



Nordic Society Oikos

Differential Dispersal Tendencies among *Enallagma* damselflies (Odonata) Inhabiting Different Habitats

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Source: *Oikos*, Vol. 56, No. 2 (Oct., 1989), pp. 187-195

Published by: Blackwell Publishing on behalf of Nordic Society Oikos

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Differential dispersal tendencies among *Enallagma* damselflies (Odonata) inhabiting different habitats

Mark A. McPeck

McPeck, M. A. 1989. Differential dispersal tendencies among *Enallagma* damselflies (Odonata) inhabiting different habitats. – *Oikos* 56: 187–195.

I examined the propensity and mechanism of dispersal for adults of *Enallagma* species (Odonata: Zygoptera) whose larvae are differentially able to survive in fishless and fish-containing lakes. Two species, found as larvae in fishless lakes, and two species, found as larvae in lakes supporting well-developed fish faunas, dispersed very few adults to adjacent lakes (≤ 1 km apart). Another species, found in winterkill lakes that periodically cycle between the fish-containing and fishless condition, dispersed large numbers of adults to adjacent lakes. The results of mark-release experiments suggested that the species inhabiting fishless lakes cannot discriminate between fishless and fish-containing lakes. Species differences in the propensity to disperse are attributed to the constancy of the fishless and fish-containing condition of the lakes inhabited by species. The mechanisms causing species differences in movement between lakes appear to be differences in their propensity to leave natal lakes, and not active selection of different lake types.

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Introduction

Species obtain different fitnesses in different habitats. Therefore, the mechanisms determining whether and how the individuals of a species move between habitats can be critical to determining their fitnesses (Templeton and Rothman 1981). If organisms are able to select habitats, they should restrict their use to the set of habitats that maximizes their average fitness across habitats (Fretwell and Lucas 1970). Even if organisms cannot discriminate between habitats, mechanisms that reduce dispersal to poor quality habitats should be favored by natural selection.

The larvae of species in the genus *Enallagma* (Odonata: Coenagrionidae) are differentially able to survive in two different habitats, namely lakes that do and do not support fish populations. One group of species is found as larvae only coexisting with fish, while the remaining species are found as larvae only in the absence of fish (Johnson and Crowley 1980, McPeck, in press). Alternative sets of predators in these two habitats are major environmental factors restricting the lar-

vae of these species to only one of the two habitats (McPeck, in press): A number of dragonfly species are predominantly found in fishless lakes, and these predators limit the ability of larvae in one group of *Enallagma* species (those found in lakes containing fish) to survive in fishless lakes. Similarly, fish predation strongly contributes to the exclusion of larvae in the second group of *Enallagma* species (those found in fishless lakes) from lakes containing fish. Dispersal of *Enallagma* among lakes occurs in the adult phase of the life cycle (Corbet 1962, 1980). Natural selection should strongly favor dispersal mechanisms that prevent *Enallagma* adults from dispersing to the wrong habitat.

In this paper I present observational and experimental results examining the propensity and mechanisms of dispersal for *Enallagma* species found in southwestern Michigan, USA. I first present the results of a survey of lakes to characterize the distributions of five species among lakes early in their adult period. I then evaluate whether significant dispersal occurs among lakes by following the species compositions through the flight season at pairs of closely adjacent lakes that have different

Accepted 11 May 1989

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initial species compositions. Finally, I examine the mechanisms of dispersal in observations and experiments performed at a series of small ponds.

Methods

Species composition

I surveyed 21 lakes in Barry and Kalamazoo Counties, Michigan, USA, to determine the adult species composition of early emerging *Enallagma* species (i.e. spring species of Corbet 1962, 1980) at three lake types: 8 fishless lakes, 6 winterkill lakes supporting depauperate fish faunas (fish populations in these lakes periodically are reduced to very low numbers or become extinct, because of low winter oxygen concentrations in some years [Tonn and Magnuson 1982, Rahel 1984, Hall and Ehlinger 1990]), and 7 lakes supporting well-developed fish faunas (e.g., see Hall and Werner 1977, Werner et al. 1977). The locations and major fish species inhabiting these lakes are given in the Appendix. I surveyed the *Enallagma* species composition at each lake during roughly the first week of their adult period (31 May–10 June), by collecting 50–100 adults combined of all *Enallagma* species while slowly wading >50 m of shoreline in two areas of each lake. Lakes were sampled on sunny, relatively windless days between 1300–1730 hours. Quantitative sampling of larvae in a subset of these lakes demonstrated that larvae of each species were associated with only one lake type (McPeck, in press). Therefore, the distributions of adults immediately following emergence should strongly reflect the larval composition of a lake. All adults were identified to species according to Walker (1953).

