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## Negative effects of habitat drying and prior exploitation on the detritus resource in an ephemeral aquatic habitat

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**Abstract** Ephemeral aquatic habitats are characterized by cycles of drying and subsequent inundation, and by production of sequential non-overlapping cohorts of organisms. Both processes may alter the quantity or quality of resources, and may therefore affect survival and development of cohorts that subsequently colonize ephemeral habitats. We examined these effects of habitat drying and non-overlapping cohorts on experimental cohorts of the tree hole mosquito *Aedes triseriatus*, testing specifically whether the value of leaf litter as a food resource is altered by cycles of inundation and drying, or by exploitation by a prior non-overlapping cohort. We created four treatments of leaf litter: (1) no prior cohort, continuously wet; (2) no prior cohort, one wet/dry cycle; (3) prior cohort, continuously wet, and (4) prior cohort, one wet/dry cycle, and tested for effects on individual fitness components (survivorship, mean dry mass at, and median days to eclosion) and on population growth (estimated finite rate of increase  $\lambda'$ ). Both resource drying and the presence of a prior cohort negatively affected individual fitness components in tires, increasing days to eclosion, and decreasing mean dry mass at eclosion for both sexes. Resource drying also negatively affected estimated rates of increase ( $\lambda'$ ) in tree holes. A prior cohort had no significant effects on  $\lambda'$ . These results indicate that intraspecific interactions among mosquito larvae may include amensalistic effects of earlier, non-overlapping cohorts, and that resource drying reduces resource quality. The latter effect indicates that enhanced production of *A. triseriatus* from recently filled containers is not due to resource drying

per se, and may result from more complex community-level effects of habitat drying. Extreme cycles of drying and inundation seem likely to increase intraspecific resource competition among drought-adapted species like *A. triseriatus*.

**Key words** *Aedes triseriatus* · Disturbance · Ephemeral aquatic habitats · Habitat drying · Resources

### Introduction

Effects of disturbances in aquatic communities have been well studied (reviewed by Sousa 1984). In freshwater stream systems, physical disturbance from flooding can have negative effects on populations (McAuliffe 1984a, b; Feminella and Resh 1990), and these effects may fall into two categories: mortality caused directly by the disturbance of a flash flood (e.g., Boulton et al. 1992; Grimm 1993), and indirect effects of disturbance that reduce resource availability (e.g., Fisher et al. 1982; Grimm and Fisher 1989) or enhance competitive or predatory interactions (e.g., Hemphill 1991; Grimm 1993), and so reduce populations. The same is true for ephemeral aquatic habitats, including ponds, streams, and containers (e.g., tree holes), in which habitat drying may have the same kinds of negative effects that flooding has in streams (e.g., McLachlan and Cantrall 1980; Boulton and Lake 1992; Grimm 1993). Drying is a disturbance because it causes mortality, decreasing populations of aquatic organisms, and disrupting density-dependent processes that may affect populations (Corti et al. 1997). The direct effects of habitat drying on mortality have been documented in benthic stream communities (e.g., Cummins and Klug 1979; Ward and Cummins 1979; Feminella and Resh 1990; Grimm 1993), tadpole assemblages (e.g., Dickman 1968; Seale 1980; Smith 1983; Crump 1989), container insects (Fincke 1994), and salamanders that develop in ephemeral habitats (Semlitsch 1987a, b; Petranka 1989). Indirect effects of drying and subsequent inundation on aquatic animals

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may occur via changes in the quantity or quality of resources, such as the detritus that forms the base of many aquatic food chains (Bärlocher et al. 1978), or via changes in species interactions, such as reductions in competition or predation (e.g., Bradshaw and Holzapfel 1983, 1988; Grimm 1993), but such indirect effects have rarely been studied (e.g., Corti et al. 1997). Further, it is not obvious whether indirect effects of drying on resources for aquatic animal populations should be positive or negative. Drying of an aquatic habitat could increase the quality or quantity of plant detritus as a resource by removing aquatic consumers (Lounibos 1985). For this effect to occur, exploitation of the resources by terrestrial consumers during the dry phase must be less than the exploitation of that resource by aquatic consumers during an equivalent wet phase. Alternatively, drying of the habitat may reduce the quality or quantity of detritus as a resource by inhibiting the growth of edible microorganisms, which are often essential for growth of detritivorous animals (Cummins and Klug 1979). For this effect to occur, decomposers growing on detritus during the wet phase must in some way provide a better resource than would comparable decomposers growing on detritus during an equivalent dry phase. Thus, though drying may alter resources, it is unclear whether resource quality will increase or decrease.

Intraspecific competition and food limitation among larvae negatively affect the individual growth rates of many aquatic insects (e.g., Lamberti et al. 1987; Hawley 1985; Quiring and McNeil 1984; Gribbin and Thompson 1990; Hemphill 1991), and probably ultimately affect populations of adults. Resource competition is usually thought of as involving individuals that simultaneously exploit a resource. However, in aquatic habitats, especially those that are ephemeral, resources such as plant detritus may be exploited and depleted by cohorts that complete development before another cohort occupies the habitat. Such non-overlapping cohorts are particularly likely for organisms that undergo an ontogenetic niche shift (Werner and Gilliam 1984), and move to a different habitat upon completing larval development. If this impact of prior exploitation by an earlier cohort involved two different species, it would be termed amensalism, or extremely asymmetrical resource competition (Lawton and Hassell 1981). The intraspecific effect we are describing, where an early cohort has a negative effect on a later cohort, but not vice versa, might best be characterized as intraspecific amensalism. Whatever the effect is called, it is clearly produced by the same process (resource depletion) that mediates more symmetrical resource competition (Keddy 1989). The negative effects of an earlier cohort may also include an increase in competition for limited resources within the later cohort. Drying and prior exploitation may occur in combination and interact to affect resource quantity or quality. For example, if resource depletion by early cohorts negatively affects later cohorts, drying, by reducing or eliminating early cohorts, may reduce the impact of

this intraspecific amensalism on later cohorts that recolonize after flooding.

