DIEL PATTERNS OF HABITAT USE: CRAYFISH COMPETITION

Erik W. Oswald
University of Notre Dame
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ABSTRACT

Invasions by nonindigenous organisms can be lethal to many different kinds of ecosystems. *Orconectes rusticus* is replacing its congener crayfish species *O. propinquus* and *O. virilis* in northern Wisconsin Lakes. *O. propinquus,* possibly an earlier invader, may be interacting with *O. virilis* in a similar fashion, but the mechanisms of this are poorly understood. This study of *O. propinquus* and *O. virilis* tests the hypothesis that the presence of one species affects the habitat choice of the other and looks at patterns of diel periodicity. Competitive exclusion of the species was tested via habitat use in experimental pools (1.4m in diameter). Each pool was divided equally into segments of cobble, open sand, macrophytes in organic sediments (muck), and macrophytes in sand. No difference was found in crayfish distributions between single- and two-species treatments. While this result was not anticipated, it is consistent with observational data in the field. Both species *were* found to significantly decrease their use of open habitat during the day. This is consistent with the crayfishes' need to hide from visual predators during the day and to forage at night.

INTRODUCTION

Whether it be through ballast water from cargo ships, or anglers releasing excess live bait into a lake, nonindigenous organisms find a way into ecosystems. Once established, these 'outsiders' can have devastating economic impacts, affect the health of humans, or threaten native biodiversity and ecosystem function (Kolar 2001). For example, the predacious Nile perch was introduced into Lake Victoria, East Africa in the 1950's. It has led to the largest modern vertebrate extinction, over 200 species of fish (Kolar 2001).

When a new species is introduced to an area such as a lake, the stage is set for competitive interactions between the native species and the invader. This competition may take a couple of forms. A common one is interference competition, or direct aggressive interaction between individuals (Birch 1957). Paine (1980) found that predation by starfish altered competition and diversity. We are investigating the opposite: how competition affects one species' ability to occupy optimal habitat while excluding the other species, hence increasing the second species vulnerability to predation.

Crayfish in the northern Wisconsin/Upper Peninsula of Michigan watershed are good models for interspecific competition and invasion. The native species *Orconectes virilis* and the probably nonindigenous *O. propinquus* have been compared extensively to the dominant species *O. rusticus,* whose invasion occurred more recently than that of *O. propinquus.* The effects of the *O. propinquus* invasion are poorly understood, and the direct competitive interactions between *O. virilis* and *O. propinquus* have never been studied separately from the presence of *O. rusticus.* The purpose of this study will be to examine the effects of interspecific competition between the native *O. virilis* and *O. propinquus* and predation risk on habitat selection of the crayfish.

Predation risk affects habitat choice by indirectly influencing prey behaviors and hence, prey resource use (Garvey 1994). Both noncompetitive and competitive interactions among prey can alter predation results. In this way, predation and competition interact to determine community structure (Garvey 1984). Predation risk may intensify competition among species by forcing them into common refugia. By including the predation risk factor in the study, the crayfish will act as they would in a natural environment. Therefore, the study will see how crayfish interact and compete to attain their optimal habitat as they would to avoid predation.

The second goal of this study is to obtain comprehensive data on the crayfish species composition and abundance in lakes on the University of Notre Dame Environmental Research Center (UNDERC) property as well as those upstream in the watershed. To achieve this goal, the lakes will be surveyed using standard methods of trapping (see Olsen et. al. 1991, Capelli 1982). UNDERC lakes are unique in that to this date, no crayfish invasions have been recorded on the property due largely to fishing controls, restricted access to the property, and the relative hydrologic isolation of the watershed. Also, a few rare species of crayfish may inhabit the lakes.

