

Evolution of aquatic insect behaviours across a gradient of disturbance predictability

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Natural disturbance regimes—cycles of fire, flood, drought or other events—range from highly predictable (disturbances occur regularly in time or in concert with a proximate cue) to highly unpredictable. While theory predicts how populations should evolve under different degrees of disturbance predictability, there is little empirical evidence of how this occurs in nature. Here, we demonstrate local adaptation in populations of an aquatic insect occupying sites along a natural gradient of disturbance predictability, where predictability was defined as the ability of a proximate cue (rainfall) to signal a disturbance (flash flood). In controlled behavioural experiments, populations from predictable environments responded to rainfall events by quickly exiting the water and moving sufficiently far from the stream to escape flash floods. By contrast, populations from less predictable environments had longer response times and lower response rates, reflecting the uncertainty inherent to these environments. Analysis with signal detection theory showed that for 13 out of 15 populations, observed response times were an optimal compromise between the competing risks of abandoning versus remaining in the stream, mediated by the rainfall–flood correlation of the local environment. Our study provides the first demonstration that populations can evolve in response to differences in disturbance predictability, and provides evidence that populations can adapt to among-stream differences in flow regime.

Keywords: disturbance; information theory; natural flow regime; signal detection theory; flooding; drought

1. INTRODUCTION

Disturbance regimes play a central role in the regulation of populations (MacArthur & Levins 1967; Lavorel & Chesson 1995), the structuring of communities (Fisher *et al.* 1982; Townsend *et al.* 1997; Collins 2000) and the functioning of ecosystems (Turner *et al.* 1997, 1998; Townsend *et al.* 1998). While the ecological effects of disturbances such as fires, floods and droughts are well appreciated, it is less clear how organisms evolve in response to these phenomena. Theory suggests that traits allowing escape from disturbance can evolve if disturbance events are sufficiently predictable, i.e. if they occur with sufficiently regular periodicity (Lytle 2001; Roff 2002) or if they are sufficiently correlated with an environmental cue (Cohen 1967). The salient issue here is what constitutes ‘sufficient’. At one extreme, large infrequent disturbances such as hurricanes and tsunamis may devastate populations, but they are difficult for organisms to anticipate (Turner *et al.* 1997, 1998; Allison *et al.* 2003). Thus, it is not clear how organisms might evolve strategies to escape these disturbances (although bet-hedging strategies may evolve to spread risk among offspring; Cohen 1966, Hopper 1999). At the other extreme, disturbances such as winter frosts can be predicted from environmental cues such as changes in photoperiod, and populations can evolve strategies that allow dormancy or migration in advance of the disturbance (Blanckenhorn & Fairbairn 1995; Nylin *et al.* 1995; Burke *et al.* 2005).

Flash floods in arid climates provide a model system for understanding how populations evolve in response to disturbance predictability. In Madrean Sky Island streams of the desert southwestern USA and northern Mexico, sudden floods generated by monsoon thunderstorms (Douglas *et al.* 1993) can kill or displace over 95% of aquatic organisms (Gray 1981; Fisher *et al.* 1982; Molles 1985; Lytle 2000). The flightless aquatic insect *Abedus herberti* (Hemiptera: Belostomatidae) uses rainfall response behaviour (RRB) to escape streams immediately prior to flash floods: after some critical duration of heavy rainfall, individuals crawl out of the stream to riparian areas where they are safe from floods but vulnerable to terrestrial predators and desiccation (Lytle & Smith 2004). Individuals return to the same stream post-flood. Populations have a characteristic response time (the duration of rainfall required to trigger RRB) and response rate (percentage of individuals in a population that respond to rainfall with RRB) that can be quantified in the laboratory (Lytle 1999; Lytle & Smith 2004).

Isolated populations of *A. herberti* are found in catchments throughout the Sky Island region (figure 1; Finn *et al.* 2007), and the differences in catchment geometry create a spectrum of disturbance regimes ranging from predictable to unpredictable. In the mid-sized catchments (approx. 10 km²), rainfall cues and floods are well correlated, in part because monsoon storms occur at this spatial scale (9 km²; Syed *et al.* 2003). Thus, flood events can be predicted from rainfall events somewhat reliably in the mid-sized catchments. In larger catchments (more than 30 km²), flash floods can be generated by distant thunderstorms, rendering local