Tree holes and discarded tires are ephemeral aquatic habitats occupied by aquatic invertebrates (Frank and Lounibos 1983). These containers have been useful systems for testing inter- and intraspecific effects within aquatic systems using mosquitoes (the dominant organisms in these habitats) as model organisms (e.g., Fish and Carpenter 1982; Livdahl 1984; Chambers 1985; Hawley 1985; Bradshaw and Holzapfel 1988; Walker and Merritt 1988; Hard et al. 1989; Juliano 1989, 1998; Fisher et al. 1990; Broadie and Bradshaw 1991; Livdahl and Willey 1991; Walker et al. 1991; Copeland and Craig 1992; Lounibos et al. 1993; Léonard and Juliano 1995). In such aquatic habitats, drought may alter the roles of competition and predation by inhibiting certain species that are drought intolerant (Bradshaw and Holzapfel 1983, 1988). Drying may also affect the quantity or quality of resources. Leaf litter and other organic matter that accumulate in these containers form an important part of the energetic base of these communities (Walker et al. 1991; Lounibos et al. 1993; Léonard and Juliano 1995). This detritus may change in quality or quantity over time due to activities of earlier cohorts of tree hole insects, colonization and exploitation by aquatic microorganisms, and physical effects of drying and subsequent inundation (Lounibos 1985; Bradshaw and Holzapfel 1988). In some aquatic systems, the quality of plant detritus is primarily determined by colonization of that detritus by bacteria and fungi, and is a major determinant of detritivore populations (Cummins and Klug 1979; Ward and Cummins 1979). The importance of effects of drought on resource quality in container systems has not been fully investigated, so we do not yet completely understand how drying may alter productivity and competitive interactions within these ephemeral aquatic habitats.

*Aedes triseriatus* is a dominant container mosquito in much of wooded eastern North America (Bradshaw and Holzapfel 1985). Eggs are laid above the water line in containers, and hatch when flooded (Novak and Shroyer 1978). Larvae of this species filter feed or browse on bacteria, fungi, and protozoa associated with leaf litter and other detritus that accumulates in tree holes and tires (Bradshaw and Holzapfel 1988). The quantity of leaf litter has been demonstrated to be an important factor for growth and survival of *A. triseriatus* both in the laboratory (Fish and Carpenter 1982; Carpenter 1983), and in the field (Walker et al. 1991; Lounibos et al. 1993; Léonard and Juliano 1995). In addition to quantity, leaf litter quality may also affect *A. triseriatus* survivorship and development (Carpenter 1983). The effect of drying followed by inundation on the quality of litter for *A. triseriatus* has not been investigated. Some tree holes and tires dry out and are subsequently refilled with rainwater, whereas other containers remain full throughout the season (Lounibos 1985; Bradshaw and Holzapfel 1988). The duration of dry periods also varies among containers (Lounibos 1985), and production of

pupae increases with the duration of a preceding dry period for tree holes that dry out and refill (Lounibos 1985). Lounibos (1985) suggested that this positive effect of habitat drying on *A. triseriatus* could result from (a) accumulation of detritus during the dry phase, (b) increased litter quality due to microbial decomposition during the dry (rather than the wet) phase, or (c) reductions in predator abundance. Experiments are necessary to test these hypotheses.

The quantity or quality of leaf litter as a resource for *A. triseriatus* may also change as a result of colonization of a container by sequential cohorts of mosquitoes (Lounibos 1985). Non-overlapping cohorts arise when one cohort completes development prior to the hatch of another cohort. Hatching occurs when rainfall raises the level of water within a tree hole, flooding eggs that were laid above the water line, and stimulating hatching. Effects of non-overlapping cohorts may be the result of feeding by mosquitoes on microorganisms that grow on the detritus (Kurihara 1983; Walker and Merritt 1988; Walker et al. 1991; Merritt et al. 1992), or of the physical breakdown of the detritus into smaller particles (e.g., Heard 1994). Intraspecific resource competition has been clearly demonstrated between fully overlapping (synchronous) cohorts of container mosquitoes (Dye 1984; Livdahl 1984; Fisher et al. 1990; Broadie and Bradshaw 1991; Léonard and Juliano 1995), and between overlapping but asynchronous cohorts of different ages (Livdahl 1982; Edgerly and Livdahl 1992). The possibility of asymmetrical intraspecific effects when there is no temporal overlap between cohorts of container mosquitoes has not been examined.

Our goal in this study is to use *A. triseriatus* in natural containers as a model system to test the hypotheses that (1) the presence of a prior non-overlapping cohort affects growth rate of the next cohort by altering the quality or quantity of leaf detritus as a food resource, and (2) drying and subsequent inundation affect the growth rate of a subsequent cohort by altering the quality of the detritus as a food resource. The effects of both a prior cohort or of drying on population growth and fitness components of *A. triseriatus* could be either positive or negative, and could interact. A positive effect of a prior cohort would suggest that a prior cohort facilitates the growth of edible microorganisms on the leaf litter (e.g., by reducing litter particle size). A negative effect would suggest significant resource depletion. A positive effect of habitat drying would suggest greater growth of edible microorganisms during dry spells, and would support the hypothesis that it is resource drying per se that explains the observation that tree holes that are dry longer before reflooding support greater *A. triseriatus* production (Lounibos 1985). A negative effect of drying would suggest death or inhibition of the microorganisms responsible for conversion of cellulose and lignin to edible biomass, and would imply that greater *A. triseriatus* production following long dry periods is not a product of effects of drying on the resource.

We are interested in the effects of these variables on fitness components and population growth of the test species, *A. triseriatus*. Estimates of population growth for experimental cohorts often facilitate interpretation of complex effects of treatments (Livdahl and Sugihara 1984; Léonard and Juliano 1995; Grill and Juliano 1996; Juliano 1998). Fitness correlates such as growth, development rate, and survivorship may be affected in various ways by manipulations, and some such effects may be negatively correlated (e.g., manipulations that increase survival, thereby increasing average density, may decrease individual growth rates; Livdahl and Sugihara 1984; Juliano 1989). In this circumstance, interpreting resulting effects of manipulations on populations is difficult unless some overall demographic parameter can be estimated. We therefore determined effects of drying and a prior cohort on both fitness components, and on a composite estimate of population growth.

