

Extreme weather change and the dynamics of oviposition behavior in the pipevine swallowtail, *Battus philenor*

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Abstract Prospects of global increases in extreme weather change provide incentive to examine how such change influences animal behavior, for example, behavior associated with resource use. In this study, we examined how oviposition behavior in a southern Arizona population of pipevine swallowtails (*Battus philenor* L.) responded to changes in their *Aristolochia* host resource and vegetative background caused by the North American monsoon system. Summer monsoon rains resulted in a flush of non-host vegetation and a more than doubling in rate of landings by host-searching females on non-host vegetation. Rates of discovery of the host species *A. watsoni* Woot. Standl. decreased by 50% after monsoon rains. Rains did not alter host density appreciably, but resulted in significant increases in host plant size and new growth, two indicators of host suitability for *B. philenor* larvae. After the rains, mean clutch size on individual host plants increased by a factor of 2.5; the mean proportion of host plants encountered on which a female laid eggs

also increased significantly. Females were discriminating about the host plants on which they laid eggs after alightment; plants accepted for oviposition were larger, bore more new growth, and bore fewer larvae than rejected plants. Contrary to predictions from foraging theory, degree of discrimination did not change seasonally. Finally, the rate at which eggs were laid increased seasonally, suggesting that oviposition rates were limited more before monsoon rains by the relatively low quality of hosts than they were after the rains by the relatively low rate at which hosts were found. This latter result suggests that, while butterflies possess behavioral flexibility to respond to extreme weather change, such flexibility may have limits. In particular, expected increases in the severity and frequency of droughts may result in reduced oviposition rates, reductions that could have adverse demographic consequences.

Keywords Climate change · Host selection · Egg load · Clutch size · Butterfly

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Introduction

The literature on how weather affects foraging behavior in animals is relatively sparse and scattered. Yet weather can have striking effects on resource use. In insects that utilize hosts, the subject of the present study, weather change has been shown to influence host selection behavior both before and after a weather event. Female swallowtail butterflies respond to periods of inclement weather during which they cannot fly by foraging more actively for host plants once the weather clears and laying larger clutches when plants

are found, results consistent with dynamical foraging theory (Odendaal and Rausher 1990). Parasitoids respond to simulated barometric changes predictive of approaching storms by increasing the rate at which they superparasitize (i.e., parasitize insect hosts that have already been parasitized) (Roitberg et al. 1993). The latter result also follows from foraging theory—storms are a source of mortality and faced with prospects of a shorter time horizon for foraging, parasitoids allocate more eggs to lower-quality hosts to avoid dying with eggs unlaidd. These two studies focused on short-term, resource-independent effects of changes in weather. However, weather change might affect behavior indirectly through effects on host resources and the associated host environment. If and how herbivorous insects respond behaviorally to such aspects of extreme change in weather in nature has been given little attention.

The onset of global climate change provides added incentive for understanding how weather affects host use. Global changes in climate are having documented effects on animal biology, including behavior (Parmesan and Yohe 2003; Parmesan and Galbraith 2004). Global warming has influenced insect movement (Parmesan 2001) and avian breeding behavior (Rubenstein 1992). Some aspects of weather are less easily evaluated and their effects on behavior less well understood, though potentially important. For instance, weather has become more variable; this trend is expected to continue, with more frequent fluctuations in precipitation and temperature, and more severe extremes in such variables in mid to high latitudes (Karl et al. 1995; Easterling et al. 2000; Meehl et al. 2000; IPCC 2001; Knapp et al. 2002). It would be useful to know if and how host selection behavior is altered in response to extreme changes in weather. Even if such changes are not generated by climate change per se, this information

could provide valuable insight into how insects will respond to anticipated changes in weather. Such a perspective was adopted recently by Bolger et al. (2005), who described striking differences in reproduction in passerine bird populations in dry versus wet years.

Monsoon weather systems provide a convenient context in which to address the issue of extreme weather change and host selection behavior. A monsoon is a seasonal pattern of wind shift often accompanied by an abrupt transition in the amount of precipitation. In southern Arizona, site of the present study, frequent thunderstorms associated with the North American summer monsoon system (Adams and Comrie 1997; Ellis et al. 2004) contribute most of the annual precipitation in the region and result in a rapid flush of vegetative growth in desert biota. In the present study, we examined how monsoonal effects on host and host environment influenced patterns of oviposition by pipevine swallowtail butterflies (*Battus philenor* L.; Papilionidae).

We reasoned that monsoon rains could have three possible effects on plants that could influence butterfly behavior. First, the associated sharp increase in abundance of non-host vegetation, particularly grasses, could reduce the apparency of host plants (sensu Feeny 1976), thereby decreasing the rate at which host plants are discovered. Foraging theory (Mangel 1987, 1989; Minkenberget al. 1992) predicts that reduced discovery rate should in turn have the following effects on oviposition behavior: an increase in the size of a female's clutch on any given plant, an increase in the proportion of plants accepted for oviposition, and a decrease in how discriminating ovipositing females are with respect to the suitability of accepted host plants for juvenile survival (see summary in Table 1). All of these behavioral responses would lessen the effects of reduced host discovery on rate of oviposition.