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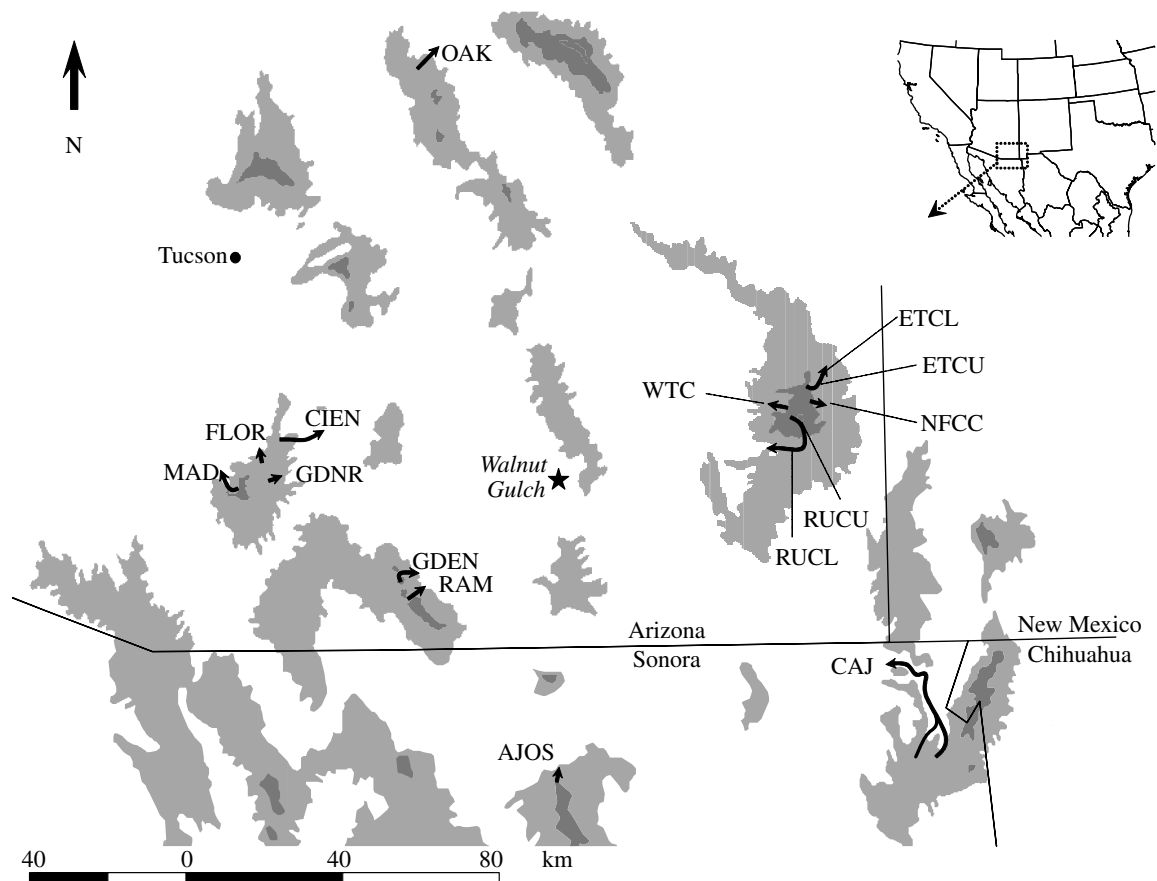


Figure 1. Map of *A. herberti* study populations in the Madrean Sky Island region (see table 1 for population codes). Light grey corresponds to approximately 1300 m elevation, and dark grey to approximately 2200 m. Stream vector lengths are proportional to study catchment areas.

rainfall cues ambiguous or even misleading. The latter is the 'classic' flash flood scenario, where a violent flood arrives suddenly on an otherwise calm sunny day. Thus, floods in large catchments are unpredictable due to the poor correlation between rainfall cues and flash flood events. Conversely, floods are often rare in small catchments (less than 10 km²) because small drainage areas rarely capture enough rainfall to generate floods. This situation can also generate false alarms, causing individuals to respond to rainfall events that never produce a flood. Owing to these hydrological characteristics, the relationship between catchment size and disturbance predictability should be hump shaped, with maximum flood predictability occurring in the mid-sized catchments. We therefore hypothesized that animals from populations inhabiting mid-sized catchments should respond quickly to rainfall cues. In smaller or larger catchments where rainfall cues are more ambiguous, uncertainty about the reliability of rainfall cues may favour longer response times.

Signal detection theory (SDT) provides a robust framework for exploring how disturbance predictability can drive the evolution of traits (Getty & Krebs 1985; Reeve 1989; Wiley 1994). As a branch of information theory (*sensu* Shannon & Weaver 1949), SDT provides a modelling framework that describes how decision makers—be they humans, birds, insects or computers—can make optimal choices when faced with noisy signals. SDT has been used to interpret the adaptive value of foraging behaviour (Getty & Krebs 1985; Lynn *et al.*

2005; McClinn & Stephens 2006), phenotypic plasticity (Getty 1996), mimicry (Rodríguez-Gironés & Lotem 1999), mate choice in birds (Getty 1995), colour polymorphism in odonates (Sherratt 2001; Fincke 2004), and pain, fever and fear in humans (Nesse 2005). However, the ability of SDT to predict phenotypes accurately across a wide gradient of environments has not been demonstrated in the field or in the laboratory.

The general SDT framework neatly encompasses the problem of flood escape in flash-flooding streams. In order to maximize survival, individuals choose the threshold duration of rain that makes the benefit of leaving the stream (flood escape) outweigh the cost of a false alarm (predation or desiccation in the terrestrial environment; Smith 1997, Lytle 1999), given the information content of the local environment. At any given duration of rainfall x , an individual can choose to remain in or exit the stream. The consequences of this decision will depend on whether or not a flood actually occurs (denoted F or NF). There are four possible outcomes: an individual can (i) leave the stream and avoid a subsequent flood (a 'hit', with a pay-off of V_H), (ii) leave the stream and then no flood occurs (a 'false alarm', V_{FA}), (iii) remain in the stream and then a flood occurs (a 'miss', V_M) or (iv) remain in the stream and no flood occurs (a 'correct rejection', V_{CR}). At the optimal rainfall duration x^* , the expected cost of leaving the stream equals the cost of remaining, and so individuals should choose to exit the stream after rainfall events longer than x^* . The value of x^* also depends on the degree to which rainfall cues predict (or fail to predict) flash floods, and the overall

Table 1. Sample sizes and catchment attributes of *A. herberti* populations used in behavioural experiments. (AZ, Arizona, USA; SON, Sonora, Mexico.)

