength of biotic processes that control population size by predictably changing interaction strength. Moreover, this study demonstrates that variation in interaction strength can produce more variation in the intensity of a species interaction than variation in the densities of the interacting species. Hence, ecological models describing the role of environmental variation on the dynamics of a population should include the physiological and behavioral responses of a species to environmental stimuli.

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