Table 1 Predicted effects of monsoon rains on host plant (vegetative background, host density and host suitability) and herbivore [host discovery rate (HDR), clutch size, host acceptance,

degree of discrimination and oviposition rate]. See Introduction for further explanation

	Vegetative background effects	Host density effects	Host suitability effects
Presumed post-rain pattern	More non-host vegetation	Hosts more abundant	Hosts more suitable
Predicted change in HDR	Decrease	Increase	No change <i>or</i> increase
Predicted change in clutch size	Increase	Decrease	Increase
Predicted change in propensity to oviposit	Increase	Decrease	Decrease (via increased HDR)
Predicted change in discrimination	Decrease	Increase	Increase
Predicted change in oviposition rate	No change or decrease	Increase if HDR increases	Decrease (via increased HDR)

A second possible monsoonal effect is an increase in host density. Although the local host species, *Aristolochia watsoni*, is a long-lived perennial, its above-ground growth is labile. Some plants appear not to bear foliage in a dry year, while neighboring plants put foliage on and off multiple times in the same year (D. Papaj and C. Heinz, unpublished data). Monsoon rains could conceivably increase the density of plants bearing foliage. Such an increase might increase the rate at which hosts are discovered and exert effects on oviposition behavior opposite to those predicted by changes in vegetative background: a decrease in clutch size, a decrease in proportion of plants accepted for oviposition, and an increase in degree of discrimination (summarized in Table 1).

Third, monsoon rains could alter aspects of a given host plant's suitability for juvenile survival, to which oviposition behavior is sensitive. For instance, *Aristolochia* plants may grow larger and bear more young leaf tissue in response to rains, changes which should improve juvenile performance in this butterfly (Rausher 1981a; Rausher and Papaj 1983; Papaj 1986a; Papaj and Rausher 1987). Enhancement of host suitability should have the following direct effects on oviposition behavior: an increase in clutch size, an increase in proportion of host plants accepted for oviposition, and, assuming more plants cross some presumed threshold of acceptability, a decrease in degree of discrimination (Table 1). Changes in host characteristics may also affect behavior via effects on host discovery rate. For instance, larger, lusher plants may be more apparent to the butterfly. If changes in the host increase host discovery rate, they would exert opposing, indirect effects: a decrease in clutch size, a decrease in proportion of plants accepted, and an increase in degree of discrimination (Table 1). The presumed effects of monsoon rains on plants carry implications for overall rate of oviposition (Table 1). Additionally, the effects are not mutually exclusive and host selection behavior may be a composite of them.

The *Battus*–*Aristolochia* system is in many ways an ideal one in which to evaluate effects in situ, the dynamics of host selection behavior having been studied intensively in the field. For instance, work of Rausher (1983) suggested that females became more discriminating as host density increased seasonally, such that proportionally more eggs were allocated to higher-quality host plants. Rausher (1981b) additionally demonstrated that removing non-host vegetation around a host plant increases the susceptibility of the plant to oviposition, as presumed by the vegetative background hypothesis. Tatar (1991) described seasonal dynamics in the relationship between clutch size

and egg load (defined as the number of mature eggs in a female's ovaries) in a Californian *B. philenor* population. Like Tatar, we adopted non-manipulative survey and observational approaches, with the goal of describing field patterns that could guide experimental manipulation in future studies.

Materials and methods

Natural history and study site

The pipevine swallowtail butterfly, *Battus philenor* L., is a specialist papilionid butterfly whose larvae feed exclusively on members of the genus *Aristolochia*. In southern Arizona, there is a single host species, *Aristolochia watsoni* Woot. Standl. *A. watsoni* is a small perennial, deciduous, recumbent vine with multiple stems that is abundant in washes and bordering areas at low to middle elevations. We worked on a 25-ha site in Pasture 1 on the University of Arizona Santa Rita Experimental Range in Pima County, Arizona (31°47.049'N, 110°49.524'W). This site consists of mesquite grassland and is bisected by a wash; the wash represents less than 5% of the area of the site. The butterfly has in the order of four broods in southern Arizona, but timing and discreteness of broods varies substantially from year to year and site to site. The plant dies back in the winter though not always completely; adults are occasionally observed even in mid winter.

Weather information and timing of observations

The 2003 summer monsoon was in many respects a "typical" monsoon, beginning officially in Tucson (ca. 65 km north of our study site) on 11 July, just ca. 6 days later than average and resulting in an average amount of rain (National Weather Service, Tucson). Observations of ovipositing females were conducted during two distinct periods, one before the onset of the monsoon and one after: 29 May–19 June and 30 August–17 September. An automated USDA rain gauge located at our site reported that precipitation totaled 28.1 cm during the period between the observation phases (Fig. 1; W. Emmerich, USDA–ARS, Tucson, Ariz.).

