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Drought-Induced Decreases in Abundance of Emergent Midge Subsidies Are Offset by Increased Body Size in a Prairie Stream

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ABSTRACT

1. Emerging aquatic insects can be an important resource subsidy for a variety of terrestrial consumers, including spiders, birds, bats and lizards. Emergence flux is influenced by a variety of abiotic and biotic variables, such as temperature, drying, and predators and these variables can also control the body size of emergent insects. Despite their importance, these variables can change rapidly during drought conditions as water temperatures rise, surface area decreases and predator densities increase.
2. During 2018, the Konza Prairie Biological Station experienced a record drought: flow ceased in the lower reaches of Kings Creek for the first time in over 40 years of observation, leaving a series of isolated pools. We studied how the drought affected aquatic insect emergence in 12 of these pools via elevated temperatures, decreased surface area, and concentration of predators (e.g. fishes and crayfish) over a four-week period. We returned in 2020 and sampled emergence in the same pools over 2 weeks under non-drought conditions to compare emergence between drought and non-drought conditions.
3. We found three overall patterns: (1) rates of areal emergence abundance and biomass (number or mg DM m^{-2} d^{-1}) did not differ between drought and non-drought conditions. In contrast, pool-scale emergence abundance, but not biomass (number or mg DM $pool^{-1}$ d^{-1}), was lower during drought conditions; (2) average midge body size was larger during the drought relative to the non-drought conditions; (3) environmental variables (e.g. temperature, pool surface area, predator biomass) were not predictive of emergence during drought and non-drought conditions.
4. Fewer, but larger emergent midges (as seen under drought conditions) may represent a higher quality resource for terrestrial consumers than many smaller midges due to increased per-capita energy yield. However, due to the overall decrease in water availability throughout the stream network, the overall emergence flux was concentrated in reaches with remaining water during the drought, making pools emergence subsidy hotspots. Overall, these contrasting responses underscore the complex nature of community responses to shifting climatic conditions.

1 | Introduction

Aquatic insect emergence is an important resource subsidy, which can concentrate and subsidise consumers such as birds, bats, lizards, spiders and fish (Baxter et al. 2005; Heinrich et al. 2014; Metcalfe et al. 2023). Despite the importance of emerging adult aquatic insects, factors affecting emergence are not well understood. Factors that affect benthic insect abundance and biomass should also affect emergent insects. Abiotic factors influencing benthic or emergent insects include water temperature (Sweeney and Vannote 1978; Nordlie and Arthur 1981; Kominoski et al. 2012), water velocity (Wallace and Merritt 1980; Harper and Peckarsky 2006; Bogan et al. 2015) and water level in pool habitats (Robinson and Buser 2007; Drummond et al. 2015; Nelson et al. 2021). Biotic factors known to affect benthic or emergent insects include leaf litter characteristics (Kraus and Vonesh 2012; Compson et al. 2016) and predatory invertebrates and fishes (Forrester 1994; Dahl 1998; Wesner 2016). The relative influence of these abiotic and biotic factors on benthic and emerging insects is likely modified by the broader environmental context. For example, drought conditions alter many of these factors, exposing benthic insects to environmental challenges that intensify over time (Boulton 2003).

Understanding how drought and drying conditions affect emergent insect flux, and the relative importance of abiotic and biotic variables on emergence during drying conditions, is important given that stream drying is increasingly common and the number of perennial streams becoming intermittent is increasing due to climate change and increased water demands (Zipper et al. 2021; Datry et al. 2023). Stream drying is expected to homogenise invertebrate assemblages, favouring taxa with life history traits suited to lentic conditions (Boulton 2003; Bogan et al. 2015). During drying, flow may cease, decreasing pool surface area and leading to increasing temperature and siltation but decreasing dissolved oxygen. These factors can decrease the abundance and richness of sensitive fish and invertebrate taxa (Wright and Berrie 1987; Bogan et al. 2015) and increase predatory invertebrate abundance (Hynes 1975; Stanley et al. 1994). These abiotic and biotic changes during drought may increase emergence by functioning as escape cues for emerging insects (Velasco and Millan 1998; Lytle et al. 2008; Drummond et al. 2015). For example, decreasing water levels and increased densities of individuals functioned as emergence escape cues for Leptophlebiid mayflies (Robinson and Buser 2007), and disconnection of pools associated with decreasing water levels resulted in higher emergence rates of Trichoptera in New Zealand scour pools (Drummond et al. 2015).

One of the most widely reported effects of stream drying is increased water temperature (Boulton 2003; Lake 2003; Bogan et al. 2015). Increased water temperature can accelerate the onset and duration of aquatic insect emergence (Hogg and Williams 1996; Harper and Peckarsky 2006; Cheney et al. 2019), and water temperature is probably the most important factor controlling aquatic insect growth and development (Sweeney 1984). Increased water temperature has been shown to accelerate aquatic insect development rates more than growth rates, resulting in smaller and less fecund individuals at emergence (Sweeney 1978; Sweeney and Vannote 1978). Recent reviews suggest that as stream temperatures increase, smaller individuals should be selected for as temperature increases metabolic rates and organisms must allocate resources to maintenance, growth, and reproduction (Sheridan and Bickford 2011; Ohlberger 2013, but see Siepielski et al. 2019). Therefore, as water temperatures warm during drought conditions, we might expect the body size of emerging insects to be smaller than under non-drought conditions.