METHODS

Competition for Habitat

To test the effects of interspecific competition and predation risk on habitat selection, we used the methods of Hill and Lodge (1994). By replicating their experiment closely, we can compare the results of *O. virilis* and *O. propinquus* interspecific competition to their study which additionally included the dominant invasive *O. rusticus*. Our experiment included three treatments run in two time blocks of two replicates each (n=4 for each treatment). The treatments consisted of one pool of *O. virilis,* one pool of *O. propinquus,* and one pool of both species together in a 1:1 ratio to test for competitive exclusion. Each pool had 24 crayfish with 12 of each species in the two-species treatment. This ensures densities of 16 individuals/m^2, which is on the high end of natural crayfish densities in Northern Wisconsin Lakes (see Olsen et. al 1991 and others). To ensure the crayfish acted as if predators were present in the pools, they were kept in the presence of largemouth bass (a main predator of the crayfish) constantly prior to insertion into the experimental pool.

The experiment was carried out in six outdoor wading pools approximately 1.4 m in diameter, 30 cm deep. Each pool bottom was divided evenly into sections of cobble (rocks) on sand, sand only, sand with macrophytes, and organic sediments (muck) with macrophytes. Sediments and macrophytes were mixed from Tenderfoot Lake, Morris Lake, and Brown Lake. The sand was collected near shore with a shovel while cobble was collected by hand. Muck collection required a shovel and an Eckman Grab. Macrophytes (*Elodea Canadensis, Ceratophyllum demersum,* and *Potamogeton richardsonii)* were collected via uprooting with a leveling rake as well as by hand, and were controlled in the pools for size and density (15-20 cm shoots, 250 shoots/m^2). Invertebrate organism loss from the plants was minimized as much as possible to allow for a natural food resource for the crayfish. Qualitative analysis of sediment sub samples showed that snails, odonates, mayflies, and chironomids were present in abundances similar to those of local lake littoral zones.

The Crayfish were placed in the center of the experimental pools in the afternoon and the numbers occupying each habitat were recorded twice that night and twice the following day twelve hours later. The average of the two night values and the average of the two daytime values were used for statistical analysis.

The experimental crayfish specimens were maintained separately by species in aerated laboratory aquaria and fed Tetramin (TetraWerke, Melle, Germany) fish food daily until used. The crayfish used in the experiment were Form II (nonreproductive adult molt stage) males of carapace length between 27 and 32mm and were controlled for size not only within each pool, but in each replicated group of three different treatments (see fig 1).

Survey of UNDERC Lakes

UNDERC lakes were surveyed following standard methods using modified minnow traps baited with beef liver and placed every 100m (Capelli 1982). The traps were set and checked approx 24 hours later.

RESULTS

Competition for Habitat

Crayfish in single species treatments are assumed to occupy the habitat in which they would prefer to live when alone in their natural habitat. For this reason the single species data were set as the expected values. Crayfish in two-species treatments may interact in such a way as to alter the substrate choice of the other species making data from these treatments the observed values. Running a G-test on observed values vs. expected values would thus show if indeed any difference existed between expected and observed distributions (Zar 1999).

The presence of the congener had no effect on distribution of either crayfish species' substrate use neither at night ($G < 0.026$, $df = 3$, $P > 0.995$ for both species) nor during the day ($G = 0.274$ and 0.1135 for *O. virilis* and *O. propinquus* respectively, $df = 3$, $P > 0.975$ and $P > 0.995$).

Observationally, it appeared that crayfish used cobble, macrophyte muck, and macrophyte sand habitats fairly evenly with less use of the open habitat. Statistically, both crayfish species significantly decreased their use of the open habitat during the day ($G = 24.978$ and 31.369 for *O. virilis* and *O. propinquus* respectively, $df = 1$, $P < 0.001$ for both species). (See Figs 2 and 3)

Survey of UNDERC Lakes

Of the eight lakes surveyed in the UNDERC watershed, trapping on three of them yielded no crayfish. These were Langford (23 traps), Roach (14 traps), and Hummingbird (14 traps). Plum Lake (0.65 males/trap), Palmer Lake (0.167 males/trap), Kickapoo Lake (0.071 males/trap), and Morris Lake (0.9 males/trap) all yielded traps with *O. virilis* in them while only Tenderfoot Lake yielded traps with *O. propinquus* (0.571 males/trap) *and O. Virilis* (0.095 males/trap). No rare species of crayfish were found in the traps as well as no *O. rusticus*. (See Fig. 4)

DISCUSSION

Competition for Habitat

Consistent with expectations set forth by results from Hill and Lodge (1994), the nighttime distributions of combined species treatments did not differ from single species distributions. At night the crayfish are more likely to be active and worry less about defending their preferred hiding space due to decreased threat from visual predators.