Dispersal between pairs of lakes

I next examined if significant dispersal occurred between lakes by following the *Enallagma* species composition at three pairs of lakes through the flight season. Dispersal between pairs of lakes with different species compositions would be expressed as a change in adult species composition at one or both of the lakes through time. I chose pairs of lakes in which one contained fish and one was fishless. The lakes of one pair, Turkey Marsh (fishless) and Duck Lake (winterkill), were 1.0 km apart. The lakes of the second pair, Marshfield Rd. Marsh (fishless) and Sheffield Rd. Marsh (winterkill), were 0.2 km apart. The lakes of the third pair, Deep Lake Marsh (fishless) and Deep Lake (well-developed fish fauna), were 0.6 km apart. The lakes in a pair were chosen so that they were nearest neighbors. Little is known about the flight abilities of *Enallagma* adults. However, *Enallagma* adults have been found up to 2.7 km from source populations (Moore 1954), indicating that the distances between these pairs of lakes were not prohibitive to dispersal by *Enallagma*.

To estimate the relative abundances of species at each

lake, I collected adults from two areas at each lake on three different dates. The first date was within one week of emergence of adults, the second date was in the middle of the adult period for species considered in this paper, and the third date was approximately one week before all adults of the species considered in this paper had died. (No adults of the five species discussed in this paper were observed in counts of adults made 1–2 wk after the last date.) Lakes were censused on sunny, relatively windless days between 1300–1730 hours.

A contingency table of the number of each species captured on each census date was constructed for each lake. To increase cell frequencies I pooled the counts for *E. boreale* Selys and *E. cyathigerum* (Charpentier) for analysis. Each contingency table was analyzed using the G-statistic (Sokal and Rohlf 1981) to test the hypotheses of no change in the relative abundances of the species over the three census dates at each lake. Only the contingency tables for Marshfield Rd. Marsh and Turkey Marsh could be tested, because of the large number of cells with zero counts in the tables for the other four lakes.

Experiments on dispersal

I found very few adults of four *Enallagma* species moving between lakes in observations of pairs of lakes just described (see below). Two mechanisms can potentially explain why these species did not move between the lakes in a pair: (1) adults of these four species can discern whether or not a lake contains fish, and they only remain at lakes in which their offspring can survive as larvae, or (2) adults of these four species rarely disperse away from their natal lake.

I evaluated these two mechanisms for *E. boreale* and *E. cyathigerum* populations inhabiting the ponds at the Kellogg Biological Station Pond Laboratory by determining if these species were more abundant at fishless ponds than at ponds containing fish throughout their adult period, and by evaluating the ability of these species to discriminate between fishless and fish-containing ponds. Fishless ponds at the Pond Laboratory are similar to natural fishless habitats, and support large populations of both *E. boreale* and *E. cyathigerum* (McPeck, in press). *E. ebrium* (Hagen) inhabit ponds containing fish, but *E. ebrium* adults also immigrate to the Pond Laboratory from nearby Duck Lake. To test if the *E. boreale* and *E. cyathigerum* adults were more abundant over fishless ponds, I censused two pairs of adjacent ponds that were similar in most respects, except that one pond of each pair contained 300–400 bluegill sunfish (*Lepomis macrochirus* Rafinesque) and the other did not. Each fish pond had contained fish for ≥ 2 yr. The ponds of one pair (ponds 15 and 16) were 6.5 m apart, and each was 27 m in diameter with cattails (*Typha latifolia* L.) growing along most of the shoreline of each pond. Ponds of the second pair (ponds A and B)

Tab. 1. *Enallagma* species present at lakes surveyed in Barry and Kalamazoo Counties, Michigan, USA. The locations and major fish species inhabiting these lakes are given in the Appendix.

	<i>E. boreale</i>	<i>E. cyathigerum</i>	<i>E. ebrium</i>	<i>E. geminatum</i>	<i>E. hageni</i>
<i>Fishless</i>					
Turkey Marsh	×	×			
Yorkshire Rd. Pond		×			
Marshfield Rd. Marsh	×	×			
Long Woods Pond	×	×			
Manning Rd. Marsh	×				
Deep Lake Marsh	×	×			
Duck Marsh	×	×			
Otis Lake Marsh	×	×			
<i>Winterkill</i>					
Duck Lake			×		
Sheffield Rd. Marsh			×		
Wintergreen Lake			×		
Long Swale Pond			×		
Pond Lily Pond			×		
Otis Lake			×		
<i>Fish</i>					
3 Lakes II			×	×	×
3 Lakes III			×	×	×
Lawrence Lake				×	×
Palmatier Lake				×	×
Dunn Lake				×	×
Hamilton Lake				×	×
Deep Lake				×	×

were 9 m apart, and each was 31 m in diameter with one clump of small willows on the shoreline.