In addition to the effects of temperature and other abiotic drivers, biotic drivers can influence aquatic insect emergence. Fishes and predatory invertebrates can have varied effects on benthic invertebrate communities and emergence. Predatory benthic insects are thought to have a larger impact on benthic insect biomass than predatory fishes because fishes tend to have a broader range of prey (Wooster 1994). The generally high habitat heterogeneity in the benthic zone creates refuges from fish predators for larval insects, which may lead to fishes having more dramatic effects on emergent than benthic insect biomass (Wesner 2016). However, the feeding strategies of fishes (benthic versus water column) can also affect benthic and emergent biomass (Warmbold and Wesner 2018). Emerging insects are more exposed to predation due to the lack of refuges, although drought can also reduce benthic refuge availability due to increased siltation (Wright and Berrie 1987; Boulton 2003).

To better understand the effects of drought on emergence and the abiotic and biotic factors influencing insect emergence under drought conditions, we quantified adult aquatic insect emergence from isolated pools during a record drought in 2018 at the Konza Prairie Biological Station (KPBS). Throughout this drought, fish densities within the pools were high (Hopper et al. 2020). To establish how emergence during drought compared to non-drought conditions, we quantified adult aquatic insect emergence from the same pools in summer 2020 (non-drought conditions) when pools were connected to streamflow under typical hydrological conditions. Our overarching questions were how does drought affect emerging aquatic insect subsidies and which abiotic and biotic factors were related to emergence dynamics? We predicted that (1) areal emergence abundance and biomass rates (number or mg DM m^{-2} d^{-1}) would be higher during drought than non-drought conditions because escape cues would trigger emergence; (2) pool-scale emergence abundance and biomass (number or mg DM $pool^{-1}$ d^{-1}) would be lower during drought than non-drought conditions due to decreased pool surface area negatively affecting emergence; (3) the body size of emerging midges would be smaller during drought than non-drought conditions, and would be related to abiotic and biotic variables; (4) areal emergence abundance and biomass rates would increase as pool conditions became harsher during the drought due to drought-induced escape cues.

2 | Methods

2.1 | Study Site

This study took place in Kings Creek, a tallgrass prairie stream located on the KPBS, a 3487 ha tallgrass prairie preserve and Long-Term Ecological Research station located in the Flint Hills of eastern Kansas, USA. Streams at KPBS can be perennial near spring-fed headwaters and downstream where tributaries contribute to flow, or intermittent in reaches lacking springs or tributary inputs (Dodds et al. 2004). Flooding after spring rains and drying during summer months are common at KPBS. The lower reaches of Kings Creek have extensive canopy cover and tend to be less prone to drying. Given the intermittent nature of streams at KPBS, fauna inhabiting the streams have high resilience and rapidly recover following flooding or drying (Murdock et al. 2010).

We measured emergence weekly at a series of 12 isolated pools in the lower reaches of Kings Creek over a four-week period during the 2018 drought conditions from July 2 to 27, and weekly at the same 12 pools for 2 weeks when the pools were connected under non-drought conditions from July 22 to 30, 2020. Reduced sampling frequency during the non-drought period was necessary due to restrictions enacted during the COVID-19 pandemic. During the drought conditions, each pool was disconnected from streamflow except for the two most downstream pools, where flow remained throughout the study. Pool 1 was the most upstream pool we sampled, and pool 12 was the most downstream. During the drought, pool 5 dried completely after the first sampling week and was not sampled during the second week. Between sampling in Weeks 2 and 3 during the drought, it rained 45 mm in a single day and refilled pools to levels similar to Week 1; pool 5 was sampled again in Week 3 but dried again prior to Week 4 and was not sampled in Week 4. Pool 6 also dried over the day the emergence nets were deployed in Week 4, and we were therefore unable to sample benthic invertebrates at this site during this week. During the non-drought conditions, all pools were connected to streamflow except for pool 10, which was laterally disconnected from the main channel. Stream geomorphology changed little between the drought and non-drought conditions, except a large tree fell into pool 7, altering the morphology and resulting in decreased pool surface area.

2.2 | Sampling Methods

At each pool, we measured emergence using 25 × 25 cm floating emergence nets. Emergence nets were constructed using a wire frame enclosed in fine mesh (mesh size <0.5 mm) with a floating foam noodle to provide buoyancy and allow insects to emerge from water prior to capture. Five emergence nets were placed in each pool for a 24-h period, after which insects were removed from the net using a BioQuip Hand-Held Vac/Aspirator (BioQuip Products, Rancho Domingues, CA, USA). Invertebrates removed from emergence nets were preserved in 10% formalin or 70% ethanol. In the laboratory, emergent invertebrates were identified to family, counted, and measured to the nearest mm (Merritt et al. 2008). Areal emergence abundance was calculated as the total number of invertebrates that emerged per m^2 over the 24-h period, and we estimated areal emergence biomass using published length-mass regressions (Sabo et al. 2002). Each pool was treated as a replicate, with individual emergence traps considered as field replicates (e.g. pool emergence estimates were calculated as the mean of all emergence traps within that pool for a given sampling week). Emergence traps were occasionally disturbed by wildlife. On those occasions, not all replicates could be measured, and the pool-wide emergence estimate was calculated only from intact field replicates.

Benthic invertebrates were sampled during weeks one and four (except for pools 5 and 6, which dried by Week 4) only during the drought conditions by sweeping a 25 × 45 cm net with 1 mm mesh through the water until the net reached the sediment and then gently bumped the sediment with the net to dislodge invertebrates. Contents of sweep nets were emptied into a bucket and elutriated before passing the sample contents through a 250 μm sieve. Sieve contents were then preserved in 10% formalin containing Phloxine-b dye to assist with post-sample processing. We took five sweeps per pool in different locations. The sweep net sampling was conducted by the same person using the same sampling effort throughout the study to standardise sampling over time and across pools. Emergent adults and benthic larvae were sampled on opposite days so benthic sampling would not interfere with emergence sampling. In the laboratory, preserved insects were passed through a 1 mm mesh sieve stacked over a 250 μm mesh sieve and contents were partitioned into coarse (retained in 1 mm sieve) and fine (retained in 250 μm sieve) fractions. All invertebrates in coarse fractions were counted, measured to the nearest mm, and identified to the lowest practical taxonomic level, typically genus (Merritt et al. 2008). When invertebrates in fine fractions were abundant, we subsampled the fine fraction using a Folsom plankton wheel (Wildlife Supply Company, Buffalo, NY, USA) so that subsamples contained a minimum of 75 invertebrates before they were counted, measured, and identified using the same approach as with coarse samples. Chironomidae were categorised as Tanypodinae (predatory) and non-Tanypodinae (non-predatory) subgroups. Benthic abundance was considered as the total number of invertebrates captured per unit effort (sweep) and biomass as mg dry mass captured per unit effort based on published length–mass regressions (Benke et al. 1999). We also calculated predatory invertebrate abundance as the biomass of all invertebrates considered predators (Merritt et al. 2008).