Daytime distributions, on the other hand, were found to be contrary to Hill and Lodge (1994). *O. propinquus* and *O. virilis* did not alter their distributions in the two-species treatment from the expected values of their single-species treatments. The replication of the experiment was low (n=4), and the p value (>0.995, and >0.975) was rather large. This could mean that the replication was *too* low to reject the null hypothesis that *O. propinquus* does not alter *O. virilis* substrate choice. Another possibility is that this shows *O. propinquus* to be much less likely to exclude *O. virilis* than is *O. rusticus*. In support of this possibility, *O. propinquus and O. virilis* have been seen to coexist in the absence of *O. rusticus*. Tenderfoot Lake has had both species for nearly two decades and they have been seen coexisting in Crab Lake (Vilas Co, WI) for over

25 years; whereas *O. rusticus* will routinely eliminate *O. virilis* (Olsen et al. 1991, Hill and Lodge 1994, and Lodge unpublished data).

Also consistent with expectations was the decreased use of open habitat during the day. Having been kept in a tank in the presence of a predator, the crayfish continue to act in ways to avoid that predator even in the pools. In the absence of cover, crayfish are quite vulnerable to predation and thus the minimization of time spent in the open increases a crayfish' chances of survival. Of the crayfish observed in the open quadrant of the pools during the daytime, most were seen up close to the pool wall which acted as pseudo cover. Otherwise, they would be more visible and thus more susceptible to predation. During the night, the crayfish are in less danger of visual predation and thus have less reason to avoid the open habitat. Hill and Lodge (1994) refer to these times as low risk or high risk regarding predation.

Survey of UNDERC Lakes

The most significant aspect of the survey is that no *O. rusticus* were found on UNDERC property. In addition to this, no *O. propinquus* were trapped in the non-public lakes. (Tenderfoot Lake has public access through the Ontonagon River to Palmer Lake. There is a public boat launch on Palmer Lake). UNDERC has done a tremendous job of preventing the introduction of the nonindigenous *(O. rusticus)* and the possibly nonindigenous *(O. propinquus)* crayfish. Through the privatization of the property and the carefully observed watershed, UNDERC is one of the few remaining areas with truly native crayfish lakes. These lakes are important for ecological research and the introduction of *O. rusticus* could have serious detrimental effects. Through the continued study of crayfish interactions we may come to a full understanding of the mechanisms at work in species invasions.