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## Materials and methods

### Origin of leaf litter and mosquitoes

White Oak (*Quercus alba*) leaf litter was collected from ParkLands Merwin Nature Preserve, McLean County, Ill., dried for 48 h at 60°C, broken into pieces approximately 6 mm<sup>2</sup>, and allotted into 2.0-g portions. *A. triseriatus* larvae were collected from tires and tree holes at ParkLands Preserve and nearby private land (hereafter collectively referred to as 'ParkLands'), raised to adulthood on bovine liver powder (ICN Biochemicals, Cleveland, Ohio), then released into 0.6-m<sup>3</sup> cages. These *A. triseriatus* (P generation) were blood fed on anesthetized laboratory mice (handled in accordance with NIH guidelines for animal care), and reared as described by Juliano (1989) and Munstermann and Wasmuth (1985) in order to produce eggs (F<sub>1</sub> generation) for the experiment.

### Preparation of leaf litter

The experiment began with the preparation of leaf litter with different regimes of drying and exploitation by an initial cohort of *A. triseriatus*. Replicates consisted of cages composed of a 35-mm-diameter cylinder constructed of 150- $\mu$ m nylon mesh, attached at the bottom to a 30-ml plastic jar which held leaf litter. The top of the nylon mesh cylinder was folded over and closed with a binder clip. The entire cage measured 221 mm in height, and when suspended in the water, each cage held 77–125 ml of water (Juliano 1998). The mesh size used allows fluid and microorganisms to pass, but excludes most particulate matter, including eggs of most other aquatic insects. Each replicate cage received 2.0 g of dry White Oak leaf litter, and was placed in a plastic beaker with 400 ml deionized (DI) water. The beakers were placed in an environmental chamber in the laboratory at 22°C and 16:8 light:dark photoperiod. On 17 May 1995 (day 0), after the litter had soaked and settled for 4 days, F<sub>1</sub> eggs were synchronously hatched (Novak and Shroyer 1978) to produce larvae of the first cohort. Half of the 64 cages, chosen at random, received 25 of these newly hatched *A. triseriatus* larvae. After 14 days, adults began to emerge, and were collected daily, dried, sexed, and weighed on a Cahn C-31 microbalance. The final adults were collected on day 55 after hatching.

On day 26, desiccant was added to the environmental chamber. Equal numbers of cages with and without first cohorts of *A. triseriatus* were randomly assigned to one of two drying regimes (continuously wet, or one cycle of drying and inundation). Thus, combinations of prior cohort (present or absent) and drying regime

(continuously wet, one cycle of drying) formed four equally replicated treatments. Volumes in beakers assigned to the 'wet' treatment were maintained at 400 ml by daily addition of DI water. Water in beakers assigned to the 'dry' treatment was allowed to evaporate until the leaf litter in the cages was completely dry. On day 34, all the beakers in both the 'wet' and 'dry' treatments were transferred to a greenhouse in order to hasten the drying process. By day 70, all the beakers in the 'dry' treatment had dried completely (i.e., litter was not detectably damp). Beakers varied in drying time, hence the time that litter was totally dry varied from 1 to 6 days.

### Field experiment

On 21 July 1995 (day 70), cages were transferred to the ParkLands field site. This experiment took place in tree holes and tires that held sufficient water at the beginning of the experiment, so that no water was added initially to containers. We do not know the history of the fluctuations of the water level in these containers prior to the start of the experiment. These tree holes and tires were covered with hardware cloth to exclude vertebrates (Léonard and Juliano 1995). We used two tree holes, each with 16 cages, and four tires, each with 8 cages. Volumes in tree holes and tires were maintained at maxima by weekly additions of DI water, which was poured down the trunk into tree holes, or directly into tires. We did not add sufficient water to overflow the tree holes or tires, hence flushing (Walker et al. 1991) could only have resulted from natural rainfall. The four treatments in this experiment were (1) prior cohort, continuously wet, (2) prior cohort, one wet/dry cycle, (3) no prior cohort, continuously wet, and (4) no prior cohort, one wet/dry cycle. Each treatment was replicated four times in each tree hole, and twice in each tire. Ambient dissolved nutrients in each individual tree hole or tire (collectively referred to as containers) could affect microbial resources available to mosquitoes in all cages in that container. Because of the fine mesh used, mosquitoes in each cage had access only to the litter within their cage.

On day 74, 25 newly and synchronously hatched *F<sub>1</sub> A. triseriatus* larvae were added to each cage. After 17 days, the first adults eclosed. Adults were collected daily, dried, sexed, and weighed using a Cahn C-31 microbalance. Wing length of females was also measured to the nearest 0.033 mm using a Wild M3Z dissecting microscope with an eyepiece micrometer. After 40 days, all mosquitoes that survived had completed development.

### Statistical analyses

We analyzed proportion surviving (sexes pooled and each sex individually), mean dry masses of males and females, and median days to eclosion of males and females. Median days to eclosion (rather than the mean) was used to minimize effects of a few individuals that had an extremely long development time. Survivorship, dry mass at, and time to eclosion of females were used to estimate the composite index of performance,  $r'$  (Livdahl 1982; Livdahl and Sugihara 1984). This index gives an estimate of the per capita exponential rate of increase for a cohort ( $r = dN/Ndt$ ), and is used when survivorship, development rate, and adult dry mass all vary in response to treatments (Livdahl 1982, 1984; Livdahl and Sugihara 1984). The formula for this index is:

$$r' = \{ \ln[(1/N_0) \sum A_x f(w_x)] / \{ D + [\sum x A_x f(w_x)] / [\sum A_x f(w_x)] \} \}$$

where,  $N_0$  is the original number of females in a replicate (assumed to be 50% of the original 25 larvae),  $A_x$  is the number of females eclosing on day  $x$ ,  $w_x$  is the mean wing length of females eclosing on day  $x$ ,  $f(w_x)$  is a function relating production of female offspring to wing length of a female, and  $D$  is the estimated time between adult eclosion and reproduction (assumed to be 12 day; Léonard and Juliano 1995). We used the following regression to estimate production of female offspring (as eggs) as a function of wing length (in mm) in this population of *A. triseriatus*:  $f(w_x) = 0.9272$

(mean wing length<sup>3.0024</sup>); exponent significantly greater than 0,  $P = 0.0001$  ( $r^2 = 0.55$ ,  $n = 36$ )

Because some cohorts yielded no female survivors, we analyzed an alternative form of this index of population growth rate,  $\lambda'$  ( $\lambda' = e^{r'}$ ), which is an estimate of the finite rate of increase of a cohort ( $\lambda = e^r$ ), or the multiplicative rate of increase (Pianka 1983). This population parameter is estimable regardless of whether there are survivors in a given cohort (Lenski and Service 1982; Grill and Juliano 1996). When no females survive,  $\lambda' = 0$ . Increasing cohorts have  $\lambda' > 1$ , whereas decreasing cohorts have  $\lambda' < 1$ .