Assessment of female landings on hosts and non-hosts

Between the hours of 0900 and 1600, we followed individual females engaged in host search, by walking through the site until a female searching for hosts was sighted. Host search is a highly stereotyped, readily

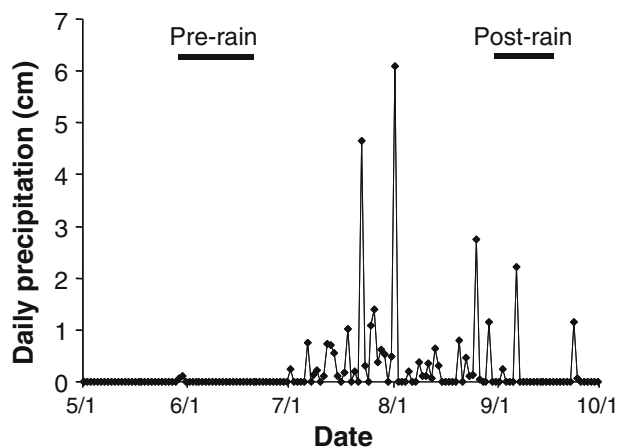


Fig. 1 Daily precipitation (cm) at the Santa Rita Experimental Range study site in Pima County, Arizona, from 1 May up to and including 1 October 2003. The 2003 monsoon season began officially in Tucson, Arizona, on 11 July. Bars above plot indicate periods over which pre-rain and post-rain observations were conducted. The pre-rain period lasted from 29 May up to and including 19 June; the post-rain period lasted from 30 August up to and including 17 September

identified pattern of behavior in which females flutter close to the vegetation, making frequent turns and landing periodically on both host and non-host vegetation, but laying eggs exclusively on *A. watsoni*. We followed a female either for 15 min search time (search time = time followed, exclusive of time spent nectaring, inspecting host plants, or laying eggs) or, commonly, until the female was lost from view. We recorded the duration of an observation, as well as the time that a female spent inspecting any host plants that she discovered over the observation period. Regardless of time of season, females were observed only during periods of sunny weather (which dominated the period of 0900–1600 hours throughout the summer, clouds and rain generally appearing in late afternoon or evening after observations ended). Nothing in our observations gave us reason to believe that seasonal changes in weather had direct effects on female behavior.

Host discovery rates were estimated as the number of hosts found per unit time spent searching for hosts, exclusive of time spent nectaring, inspecting hosts, or laying eggs. Because females were followed for variable periods of time and because host discovery rate should be a function of length of observation period, we analyzed the effect of monsoon rains on host discovery rates using analysis of covariance (ANCOVA) on number of hosts found with total search time in an observation as a covariate.

While we did not mark females and thus could not absolutely rule out the possibility that we never followed the same individuals more than once, it is

unlikely on several counts. First, females varied sufficiently in size, wing wear and behavior that we could readily avoid repeated observations of the same females within a given day. Second, pipevine swallowtail butterflies are large, highly vagile insects, and our study site probably represents just a small portion of the area over which a female ranges in this locale. It thus seems unlikely that we followed the same individuals on different days. In a mark–release effort unrelated to this study, release of ca. 100 marked females at our study site yielded no recoveries in ensuing days (D. Papaj, unpublished data). Third, since pipevine swallowtail butterflies appear to live only a few weeks in the field (Papaj 1986b), it is virtually certain that individual butterflies followed before monsoon rains were not followed after the rains, the two observation phases in 2003 being separated by almost 10 weeks.

In 2004, we conducted similar observations, this time focusing on “mistakes” made by searching females, i.e., landings on non-host plants. We again made observations before monsoon rains began (2–24 June) and again following the flush of vegetation resulting from monsoon rains (3 August–3 September). Observations were made as above except that we counted the number of landings made by searching females on anything that was not an *Aristolochia*. We analyzed the effect of monsoon rains on rate of landing mistakes using ANCOVA on number of non-host landings, with total search time in an observation as a covariate.

Assessment of female oviposition behavior

Assessment of female oviposition choices was made in 2003 as part of the same observations in which host discovery rates were estimated. When a female landed on a host plant, we recorded her response to the plant (oviposition vs. rejection). After a female left the plant, we placed a uniquely numbered flag near the plant. If the female appeared to lay eggs on the plant (as indicated by a stereotyped curling of the abdomen), we searched the plant after she left, in the place where abdominal curling was observed, and recorded the number of any eggs found. Abdominal curling is not always accompanied by egg deposition; hence, oviposition was inferred only if eggs were found at the site of curling.

At the end of the day, we returned to flagged plants. We measured the following characteristics for all host plants: number of stems, individual stem length, number of eggs not laid by the focal female, number of larvae, relative amount of new growth, and leaf color. Some host characteristics were chosen because previous studies indicated their importance in this system (plant size, presence of new growth, and presence of

previously laid eggs and larvae; Rausher 1979, 1981a; Rausher and Papaj 1983; Papaj 1986a; Papaj and Rausher 1987; Papaj and Newsom 2005). Intuition guided selection of leaf color as a characteristic of interest. *A. watsoni* plants vary strikingly in color from bright green to dark green to red to a very dark red.

Plant size was assessed in terms of number of stems and length of each stem. New growth was coded as 0–5 where 0 meant that there was no new growth, as judged by the presence or absence of unexpanded leaves, and 5 meant that foliage consisted entirely of new growth. Leaf color was assessed using an index estimating the percentage of leaf tissue that was red vs. bright green vs. dark green; in the analysis, we analyzed percentage red tissue and percentage bright green tissue.

