Association of immature mosquitoes and predatory insects in urban rain pools

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Received 15 June 2007; Accepted 9 November 2007

ABSTRACT: Distribution among pools of six mosquito species and 23 predatory insect taxa were studied in temporary rain pools during the summer and fall season in Buenos Aires city. Both mosquito immatures and predators were disproportionally more abundant in pools with high flooded surface, depth, and duration. Mosquito immatures differed in their habitat use with respect to predators. Among mosquitoes, *Ochlerotatus albifasciatus* showed a different pattern when compared to the remaining culicids. More culicid and predatory insect taxa colonized the pools in those flooding events of longer duration. *Ochlerotatus albifasciatus* was the only mosquito species recorded during short duration events and the first one in colonizing the pools in long duration events. This species shared the pools mainly with early arriving adult predators. Three *Culex* species were recorded later and showed higher coexistence with most of the predatory taxa, mainly immatures of the genera *Tropisternus, Rhantus, Liodessus*, and *Belostoma*. A high heterogeneity between pools and seasons was observed. Multiple regression analyses showed a negative relationship of per capita change of *Culex* species with large-sized predators only in those cases where predators were collected in high abundances during the summer. No negative relationship of predators was detected in relation to per capita change and abundance of *Ochlerotatus albifasciatus*. Differences in duration of about two to three weeks seemed to significantly affect the abundance of both culicid and predatory taxa, suggesting that the urban pools analyzed in this study are on the extreme of suitable conditions for these aquatic insects. *Journal of Vector Ecology* 33 (1): 46-55. 2008.

Keyword Index: Culicidae, predation, urban pools, temporary waters, Argentina.

INTRODUCTION

Many mosquito species use temporary bodies of water as breeding sites (Laird 1988). Species that colonize temporary habitats probably take advantage by exploiting the abundant resources offered by the pools and the reduced predation pressure as compared to more permanent pools (Williams 1997). Although predation in temporary habitats is expected to be less important than in permanent waters (Wellborn et al. 1996, Schneider and Frost 1996), several species of Coleoptera, Hemiptera, and Odonata are common predators in temporary waters and wetlands (Laird 1988, Nilsson and Svensson 1994, Williams 1996, Schneider and Frost 1996, Blaustein 1998).

The presence of predators is important in structuring temporary pool communities and controlling mosquito populations (Blaustein 1998, Stav et al. 2000, Chase and Knight 2003). In extremely ephemeral habitats, the relative importance of predators coexisting with mosquito immatures is dependent on water permanence; the water must persist long enough to allow colonization by predatory species (Wellborn et al. 1996, Schneider and Frost 1996).

The effect of predators on mosquito abundance is expected to be strongly related to their ability to colonize the pools at the same time as their prey, as well as to the similarity in habitat preference they show. On the other hand, mosquito prey could reduce predation by different habitat use, i.e, by using habitats where predators can not or have not colonized yet or by avoiding colonizing those habitats where predators are already abundant (Stav et al. 1999, Blaustein et al. 2005).

Ochlerotatus albifasciatus and three Culex species (Culex pipiens, Cx. dolosus, and Cx. maxi) breed frequently in temporary rain pools of Buenos Aires city, representing 76% of the insects collected during a one-year study (Fischer et al. 2000, Fontanarrosa et al. 2004). All four mosquito species showed a similar pattern of association with pool characteristics: a positive relationship to pools with greater surface area and depth and to the presence of vegetation. On the other hand, they differed in their breeding season: Oc. albifasciatus was recorded mainly during the fall and winter, Cx. pipiens mainly in the summer, Cx. maxi in the fall, and Cx. dolosus year-round (Fischer et al. 2002, Fischer and Schweigmann 2004). Therefore, summer and fall are the seasons when mosquito abundance reaches highest values in these rain pools. The two genera show differences in their life cycle type and adaptation to ephemeral habitats and should be classified in different functional groups when considering ecological strategies (Wiggins et al. 1980) or life cycles (Crans 2004). Oc. albifasciatus, like other floodwater mosquitoes, lay their drought-resistant eggs on the humid soil surrounding temporary waters, while the Culex species are dependent on water to lay their non-drought-resistant egg rafts (Clements 1992). In addition, Anopheles sp. and Psorophora sp. were recorded occasionally in the same rain pools. The latter species show an ecological strategy

comparable to *Oc. albifasciatus*, while *Anopheles* mosquitoes lay non-resistant eggs like *Culex* species.