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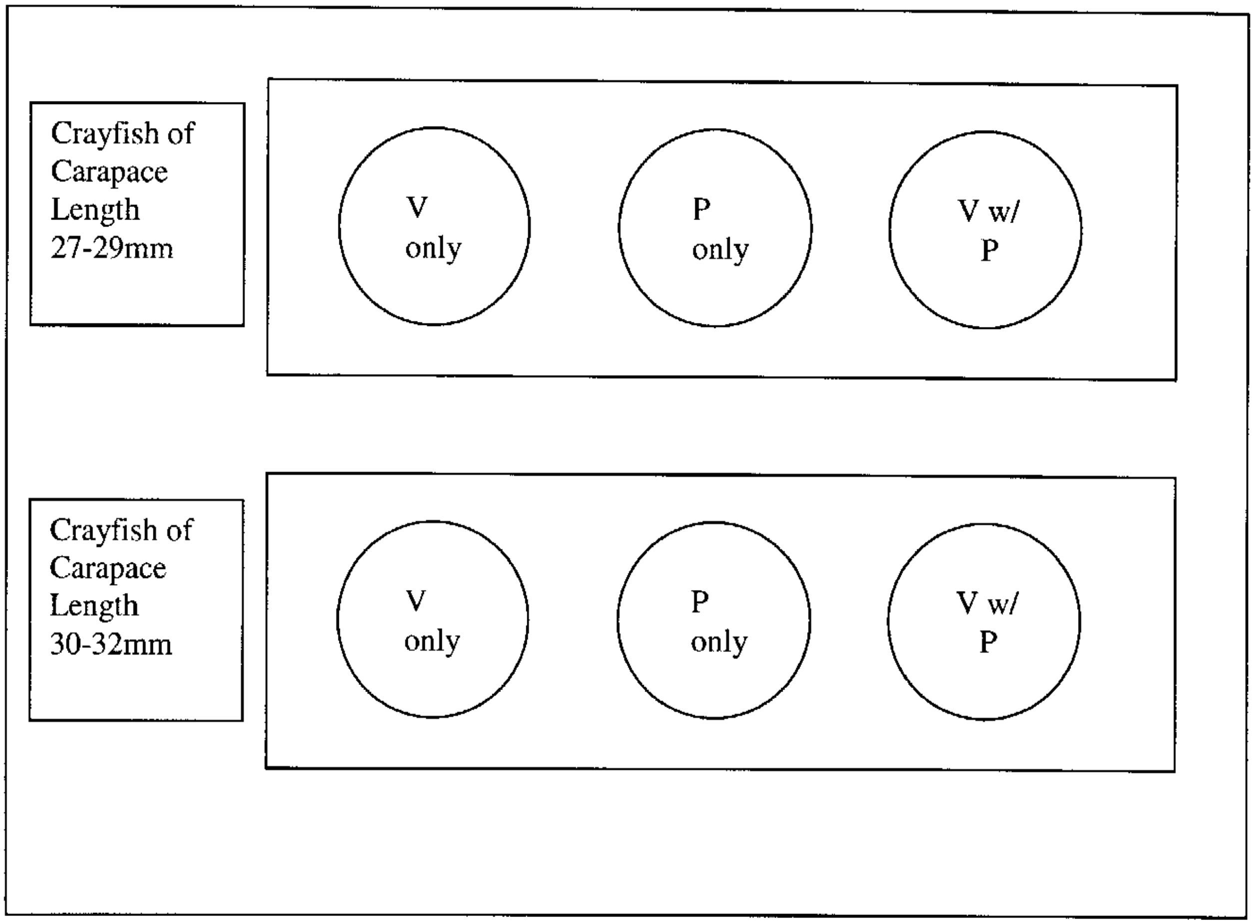


Fig 1: Experimental setup of the 6 outdoor wading pools. Circles represent pools.
V = *O. virilis*   P = *O. propinquus*