In calculating  $r'$  and  $\lambda'$ , if a female escaped or was damaged during collection, her wing length was estimated as the mean wing length for other females that eclosed from the same cage on the same day (as was the case for 9 out of 301 females). If no such females were available (as was the case for 21 out of 301 females), her wing length was estimated as the mean wing length for other females that eclosed from the same treatment from all the replicates within either tires or tree holes, whichever was appropriate.

Mean dry mass and median days to eclosion for both males and females, survivorship (sexes pooled), and  $\lambda'$  were analyzed using a split-plot analysis of variance (AOV). Container type (tree hole, tire) was the whole-plot factor and the individual containers (container nested in type) the whole plots. Container nested in type was a random effect. Treatment was the split-plot factor, with four levels (prior cohort-wet, no prior cohort-wet, prior cohort-dry, no prior cohort-dry). Because of the unbalanced design, our split-plot AOV required the use of Satterthwaite's synthetic mean squares (Montgomery 1976; SAS 1989) to obtain an appropriate denominator for  $F$ -tests, resulting in non-integer degrees of freedom (see Table 1). We used contrasts to partition treatment effect into effects of a prior cohort, or of a cycle of drying and inundation within tires and within tree holes. This resulted in a two-way AOV with interaction for the split-plot factor within container types, with main effects being prior cohort and drying regime, and the interaction between prior cohort and drying regime. Contrasts were done within tires and within tree holes because the numbers of containers within each type were not the same, resulting in an unbalanced pooled analysis, which can render mixed-model analysis of overall effects of a split-plot factor complicated.

The estimated finite rate of increase  $\lambda'$  yielded highly non-normal data, and no transformation could correct this problem. In order to analyze  $\lambda'$ , we used a rank transformation approach, conducting a parametric AOV on the ranks of the data instead of the raw data (Conover and Iman 1981). Such ranked data usually meet assumptions of parametric AOV (Conover and Iman 1981) and we verified that they did so in our data set. All observations were ranked from smallest (rank = 1) to largest, with average ranks assigned in cases of ties (Conover and Iman 1981). The rank transformation approach yields good tests in one-way models, but may produce questionable results for models with interactions when there are more than two levels for any factor (Seaman et al. 1994). Because our split-plot factor consists of a  $2 \times 2$  factorial, and because our data on  $\lambda'$  so clearly violated the assumptions of parametric AOV, we felt that use of the rank transformation was the best analysis for these data. Parametric statistical tests may be superior in power to non-parametric tests, but only if the assumptions of the parametric test are met (Sokal and Rohlf 1995). For our data, statistical conclusions for both types of tests were similar for all model effects but one, which was significant in our non-parametric analysis (see Table 1), but not in a similar parametric analysis, suggesting that lack of power of the non-parametric test is unlikely to be a major problem. For median days to eclosion, mean mass at eclosion, and survivorship, untransformed data were analyzed by parametric AOV as they more closely approximated a normal distribution with homogeneous variance than did log- or square-root-transformed data.

We tested whether variation in the response variables for the second cohort was related to production in the first cohort (cumulative milligrams of adults produced) by testing correlations between total dry mass produced in the first cohort and residual variation remaining after AOV with drying as a factor. Because production in the first cohort was clearly dependent on the prior

cohort treatment (i.e., if there was no prior cohort, production in the first cohort must be 0), the prior cohort effect was omitted from this analysis. We found no significant correlations for any response variable, hence we did not pursue this analysis further.

**Results**

**Survivorship**

There were no significant effects of Treatment or Treatment\*Type on survivorship to adulthood (Table 1). There were no significant effects of prior cohort, drying regime, or interaction on survivorship in either tree holes or tires (Table 1, Figs. 1, 2). There was no significant effect of Type on survivorship, indicating survivorship within cages was similar in tires and in tree holes (Table 1). Additional analyses of survivorship of each sex individually, assuming each sex was represented by one-half the initial cohort of 25 larvae, also yielded no significant effects of any factor (analysis omitted for brevity).

**Mean dry mass at eclosion**

*Females*

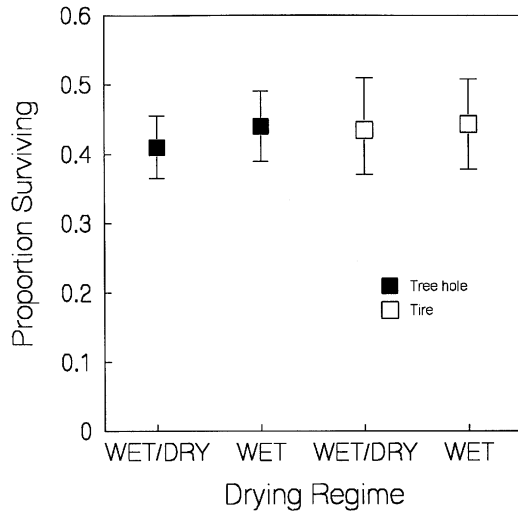
There was a significant effect of Treatment, but not of Treatment\*Type on female mean dry mass at eclosion (Table 1). There were significant effects of prior cohort and drying regime on female mean dry mass at eclosion in tires, but not in tree holes (Table 1). In tires, mean dry mass at eclosion was significantly greater for females from cages with leaf litter that had been kept continuously wet (Table 1, Fig. 3), and for females from cages with leaf litter that had not been exploited by a prior cohort (Table 1, Fig. 4). There were no significant effects of prior cohort or drying regime in tree holes, although the trends within tree holes were the same as those within tires (Figs. 3, 4). There were no significant interaction effects in either type of container, nor was there a significant effect of container type (Table 1).