Potential aquatic insect predators (i.e. fishes, crayfish, and tadpoles) were sampled in each pool once before, during, and after (June, July, August) the four-week period of emergence sampling during the drought conditions, using one or multiple seine hauls with a 4.6 × 1.8 m seine with 3.2 mm mesh (Hopper et al. 2020) and once during the non-drought conditions at the same pools 3 weeks prior to emergence sampling. All predators were identified to species, counted and total length was measured in the field to the nearest mm. Length measurements were converted to wet mass using length-mass relationships. Fish species with fewer than five occurrences were excluded from analysis. Tadpoles were considered in predator abundance and biomass calculations because in certain pools they made up the majority of the biomass and because they can exhibit a high degree of omnivory (Whiles et al. 2010). Because predator sampling did not always coincide with emergence sampling during the drought conditions, we used linear interpolation between consumer sampling events to estimate predator abundance and biomass for three of the four emergence sampling weeks. Pool temperature was measured hourly over the duration of the study using HOBO pendant loggers (Onset Computer Corporation, Bourne, MA, USA). Pool length and average pool width were measured weekly by taking 3–7 measurements depending on pool size. Depth was measured using either transects where pool widths were measured or haphazard sampling (e.g. zig-zag).

2.3 | Data Analyses

We calculated mean areal emergence abundance and biomass rates (number or mg DM m^{-2} d^{-1}) for each of the 12 pools over the 4 weeks sampled during the drought conditions and the 2 weeks sampled during the non-drought conditions. As pool surface area was generally smaller during the drought (except for pool 7, see above), we also calculated pool-scale emergence abundance and biomass (number or mg DM $pool^{-1}$ d^{-1}) for each pool to account for the changing pool surface area during the drought. Pool-scale emergence was calculated by multiplying emergence rates (abundance and biomass) by the pool surface area at each time point sampled. Changes in areal emergence rates may indicate changes occurring due to within-pool factors (e.g. temperature or predation), whereas changes in pool-scale emergence also account for the contracting pool size and may be more relevant for understanding the impact of drought on emerging insects as potential subsidies for riparian consumers.

We established whether drought affected the response variables: areal emergence abundance and biomass (number or mg DM m^{-2} d^{-1}), pool-scale emergence abundance and biomass (number or mg DM $pool^{-1}$ d^{-1}), emergent midge body size. We first calculated the average pool emergence response metrics for each pool across the drought conditions (average of four sampling events) and non-drought conditions (average of two sampling events). We then used paired *t*-tests to determine if areal emergence rates or pool-scale emergence differed between drought and non-drought conditions. We focused body size comparisons explicitly on midges (using the Nematoceran equation from (Sabo et al. 2002)), as they were the dominant taxa in emergence traps throughout the entire study. Samples containing no midges were excluded from the midge body size analysis.

To establish whether emergence changed during drought conditions, we used repeated measures analysis of variance (rmANOVA) tests to assess if areal emergence abundance and biomass rates, or midge body size, differed across sampling weeks or among pools during the drought. We $\log_{10}(x+1)$ transformed areal emergence abundance and biomass data to improve assumptions of equal variance and accommodate 0 values.

We used analysis of covariance (ANCOVA) tests to establish which continuous predictor variables explained areal emergence abundance, areal emergence biomass, and emergent midge body size under drought and non-drought conditions. For ANCOVAs, we used the average values of drought and non-drought conditions for predictor and response variables for each individual pool, as we did for the paired *t*-tests. Sampling conditions (drought vs. non-drought) were included as a categorical predictor variable in all ANCOVA models. For ANCOVAs using areal emergence abundance or biomass as the response variable, model co-variates were pool surface area, mean daily temperature, maximum daily temperature, predator abundance (fishes, crayfish, and tadpoles) and predator biomass. For ANCOVAs using average midge body size as the response variable, model co-variates included mean daily temperature, maximum daily temperature, predator abundance, predator biomass and biomass of orangethroat darters (*Etheostoma spectabile*), which have been previously shown to be predictive of midge body size (Bonjour et al. 2020).

Because benthic insect biomass and predatory benthic insect biomass were only sampled during the drought conditions, we used simple linear regressions to test if these variables were predictive of areal emergence abundance or biomass. Preliminary visual inspection of these data indicated that there was an outlier for mean and maximum temperatures during the non-drought conditions in which pool 10 was substantially warmer than all other pools, likely because it remained spatially isolated from the stream. This point was omitted from ANCOVAs with predictor variables of mean and maximum temperature for areal emergence abundance and biomass. A separate outlier was identified from the drought sampling: pool 5 dried completely and the drying concentrated benthic invertebrates, leading to much higher abundance and biomass. This outlier was omitted from simple linear regression models where we regressed areal emergence abundance or biomass against benthic or predatory insect biomass.