We followed procedures by Rausher and Papaj (1983) and Papaj and Rausher (1987) in analyzing the pattern of host discrimination. Because individual females generally did not furnish enough accepted and rejected plants to allow us to analyze by female [median no. hosts found per female = 3, range 1–8, $n(\text{females})_{\text{max}} = 98$], we pooled host plants across observations into accepted (= received at least one egg) and rejected (= received no eggs) categories. We then employed a multivariate ANOVA (MANOVA) of plant characteristics in which host category and monsoon were main effects. In this MANOVA, a significant effect of host category indicates that females are discriminating with respect to plants on which they lay their eggs. A significant effect of monsoon rains indicates that found plants differ according to period of observation. A significant interaction between host category and monsoon rains indicates that degree of discrimination depends on whether females were observed before versus after onset of monsoon rains.

Assessment of host density and suitability

We evaluated changes in host density and suitability using an independent set of 212 individually tagged host plants at the same site in which females were followed. Plants were tagged in the previous year and the early spring of the study year. Approximately every 2 weeks, we surveyed plants, noting the number of plants that had some amount of edible foliage and were therefore available for oviposition. Plant size was scored from 0 (no foliage present) to 8. New growth was categorized from 0 (no new growth) to 8 (entirely new growth). Because we tagged most of our plants in the early spring of the study year, it is possible that we missed plants that did not leaf out in the spring but did so later, perhaps after the monsoon rains. Hence, increases in host density might have been underestimated by our

method. However, our methods should have allowed us to detect a significant decrease in host density which, as will be apparent below, was more crucial to our inferences.

Statistical analyses

All statistical analyses were conducted with JMP-IN version 4 software (SAS 2000).

Results

Changes in host discovery rate

The onset of the summer monsoon and resulting flush of non-host vegetation, was accompanied by a 50% decrease in host discovery rate, measured in terms of number of hosts found per unit search time (Fig. 2; median before = 16.0 hosts discovered per hour, $n = 86$; median after = 7.8 hosts discovered per hour, $n = 54$). ANCOVA of effect of monsoon rains on number of hosts found, with total search time as a covariate confirmed that host discovery rate dropped significantly after the monsoon began; in this analysis, the slope, which is an estimate of host discovery rate (with units equal to number of hosts found divided by search time), is significantly steeper before the onset of monsoon rains than after the rains (Fig. 2; $R^2 = 45.0\%$; test for slope heterogeneity, $F_{1,136} = 7.56$, $P < 0.007$).

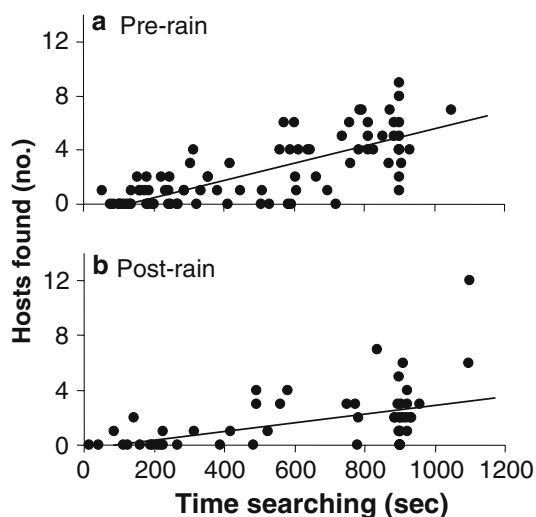


Fig. 2 Relationship between the number of *Aristolochia watsoni* host plants found and time spent searching for host plants (slope = host discovery rate) for pipevine swallowtail (*Battus philenor* L.) females observed **a** prior to onset of monsoon rains ($n = 86$) and **b** after monsoon rains subsided ($n = 54$). Lines indicate fit to analysis of covariance (ANCOVA) model. *sec* Seconds

Changes in rate of non-host landings

In 2004, numbers of butterflies after monsoon rains were low. Nevertheless, we were able to show that the frequency with which searching females landed on non-host vegetation increased significantly with the summer monsoon rains. The flush of non-host vegetation resulting from monsoon rains was accompanied by more than a doubling in the estimated number of landings made on non-host vegetation, measured in terms of number of non-hosts landed on per unit search time (Fig. 3; median before rains = 138.0 non-host landings per hour, $n = 76$; median after = 304.0 non-host landings per hour, $n = 16$). ANCOVA of effect of monsoon rains on number of non-host landings, with total search time as a covariate (Fig. 3), confirmed that rate of non-host landings increased significantly after the monsoon rains; in that analysis, the slope, which is an estimate of non-host landing rate (with units equal to number of non-host landings divided by total search time), is significantly steeper for data collected after the monsoon rains (Fig. 3; $R^2 = 69.6\%$; test for slope heterogeneity, $F_{1,88} = 12.85$, $P = 0.0006$).