*Males*

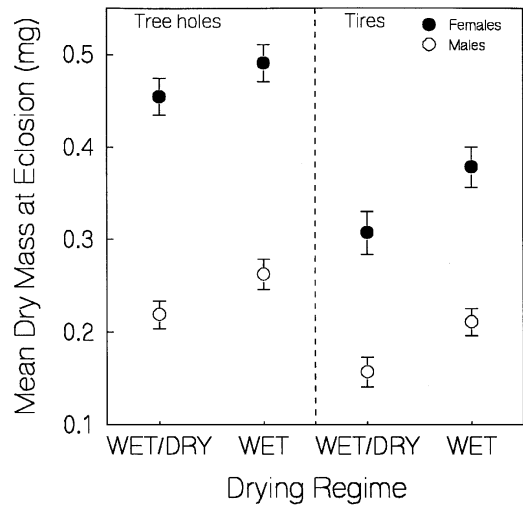
There was a significant effect of Treatment, but not of Treatment\*Type on male mean dry mass at eclosion (Table 1). There were significant effects of drying regime on male mean dry mass at eclosion in both tires and tree holes and also significant effects of prior cohort on male mean dry mass in tires (Table 1). For both tires and tree holes, male mean dry mass at eclosion was significantly greater for cages with litter that had been kept continuously wet (Table 1, Fig. 3). For tires only, mean male dry mass at eclosion was significantly greater for cages with litter that had not been exploited by a prior cohort (Table 1, Fig. 4). There was a significant effect of Type, with tree holes producing larger males than tires (Table 1, Figs. 3, 4).

**Table 1** Analysis of variance for effects of prior cohort in tree holes and tires, and drying in tree holes and tires for survivorship, mean mass at eclosion (females and males), median days to eclosion (females and males), and  $\lambda'$  (rank transformed). *F*-tests significant at  $P < 0.05$  are highlighted in italics. Denominator *df* are given in parentheses. The Treatment\*Container (Type) effect (*df* = 12) was the denominator for all *F*-tests for contrasts. Type refers to either tire or tree hole, and was tested using Container (Type) as the denominator for the *F*-tests. Container refers to individual tires (1–4), or tree holes (1, 2)

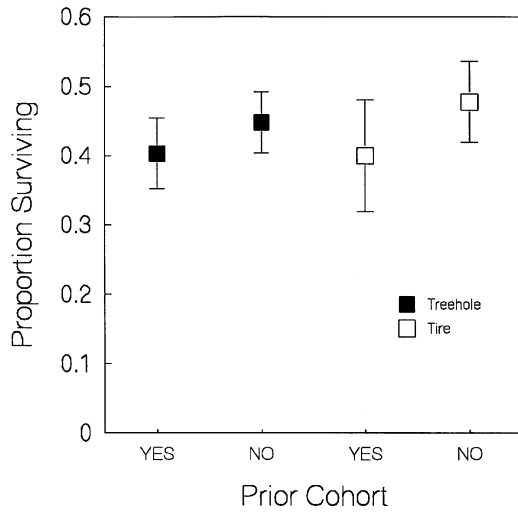
Source	<i>df</i>	Survivorship			Mean mass at eclosion						Median days to eclosion						$\lambda'$	
					Females			Males			Females			Males				
		<i>F</i>	<i>Pr</i> > <i>F</i>	<i>F</i>	<i>F</i>	<i>Pr</i> > <i>F</i>	<i>F</i>	<i>F</i>	<i>Pr</i> > <i>F</i>	<i>F</i>	<i>F</i>	<i>Pr</i> > <i>F</i>	<i>F</i>	<i>F</i>	<i>Pr</i> > <i>F</i>	<i>F</i>	<i>Pr</i> > <i>F</i>	
Type	1	0.02 (3.8)	0.896	7.31 (3.9)	0.055	23.24 (3.0)	0.017	1.93 (3.9)	0.240	8.06 (2.2)	0.094	0.28 (3.8)	0.625					
Treatment	3	0.53 (10.9)	0.671	9.00 (10.6)	0.003	10.67 (10.0)	0.002	9.16 (11.2)	0.002	2.99 (10.8)	0.078	3.35 (8.9)	0.069					
Treatment*Type	4	0.12 (10.4)	0.949	1.78 (9.5)	0.218	1.72 (9.0)	0.232	3.83 (10.6)	0.044	2.71 (10.1)	0.101	1.07 (7.6)	0.573					
Contrasts in tree holes																		
Prior	1	0.41	0.534	1.83	0.201	1.53	0.239	0.03	0.860	0.16	0.699	0.00	0.951					
Drying	1	0.18	0.677	3.12	0.103	7.72	0.017	2.80	0.120	0.22	0.648	6.93	0.022					
Interaction	1	0.13	0.723	1.29	0.278	0.60	0.452	0.08	0.782	1.09	0.316	0.15	0.703					
Contrasts in tires																		
Prior	1	1.22	0.292	13.11	0.004	13.89	0.003	20.33	0.001	8.57	0.013	4.01	0.068					
Drying	1	0.01	0.917	10.25	0.008	11.67	0.005	11.08	0.006	6.98	0.022	1.75	0.211					
Interaction	1	0.10	0.754	0.06	0.815	1.31	0.275	1.94	0.189	0.25	0.626	0.17	0.685					



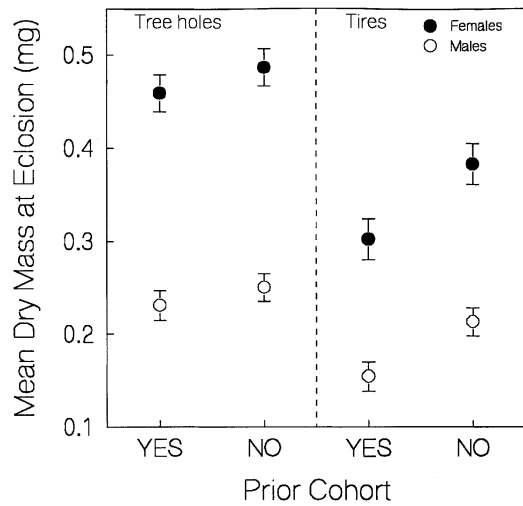
**Fig. 1** Effect of drying regime on survivorship in tires and tree holes. Plotted are means  $\pm$  1 SE for replicate cages