3 | Results

Mean daily pool temperature was 25.8°C ± 0.9°C (mean ± 1 SE) during drought conditions, and maximum daily pool temperature averaged 30.1°C ± 1.5°C (Table 1). During non-drought conditions, mean daily pool temperature averaged 20.9°C ± 0.4°C, and maximum daily temperature averaged 23.0°C ± 0.5°C. During drought conditions, pool surface area was, on average, 44% smaller than during non-drought conditions (Table 1). Pool depth during drought conditions (0.13 ± 0.2 m) was about half that of non-drought conditions (0.28 ± 0.03 m; Table 1), which also resulted in decreased pool volume during the drought by a median of 169% relative to the non-drought conditions.

Eleven emergent insect families were identified during the drought, including two distinct morphs of Ephydridae (Diptera), Dolichopodidae (Diptera) and Empididae (Diptera). Families identified during drought conditions that were not found during non-drought conditions were Empididae (Diptera), Ephemeridae (Ephemeroptera) and Pompilidae (Hymenoptera). Ten emergent insect families were identified during the non-drought conditions. Families only identified during non-drought conditions were Leptophlebiidae (Ephemeroptera) and Caenidae (Ephemeroptera). Eight families were identified during both sampling conditions, including Chironomidae (Diptera), Hydroptilidae (Trichoptera), Ceratopogonidae (Diptera), Phoridae (Diptera), Ephydridae (Diptera), Dolichopodidae (Diptera), Figitidae (Hymenoptera) and Braconidae (Hymenoptera). Emergent Chironomidae biomass accounted for approximately 80% of the total biomass sampled among pools during both drought and non-drought conditions.

Predator biomass (fishes, crayfish, tadpoles) in the pools was high during drought conditions, averaging 30.4 ± 9.9 g wet mass m^{-2} (range: 0–105 g wet mass m^{-2}; Table 1). During the

TABLE 1 | Mean daily temperature, maximum daily temperature, pool surface area, pool depth, predator (fishes, crayfishes, tadpoles) abundance and biomass under the drought and non-drought conditions.

		Pool												
Conditions	**Variable**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**Mean**
Drought	Mean temperature (°C)	24.5	28.4	22.9	25.5	26.7	22.9	27.0	28.9	28.3	28.6	26.2	18.9	25.7
Non-drought	Mean temperature (°C)	20.0	19.7	19.5	19.7	19.7	20.2	21.1	21.0	21.2	25.0	21.5	21.4	20.8
Drought	Max temperature (°C)	26.8	34.8	24.6	27.2	33.1	24.6	31.3	34.9	35.3	36.9	29.9	21.1	30.0
Non-drought	Max temperature (°C)	21.9	21.8	21.5	21.6	21.8	22.3	22.9	23.1	23.1	27.9	23.9	23.5	22.9
Drought	Surface area (m^2)	63.9	21.8	108	62.6	2.03	7.22	51	20.3	41.8	18.4	50.4	61.9	42.4
Non-drought	Surface area (m^2)	90.5	25.1	172	91.2	214	58	12.3	73.5	103	33.1	68.6	51.1	82.7
Drought	Depth (m)	0.24	0.1	0.19	0.14	0.02	0.1	0.13	0.14	0.09	0.1	0.13	0.15	0.1
Non-drought	Depth (m)	0.33	0.16	0.21	0.28	0.45	0.44	0.15	0.34	0.25	0.24	0.26	0.17	0.3
Drought	Predator abundance (# m^{-2})	18.8	11.7	22.2	4.94	24.5	3.14	30.3	18.8	14.2	0.9	10.8	6.28	13.9
Non-drought	Predator abundance (# m^{-2})	6.47	0.96	0.84	0.97	0.19	1.25	0.88	4.67	2.4	3.87	2.69	0.59	2.1
Drought	Predator biomass (g wet mass m^{-2})	105	16.6	86.7	15.8	0	17	56.6	26.5	9.02	1.9	13.7	14.7	30.3
Non-drought	Predator biomass (g wet mass m^{-2})	25.3	0.37	0.94	2.7	3.45	7.62	1.04	6	2.79	3.46	3.37	0.54	4.8

Note: Each value represents the average of the 4 weeks under the drought and 2 weeks under the non-drought sampling conditions.

drought, seven fish taxa, two crayfish taxa, and one tadpole taxon accounted for the majority of predator biomass. Fish biomass was dominated by southern redbelly dace (*Chrosomus erythrogaster*) and western mosquitofish (*Gambusia affinis*), whereas crayfish biomass was dominated by water nymph crayfish (*Faxonius nais*). In the non-drought conditions, predator biomass averaged 4.8 ± 2.0 g wet mass m^{-2} and ranged from 0.54–25.3 g wet mass m^{-2}. During the non-drought conditions, 10 taxa accounted for the majority of the predator biomass, with southern redbelly dace and creek chub (*Semotilus atromaculatus*) dominating biomass among pools. When present, white sucker (*Catostomus commersonii*) biomass was very high, but they were only present in three pools. During the non-drought conditions, western mosquitofish were not captured, and tadpoles did not contribute an appreciable amount of biomass.