Several predatory insects were reported in temporary pools in natural areas of Buenos Aires province (Von Ellenrieder and Perez Goodwyn 2000, Von Ellenrieder and Fernandez 2000, Campos et al. 2004) and in urban environments (Fischer et al. 2000, Fontanarrosa et al. 2004). During the summer season, these insects showed the highest abundance (Fischer et al. 2000) and diversity (Campos et al. 2004).

The aims of the present study were to analyze the distribution pattern of culicid immature stages and their potential predators in ephemeral rain pools, describe the colonization sequence of immature mosquitoes and the associated predatory insects in temporary pools, compare flooding events with contrasting duration, and explore the relationships among abundance patterns of mosquito genera, flooding dynamics, and the presence of functional groups of predatory insects.

MATERIALS AND METHODS

The study was carried out in the Saavedra Park (34°33'S - 58°29'W), located over the piping of Medrano Spring near the northern limit of the city. The terrain, historically subjected to flooding, has an irregular topography where numerous rain pools form after rain. Those ephemeral and temporary rain pools are variable in size (0.1 to 600 m2), depth (1 to 24 cm), and duration (one to eight weeks in the summer). Vegetation cover within the pools is mainly composed of periodically cut Gramineae, and trees providing different shading degrees to the pools. Buenos Aires city is located in a humid temperate climatic region, with an annual mean temperature of 17.6° C and an annual rainfall exceeding 1,000 mm. The study was performed during the summer and fall seasons when mosquitoes and predatory insects attained their highest richness and abundance. All samples were taken from December 1998 through May 1999.

To analyze differences in mosquito and predatory insect composition among pools, a total of 67 rain pools were sampled 25 times on a weekly basis. To analyze the colonization time and population dynamics, two pools (pool A = maximum flooded area 1,123 m², pool B = maximumflooded area 114 m²) were sampled three times a week during the study period. The pools were selected based on preliminary data collected in the previous fall season and were considered representatives of a high abundance of predators (pool A) and mosquitoes (pool B).

Water presence, flooded area, and maximum depth were assessed every sampling date for each pool. The methods for estimation of environmental variables and insect sampling are described in Fischer et al. (2000). Culicids were sorted by stage and identified to generic level for larval instars 1-2 and pupae, and to species level for larval instars 3-4 (Darsie 1985, Almirón and Harbach 1996, Almirón and Brewer 1995, Rossi 2000). Adult and larval instars of Coleoptera and Heteroptera were identified to specific or generic level and Odonata to suborder, following the systematic keys and specialized literature for local fauna (Angrisano and Trémuilles 1995, Bachmann and Mazzucconi 1995, Trémuilles et al. 1995, Bachmann and Angrisano 1998¹). Non-predatory insects such as adult Hydrophilidae were not considered in this study.

Maximum flooded area, maximum depth, and number of times when the pool contained water were obtained for each of the 67 pools based on information from the whole study period. Cumulative abundance of mosquitoes (larval instars 3-4 of *Cx. pipiens*, *Cx. maxi*, and *Cx. dolosus*, larval instars 1-2 and pupae of *Culex* spp., larvae and pupae of *Oc. albifasciatus*, all instars of *Anopheles* sp., and all instars of *Psorophora* sp.) and predators (adults and immature for each taxon) were calculated for each pool.

Four categories of pools were defined based on their percentage contribution to total abundance of collected insects: high abundance (more than 10% of organisms), intermediate abundance (1 to 10% of organisms), low abundance (less than 1% of organisms), and without insects (where neither culicids nor predators were collected). Depth, flooded area, and number of dates with water were compared among categories by means of the Kruskal Wallis test. Cumulative sampling effort, number of culicids and predatory insects, and number of taxa were calculated for each pool category.

Correspondence analysis (CA) was used to explore differences in taxonomic composition among pools. Abundance data were transformed to log (n+1), and only taxa with more than five individuals were included. Pools were grouped in categories based on the CA results. Flooded area, depth, and number of dates with water were compared among these groups with the Kruskal Wallis test. The Chi square test was used to assess the independence of pool classification based on abundance (percentage of the collected fauna), and the composition criteria. Intermediate and high abundance categories were grouped because of the low numbers in each of them (Zar 1999).