**Fig. 3** Effect of drying regime on mean mass at eclosion for females and males in tires and tree holes. Plotted are means  $\pm$  1 SE for replicate cages



**Fig. 2** Effect of prior cohort on survivorship in tires and tree holes. Plotted are means  $\pm$  1 SE for replicate cages



**Fig. 4** Effect of prior cohort on mean mass at eclosion for females and males in tires and tree holes. Plotted are means  $\pm$  1 SE for replicate cages

Median days to eclosion

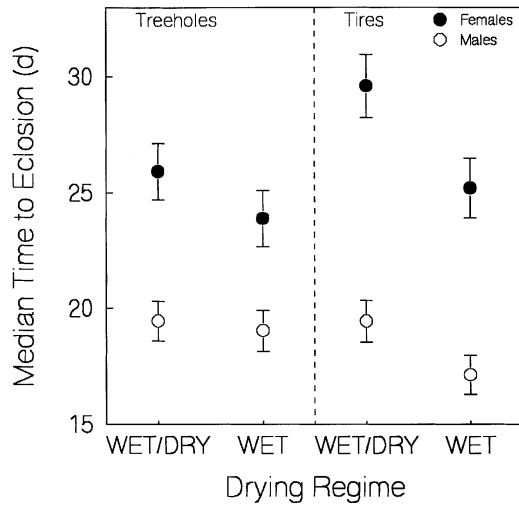
*Females*

There was a significant effect of Treatment and Treatment\*Type on female median days to eclosion (Table 1). There were significant effects of both prior cohort and drying regime on median days to eclosion for females in tires, but not in tree holes (Table 1). There were no significant interaction effects in either container type (Table 1). Days to eclosion for females in tires was significantly less for cages with leaf litter that had remained continuously wet, and also for cages with litter that had not been exploited by a prior cohort (Table 1, Figs. 5, 6).

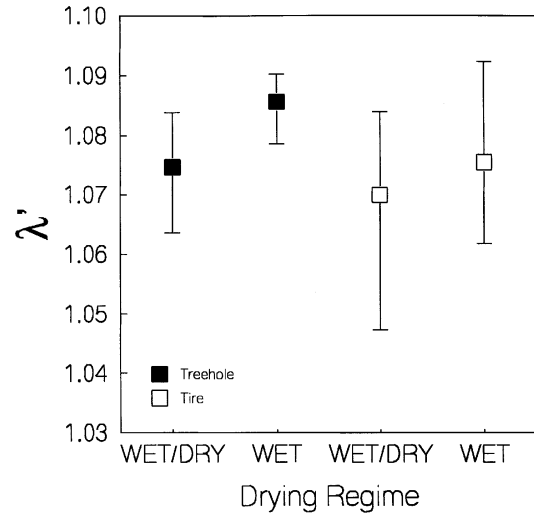
Once again, although not significant, trends within tree holes were similar to those observed in tires (Figs. 5, 6). There was no significant effect of container type (Table 1).

*Males*

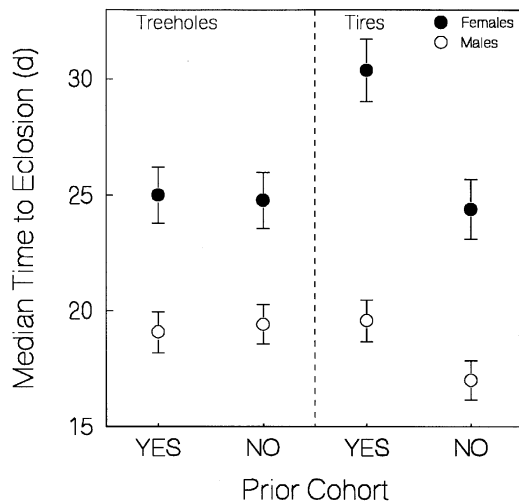
There were no significant effects of Treatment or Treatment\*Type on male median days to eclosion (Table 1). There were significant effects of both prior cohort and drying regime on median days to eclosion for males in tires, but not in tree holes (Table 1). There were no significant interaction effects in either container type



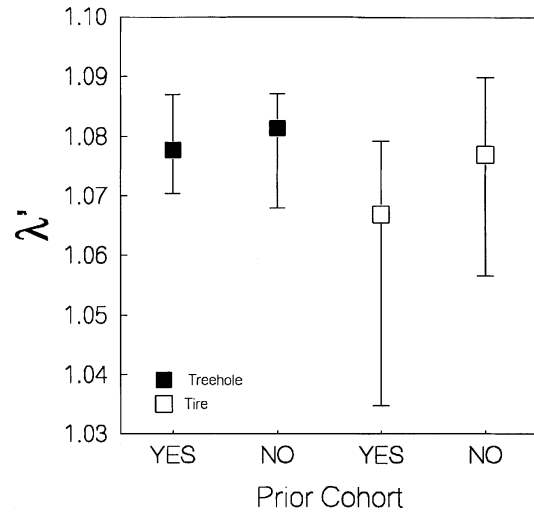
**Fig. 5** Effect of drying regime on median days to eclosion for females and males in tires and tree holes. Plotted are means  $\pm$  1 SE for replicate cages



**Fig. 7** Effect of habitat drying on  $\lambda'$  in tires and tree holes. Plotted are medians  $\pm$  interquartile ranges



**Fig. 6** Effect of prior cohort on median days to eclosion for females and males in tires and tree holes. Plotted are means  $\pm$  1 SE for replicate cages



**Fig. 8** Effect of prior cohort on  $\lambda'$  in tires and tree holes. Plotted are medians  $\pm$  interquartile ranges

(Table 1). Days to eclosion for males in tires was significantly lower for cages with leaf litter that had remained continuously wet, and also for cages with litter that had not been exploited by a prior cohort (Table 1; Figs. 5, 6). There was no significant effect of container type (Table 1).

Estimated finite rate of increase ( $\lambda'$ )

There was no effect of Treatment or Treatment\*Type on  $\lambda'$  (Table 1). The only significant treatment effect on  $\lambda'$  was drying regime in tree holes (Table 1). In tree holes,  $\lambda'$  was significantly less when there was a cycle of drying and inundation (Table 1, Fig. 7). In tires the trend was

similar but not significant (Table 1, Fig. 7). A prior cohort had no significant effect on  $\lambda'$  in either tree holes or tires (Table 1, Fig. 8). There was no significant effect of container type (Table 1).