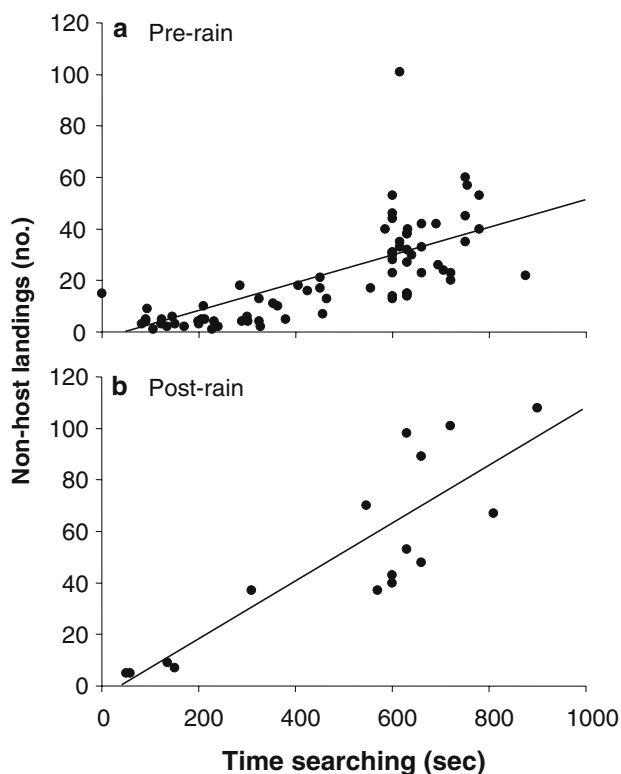


Fig. 3 Relationship between the number of landings on non-host plants and time spent searching for host plants (slope = non-host landing rate) for pipevine swallowtail females observed **a** prior to onset of monsoon rains ($n = 76$) and **b** after monsoon rains subsided ($n = 16$). Lines indicate fit to ANCOVA model

Changes in clutch size and propensity to oviposit

Mean clutch size increased by almost 150% after monsoon rains (mean clutch size before = 1.60, SE = 0.20, $n = 42$; mean clutch size after = 3.99, SE = 0.25, $n = 23$). We conducted a nested ANOVA in which clutch size data were nested within females. The model explained 74.6% of variation in clutch size. The nesting factor, female, was not significant (nested ANOVA, $F_{64,49} = 1.31$, $P < 0.20$), indicating that variation in clutch size among females was not significantly greater than variation within females. The difference in clutch size before versus after monsoon rains was highly significant ($F_{1,49} = 53.16$, $P < 0.0001$).

Monsoon rains were also associated with a highly significant increase in a female's propensity to oviposit after alightment, measured as the proportion of those hosts found by a female that received eggs (mean proportion hosts accepted before rains = 0.31, SE = 0.035, $n = 61$; mean proportion hosts accepted after = 0.54, SE = 0.05, $n = 35$). The difference in propensity to oviposit in relation to monsoon rains was highly significant (ANOVA, $R^2 = 13.1\%$, $F_{1,94} = 14.17$, $P = 0.0003$).

Pattern of female discrimination after alightment

A multivariate ANOVA of assorted plant characteristics yielded the following inferences. First, the highly significant effect of host category (accepted for oviposition vs. rejected) indicated that the plants on which females laid eggs differed in one or more measured characteristics from the plants on which females landed but did not lay eggs (MANOVA, $F_{7,287} = 5.96$, $P < 0.0001$). In terms of the individual plant characteristics measured, plants accepted for oviposition tended to bear fewer larvae, more new growth, and longer stems (Table 2). Females showed no tendency to reject hosts according to the number of previously laid eggs, nor was number of stems a factor in host acceptance.

Second, a highly significant effect of time of observations (before vs. after rains) suggested that monsoon rains significantly altered host plant characteristics (MANOVA, $F_{7,287} = 91.91$, $P < 0.0001$), including some that affected oviposition decisions. Following monsoon rains, host plants bore longer stems, more green leaf tissue, more new growth, and bore more previously laid eggs (Table 2). In conjunction with host acceptance patterns, overall host suitability in terms of new growth and plant size (specifically, stem length) thus improved with monsoon rains. Females were agnostic with respect to other characteristics that changed seasonally, specifically amount of green leaf tissue and number of previously laid eggs (Table 2).

Table 2 Results of univariate ANOVA on assorted host characteristics in relation to whether eggs were laid on a host (*Accept*) or not laid (*Reject*), whether females encountered hosts before versus after monsoon rains, and the interaction of those two factors

Trait	Mean values ($\pm 1SE$)				Host acceptance		Rains		Acceptance \times Rains	
	Pre-rains		Post-rains		$F_{1,293}$	<i>P</i> -value ^a	$F_{1,293}$	<i>P</i> -value ^a	$F_{1,293}$	<i>P</i> -value ^a
	Accept	Reject	Accept	Reject						
No. previous eggs	0.94 (± 0.26) <i>n</i> = 67	0.94 (± 0.14) <i>n</i> = 141	2.09 (± 0.51) <i>n</i> = 53	1.96 (± 0.41) <i>n</i> = 46	0.02	n.s.	13.32	0.0003	0.02	n.s.
No. previous larvae	0.06 (± 0.03) <i>n</i> = 67	0.51 (± 0.07) <i>n</i> = 141	0.23 (± 0.13) <i>n</i> = 53	0.50 (± 0.15) <i>n</i> = 46	14.05	0.0002	0.65	n.s.	0.46	n.s.
% Green leaves	13.03 (± 3.47) <i>n</i> = 66	13.99 (± 2.47) <i>n</i> = 138	22.45 (± 4.32) <i>n</i> = 53	24.32 (± 5.26) <i>n</i> = 44	0.25	n.s.	7.37	0.007	0.05	n.s.
% Red leaves	60.76 (± 4.84) <i>n</i> = 66	60.0 (± 3.19) <i>n</i> = 138	64.72 (± 4.46) <i>n</i> = 53	66.36 (± 5.04) <i>n</i> = 44	0.0002	n.s.	0.71	n.s.	0.01	n.s.
New growth index	1.12 (± 0.19) <i>n</i> = 66	0.81 (± 0.11) <i>n</i> = 139	2.42 (± 0.18) <i>n</i> = 53	1.70 (± 0.22) <i>n</i> = 46	8.01	0.005	41.55	<0.0001	1.25	n.s.
No. stems	11.20 (± 0.68) <i>n</i> = 66	11.36 (± 0.44) <i>n</i> = 138	11.11 (± 0.83) <i>n</i> = 52	11.0 (± 0.89) <i>n</i> = 45	0.003	n.s.	0.05	n.s.	0.01	n.s.
Mean stem length (mm)	58.68 (± 4.09) <i>n</i> = 66	51.67 (± 2.19) <i>n</i> = 138	183.88 (± 8.72) <i>n</i> = 52	158.83 (± 9.91) <i>n</i> = 44	9.06	<0.003	436.05	<0.0001	3.09	0.080