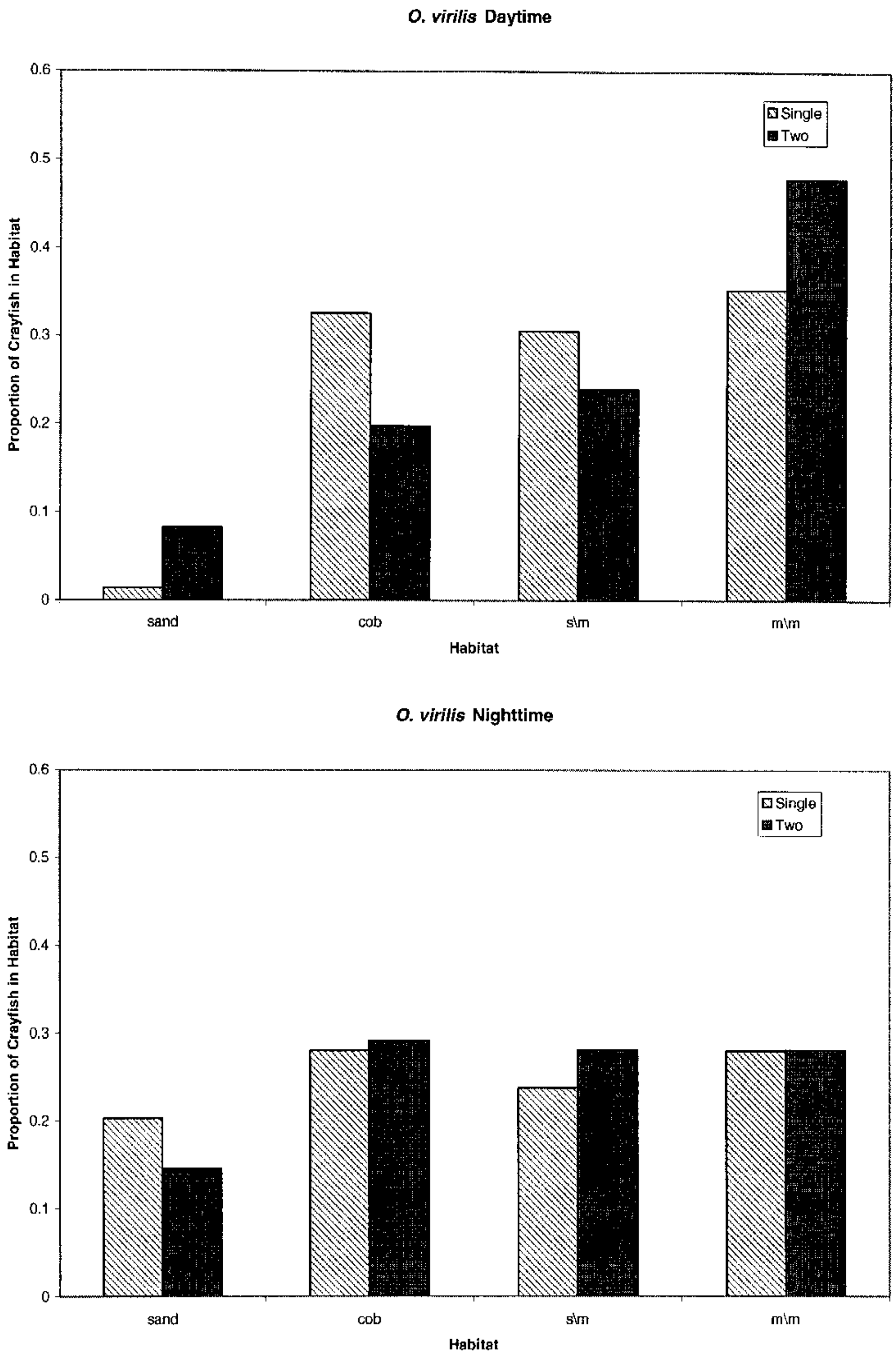
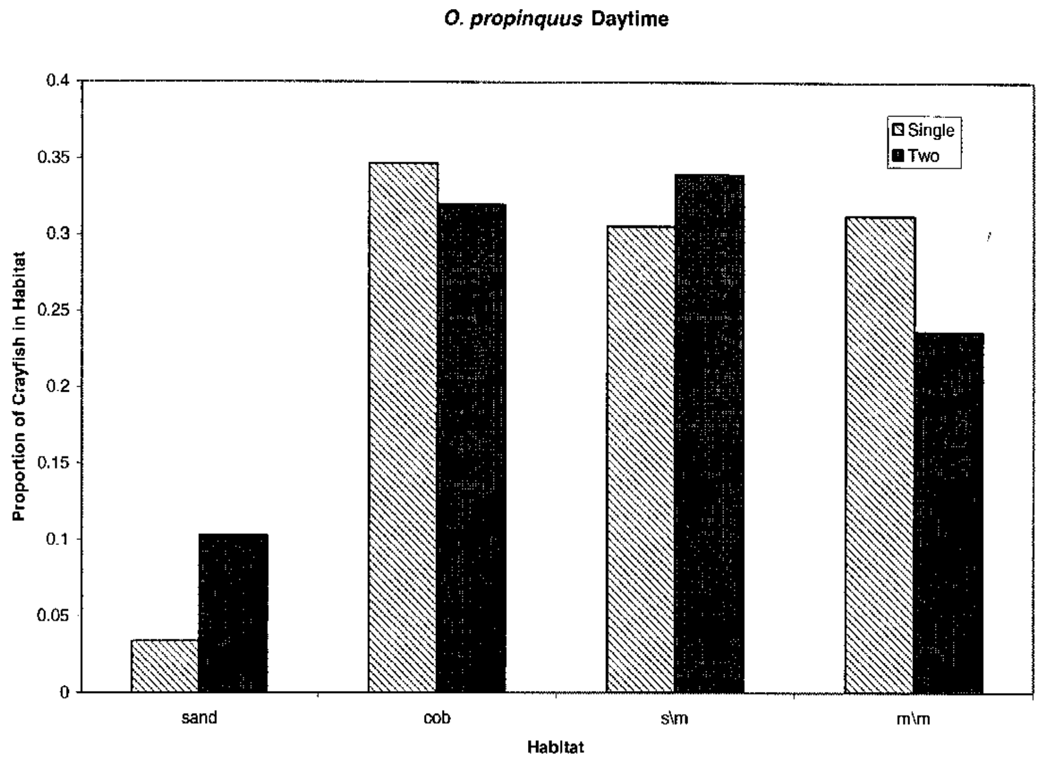