I censused the ponds by slowly walking around each pond and recording the number of *Enallagma* adults flying over and perched on vegetation at the edge of each pond. Ponds were censused on sunny, relatively windless days at roughly one week intervals, and all ponds were censused on the same day. I could not discriminate between *E. boreale*, *E. cyathigerum* and *E. ebrium* in these visual counts: these species are only distinguishable by examining the anal appendages of males and the mesostigmal plates of females under magnification. Therefore, I made collections of the three species immediately following the census of each pond to assess relative abundances at each pond. The number of adults for each species was calculated by multiplying the total number of adults counted at the pond by the relative abundance of each species in the collection. A contingency table of the calculated number of adults at each pond in a pair on each census date was constructed for each species. I analyzed each contingency table (6 total: 3 species at two pairs of ponds) using the G-statistic (Sokal and Rohlf 1981) to test the hypotheses that adults of each species were equally abundant at both ponds in a pair throughout its adult period.

To evaluate if *E. boreale* and *E. cyathigerum* can distinguish between fish-containing and fishless ponds, I performed two mark-release experiments at ponds A and B. This pair was chosen because the *Enallagma* were easier to census due to the lack of *Typha*. The first

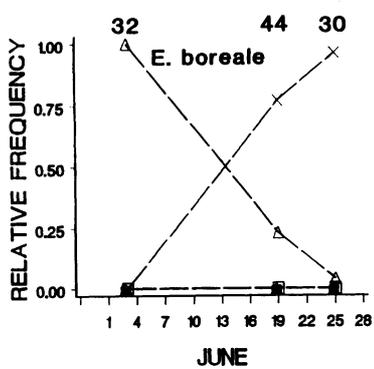
release was performed on 18 June 1986, and the second on 20 June 1986. Immediately before releasing the adults for the second experiment, I censused the two ponds for marked adults released in the first experiment, and found none. I collected 87 males of the two species for the first release and 94 male for the second release. Males were collected at Turkey Marsh and each was marked with a large black spot of indelible ink on the base of each wing. The marks were easy to see at a considerable distance when a male was resting on a plant stem or flying. The marked males were placed in a small frame box covered with mosquito netting and released midway between the two pond. Marked males were then recounted at 45 min intervals the first day and 30 min intervals the second day until all flight activity ceased for that day.

Results

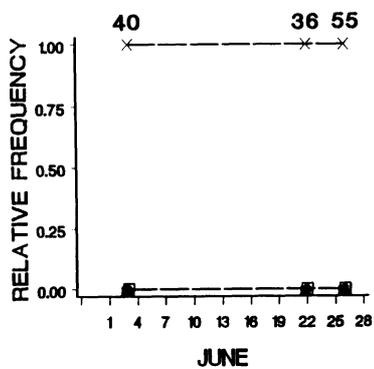
Species composition

Adults of five *Enallagma* species dominated the collections (Tab. 1). A number of other *Enallagma* species were either very rare or emerged later in the summer, and therefore are not reported here. *Enallagma boreale* and *E. cyathigerum* were found exclusively at fishless lakes, and both species were found together at most fishless lakes. *E. geminatum* Kellicott and *E. hageni*

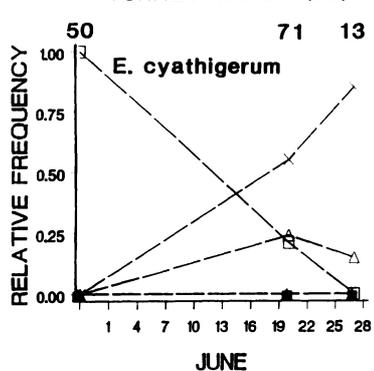
MARSHFIELD RD. MARSH (FL)



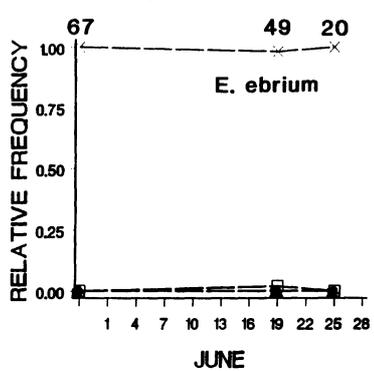
SHEFFIELD RD. MARSH (WK)



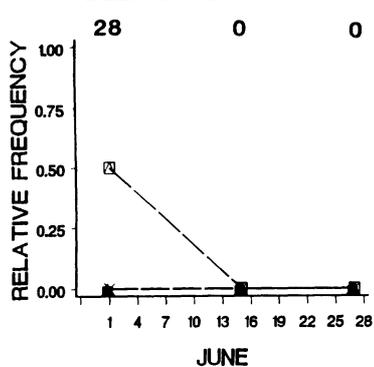
TURKEY MARSH (FL)



DUCK LAKE (WK)