^a *P*-values shown before Bonferroni correction. *P*-values in **bold** are those that remained significant after Bonferroni correction

Third, the lack of a significant interaction between time of observation and host category (MANOVA, $F_{7,287} = 0.98$, n.s.) indicated that, contrary to predictions (Table 1), the extent to which females discriminated among hosts after alightment did not change with onset of the monsoon.

Changes in oviposition rate

Despite reductions in host discovery rates, rates of oviposition were greater after the monsoon rains than before (Fig. 4; median before = 8.14 eggs laid per hour, *n* = 86; median after = 16.55 eggs laid per hour, *n* = 52). To quantify this pattern, we applied an ANCOVA approach to oviposition rate similar to that used above for host discovery rate. ANCOVA of effect of monsoon rains on total eggs laid in an observation period with time spent in host search as a covariate, confirmed that oviposition rate increased after the rains; in this analysis, the slope, which is an estimate of oviposition rate (with units equal to total number eggs laid divided by time spent engaged in host selection), was significantly steeper after the monsoon rains than before (Fig. 4; ANCOVA, $R^2 = 26.3\%$; test for slope heterogeneity, $F_{1,134} = 4.50$, $P < 0.04$). This difference appears to be due primarily to the difference in clutch size reported above, because clutch deposition rate did not depend on monsoon rains: ANCOVA of the effect of rains on number of clutches, with time engaged in host selection as a covariate, failed to show significant heterogeneity of slope ($R^2 = 23.2\%$; test for slope heterogeneity, $F_{1,136} = 0.55$, n.s.).

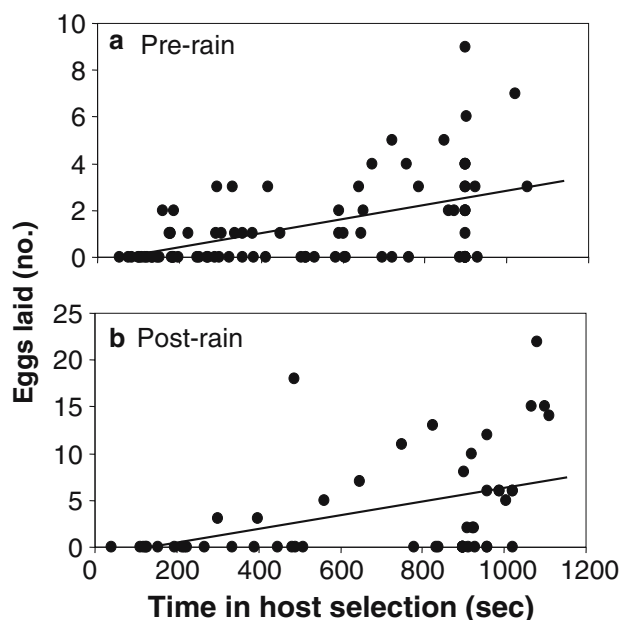


Fig. 4 Relationship between total number of eggs laid in an observation period and time engaged in host selection (slope = oviposition) for pipevine swallowtail females observed **a** prior to onset of monsoon rains (*n* = 86) and **b** after monsoon rains subsided (*n* = 52). Lines indicate fit to ANCOVA model. Note different scales on y-axes of two plots

Changes in host density and suitability

Monsoon rains were not accompanied by a measurable change in the number of plants bearing foliage and available for oviposition, as determined by biweekly surveys of 212 tagged plants that bounded our two

observation phases (mean proportion plants available for oviposition before rains = 0.894, SE = 0.027, $n = 3$ surveys; mean proportion after rains = 0.892, SE = 0.080, $n = 3$ surveys; t -test, n.s.). Hence, changes in host density can account neither for the seasonal decline in host discovery rates nor for the increase in oviposition rates.

Both size and amount of new growth of a representative set of host plants in the local population increased after the monsoon rains. In biweekly surveys of 212 plants, 103 had complete records for indices of size and new growth during three surveys bounding each time of season. Host plants were significantly larger after rains than before (median score = 3 before rains and = 4.5 after rains; sign test, $Z = 45.5$, $P < 0.0001$). Host plants bore significantly more new growth after rains than before (median score = 0 before rains and 6 after rains; sign test, $Z = 25.5$, $P < 0.0001$).