Fig 2: Day- and nighttime distributions of habitat use by *O. virilis*. Habitats were sand, cobble (cob), sand with macrophytes (s\m), and muck with macrophytes (m\m). *O. virilis* significantly decreased its use of the open habitat during the day (G test: $P < 0.001$).



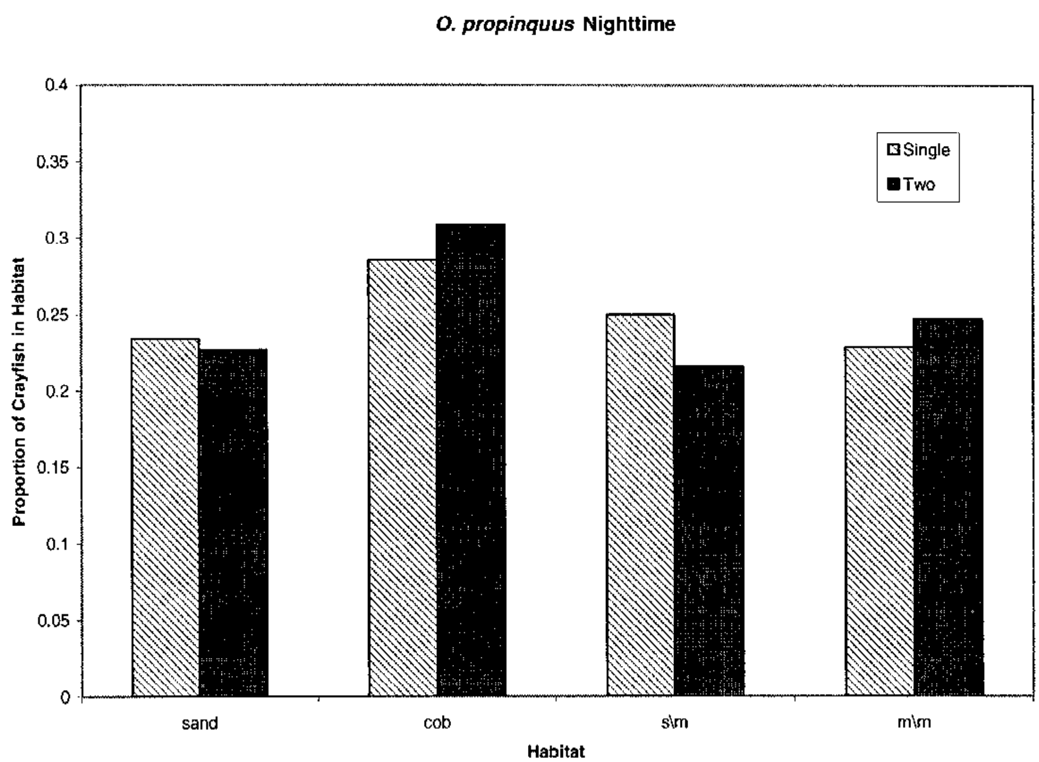


Fig 3: Day- and nighttime distributions of habitat use by *Orconectes propinquus.* Habitats were open sand, cobble (cob), sand with macrophytes (s\m), and muck with macrophytes (m\m). *O. propinquus* significantly decreased its use of the open habitat during the day (G test: $P < 0.001$).