code	stream	mountain range	area (km ²)	N
AJOS	Arroyo Claro	Sierra los Ajos, SON	4	22
CAJ	Cajon Bonito	Sierra San Luis, SON	440	41
CIEN	La Cienega	Santa Rita Mtns, AZ	37.6	21
ETCL	Lower E. Turkey Cr.	Chiricahua Mtns, AZ	11.2	58
ETCU	Upper E. Turkey Cr.	Chiricahua Mtns, AZ	5.7	76
FLOR	Florida Canyon	Santa Rita Mtns, AZ	4.9	50
GDEN	Garden Canyon	Huachuca Mtns, AZ	8.9	37
GDNR	Gardner Canyon	Santa Rita Mtns, AZ	4.6	52
MAD	Madera Canyon	Santa Rita Mtns, AZ	18.3	51
NFCC	N. Fork Cave Cr.	Chiricahua Mtns, AZ	5.5	36
OAK	Oak Cr.	Galiuro Mtns, AZ	15.5	56
RAM	Ramsey Canyon	Huachuca Mtns, AZ	8.2	36
RUCL	Lower Rucker Canyon	Chiricahua Mtns, AZ	91.4	58
RUCU	Upper Rucker Canyon	Chiricahua Mtns, AZ	16.9	123
WTC	W. Turkey Cr.	Chiricahua Mtns, AZ	7.4	36

probability of a flood occurring. Following the notation of Getty (2002), these trade-offs can be written as

$$\frac{f(x^*|F)}{g(x^*|NF)} = \frac{1-\alpha}{\alpha} \cdot \frac{V_{CR} - V_{FA}}{V_H - V_M} = \frac{1-\alpha}{\alpha} \cdot \frac{c}{t-c}, \quad (1.1)$$

where the environmental signal f is the probability density distribution of rainfall events of duration x conditioned on a flood disturbance occurring (F); the environmental noise g is the probability density distribution of x conditioned on a flood not occurring (NF); c is the mortality risk of abandoning the stream; t is the mortality risk of being caught in a flood; and α is the prior probability of a flood occurring. The shapes of $f(x|F)$ and $g(x|NF)$ will vary depending on catchment size, so the value of x^* which satisfies the equation likewise should vary among populations. According to SDT, individuals that abandon the stream after rainfall events of duration x^* have the highest survival fitness. If the f and g distributions are very similar, as may occur in highly unpredictable environments, there may exist no f/g that satisfies equation (1.1) and thus no optimal value of x^* .

For the purpose of analysing empirical data, equation (1.1) can be further simplified. Noting that $\alpha = P(F)$, by Bayes' rule the conditional probability of observing x given a flood can be rewritten as the probability of observing a flood given x

$$P(x|F) = P(F|x) \frac{P(x)}{\alpha}. \quad (1.2)$$

Similarly, for the case of no floods

$$P(x|NF) = P(NF|x) \frac{P(x)}{1-\alpha}. \quad (1.3)$$

Substituting equations (1.2) and (1.3) into equation (1.1), and observing that $P(F|x) = 1 - P(NF|x)$, yields the simplified form

$$P(F|x^*) = \frac{c}{t}. \quad (1.4)$$

Equation (1.4) shows that flood escape should occur at the rainfall duration where the per-interval probability of a flood occurring equals the cost ratio c/t . Note that equations (1.1) and (1.2) are equivalent and make the same predictions with respect to optimal behaviours.

Equation (1.4) is a more compact form than equation (1.1), and it is presented here because it may be more useful in cases where the signal data are obtained as per-interval probabilities rather than probability density distributions.

In this study, we used behavioural experiments to quantify how multiple populations of an aquatic insect have evolved along a flood disturbance gradient that ranges from highly predictable to highly unpredictable. We used mtDNA analysis to demonstrate that most populations are independently evolving units, and that shared behavioural traits among populations can be attributed to convergent local selection pressures rather than shared descent. We then used SDT to explore the mechanism by which disturbance predictability has determined the local phenotype of each population. This is the first demonstration of how populations evolve across a gradient of disturbance predictability, and the first empirical test of SDT across multiple populations.

2. MATERIAL AND METHODS

Our 15 study populations inhabit catchments spanning two orders of magnitude in size, from 4 to 440 km² (table 1). These catchments are located across six mountain ranges with similar geological settings (mixture of rhyolite and limestone bedrock). *Abedus herberti* is one of the dominant predators in these streams and, due to its ability to escape flash floods, it is the most abundant aquatic insect following flash floods (Lytle 2000). Although there is a distinct among-population size variation, individuals from most populations are 35–39 mm in length (Pelegrin 2006). *Abedus herberti* is long lived and iteroparous; we have recaptured marked individuals in the wild that are at least 2 years old (D. A. Lytle 2006, unpublished data). Like other belostomatine species, *A. herberti* males provide exclusive parental care by brooding eggs on their backs (Smith 1976).

(a) Streams with a single population

Out of the 15 populations, 13 are restricted to short (several km) sections of perennial stream between approximately 1300 and 2000 m in elevation, where water is forced to the surface by local geology. These small sections of perennial 'Sky Island' habitat are isolated from one another by long

intermittent reaches on the valley floors, where deep alluvial fill prevents surface flow for most of the year (Bogan & Lytle 2007). Owing to this isolation, there is a little or no contemporary gene flow among populations (Finn *et al.* 2007; also see genetic analysis below). Each population occupies a fairly discrete catchment size, so all individuals within each population probably experience the same selective regime. These single-population streams constitute the main focus of our study, because they consist of isolated independently evolving units that are subject to relatively uniform flood regimes.

(b) Streams with multiple subpopulations

Some of the larger streams (Cajon and Rucker; table 1) harbour multiple subpopulations ranging from the upper headwaters (small catchment size) to the lower reaches (large catchment size). The different subpopulations could experience different selective regimes, producing a sequential behavioural polymorphism from up- to downstream. To test whether different behaviours occur up- versus downstream, we sampled subpopulations at the up- and downstream extremes of one of the larger streams (Rucker, sampled at locations representing catchments areas of 16.9 and 91.4 km²). For comparison, we sampled a single-population stream at the upper and lower bounds of the population (E. Turkey, sampled at 5.7 and 11.2 km²).