Discussion

Our results suggest strong effects of monsoon rains on a butterfly's host plant and surrounding vegetation, effects which in turn exert striking effects on oviposition behavior. Our results are correlative in nature and our inferences about cause and effect need to be supported by experimental manipulations. In the following sections, we explore our inferences with a view towards the kind of manipulations that should be done.

Monsoonal effects on non-host vegetation

Extreme weather change in the form of monsoonal precipitation affected non-host vegetative background in ways that appeared to alter host selection by

pipevine swallowtail butterflies (see summary in Table 3). Monsoon rains generated a flush of non-host foliage. Host discovery rates after the rains were sharply reduced, as predicted by the vegetative background hypothesis. Increases in non-host biomass probably reduced host discovery in several ways (Rausher 1981b; Snell-Rood and Papaj 2006). Casual observations suggest that non-host vegetation physically masks hosts visually (perhaps olfactorily too) and sometimes physically prevents a female from making contact with a host to which she is orienting. Such obstruction is rarer prior to monsoon rains. In addition, the increase in non-host vegetation accompanying monsoon rains resulted in significantly more "mistaken" landings on non-host vegetation (Fig. 3). Non-host landings are presumed to reflect detection constraints; females cannot identify a host absolutely prior to alightment (Rausher 1978). Identification is made via chemotactile input involving receptors on the female's foretarsi. Application of functional response models to analysis of such "false alarms" suggest that host discovery rates can decline severely if a non-host landing consumes as little as 1–2 s (Papaj 1990). In short, the flush of non-host vegetation accompanying monsoon rains can be considered to generate sensory noise that reduces host discovery rate. Testing an hypothesis of sensory noise would involve manipulation of the nature and density of non-host foliage (Rausher 1981b; see also Snell-Rood and Papaj 2006); ideally, such manipulations would distinguish between physical obstruction and sensory noise.

Monsoonal effects on host plant suitability

Monsoon rains also caused a striking change in host plants, including changes that are likely to improve juvenile growth and/or survival. Most notably, *A. watsoni*

Table 3 Predicted effects^a of monsoon rains on plants (post-rains pattern) and herbivore (HDR, clutch size, host acceptance, degree of discrimination and oviposition rate)

	Vegetative background effects	Host density effects	Host suitability effects
Presumed post-rain pattern	<i>More non-host vegetation</i>	Hosts more abundant	<i>Hosts more suitable</i>
Predicted change in HDR	<i>Decrease</i>	Increase	No change or increase
Predicted change in clutch size	<i>Increase</i>	Decrease	<i>Increase</i>
Predicted change in propensity to oviposit	<i>Increase</i>	Decrease	<i>Decrease (via increased HDR)</i>
Predicted change in discrimination	Decrease	Increase	<i>Increase (via increased HDR)</i>
Predicted change in oviposition rate	No change or decrease	Increase if HDR increases	<i>Increase</i>
			<i>Decrease (via increased HDR)</i>

^a Comments in *italics* indicate presumptions and predictions that were met by the data. See Results for further explanation

plants bore more foliage after monsoon rains began. In studies of this association in east Texas, the amount of edible foliage on an *A. serpentaria* plant was a good predictor of juvenile performance and of female oviposition behavior (Papaj and Rausher 1987). Larger plants should be more suitable for larval performance because *Battus* larvae commonly require a number of host plants in order to complete development (D. Papaj and C. Heinz, personal observation) and because the probability of a dispersing larva reaching a new plant without dying increases with size at which they leave the defoliated plant (Rausher 1980). Plants also bore more new growth following monsoon rains; amount of new growth was shown previously to be a strong indicator of host suitability in other locales (Rausher 1981b; Rausher and Papaj 1983).

Both changes in vegetative background and in host suitability might be expected to contribute to the increases in clutch size and propensity to oviposit observed here. Odendaal and Rausher (1990) found that clutch size and propensity to oviposit increased following periods of inclement weather during which *B. philenor* could not lay eggs. The same effects might be observed if an increase in non-host vegetation reduced host discovery rates. Pilson and Rausher (1988) reported that *B. philenor* females adjust clutch size in response to host suitability in terms of new growth. For several reasons, we believe increases in clutch size to be due mainly to changes in host suitability. First, data collected in 2004 failed to detect a significant cross-monsoon difference in egg load (D. Papaj and B. Worden, unpublished data). These data tend to discount the possibility that increases in non-host vegetation increase clutch size and propensity to oviposit by reducing host discovery rate and increasing egg load. Second, the monsoon-based decline in host discovery rate wrought by increases in non-host vegetation ought to have generated not only increases in clutch size but also reductions in degree of discrimination (Mangel 1989). While we found strong evidence of discrimination after alightment (specifically, discrimination against larval presence and in favor of large plants bearing more new growth), the degree of discrimination did not change in relation to the rains. Confirmation that changes in host suitability drive changes in clutch size and propensity to oviposit would involve manipulation of host characteristics such as plant size and amount of new growth, perhaps through fertilization experiments.