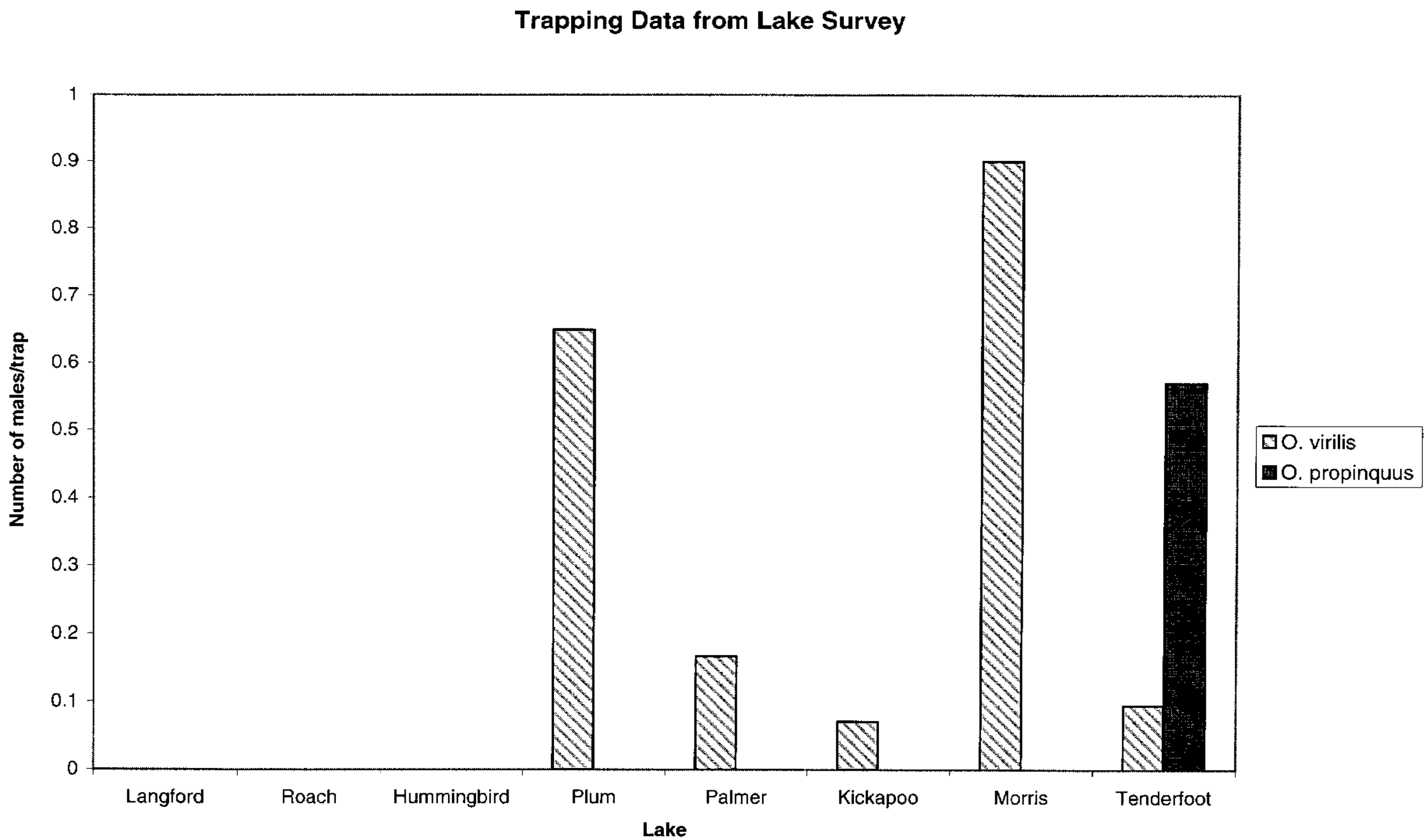


Fig 4: Numbers of *Orconectes propinquus* and *O. virilis* males collected per trap

Erik Oswald Crayfish pools Raw Data ~Lodge

7/17/2002 1200

	Sm Virilis	Sm Prop	Sm Both P	Sm Both V	Lg Prop	Lg Virilis	Lg Both P	Lg Both V
open	0	2	4	0			0	0
macromuck	8	9	3	8			6	7
cobble	8	8	1	2			2	2
macrosand	8	5	4	2			4	3

7/17/2002 1700

	Sm Virilis	Sm Prop	Sm Both P	Sm Both V	Lg Prop	Lg Virilis	Lg Both P	Lg Both V
open	0	0	0	5			0	1
macromuck	10	8	4	2			4	9
cobble	8	10	5	5			3	1
macrosand	6	6	3	0			5	1

7/17/2002 2250

	Sm Virilis	Sm Prop	Sm Both P	Sm Both V	Lg Prop	Lg Virilis	Lg Both P	Lg Both V
open	5	2	5	4	7		2	1
macromuck	7	8	2	4	6		1	4
cobble	5	7	3	1	8		4	4
macrosand	7	7	2	3	3		5	3

7/17/2002 2330

	Sm Virilis	Sm Prop	Sm Both P	Sm Both V	Lg Prop	Lg Virilis	Lg Both P	Lg Both V
open	3	5	1	4	5		4	1