Data analysis included those flooding events when water permanence lasted at least the time estimated for *Oc. albifasciatus* to complete the aquatic phase at different temperatures (following Fontanarrosa et al. 2002). A total of six data sets matching the former criterion were recorded, corresponding to December (11 days pool A), January (8 days pool A), end of January through first days of March (35 days pool A) and 32 days pool B), end of March through April (30 days pool A), and May (16 days pool A). Flooding events were classified as short duration events when water permanence was proximate to *Oc. albifasciatus* development time (8, 11, and 16 days). Flooding events that lasted at least twice the time needed to complete *Oc. albifasciatus* aquatic phase (35, 32, and 30 days) were classified as long duration events.

¹Bachmann, A.O. and E.B. Angrisano. 1998. Diversidad y bionomía de insectos acuáticos. Curso de postgrado, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. MS, 289 pp. Culicidae instars 1-2, 3-4, and pupae, predatory insect immatures, and adult stages of each taxon, were counted separately and summed for each of the six analyzed events. Temporal pattern of colonization was synthesized by grouping short term and long term events (three in each category). Mean abundance of each taxon were calculated for three-day intervals, transformed to $\log(n+1)$, and plotted against time since flooding for both duration categories. Only taxa with more than five individuals were included.

We assessed the relationship of mosquito abundance (Nt) with predator abundance, water availability, and permanence of the water through multiple regression analyses. Only data from long duration events were included, and three models were adjusted for Culex spp. (one for each flooding event) and one for Oc. albifasciatus (this species showed very low abundance in the summer events). The independent variables included were flooded area (log transformed), days since flooding, and log transformed abundance of each of four categories of predators (small adults, small larvae, large adults, and large larvae). Predators smaller than 3 mm were assigned to the small predator category, while predators exceeding this size were included in the large predator category. Multiple regression analyses were also used to explore the relationship of per capita decrease of abundance $(dN=(N_t-N_{t-1})/N_{t-1})$ of both mosquito genera with the abundance of the same categories of predators and with the variation of flooded area. All statistical analyses were performed with Statistica 7.1 (Statsoft, Inc. 2005).

Monthly mean temperature and accumulated rainfall data for nine months including the sampling period were compared to the 30-year mean (1961-1990), in order to discuss the differences between the study period and average years. Meteorological data were provided by the National Meteorological Service.

RESULTS

Differences among pools

The percentage abundance of both culicids and predatory insects varied greatly among the 67 studied pools. Significant differences of maximum surface area (H=21.30; N=67; p<0.001), maximum depth (H=22.80; N=67; p<0.001), and number of dates with water (H=30.26; N=67; p<0.001) were detected among abundance categories. With less than 50% of total sampling effort, 91% of culicids and 77% of predatory insects were collected in intermediate and high abundance pools (Table 1). In general, all culicid taxa were present in pools of the three abundance categories, except Anopheles genus, which was not recorded in high abundance pools. The most abundant predators were collected in all abundance category pools, while less abundant taxa were recorded in one or two pool categories. All culicid and predatory taxa with more than five individuals showed higher abundance in intermediate and high abundance pools, with always more than 40% of individuals in these water bodies (Figure 1). The first two dimensions of the CA explained 32% of inertia, and according to the ordination diagram, we differentiated three groups of pools (Figure 2). Twenty-four pools were included in the first group characterized by a high abundance of Liodessus sp. larvae, together with all mosquito taxa except Oc. albifasciatus. The 17 pools of Group 2, characterized by positive values on the first axis and negative values on the second dimension, showed a high abundance of Oc. albifasciatus immatures and Liodessus sp. adults. The third group included only six pools with positive values on both principal dimensions and was characterized by the high proportion of the remaining larval and adult predatory insects. Kruskal Wallis tests showed differences in depth (H=12.20; N=47; p<0.005) and flooded

Table 1. Environmental and biological characteristics of pools categorized by mosquito and predatory insect abundance.

	High abundance pools x>10%	Medium abundance pools 10%>x>1%	Low abundance pools 1%>x>0%	Pools where no culicid or predators were collected
No. of pools	3	8	36	20
Depth (cm) mean (range)	16.0 (13-20)	12.8 (6-23)	9.1 (2-18)	5.5 (1-13)
Surface area (m ²) mean (range)	337.9 (60-594)	52.1 (10-177)	28.1 (0.6-229)	16.9 (0.3-259)
No. of dates with water mean (range)	13.7 (9-20)	11.9 (7-16)	7.3 (1-20)	2.4 (1-8)
Percentage of sampling effort	23%	25%	42%	10%
Percentage of total collected mosquitoes	68%	23%	9%	-
Percentage of total collected predators	51%	26%	23%	-
No. of Culicid taxa	5	6	6	-
No. of predatory taxa	19	18	14	-