(c) Sampling

Individuals were collected using nets and by hand during the pre-monsoon dry season of June to early August, ensuring that most individuals were naive to monsoon rainfall (from mark-recapture data, few individuals would have experienced the previous year's monsoon season; D. A. Lytle 2006, unpublished data). Individuals were transported to a field laboratory, placed in tanks filled with stream water and numbered with a fine-tipped permanent marker. Food was not provided since prey is scarce in natural streams during the pre-monsoon dry period (Bogan & Lytle 2007), but behavioural trials commenced within several days of capture.

(d) Behavioural experiments

We used controlled, replicated behavioural experiments to quantify response time and response rate for each population (Lytle & Smith 2004). Individuals were randomly assigned to one of the two behavioural arenas (42 × 32 × 23 cm plastic bins fitted with 0.5 m walls that allow individuals to exit the water by climbing vertically; usually six individuals per arena) and allowed to acclimate for at least 30 min. One arena was selected at random and exposed to simulated rainfall (sprayed stream water) for 60 min, and the other arena served as a control. Response time was scored as the minutes of rainfall required to trigger RRB, which we defined as the crossing of a line 35 cm above the water surface (this distance allowed us to observe the negatively geotactic movement that is characteristic of RRB; Lytle & Smith 2004). Most individuals were run in experiments at least three times, never on the same day. Mean response time per individual was used in later analyses. For individuals that exhibited RRB in more than one trial, we used a Wilcoxon signed-rank test to determine whether learning occurred across consecutive trials. Response rate was calculated as the percentage of individuals in the population that exhibited RRB at least once. To avoid conflating response time and response rate, only individuals that responded at least once were used to calculate response time.

To ensure that behaviours remained consistent across years and during the course of a season, we selected a control population (ETCL) that was sampled and tested at the beginning and the end of the field season in 2003 (late June and early August, respectively) and again in June 2004. Another population (RUCU) was assayed once per year over three consecutive years. Comparisons were made using ANOVA with mean response time per individual as the unit of replication.

We used polynomial regression to examine both response time and response rate as a function of catchment area. Because the populations from the two largest catchments were possible outliers, we ran analyses including ($N=15$) and excluding them ($N=13$). If a regression appeared to be hump shaped, the method of Mitchell-Olds & Shaw (1987; hereafter the MOS test) was used to determine whether the response variable reached a maximum (or minimum) within the observed data range. Tests used mean population response time or response rate as the unit of replication. Residual plots were examined to ensure that parametric test assumptions were met.

We calculated the repeatability (r_F) of response time across successive rainfall experiments as the correlation between the first and last response times for each individual that responded more than once during the rainfall experiments. Repeatability provides an upper bound estimate of H^2 , the broad-sense trait heritability (Lynch & Walsh 1998).

(e) Molecular analysis

We assessed the patterns of mitochondrial COI–COII sequence variation to ask whether populations functioned as evolutionarily independent units, and to test whether observed behavioural phenotypes are due to shared population history versus local adaptation. Following behavioural experiments, we preserved individuals in 95% ethanol, and a subset of 19–24 individuals from each population was used for molecular analyses. PCR and sequencing protocols were described by Finn *et al.* (2007) and resulted in retention of a 1032 bp fragment for molecular analyses.

Sequences were aligned manually using BIOEDIT, and we used ARLEQUIN v. 2.000 (Schneider *et al.* 2000) for exploratory analyses, including calculation of haplotype frequencies, analysis of molecular variance (AMOVA) and calculation of population pairwise F_{ST} s. AMOVA and pairwise F_{ST} calculations were based on sequence divergence (Φ_{ST} ; Excoffier *et al.* 1992) according to pairwise differences. Significance was assessed by bootstrapping using 10 000 permutations of the data.

If shared evolutionary history drives similar RRB among populations, then there should be a significant correlation between population pairwise behavioural and genetic distances. Conversely, if local adaptation has caused population-level behavioural differences, then no correlation would be expected. We used a Mantel test in the software IBD (Bohonak 2002) to test the null hypothesis of no correlation between pairwise distance matrices using Slatkin's linear F_{ST} as the genetic distance measure (Rousset 1997). Behavioural distance was calculated for each population pair using absolute differences in both response time and response rate. We ran two separate tests to accommodate the two behavioural distance measures (response time and response rate), with genetic distance as the independent variable and behavioural distance as the response variable. Significance was assessed using 10 000 randomizations of the data for both the tests.

(f) Signal detection theory parameters

To quantify the relationship between catchment area and flood predictability, we analysed 42 years (1955–1996) of rainfall and discharge data from the USDA Walnut Gulch Experimental Watershed, which is located within our study region. We chose catchments that spanned a range of sizes: small (0.04 km²), medium (9.0 km²) and large (149 km²). Each catchment had a rainfall gauge (rainfall volume and intensity recorded at 1-min intervals) paired with a discharge gauge (peak discharge of all flow events). We tabulated the duration of all monsoon rainfall events that exceeded a threshold intensity of 20 mm h⁻¹, and noted whether a flood occurred during the next 4 hours. Floods were defined as events exceeding the peak discharge of the 1.5-year return interval flood event, which corresponds to bankfull conditions for most streams (Dunne & Leopold 1978). Monsoon rainfall intensities exceeding 25 mm h⁻¹ are likely to produce run-off (Syed *et al.* 2003), so 20 mm h⁻¹ was a conservative threshold. Lytle & Smith (2004) also found evidence for a threshold effect, where the rainfall intensities below 15 mm h⁻¹ produced no behavioural response from *A. herberti*, so low-intensity rainfall events are not likely to play an important role. We also tabulated flood events that occurred with no antecedent rainfall.