3.1 | Effects of Drought on Emergence

There were no differences in areal emergence abundance ($t_{1,11} = -0.93$, $p = 0.37$) or biomass rates ($t_{1,11} = 0.33$, $p = 0.75$) between drought and non-drought conditions (Figure 1A,B), in contrast to our prediction that areal emergence rates (number or mg DM m^{-2} d^{-1}) would be higher during the drought than non-drought conditions. However, pool-scale emergence abundance (number $pool^{-1}$ d^{-1}) was higher during the non-drought conditions than during drought conditions ($t_{1,11} = -2.63$, $p = 0.02$; Figure 1C) in

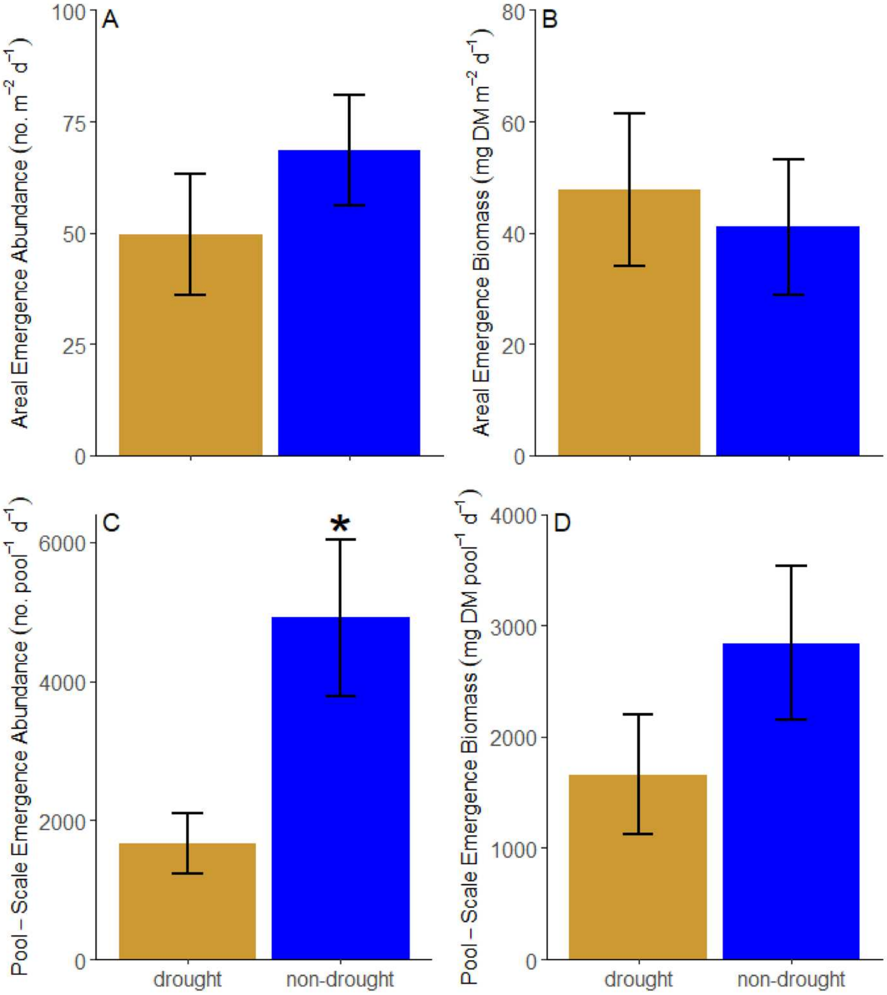

FIGURE 1 | Areal emergence abundance (A) and biomass (B) rates did not differ between drought (brown) and non-drought (blue) measurements when standardised to unit surface area (m^2). When emergence rates were standardised to the pool surface area, pool-scale emergence abundance (C) but not biomass (D) was significantly higher under non-drought conditions. Bars represent means ($n = 12$ sites averaged over 4 weeks during drought and 2 weeks during non-drought) and error bars indicate ±1 standard error.

partial support of our prediction that pool-scale emergence would be higher during non-drought conditions than under drought conditions. In contrast to pool-scale emergence abundance, there was no difference in pool-scale emergence biomass between drought and non-drought conditions ($t_{1,11} = -1.22$, $p = 0.25$; Figure 1D). In contrast to our prediction, the average length of emergent midges was 51% longer during the drought conditions than the non-drought conditions ($t_{1,11} = 9.67$, $p < 0.0001$; Figure 2).

3.2 | Emergence During Drought

During drought conditions, areal emergence abundance differed across pools (rmANOVA; $F_{11,142} = 4.09$, $p = 0.0003$), weeks (rmANOVA; $F_{3,142} = 6.50$, $p = 0.0004$), and a pool × week interaction was evident (rmANOVA; $F_{48,142} = 3.47$, $p < 0.0001$; Figure 3A). Post hoc pairwise comparisons indicated pool 4 had significantly higher areal emergence abundance than four other pools, and pool 7 had higher emergence than two other pools (Figure 3A). Week 1 had significantly higher areal emergence abundance than both Weeks 2 and 4 ($p < 0.05$ for each; Figure 3A), when drought intensified, but not Week 3, after the rain event. These results contrast our prediction that drought would increase emergence flux through inducing escape cues. Areal emergence biomass rates differed among pools (rmANOVA; $F_{11,142} = 5.76$, $p < 0.0001$), weeks (rmANOVA; $F_{3,142} = 6.33$, $p = 0.0005$) and there was a pool × week interaction (rmANOVA; $F_{33,142} = 3.29$ $p < 0.0001$; Figure 3B). Areal emergence biomass rates were higher in Week 1 than in Weeks 2 and 4 ($p < 0.05$ for each; Figure 3B). Areal emergence biomass did not differ between weeks 1 and 3 due to higher variance in Week 3. Pools 4 and 7 had higher areal emergence biomass than 7 and 6 other pools, respectively ($p < 0.05$ for each; Figure 3B). The average body size of emergent midges did not differ among pools (rmANOVA; $F_{11,40} = 1.52$, $p = 0.16$) or across weeks (rmANOVA; $F_{3,40} = 0.75$, $p = 0.53$), but there was a significant pool × week interaction (rmANOVA; $F_{27,40} = 1.52$, $p = 0.02$; data not shown).