Figure 1. Abundance of each taxon and distribution of A) mosquitoes and B) predators in three categories of pools. Notation: Oc: Ochlerotatus albifasciatus, Cxp: Culex pipiens (larvae 3 and 4), Cx: Culex spp (larvae 1, 2 and pupae), Cxd: Culex dolosus (larvae 3 and 4), Cxm: Culex maxi (larvae 3 and 4), Ps: Psorophora sp., Ano: Anopheles sp., Li: Liodessus sp., Tr: Tropisternus spp., Rh: Rhantus signatus, Be: Belostoma elegans, De: Desmopachria sp., Zy: Zygoptera, Ne: Neoplea maculosa, Th: Thermonectus succinctus, No: Notonecta sellata, An: Anisoptera, Bu: Buenoa fuscipennis, Ra: Ranatra sjostedti, La: Laccophilus sp., En: Enochrus sp., Lo: Laccornellus tristis, Su: Suphis sp., Ss: Suphisellus sp., (a): adult predator, (l): larval predator.



Figure 2. Ordination diagram of mosquitoes and predatory insects in the rain pools of Saavedra Park, Buenos Aires, Argentina. Notation same as in Figure 1.

Diptera: Culicidae ** Ochlerotatus Ochlerotatus Ochlerotatus	Taxon	colonization event Pool A (Spring- Summer)	colonization event Pool A (Summer)	onort colonization event Pool A (Fall)	Long colonization event Pool A (Summer)	colonization event Pool B (Summer)	colonization event Pool A (Fall)
Ochlerotatus Ochlerotatus	us albifasciatus (1-2)	6	11	176	I	1	366
Ochlerotatus	us albifasciatus (3-4)	35	7	72	I	2	664
t	us albifasciatus (pu)	4	ı	I	1	21	33
Psorophora s	ı sp. (1-2)	I	ı	I	I	I	2
Culex spp. (1	(1-2)	1	ı	1	97	571	59
Culex spp. (p	(nd)	I	ı	I	40	300	1
Culex pipien:	ens (3-4)	I	ı	ı	79	834	25
Culex dolosu	sus (3-4)	1	ı	I	54	31	14
Culex maxi (i (3-4)	I	ı	1	7	6	20
Coleoptera: Dytiscidae Liodessus sp.	p. (a)	12	31	6	232	74	18
Liodessus sp.	p. (l)	I	I	1	166	29	44
Rhantus sign	gnatus (1)	I	I	I	50	7	6
Rhantus sign	gnatus (a)	I	I	I	2	1	2
Thermonectu	tus succinctus (1)	I	1	I	15	-	1
Thermonectu	tus succinctus (a)	1	I	I	1	-	3
Desmopachri	<i>hria N</i> . sp. (a)	1	1	I	29	2	T
Desmopachri	hria D. sp. (a)	I	I	I	1	I	I
Laccophilus s	's sp. (a)	2	I	I	1	I	ı
Coleoptera: Hydrophilidae * <i>Tropisternus</i>	4s spp. (1)	3	3	I	236	64	4
Enochrus spi	pp. (l)	I	ı	I	3	6	·
Coleoptera: Noteridae Suphisellus sj	s sp. (a)	1	ı	I	I	I	ı
Suphis sp. (a)	(a)	1	ı	I	1	I	ı
Hemiptera: Belostomatidae Belostoma el	elegans (1)	I	I	I	129	I	I
Belostoma el	elegans (a)	I	I	I	4	I	3
Hemiptera: Nepidae Ranatra sp. (i. (a)	I	2	I	5	I	ı
Hemiptera: Notonectidae Notonecta sei	sellata (1)	ı	ı	ı	27	1	
Notonecta se	sellata (a)	2	1	I	6	I	5
Buenoa fusci	scipennis (a)	4	I	I	3	I	2
Hemiptera: Pleidae Neoplea mac	aculosa(a)	I	ı	I	38	3	ı
Odonata ** Zygoptera (1)	(1)	ı	I	I	30	I	ı
Anisoptera	1 (I) I	ı	·	ı	ı	ı	9

Table 2. Number of culicid and predatory taxa collected through intensive sampling of two pools of different flooded surface (small and large) and contrasting permanence time (short and long).