**Discussion**

Effect of prior cohort

This experiment was designed to test for effects of both a prior cohort and of resource drying on fitness components and population growth of *A. triseriatus*. Based on analysis of survivorship, either for all individuals or for each sex, there were no significant effects of a prior non-

overlapping cohort. However, for both males and females, a prior cohort had a significant detrimental effect on mean mass at, and median days to eclosion in tires, but not in tree holes. The trends were usually in the same direction in tree holes, but were not significant (Figs. 4, 6). This experiment documents a negative effect of a prior non-overlapping cohort that is caused by effects on the leaf litter resource. This asymmetrical intraspecific effect seems to be produced by the same mechanism involved in intraspecific resource competition, but because this interaction occurs between larvae that do not overlap in time, the interaction is totally asymmetrical, with the earlier cohort affecting the later cohort, but not vice versa. We call this effect intraspecific amensalism.

Two aspects of our prior cohort treatments necessarily imply that the intraspecific effects are mediated via the leaf and microbial resource. First, the first cohort was gone from all cages before the second cohort was added, hence direct interference was impossible. Second, water and any solutes in the cages during exploitation by the first cohorts was certainly flushed from the individual cages when they were placed into the field containers, hence interference via dissolved substances is impossible. Thus, it seems that prior exploitation somehow alters the litter resource. Consumers may influence both resource quantity and quality (collectively, resource value). An initial cohort of consumers may of course deplete resource quantity, resulting in amensalism or highly asymmetrical resource competition affecting a later cohort. Consumers may also alter the quality or condition of a resource in addition to reducing its quantity (Heard 1994). For interspecific effects, changes in quality produced by one consumer may often enhance resource quality for another, primarily by altering particle sizes (e.g., Cummins and Klug 1979; Heard 1994). However, within a species, it seems much more likely that changes in quality due to processing by one individual will be detrimental to other individuals, because members of the same species are likely to exploit resources in similar ways. A number of studies have now shown negative intraspecific effects caused by changes in resource quality (e.g., Livdahl 1984; Averill and Prokopy 1987; Gribbin and Thompson 1990). Older cohorts of many insect species (e.g., Averill and Prokopy 1987; Gribbin and Thompson 1990), including *Aedes* mosquitoes (Dye 1982; Livdahl 1984), can have strong negative effects on asynchronously developing younger cohorts when there is temporal overlap and high resource exploitation by older larvae. Our experiment documents negative effects of older larvae even in the absence of temporal overlap. When resources are renewed in a single annual pulse, as is the case for leaf detritus in temperate aquatic communities (Richardson 1991), such intraspecific amensalism seems likely whenever resources are exploited by cohorts that complete development before another cohort occupies the habitat. Such resource-based interactions among non-overlapping asynchronous cohorts in these systems are probably underappreciated. Inter- and

intraspecific amensalism affecting later cohorts and caused by changes in resource quality also occur in terrestrial plant-herbivore systems in which herbivory of a seasonal host plant results in induced resistance to herbivores, which negatively affects the performance of herbivorous insects developing later in the season (Haukioja and Niemälä 1979; English-Loeb et al. 1993; Brown and Weis 1995).

Our results also indicate that effects of a prior cohort on resources are not strong enough to affect significantly our composite index of performance. This result implies that although there are significant effects on individual fitness, these effects are not strong enough to produce detectable negative effects on the population growth rate of a later cohort, perhaps because resource effects on some fitness components buffer the effects of resources on other fitness components. For example, this composite index of cohort performance is strongly influenced by survivorship (Juliano 1998), a response variable for which we found no significant negative effects. The observed negative effects of prior resource exploitation on individual size and development time may enable individuals to reduce risk of death in a poor environment, and therefore may serve to buffer negative effects on survivorship, the variable most likely to determine population growth. Despite the lack of significant effects, the trend in both tree holes and tires is a decrease in  $\lambda'$  with the presence of a prior cohort (Fig. 7), as expected based on negative effects on fitness components.

#### Habitat drying

Based on the analysis of fitness components, a cycle of drying and subsequent inundation negatively affected litter as a resource, resulting in reduced size and longer development time for *A. triseriatus* in tires. Analysis of  $\lambda'$  yielded a significant negative effect of habitat drying in tree holes, but not in tires. The trend was the same in tires, though it was not significant. The implication of this result is that negative effects of habitat drying on fitness components (decreased size at and increased time to eclosion) when combined with (non-significant) trends in survivorship (see Fig. 1) were strong enough to affect our estimate of population rate of increase ( $\lambda'$ ). Thus, habitat drying may negatively affect population growth of *A. triseriatus* even if no individuals die due to desiccation. In this aquatic habitat, and perhaps in others, mortality due to desiccation would underestimate the detrimental effect on populations of this habitat disturbance.

A cycle of drought and flooding constitutes a disturbance in most aquatic systems because it disrupts the life cycles of individuals and temporarily renders the habitat unsuitable (Boulton et al. 1992; Grimm 1993), and disrupts density-dependent biotic effects (Corti et al. 1997). Such disturbances can affect resource quantity or quality (e.g., reviewed by Shapiro 1979; Ehrlich et al.



1980; McAuliffe 1984a, b; Sousa 1984). Disturbances are sources of temporal and spatial heterogeneity in natural communities, sources of mortality, and agents of natural selection in the evolution of life histories (Sousa 1984). Drying of aquatic habitats appears to act as a potent selective force shaping life histories (e.g., McLachlan and Cantrell 1980; Semlitsch 1987b), a prominent mortality source influencing individual fitness (e.g., Semlitsch and Gibbons 1985; Semlitsch 1987a), and a process that modifies species interactions (e.g., Bradshaw and Holzapfel 1988; Corti et al. 1997). To this list we now add that drying negatively affects resources for detritivorous mosquitoes, probably to a degree that can reduce population growth rate.