3.3 | Predictors of Emergence During Drought and Non-drought Conditions

Neither abiotic nor biotic variables were predictive of areal emergence abundance or biomass, as indicated by the ANCOVA

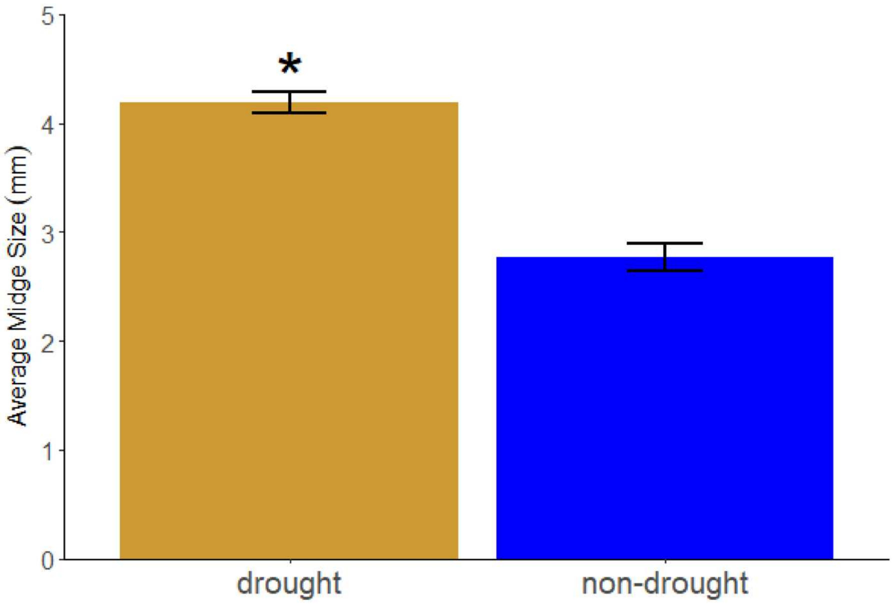

FIGURE 2 | Emergent midge body size was significantly larger when measured during the drought conditions. Bars represent means ($n=12$ sites averaged over 4 weeks during drought and 2 weeks during non-drought) and error bars indicate ±1 standard error.

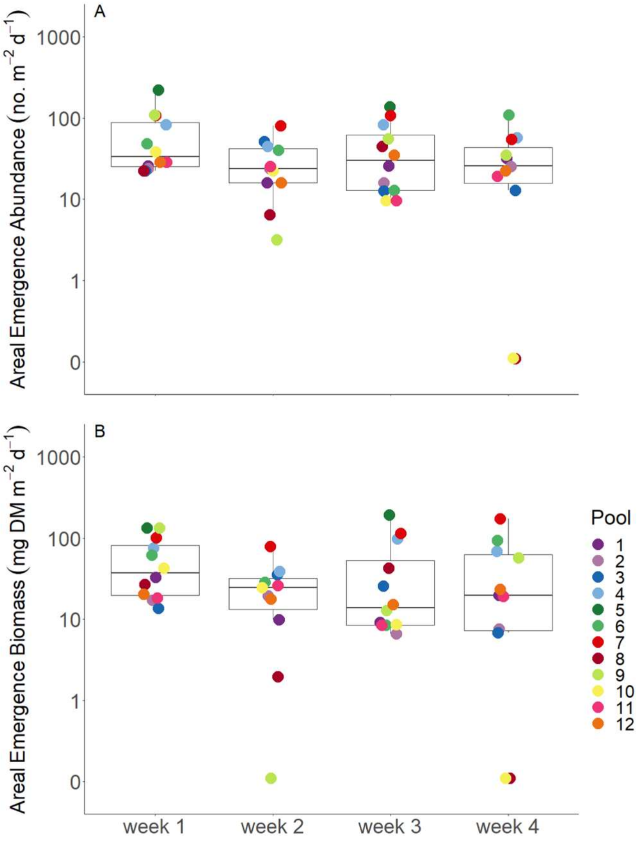

FIGURE 3 | Areal emergence abundance (A) and biomass (B) rates over the four-week period under the drought conditions. Each point represents the average from all emergence traps ($n=2$ to 5 due to wildlife disturbance) from each site for each week. Box-plots for each week show the median, inter-quartile range and 95% confidence intervals. Data are presented on $\log_{10}$-scaled axes. Statistical analyses were conducted on $\log_{10}(x+1)$ transformed data and are reported in the text.

models (Table 2). The simple linear regressions also revealed that neither benthic nor predatory insect biomass was predictive of areal emergence abundance or biomass during the drought conditions (Table S1). In contrast to our prediction, ANCOVA models revealed that neither abiotic nor biotic variables were significant predictors of emerging midge body size once accounting for the effect of sampling conditions, which was a significant predictor of midge body size (Table 3).

4 | Discussion

Overall, we found no differences in areal emergence rates (abundance or biomass m^{-2} d^{-1}) between drought and non-drought sampling conditions, despite differences in abiotic and biotic conditions. We expected emergence rates would differ between drought and non-drought conditions given the increased temperature, decreased water availability and higher concentrations of predators (fishes, crayfish, and tadpoles) during drought. Our results demonstrate that stream pool drying can decrease pool-scale emergence abundance, but not biomass. This decrease in pool-scale emergence abundance was associated with decreasing pool surface area. Despite lower pool-scale emergence abundance during drought conditions, the increased body size of emerging midges offset the decreased abundance from the pool habitats, resulting in no observable differences in pool-scale emergence biomass compared to non-drought conditions. The larger body size of emergent midges during drought was unexpected because studies have demonstrated that the body size of invertebrates should decrease under warmer conditions, as increased temperature can stimulate development rates more than growth rates and due to increased energetic allocation to metabolism potentially leaving less energy available for growth (Sweeney and Vannote 1978; Atkinson 1994; Ohlberger 2013). In fact, smaller body size in response to warming is so widespread

TABLE 2 | Model outputs for ANCOVA for areal emergence abundance (# m^{-2} d^{-1}) and biomass (mg DM m^{-2} d^{-1}).