Rates of oviposition and weather change

The vegetative background and host suitability hypotheses differ in one key respect: given the observed

pattern in host discovery rate, only the host suitability hypothesis predicts that oviposition rate would increase following onset of the monsoon (Table 1). Post-monsoon oviposition rates did indeed increase despite reduced host discovery rates. This result does not mean that changes in vegetative background did not influence oviposition rate. However, it does imply that oviposition rates prior to the onset of the monsoon were limited more by the low quality of host plants available than they were after the onset of the monsoon by the low rate at which host plants were found.

Limits on oviposition rate, whatever their cause, do not necessarily translate to limits on overall fecundity. It is possible that females suffering reduced rates of oviposition compensate for these reductions by extending the overall time engaged in oviposition each day. While we did not directly assess changes in the daily time budget devoted to oviposition, we did not observe any obvious pattern in time budget in relation to monsoon onset. However, it remains to be shown definitively that changes in oviposition rate influence lifetime fecundity.

Implications for responses to climate change

Global climate change poses documented challenges to herbivores in coevolved insect–host associations like the one examined here. For example, elevated CO₂ affected levels of plant nitrogen and defensive compounds in various systems (which generally decrease and increase, respectively; Bazzaz 1998; Coley 1998; Johns and Hughes 2002; Veteli et al. 2002). Similarly, increased levels of UV-B influenced leaf beetle herbivory (Warren et al. 2002). Global changes in climatic extremes, including more frequent and more severe droughts, could also presumably affect herbivore reproduction. The present study attempts to define plant and herbivore traits that ought to be examined in the context of extreme weather and extreme weather change. Our results with *B. philenor* butterflies suggest that these insects possess potentially adaptive flexibility in terms of oviposition decisions in the face of extreme weather change and its effects upon their host resource. However, our results also suggest that such flexibility has limits, as it pertains to climate change. For example, oviposition rates were not constant over the season, being significantly lower during the dry period. By extension, more severe droughts may be associated with more markedly reduced rates of oviposition. The link between oviposition rate and population persistence is unclear and bears scrutiny. However, to the extent that chronically low rates of oviposition translate to chronically low population

levels, they may conceivably increase the risk of population extinction, a documented consequence of climate change in butterflies and other organisms (Parmesan 1996; McLaughlin et al. 2002).

Future directions

The obvious next step in this system is to verify, via experimental manipulations, that the reported correlations among weather, vegetation and behavior truly reflect the patterns of cause and effect that were inferred above. The monsoon generated a myriad of other changes that could conceivably account for some of the observed correlations, and these need to be excluded by way of manipulations. For example, monsoon rains may have increased the abundance of nectar sources which could have boosted nectar feeding rates which in turn could have affected clutch size independent of changes in host suitability. Observations such as ours are critical to understanding what actually happens in nature; however, given how pervasively weather can affect an insect, its hosts and the biotic environment, experimental manipulations are critical to confirming the inferences drawn here.

If our inferences prove correct, our results suggest that change in clutch size was a driver of change in oviposition rate. Effects of climate change on clutch size may be deserving of special attention. First, there is a robust theoretical and empirical literature on the ecology and evolution of clutch size which provides a foundation for predictions about climate change effects. Second, work on clutch size in insects would provide a comparison with a substantial body of work on this trait in birds, which are themselves a focus of much climate change work. The pipevine swallowtail butterfly would be a particularly interesting system in which to probe for environmental correlates of clutch size, given intriguing patterns of variation in clutch size and clutch size adjustment that have been described to date. Pilson and Rausher (1988), for example, reported that females adjusted clutch size in response to quality of host foliage. In contrast, a field study by Fordyce and Nice (2004) generally failed to find correlations between the size of naturally laid clutches and assorted host characteristics. Odendaal and Rausher (1990) reported that clutch size was also a function of egg load. Tatar (1991) found that, in one California brood, clutch size varied in direct proportion to egg load; however, in another brood at the same site, clutch size was independent of egg load. Here we documented a striking seasonal change in clutch size that seems to be due to monsoon-driven changes in host suitability. Further assessment of this inference, including experiments on

clutch size on watered versus unwatered host plants, is warranted. Additionally, multiple populations should be surveyed with respect to clutch size and clutch size adjustment. Fordyce and Nice (2003), for example, speculated that differences between California and other *B. philenor* populations in clutch size may reflect genetically based differences, and presented molecular evidence suggesting that the geographically isolated California population is relatively recent in origin. The California host responds to early damage by increasing its suitability for herbivory; this short-term induction may favor larger clutches (Fordyce 2003; Fordyce and Nice 2004). In short, the available evidence suggests that clutch size in these butterflies may vary as consequences both of local adaptation and of phenotypic plasticity.

A connection between weather change and plant chemistry should also be explored in this system. *Aristolochia* plants are characterized by aristolochic acids, which defend them from most herbivores but which have no effect on *B. philenor* larvae (Fordyce 2001). In fact, aristolochic acids are sequestered by larvae and defend them from natural enemies (Fordyce 2000; Sime et al. 2000, Sime 2000). Larvae that sequester more aristolochic acids are better defended (Fordyce 2000). It would be interesting to determine how aristolochic acid levels in the plants change in relation to extremes in weather and how in turn these changes affect defense from natural enemies.

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