We used the rainfall and flood data to obtain $f(x|F)$, $g(x|NF)$ and α for each of the three catchments. To generate $f(x|F)$ for each catchment, we took all rainfall event durations (x) that resulted in a flood, binned them at 10 min intervals and divided by the total number of flood-producing events to produce a frequency histogram. This gives the probability density distribution of all the rainfall events of duration x conditioned on a flood occurring. $g(x|NF)$ was generated in a similar fashion for each catchment using all x 's that did not result in a flood. Note that $f(x|F)$ contains only information about rainfall events that produced floods and $g(x|NF)$ contains only information about rainfall events that did not result in a flood, so f/g can be understood as a signal-to-noise ratio.

Other SDT parameters were taken from the literature or allowed to vary because they were not known. We chose $t=0.95$, which is a typical mortality rate for other aquatic insects in these flash-flooding streams (Lytle 2000). Because c was not known, we re-ran SDT analysis with different values. An earlier study (Lytle 1999) recovered five out of six marked *A. herberti* that had abandoned a stream following a natural rainfall event, but this estimate of $c=0.8$ is probably not accurate given the small sample size. These parameters allowed us to calculate x^* , the theoretical optimal time to exit the stream during a rainstorm, for each catchment size.

3. RESULTS

Sample sizes ranged from 21 to 123 individuals per population, for a total of 753 individuals tested in over 400 hours of behavioural trials. Overall, one-third of individuals (243) exhibited RRB during trials. Analysis of the temporal control population (ETCL) indicated that population-level response time did not change during the study season or across years (ANOVA, $F_{0.05[2,23]}=0.8508$, $p=0.440$). Similarly, no differences in response time occurred in RUCU over three consecutive years (ANOVA, $F_{0.05[2,24]}=0.3719$, $p=0.693$). These results suggest that the exact date or year that a population was assayed did not influence RRB, and that our behavioural trials provided consistent results. For individuals that

exhibited RRB in more than one trial, no learning was apparent. A test of the difference between the first and last response times for each individual was insignificant (Wilcoxon signed-rank test; $N=98$, $p=0.459$), suggesting that individuals were neither quicker nor slower to respond to rainfall in subsequent trials.

As expected, we found no difference in response time between the upper and lower edges of the E. Turkey Creek population, which occupies a relatively discrete portion of the stream (ANOVA, $F_{0.05[1,47]}=1.556$, $p=0.218$). We also found no difference between upper and lower Rucker Canyon, despite large differences in catchment size between the two subpopulations (ANOVA, $F_{0.05[1,45]}=0.2725$, $p=0.604$). This result suggests that subpopulations within streams are not evolving independently, a result corroborated by molecular and SDT analyses (see below).

We analysed response time and response rate both with and without the two large catchment subpopulations, because our other analyses suggested that these subpopulations could be recently derived from upstream and thus not representative of local conditions. The population from the smallest catchment exhibited no RRB at all, and so was coded as having a response time of 60 min (the maximum duration of the experiments) to allow comparison with other populations.

Using all the 15 sites, response time as a function of catchment size showed a sharp decrease from small- to mid-sized catchments, and then appeared to level off for larger catchments (figure 2; inverse polynomial regression; $N=15$; $P=0.0087$ and 0.0014 for the first- and second-order terms, respectively). An inverted pattern was apparent for the percentage of response versus catchment size (figure 2), although the regression was not significant ($N=15$; $P=0.5052$ and 0.2866 for the first- and second-order terms, respectively). A strong linear relationship between response time (ln transformed) and response rate (arcsine transformed) was evident across all populations ($N=15$, $p<0.001$, $R^2=0.61$), indicating that populations with the fastest response times also had the most individuals responding. Repeatability of response time was significantly greater than zero but not large in magnitude ($r_F=0.21$ as estimated from the 98 individuals that responded during more than one successive rainfall trial; $t=2.1$, d.f. = 96, $p=0.038$).

When the two large catchments were excluded as outliers, both response time and response rate were hump shaped with respect to catchment size (figure 2). Populations from the mid-sized catchments had the fastest response time (optimum at 15 km²) and the highest response rate (optimum at 12 km²), as indicated by significant second-order polynomial regressions ($N=13$; $P=0.0022$ and 0.0092 , respectively). Both of these optima occurred within the range of the observed data (significant MOS tests; for response time: $\beta_{3min}=-248.6$, $p=0.0014$; $\beta_{3max}=-384.9$, $p=0.0017$ and for response rate: $\beta_{3min}=479.2$, $p=0.0080$; $\beta_{3max}=753.6$, $p=0.0083$).

For 322 total individuals sequenced across the 15 study populations, we recorded a total of 54 mitochondrial haplotypes (GenBank accession numbers EF090202–EF090255). Of these, 36 were restricted to a single population and 14 were singletons. There was a high degree of genetic structure among populations (overall $F_{ST}=0.40$, $p<0.0001$). Pairwise F_{ST} values ranged