What causes the negative effect of drying on resources? Our design employing cages precludes both addition of litter resources and exploitation of the litter by terrestrial invertebrates during the dry phase. The former removes any confounding effects of drying on resource quantity, whereas the latter eliminates one possible source of reduced litter quantity or quality following drying (i.e., depletion of litter by terrestrial species). Because of our design, we can rule out interference via dissolved chemicals or direct interaction (see above) – the effect of drying seems to be mediated via the litter resource. The best explanation for the negative effect of habitat drying on the litter resource is that microbial growth in the dry phase reduces litter quality to a greater extent than does microbial growth in an equivalent aquatic phase. This could occur because terrestrial microorganisms colonizing leaves are inherently less profitable or inedible for *A. triseriatus* larvae, or because aerobic microbial metabolism during the dry phase produces a greater reduction in litter energy content. It is also possible that this negative effect resulted from a failure of microorganisms (or at least edible microorganisms) to survive desiccation. In streams, it is not just the presence or size of leaf detritus, but also the extent of microbial colonization that determines resource quality for macroinvertebrates that feed on plant detritus (Cummins and Klug 1979; Petersen et al. 1989). Microbial colonization is an important parameter in models of stream detritus processing and population dynamics of stream invertebrates (Petersen et al. 1989). An alternative hypothesis for the negative effects of resource drying that we observed could be a buildup of toxins in the litter (e.g., nitrogen compounds, which may be highly toxic to *A. triseriatus*; Walker et al. 1991) during the dry phase, and resulting reduction of growth rate of mosquito larvae. Because there were no aquatic or terrestrial consumers feeding on the microorganisms during the dry phase, populations of microorganisms were not cropped, and may have produced greater amounts of waste products detrimental to *A. triseriatus* larvae. However, in our experiment, microorganisms on the litter in the continuously wet treatments were also protected from terrestrial and aquatic consumers, implying that lack of cropping by itself does not account for the negative effect of drying on resource quality. This

buildup-of-toxins hypothesis only seems viable if there is some qualitative difference in the metabolisms of the terrestrial and aquatic microorganisms colonizing the litter. We know of no data on this subject.

Because our data show that the value of the litter resource for mosquitoes is reduced by drying, it appears that it is not resource drying per se that accounts for greater production of *A. triseriatus* from refilled tree holes following longer dry periods (Lounibos 1985). The most likely effect of drying that might benefit *A. triseriatus* (at least in the southern part of North America) is elimination of the desiccation-intolerant predator *Toxorhynchites rutilus*, and the release of recolonizing *A. triseriatus* from predation (Lounibos 1985; Bradshaw and Holzapfel 1983, 1988). Addition of litter may also occur during the dry phase, but it is unclear why such additions would be less likely during an equivalent wet phase. At our site in Illinois, *T. rutilus* is sufficiently rare that in any year, few if any containers yield larvae of this predator (Juliano et al. 1993), and other predators are absent from most tree holes for much of the year (Nannini and Juliano 1998). In addition, leaf fall in the north temperate region is primarily seasonal, and during many dry phases, little or no litter will be added to containers. Thus, the processes that could enhance production of *A. triseriatus* after a prolonged dry period do not seem to be likely for our study site. Coupled with our experimental results, these observations suggest that net effects of drying on aquatic organisms in containers should be very different in different parts of North America.

We did not test for effects of the duration of the dry period on the value of the resource. It is likely that the magnitude, and perhaps the direction, of effects of habitat drying are dependent on the severity and duration of drying. In our experiment, leaf litter was completely dry for a relatively brief period of time (1–6 days). A longer period of drying may have produced a different effect, such as the positive correlation of *A. triseriatus* production with duration of a preceding dry period ranging from 1 to 32 weeks (Lounibos 1985). Perhaps the positive effect of dry periods on *A. triseriatus* production (Lounibos 1985) resulted from longer dry periods characteristic of Florida. Longer dry periods may allow for accumulation of more litter, ultimately increasing production when containers refill. What our study shows, however, is that a short dry period negatively affects the value of the litter resource. There will be great variation in the severity and duration of drying episodes among containers (e.g., due to orientation and morphology) and within a container over a single season (e.g., due to weather).

#### General implications

Our results show that drying negatively affects resource value, and that interactions among *A. triseriatus* larvae may include an intraspecific form of amensalism among

non-overlapping cohorts. There are implications of these results for natural container communities that are subject to drying, and perhaps for ephemeral aquatic communities in general. These results imply that for some species, negative intraspecific interactions involving resources in ephemeral aquatic habitats are likely to be greater in habitats subject to more extreme cycles of drying and inundation. This is somewhat counterintuitive, as a disturbance like drying, which causes mortality and reduces densities, is thought to reduce biotic interactions (Grimm 1993). However, for drought-adapted species, like *A. triseriatus* (which lays drought-resistant eggs above the water level that hatch only when submerged; Novak and Shroyer 1978), large numbers of eggs may accumulate during a long dry period, and reflooding of a dry container can submerge large areas of the container wall, which may contain large numbers of eggs. The result is likely to be a large hatch of *A. triseriatus* and subsequent high potential for intraspecific competition among the hatching cohort. Habitat drying when input of new litter is unlikely (i.e., summer in the temperate zone) should also negatively affect the resource, further increasing resource competition. Habitat drying also does not alleviate the intraspecific amensalistic effects of a prior cohort developing during a previous wet phase (note the absence of significant interactions in our study). We expect these kinds of effects of extreme cycles of habitat drying and flooding to occur in any system in which there are some species that have drought-adapted resting eggs that accumulate during dry phases, and in which plant detritus is the most important resource. Drought-adapted invertebrates in containers, temporary ponds, and ephemeral streams in the temperate zone seem to be most likely to be affected in this way.

On the other hand, if precipitation is regular, cycles of complete drying and subsequent inundation will be rare, plant detritus will stay wet, and therefore be a more valuable resource. In addition, with regular rainfall input, water levels will not fluctuate as much, resulting in smaller hatches of cohorts that will be asynchronously overlapping. So, with regular, less variable precipitation, intraspecific resource competition seems less likely to occur. However, under these circumstances of stable water levels, aquatic habitats may also be more likely to be colonized by drought-intolerant species which may be competitors (e.g., *Orthopodomyia signifera* in tree holes; Chambers 1985; Bradshaw and Holzapfel 1988) or predators (e.g., *T. rutilus* in tree holes; Bradshaw and Holzapfel 1988) that negatively affect drought-resistant species like *A. triseriatus*, and perhaps other aquatic insects.

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