Areal emergence abundance			**Areal emergence biomass**		
Predictor	*F*	*p*	*Predictor*	*F*	*p*
Conditions	1.09	0.31	Conditions	0.13	0.71
Surface area	2.06	0.17	Surface area	1.29	0.27
Conditions × surface area	0.44	0.52	Conditions × surface area	0.36	0.56
Predictor	*F*	*p*	*Predictor*	*F*	*P*
Conditions	0.24	0.62	Conditions	1.42	0.24
Mean temperature	0.11	0.74	Mean temperature	0.29	0.60
Conditions × mean temperature	0.05	0.83	Conditions × mean temperature	0.07	0.80
Predictor	*F*	*p*	*Predictor*	*F*	*p*
Conditions	0.24	0.63	Conditions	1.42	0.25
Max temperature	0.20	0.66	Max temperature	0.33	0.57
Conditions × max temperature	0.07	0.80	Conditions × max temperature	0.03	0.85
Predictor	*F*	*p*	*Predictor*	*F*	*p*
Conditions	1.00	0.33	Conditions	0.12	0.72
Predator abundance	0.50	0.49	Predator abundance	0.02	0.88
Conditions × predator abundance	0.19	0.67	Conditions × predator abundance	0.59	0.45
Predictor	*F*	*p*	*Predictor*	*F*	*p*
Conditions	1.02	0.32	Conditions	0.13	0.73
Predator biomass	0.87	0.36	Predator biomass	0.50	0.49
Conditions × predator biomass	0.20	0.66	Conditions × predator biomass	0.02	0.89

Note: Conditions (drought vs. non-drought) was a categorical predictor variable. Co-variates tested included mean pool surface area (m^2), mean daily temperature (°C), maximum daily temperature (°C), predator abundance (# m^{-2}) and predator biomass (g wet mass m^{-2}). Both predictor and response variables represent the average of the sampling weeks during the drought ($n=4$) and non-drought ($n=2$) conditions.

that it has been suggested to be the third universal response to global climate warming (Daufresne et al. 2009; Sheridan and Bickford 2011).

There are multiple drivers of emergence that may have antagonistic or synergistic effects during drought conditions. For example, emergent insect growth rates and body sizes can be affected by temperature and non-consumptive effects of fishes (Sweeney and Vannote 1978; Peckarsky et al. 2008). During drought conditions, midges were on average 1.4 mm larger than under non-drought conditions when temperature and predator biomass were lower, and pool surface area was higher. Increased temperatures can result in more rapid emergence at smaller body sizes due to development rates increasing more rapidly than growth rates (Sweeney and Vannote 1978; Harper and Peckarsky 2006). Non-consumptive effects of predators can also decrease the body size of midges and other invertebrates (Peckarsky et al. 2008; Bonjour et al. 2020). For example, a separate study of emergence in isolated pools at Konza Prairie Biological Station (KPBS) found that orangethroat darter biomass was negatively correlated with the body size of emergent midges (Bonjour et al. 2020). Similarly, emergent mayflies were smaller when larvae were reared with fish odours, which simulated predation risk (Peckarsky et al. 2008). In contrast, recent studies have shown that average invertebrate body sizes can increase under warming temperatures alone (Nelson et al. 2017) in addition to under drying conditions, which included both increased temperatures and decreased water availability (Aspin et al. 2019).

In this study, we measured between 2 and 6 times higher rates of areal emergence biomass during both drought and non-drought conditions than prior studies on aquatic insect emergence at KPBS (Gray 1989; Bonjour et al. 2020). Despite this elevated areal emergence biomass, areal emergence abundance rates were 30% and 50% lower during the non-drought and drought conditions, respectively, than areal emergence abundance rates from riffles and pools of KPBS streams (Gray 1989). However, areal emergence abundance rates in this study were similar to a prior study of emergence from isolated pools (Bonjour et al. 2020). As we measured similar or lower areal emergence abundance rates relative to prior studies, but higher areal emergence biomass rates, these findings support our result that the larger body size of emerging insects (midges) offsets reduced areal emergence abundance rates from pools. Given that midge biomass accounted for 80%–90% of areal emergence biomass in the other two studies (Gray 1989; Bonjour et al. 2020), which was similar to the approximately 80% of areal emergence biomass during both drought and non-drought conditions of the current study, this

TABLE 3 | Model outputs from ANCOVA for emergent midge body size (mm).

Emergent midge body size		
Predictor	*F*	*p*
Conditions	108	< 0.0001
Mean temperature	2.08	0.17
Conditions × mean temperature	0.04	0.83
Predictor	*F*	*p*
Conditions	105	< 0.0001
Max temperature	1.18	0.29
Conditions × max temperature	0.13	0.73
Predictor	*F*	*p*
Conditions	70.5	< 0.0001
Predator abundance	0.63	0.44
Conditions × predator abundance	1.34	0.26
Predictor	*F*	*p*
Conditions	64.5	< 0.0001
Predator biomass	0.08	0.78
Conditions × predator biomass	0.03	0.85
Predictor	*F*	*p*
Conditions	74.9	< 0.0001
Orangethroat darter biomass	0.19	0.67
Conditions × Orangethroat darter biomass	3.15	0.09

Note: Conditions (drought vs. non-drought) was a categorical predictor variable. Co-variates tested included mean daily temperature (°C), maximum daily temperature (°C), predator abundance (# m^{-2}), predator biomass (g wet mass m^{-2}) and orangethroat darter biomass (g wet mass m^{-2}). Both predictor and response variables represent the average of the sampling weeks during the drought ($n = 4$) and non-drought ($n = 2$) conditions.

shows that the increased body size of midges was the reason for increased emergence biomass, rather than changes in emergent community composition at the family level.