		Culex spp.		Ochlerotatus spp.
	Pool A (summer)	Pool A (fall)	Pool B (summer)	Pool A (fall)
Adjusted R2	0.828	0.744	0.881	0.964
Intercept	0.051	-3.036	-1.109	4.210
S Ad Pr	ns	ns	ns	ns
L Ad Pr	-0.437	ns	ns	ns
S Lar Pr	ns	ns	ns	ns
L Lar Pr	1.014	1.052	0.628	-0.367
Flooded Area	ns	1.084	0.854	ns
Days since flooding	ns	0.114	0.095	-0.156

Table 3. Multiple regression coefficients of predator abundance (small and large adult predators, and small and large larval predators), flooded area, and days since flooding related to the abundance of mosquitoes in temporary pools.



Figure 3. Abundance of mosquito immature stages (upper part) and predatory insects (lower part) in the rain pools in relation to time elapsed since flooding for long (A, C) and short (B, D) duration events. Grey circles: adults. Black circles: larvae. Notation of taxa as in Figure 1, notation of instars as in Table 2.

Table 4. Multiple regression coefficients of predator abundance (small and large adult predators, and small and large larval
predators) and variation in water availability related to the per capita change in abundance of mosquitoes in temporary
pools.

		Culex spp.		Ochlerotatus spp.
	Pool A (summer)	Pool A (fall)	Pool B (summer)	Pool A (fall)
Adjusted R2	0.843	0.924	-	0.86
Intercept	0.133	3.265	-	-0.936
S Ad Pr	1.870	ns	ns	ns
L Ad Pr	ns	ns	ns	ns
S Lar Pr	ns	ns	ns	0.560
L Lar Pr	-1.225	ns	ns	ns
Surface difference	2.117	7.665	ns	0.058

area (H=8.14; N=47; p<0.05), with higher values in Group 3 for both variables. The inclusion of pools in abundance categories was independent of the classification according to composition (Chi-Square=5.87, df=2, p>0.05).

Intensive study

Mosquito and predatory insect richness and abundance were higher in long duration flooding events and during the summer than in short duration events and during the fall (Table 2). Oc. albifasciatus was the first mosquito species recorded after flooding in long duration events and the only mosquito species collected during short duration events, with high abundances during the first three days since flooding in the fall season but not during the summer. First instars of Culex spp. were recorded in long duration events from the 4th day after flooding and from day 8 of 3rd and 4th instar larvae of Cx. dolosus, Cx. maxi, and Cx. pipiens (Figures 2A and 2B). Oc. albifasciatus abundance was highest immediately after flooding and decreased after day 13. In contrast, Culex mosquitoes increased their abundance until days 19-21 and decreased progressively thereafter. Predators that colonized the pools during the first three days were adult instars of Buenoa fuscipennis, Notonecta sellata, Thermonectus succinctus, and Liodessus sp. (Figures 2C and 2D). Neoplea maculosa, Belostoma elegans, and Desmopachria sp. were collected after day 4. Larval instars of predatory insects were generally recorded later, with the exception of Liodessus sp. and Anisopterans in low abundance. Larval Tropisternus spp. were collected after day 5, followed by Thermonectus and Rhantus larvae after day 7, Zygopterans and Belostoma after day 10, and finally Enochrus and Notonecta larvae from days 13-15 onwards. Predators showed their maximum abundance between days 15 and 18 on long duration events and decreased thereafter until total disappearance of water. Abundance of predators (mainly adults) peaked during the first week on short duration events.

Multiple regression analyses showed a positive relationship between large larval predator abundance with *Culex* spp. abundance in summer (pool A and B) and fall (pool A), and a negative relationship with *Ochlerotatus* sp. abundance in fall (pool A). Large adult predator abundance

was a significant predictor of *Culex* spp. abundance only in the summer model for pool A (Table 3). The models obtained for the large pool in the fall and for the small pool in the summer season showed positive relationships of increasing *Culex* spp. abundances with flooded area and increasing time elapsed since flooding, while these variables were not significant predictors of *Culex* spp. abundance in the summer model for pool A. On the other hand, *Ochlerotatus* sp. abundance was negatively related to the time elapsed since flooding.

Models for per capita change of Culex spp. abundance showed differences among pools and seasons. Large changes in flooded area, high abundances of large larval predators and low abundances of small adult predators were significant predictors of large per capita changes in abundance in the summer model for pool A. In the fall model for pool A, the only significant variable in predicting abundance changes of this mosquito genus was the change in flooded area. The analyzed independent variables failed in predicting the change in Culex spp. abundance in the small pool. The model adjusted for Ochlerotatus sp. predicted high abundance changes to be positively related to high abundances of small larval predators and to large decreases in flooded area (Table 4). The temperature records showed little differences between the study period and the 30-year average (Figure 4). The accumulated rainfall was remarkably low during the three months previous to the sampling period, attaining about half of the historical values. In contrast, the amount of rainfall exceeded average values during the summer season, mainly in December, January, and February.