macromuck	5	5	3	4	7		2	4
cobble	7	7	6	3	8		3	2
macrosand	9	7	2	1	4		3	5

7/22/2002 1300

	Sm Virilis	Sm Prop	Sm Both P	Sm Both V	Lg Prop	Lg Virilis	Lg Both P	Lg Both V
open	0	0	0	1	3	1	1	0
macromuck	12	10	3	7	4	8	2	4
cobble	5	7	4	1	8	8	5	4
macrosand	7	7	5	3	9	7	4	4

7/22/2002 1530

	Sm Virilis	Sm Prop	Sm Both P	Sm Both V	Lg Prop	Lg Virilis	Lg Both P	Lg Both V
open	0	0	4	1	0	1	1	0
macromuck	5	9	1	6	5	8	0	3
cobble	10	9	5	1	8	8	6	3
macrosand	9	6	3	4	11	7	5	6

7/22/2002 2145

	Sm Virilis	Sm Prop	Sm Both P	Sm Both V	Lg Prop	Lg Virilis	Lg Both P	Lg Both V
open	4	6	1	2	4	8	4	1
macromuck	8	5	2	1	6	6	5	5
cobble	6	5	5	5	9	8	2	3
macrosand	6	8	4	4	5	2	1	3

7/22/2002 2345

	Sm Virilis	Sm Prop	Sm Both P	Sm Both V	Lg Prop	Lg Virilis	Lg Both P	Lg Both V
open	4	5	3	1	11	5	2	0
macromuck	9	6	7	2	1	5	2	3
cobble	5	6	2	6	5	9	5	4
macrosand	5	7	0	3	7	5	4	5