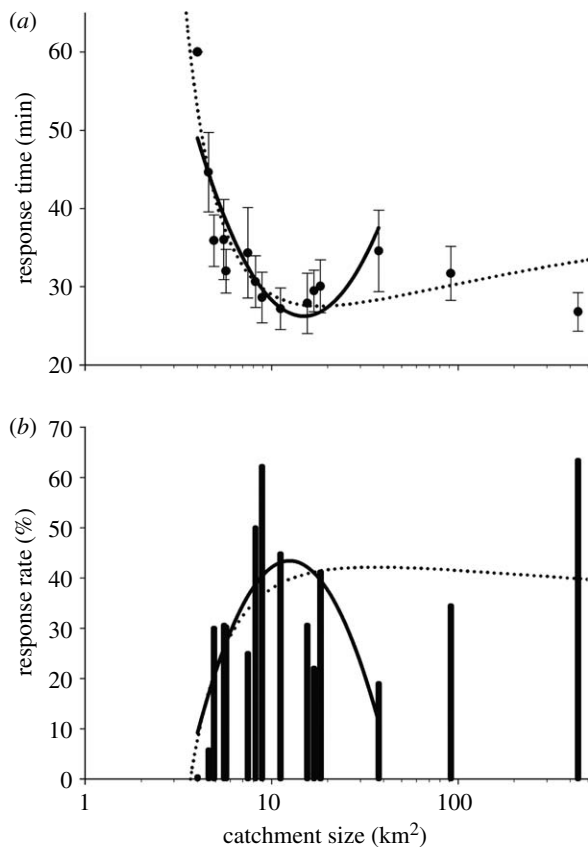


Figure 2. RRB of *A. herberti* populations as a function of catchment size. Dotted lines, regressions with all 15 populations included; solid lines, regressions excluding the two largest catchment populations. (a) Response time (minutes of rainfall required to trigger RRB) as a function of catchment area. Populations inhabiting smaller catchments, where floods are rare, required longer durations of rainfall to exit the water. Error bars show s.e.m. (b) Response rate (percentage of the population that exhibits flood escape behaviour) as a function of catchment size.

from -0.04 to 0.78 (table 2 in the electronic supplementary material) and all but four (of 105) were significant, suggesting a lengthy history of isolation and capacity for independent evolution according to local selection pressures. F_{ST} values for the two pairs of populations sampled at upstream and downstream locations on the same channel (E. Turkey Creek, ETCU/ETCL and Rucker Canyon, RUCU/RUCL) represented two of the four that were not significant. Mantel tests of the relationship between behavioural and genetic distances yielded no sign of correlation ($r = -0.08$, $p = 0.64$ for response time; $r = -0.05$, $p = 0.55$ for response rate), suggesting that differences are attributable to local adaptation within each catchment rather than shared population history.

Analysis of the Walnut Gulch hydrological data showed that rainfall cues provided the most reliable information about floods in the 9 km^2 catchment (figure 3). The probability density distributions $f(X|F)$ and $g(X|NF)$ were discriminable in both the 0.04 and 9 km^2 catchments, suggesting that in these catchment sizes rainfall event duration provides information as to whether a flood might occur. By contrast, in the 149 km^2 catchment the $f(X|F)$ and $g(X|NF)$ distributions were nearly identical, showing that in large catchments there is no reliable way to use rainfall duration to predict flash floods. Floods were the most frequent in the 149 km^2 catchment (38 floods over

407 rainfall events, $\alpha = 0.093$). Floods were slightly less frequent in the 9 km^2 catchment (37/418, $\alpha = 0.089$) and rare in the 0.04 km^2 catchment (5/454, $\alpha = 0.011$). The rarity of floods in the small catchment reduced the information content of rainfall as a cue for flash floods; when $f(X|F)$ was scaled by α (figure 3b), the probability of a flood became very low at any rainfall duration. Thus, the long-term weather data show that rainfall cues in the small catchment are unreliable due to the rarity of floods, and rainfall cues in the large catchment are unreliable due to poor signal-to-noise properties. SDT predicted the fastest response times in the mid-sized catchment (figure 4). Although all values of c produced a hump-shaped relationship between catchment size and response time or rate, the best fit to the empirical data occurred at $c = 0.6$.

4. DISCUSSION

Our analysis of long-term weather data and population genetic structure confirmed that Madrean Sky Island *A. herberti* populations constitute a unique natural experiment, with discrete populations evolving in catchments that span a wide gradient of disturbance predictability. Analysis of the Walnut Gulch dataset showed that flash floods were highly predictable from rainfall cues in the mid-sized catchments but less predictable in smaller or larger catchments, generating a gradient of disturbance predictability. Furthermore, population genetic analysis indicated that most populations of these flightless insects are evolving in isolation with little or no gene flow to overwhelm local adaptation. For these reasons, comparison of *A. herberti* populations provides a way to observe how disturbance predictability can drive the evolution of behavioural response traits.

Individuals from the smaller catchments were the most 'hesitant' to leave the stream, and this was most pronounced in the smallest catchment (AJO) where no individuals exhibited RRB. Not surprisingly, there is no evidence that floods occur in this small catchment, based on the lack of stranded woody debris and the presence of vegetation down to the waterline (D. A. Lytle 2002, personal observation). The ability to use rainfall cues to leave the stream is ancestral to the Belostomatidae, but for most taxa RRB is maintained as a cue for aerial migration to seasonal habitats, as a mechanism to escape floods, or for both purposes (Lytle & Smith 2004). The AJO population, which cannot migrate aerially and does not require RRB to escape floods, probably represents an evolutionary loss of RRB.

Results from the two largest catchments were complicated by the possibility that these subpopulations are recently derived from smaller catchments occurring upstream. Owing to this uncertainty, we analysed our behavioural data with and without these points. These possible outliers did not alter the broader conclusions of this study, but they did affect whether or not there appeared to be a hump-shaped relationship between the catchment size and the behavioural variables. When the points were excluded, the data suggested an optimum mid-sized catchment where the fastest response times and greatest response rates occurred, and this was a significant hump-shaped relationship as indicated by the MOS tests. When the points were included, the catchment-behaviour relationship seemed to level off at higher catchment sizes.