The higher areal emergence biomass in our study relative to Bonjour et al. (2020) is particularly notable given that fish biomass in the pools in our study during drought was more than seven times higher than the maximum observed fish biomass in the prior study. We found no correlation between predator metrics and areal emergence abundance or biomass during either sampling period, which agrees with Bonjour et al. (2020) who also did not find a correlation between fish and emergence. This lack of correlation in our study was surprising as predator biomass was very high. Moreover, western mosquitofish dominated predator biomass, presumably needing large amounts of prey to meet high metabolic demands due to elevated temperatures (Chipps and Wahl 2004; Merkley et al. 2015). Future studies could experimentally manipulate consumer abundance (e.g. exclosure treatments) to test the magnitude of the effect of predators on emergence under drought conditions.

Our observation of increased midge body size during drought contrasts with prior studies that suggest warmer temperatures should reduce individual body size (Sweeney and Vannote 1978; Ohlberger 2013). Multiple potential mechanisms may explain larger midge body size during drought. Firstly, the thermal equilibrium hypothesis suggests that warmer temperatures can increase insect growth if the water temperature where an insect is growing is below its thermal optimum (Vannote and Sweeney 1980). Thus, if the temperature regime during non-drought conditions was sub-optimal, the thermal equilibrium hypothesis may explain the larger midge body size. A second potential reason for increased midge body size during drought is a shift in dominant midge taxa potentially associated with the warming conditions. Nelson et al. (2017) found an increase in average body size of an aquatic invertebrate community during a two-year warming experiment, which they attributed to a shift in dominant taxa. In this study, we only identified midges to the family level due to difficulties in taxonomy with this group. However, midge communities can be quite diverse and have rapid life cycles, sometimes completing their life cycles within a week. Studies have demonstrated that midge communities can differ in ponds (Bazzanti et al. 1997) and streams (Cañedo-Argüelles et al. 2016) with different hydroperiods spanning ephemeral to permanent, and Kings Creek contains midge taxa that can dominate under these diverse hydroperiods (Stagliano and Whiles 2002). This diversity and the rapid life cycle suggest a strong potential for the dominant taxa within the community to shift in response to these rapidly changing environmental conditions. Finally, increased food quality (i.e. N and P content) is another possible mechanism explaining the increased body size of emergent midges during the drought and could be mediated through fish mortality. A concurrent study found changes in fish communities due to mortality during the drought (Hopper et al. 2020). Once fish died, they represented a high-quality detrital resource, rich in N and P relative to terrestrial detritus, which would be newly available to insects, perhaps promoting insect growth. This increase in resource availability and quality contributed by dying fish could be similar to increased macroinvertebrate biomass found in response to salmon carcasses (Chaloner and Wipfli 2002; Collins et al. 2016). Regardless of the exact causal mechanism for the increased midge body size, it is possible that several of these mechanisms worked in concert to produce this result.

Beyond the stream, drought could potentially affect terrestrial consumers of aquatic emergent insects. For example, drought can negatively affect the nesting success of insectivorous songbirds potentially due to decreased food availability and increased metabolic rates (Conrey et al. 2016; Pipoly et al. 2022). At KPBS, riparian birds are reliant on emerging aquatic insects as a food resource (Gray 1993). Given our results showing no difference in areal emergence biomass rates and pool-scale emergence biomass between drought and non-drought conditions, aquatic insects emerging from these drying pools could represent an especially important resource for terrestrial consumers during drought. Furthermore, the increased body size of midges during drought should make them a higher-quality food resource (MacArthur and Pianka 1966; Krebs et al. 1977; Mittelbach 1981).

If drought effects severely impact terrestrial predators, such as riparian birds, predation rates on emerging insects may decrease and result in decreased energy flux to higher trophic levels. This potential reduction in terrestrial predation could further lead to increased reproductive success of aquatic insects through decreased predation if larvae are then able to survive the aquatic conditions in these pool habitats. Increased body size of emergent insects has been associated with higher fecundity (Sweeney 1984). However, given the reduction in total surface area of the stream network and the loss of riffle and run habitats during the drought, the increased midge body size may not be enough to compensate for the overall loss of emergence flux for riparian predators at the reach or catchment scales.

Drought frequency and duration are expected to increase in coming decades in arid regions, mid-latitudes and subtropics (Prudhomme et al. 2014; Cook et al. 2018) and thus, it is important to gain a better understanding of how the interactive effects of increased water temperatures, drying, and changes in biotic communities resulting from drought will impact stream invertebrates and their emergent adults (e.g. Nelson et al. 2021). In streams that have experienced a transition in flow from perennial to intermittent, invertebrate taxa have been extirpated, communities have become homogenised and invertebrate life history strategies have shifted from long-lived to short-lived taxa (Bogan and Lytle 2011; Carey et al. 2021, 2023). Although previous authors have predicted that under warming scenarios, body sizes should decrease (Gardner et al. 2011; Sheridan and Bickford 2011; Ohlberger 2013), our data support recent work showing this is not always the case. Individual body size may increase with warming if resource supply rates are able to keep up with consumer demands, communities shift to better adapted taxa or predator die-offs (Nelson et al. 2017; O'Gorman et al. 2017; Carey et al. 2021). Overall, our study demonstrates how drought conditions can affect ecosystem processes in unexpected ways by altering biotic traits, such as body size, which can offset decreased areal emergence abundance, making these pools emergence subsidy hotspots.

Author Contributions

Conceptualisation: A.C.S., G.W.H., M.R.W., A.J.R., K.B.G. Developing methods and conducting the research: A.C.S., G.W.H., K.B.G. Data analysis and interpretation: A.C.S. Preparation of figures and tables: A.C.S. Writing: A.C.S., G.W.H., M.R.W., A.J.R., K.B.G.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available from authors upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.