DISCUSSION

The observed trend toward high abundance of mosquitoes and predatory insects in pools of increasing size and permanence indicate that the studied pools are at one extreme of the permanence range that represents suitable conditions for those insects. On the other hand, even in the high abundance pools not all flooding events are equally suitable for colonization. Differences of about two to three weeks in water permanence seemed to significantly affect the abundance of both culicid and predatory insects,



Figure 4. Comparison of monthly accumulated rainfall and mean monthly temperature from September 1998 through May 1999, with the 30-year average values from 1961 to 1990.

as shown when comparing the numbers of individuals collected during the short and long duration events. At this point of the permanence gradient, a prolonged drought and short duration flooding events could modulate mosquito abundance and also the abundance of potential predators. Among the possible consequences of the low rainfall amounts in the spring is a low availability of habitats for the aquatic insects during the season, thus depressing population abundance. On the other hand, the flooding events in the late spring and early summer months were characterized by their short duration, probably because of the accelerated absorption of water by the previously dry soil. These factors may explain the low abundance of mosquitoes and predatory insects in the short duration flooding events at the beginning of the summer season.

Flooding events of increasing duration after a drought could produce high mosquito abundance. The extraordinary wet summer could have favored the high abundance of *Culex* mosquitoes and predatory insects observed during the long duration flooding event in this season. Such dynamics were suggested for *Cx. pipiens* and *Anopheles quadrimaculatus* in semi-permanent wetlands (Chase and Knight 2003). On the other hand, the extended spring drought may have reduced the survival of *Oc. albifasciatus* eggs, thus preventing high abundance during the summer, even in long duration flooding events. The dominance of this species in the fall could be originated from recently laid eggs by adults dispersed from adjacent areas, as discussed by Fischer et al. 2002 and supported by Bejaran et al. (in press).

The ecological strategy observed for Oc. albifasciatus

that colonize the pools immediately after flooding allows this species to exploit the pools even when flooding events are short and complete immature development before the abundance of predators increase significantly. In contrast, species of the Culex genus were recorded only on long duration flooding events, and their colonization time differed little from the pattern observed by most of their predators. The simultaneous presence of a high number of pools provides the aquatic insects with a diversity of sites for colonization (De Meester et al. 2005). Nevertheless, the relationships of the total abundance of collected insects and sampling effort in different pool categories suggest that colonization of these taxa is not random. Some pools are colonized in an excessive proportion as compared to others, and both size and permanence of water seem to be positively related with high abundance of culicids and predatory insects. The results of the ordination analysis suggest a stronger relationship of predatory insects to these environmental variables. These organisms are probably more constrained in successfully colonizing temporary waters, since they generally attain greater size than prey and their life cycles last longer (Wellborn et al. 1996, Williams 1997, Schneider and Frost 1996, Chase and Knight 2003). Although high abundance pools contained large numbers of mosquito immature and predatory insects, differences in relative composition of these taxa were detected by the ordination analysis, and these differences were supported by the independence of abundance and composition categories. Among high abundance pools, some contained high mosquito and others high predator proportions. One possible explanation for the observed pattern could be the avoidance of oviposition sites where predators are in high abundance, as shown by several authors for different mosquito species including *Culex pipiens* (reviewed by Blaustein et al. 2005).

An alternative explanation is that the observed pattern is a consequence of the negative effect that predators exert on mosquito populations in those habitats where the former are in higher abundance, as observed in other field and experimental studies (Walton et al. 1990, Blaustein 1998). This hypothesis is partially supported by the multiple regression results. Predator abundance was shown to be related to the amount of per capita decrease in the summer (large pool) when abundance of predators was comparatively high. Future studies should experimentally assess the relative importance of the mechanisms involved in the reduction of mosquito abundances in temporary pools when high numbers of predators are present.

Acknowledgments

We thank Lic. Mariela Nieves for her field assistance and Lic. M. Cristina Marinone for her constant collaboration. This research was partially supported by a covenant endorsed by the Gobierno de la Ciudad de Buenos Aires and the Facultad de Ciencias Exactas y Naturales of the Universidad de Buenos Aires and partially by a grant from the Universidad de Buenos Aires.

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