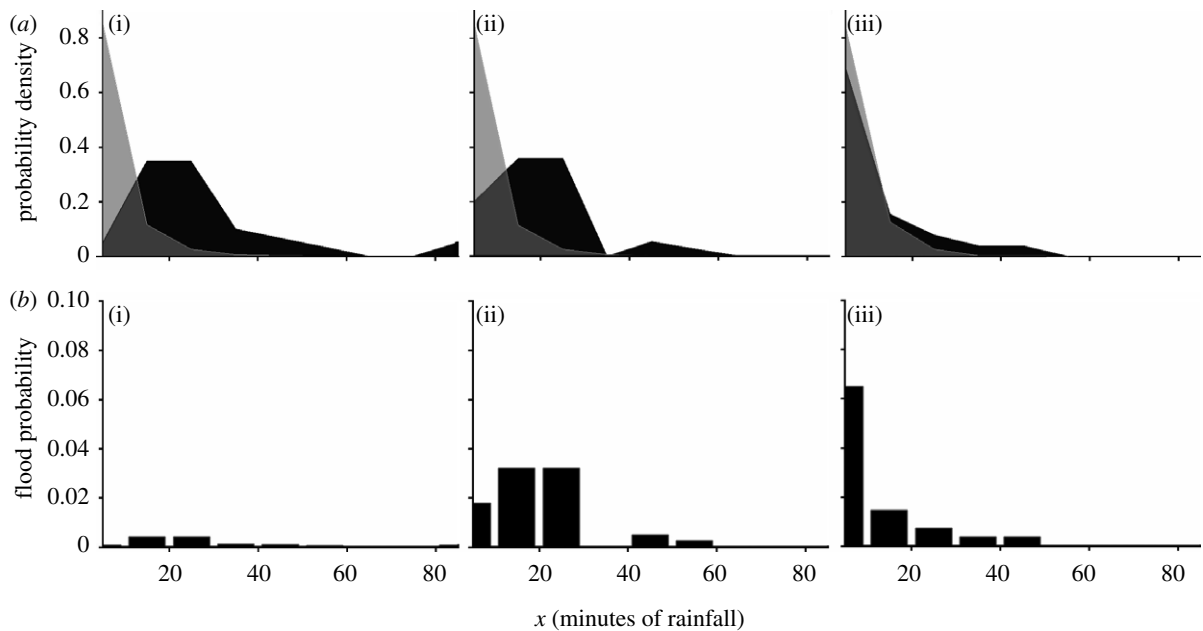


Figure 3. Flood predictability is the highest in the mid-sized catchments. Data from Walnut Gulch Experimental Watershed, 1955–1996. (a) Probability density distributions of rainfall events (x) that either resulted in a flood ($f(x|F)$, shown in black) or did not result in a flood ($g(x|NF)$, shown in grey) for three catchment sizes (i) 0.04, (ii) 9 and (iii) 149 km². f and g show good signal-to-noise characteristics in the small and medium catchments, respectively, but the distributions are indistinguishable in the large catchment, rendering floods unpredictable from rainfall cues. (b) Flood probability in the three catchments (i) 0.04, (ii) 9 and (iii) 149 km² ($f(x|F)$ scaled by α , the prior probability of a flood). Floods are rare in the small catchment, which renders them less predictable.

Three lines of evidence suggest that these two subpopulations are in fact recently derived from upstream portions of the stream. First, there was no significant difference in response time or percentage of response between up- and downstream subpopulations from the same stream, indicating that each stream harbours a single phenotype. Second, the mtDNA analysis showed no significant difference between upper and lower E. Turkey or between upper and lower Rucker, suggesting that gene flow prevents within-stream isolation of subpopulations. Third, because spring-fed headwater reaches are more reliably perennial than lower alluvial reaches in the Madrean Sky Island streams (Bogan & Lytle 2007), it is possible that lower elevation subpopulations are occasionally extirpated by drought and then recolonized by upstream individuals. This was observed at RUCL, where the population was present in 2004, appeared to be locally extirpated by drought in 2005, and was present again in 2006. At face value, it appears that data from the two large catchments may be outliers, in the sense that the observed behaviours are not a true representation of the measured catchment size. Analysis with genetic markers that evolve faster than mtDNA will be useful for determining the relative strengths of gene flow versus local adaptation for maintaining subpopulation phenotypes.

Analysis of the Walnut Gulch dataset with SDT showed that floods were the most predictable in the mid-sized catchments, approximately 10 km². In these catchments, rainfall events with a duration beyond 20–30 min carry a strong information signal: a flash flood is likely to occur soon. Part of this might be due to the geometry of convective thunderstorms relative to the catchment size. The average areal extent of monsoon storms is 9 km² (Syed *et al.* 2003), and so both rainfall and floods occur at a similar spatial scale. Thus, if a storm is present in a

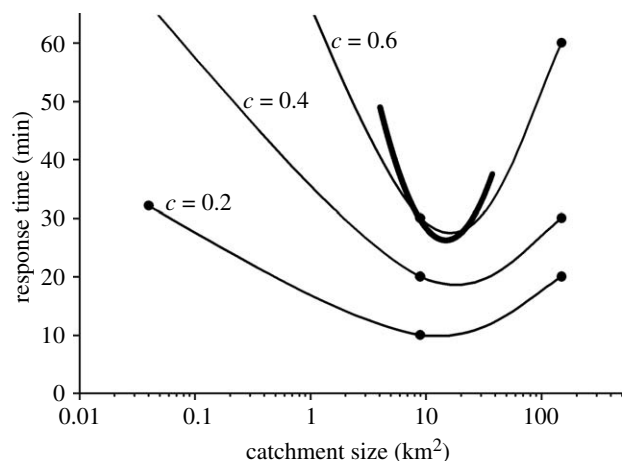


Figure 4. Optimal response time as a function of catchment size, as predicted by SDT. See text for parameter values. Several values of c were used (thin lines, fitted as spline curves through points) because it is unknown. The bold line shows the empirical curve from figure 2 (with the two large catchment populations excluded).

catchment and is producing sufficient rain to cause a flash flood, it is probable that rainfall cues will also be detected by the insects.

SDT analysis also suggested that rainfall was a poor predictor of flash floods in large catchments. In larger drainages, floods were often generated with no warning by distant thunderstorms. It might seem that in this case the correct behaviour is to abandon the stream at any sign of rain, because even traces of rain may signal that a storm is occurring somewhere upstream. However, this strategy would result in many false alarms, and the fitness cost of repeatedly abandoning the stream would be prohibitive even if the cost of abandoning the stream (c) is relatively

low. SDT also predicted long response times in large catchments, but this solution was driven entirely by minute differences in the tails of the f and g distributions and was not robust to small changes in either distribution. Because f and g are essentially identical in large catchments (figure 3), there is no way to discern rainfall events that cause floods from those that do not, and thus no optimal behaviour can evolve. Both the experiments and SDT analysis suggested that rainfall cues may not be useful for flash flood escape in larger catchments.

In the small Walnut Gulch catchment, floods were generally rare, resulting in a low value of the flood prior probability (α). Therefore, even though the density distributions of f and g were similar to those for the mid-sized catchment (figure 2a), the low α shows that floods are rare enough to be unimportant (figure 2b). In summary, the Walnut Gulch data show that in large catchments floods are common but not reliably predictable from rainfall cues. In small catchments, floods tend to occur after longer rainfall events, but floods are so rare in general that they are not a significant mortality threat. Mid-sized catchments appear to experience floods that are both frequent and predictable from rainfall cues. This general finding is congruent with the results from the theory of life-history evolution in disturbed environments, which predicts that strength of selection for an optimal phenotype is the strongest when disturbances are frequent, severe and predictable (Lytle 2001; Lytle & Poff 2004).

Despite the poor rainfall–flood correlation in large catchments, other flood avoidance strategies that do not rely on rainfall cues may be viable. For example, many smaller desert stream taxa that are multivoltine (Ephemeroptera, chironomid Diptera) appear to use rapid life cycles and fast recolonization as a means of compensating for flood mortality (Gray 1981). The life history of the univoltine sycamore caddis fly *Phylloicus mexicanus* (formerly *Phylloicus aeneus*; Prather 2003) is synchronized with the monsoon season so that most larvae emerge into the terrestrial adult stage before the flash-flooding risk becomes large (Lytle 2001, 2002). This strategy allows adults to remain away from the streams during the riskiest portion of the monsoon season and does not depend on the reliability of rainfall cues. Life-history synchronization makes sense for taxa that become fully terrestrial during the adult stage (Odonata, Plecoptera and others) but it does not work for taxa that spend the adult stage in an aquatic habitat (aquatic Hemiptera and Coleoptera) because these need to anticipate and avoid individual floods. At least one desert stream hemipteran that remains aquatic in the adult stage, the giant water bug *Lethocerus medius*, has solved this dilemma by migrating from flash-flooding streams to non-flooding rain pools during the monsoon season (Lytle & Smith 2004). Other desert stream insects are known to possess some form of RRB (Lytle & White 2007), so it is possible that the selection pressures that affect the evolution of *A. herberti* behaviours could apply to other taxa as well.

When the mortality risk of abandoning the stream was set to $c=0.6$, SDT curve matched both the shape and the minimum of the empirical curve with the two large catchments excluded. Taken at face value, our new findings produce a testable prediction that future studies of Sky Island *A. herberti* populations should find c close to 0.6. Several caveats apply here. First, the mortality risk of being caught in a flood (t) has not been measured directly

for *A. herberti*, although it is known to be high for other aquatic insects (Lytle 2000), and equation (1.4) shows that there are many combinations of c and t that could produce the same curve. Second, values of c and t could vary among catchments since both flood severity and terrestrial hazards (predators, risk of desiccation, etc.) might vary from place to place. These issues remain to be settled empirically.

5. CONCLUSIONS

Our empirical observations and theoretical analyses show that populations have adapted to a wide range of natural disturbance regimes, suggesting that populations may be able to evolve in response to disturbance regimes if given sufficient time and genetic variability. However, our study also found that the local adaptation did not occur when disturbances were highly unpredictable. This empirical finding supports the theoretical predictions of SDT, which posits that optimal phenotypes may fail to evolve in environments with very low information content.

In addition to naturally occurring differences in predictability, humans have modified disturbance regimes directly via habitat modification and indirectly via global climate change (fires, Overpeck *et al.* 1990; droughts, McCabe *et al.* 2004; floods, Nilsson *et al.* 2005; hurricanes, Webster *et al.* 2005). This is particularly true in flowing water ecosystems, where the dams for hydropower and flood control have altered historic cycles of flooding and drought (Graf 1993; Bunn & Arthington 2002; Nilsson *et al.* 2005). Changes to flow timing, magnitude and frequency have produced novel disturbance regimes that are either more predictable (e.g. homogenized flow regimes below hydropower dams; Poff *et al.* 1997) or less predictable (e.g. irregular drought occurrence due to water diversion; Rader & Belish 1999) than those occurred previously. Organisms that rely on predictable hydrological cycles to complete their life cycles, such as salmonids (Quinn & Adams 1996; Quinn *et al.* 2000), may be particularly at risk from these changes. Although populations have been observed to adapt rapidly to novel conditions if heritable genetic variation is available for selection (Hendry *et al.* 2000), our findings suggest that some disturbance regimes lie fundamentally beyond the reach of adaptation.

An earlier version of this manuscript received helpful comments from H. Araki, A. Yamamuro and several anonymous reviewers. Thanks to the AMNH Southwestern Research Station for accommodations and laboratory facilities during fieldwork, and to J. and V. Austin for access to Cajon Bonito. A. Cordova, M. Knoderbane, L. McMullen, A. Pelegrin and N. White helped with experiments. M. Blouin and A. Brower provided facilities for the mtDNA work, and A. Pelegrin provided some of the sequences. Insects were collected under USDA Forest Service Special Use permit no. SUP0092 (USA) and SEMERNAT permit no. SGPA/DGVS/04147 (Mexico). The USDA Agricultural Research Service provided the Walnut Gulch dataset. This project was supported by the National Science Foundation (USA) grant DEB-0445366 to D.A.L.

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