DEEP LAKE MARSH (FL)



DEEP LAKE (FI)

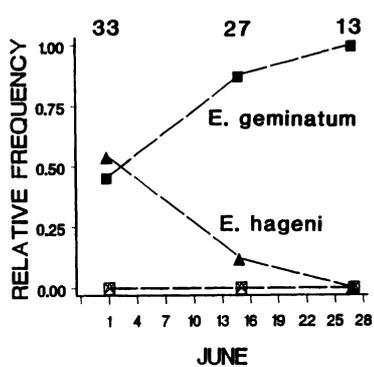


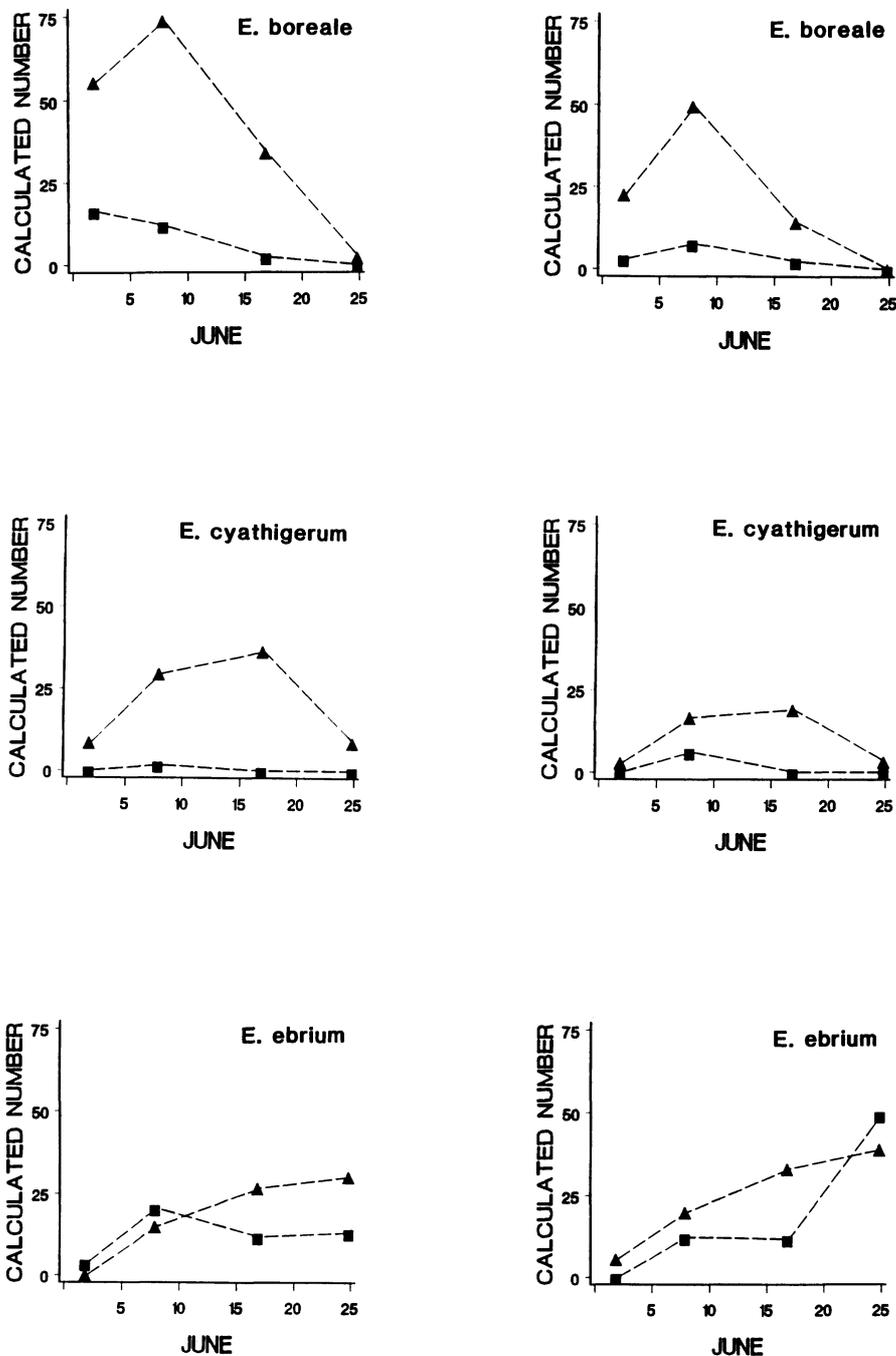
Fig. 1. The relative abundances of five *Enallagma* species found at three pairs of lakes in southwestern Michigan, USA. The two lakes in a pair are in the same row in the figure. The abbreviations in parentheses after the lake names are for fishless (FL), winterkill (WK), and well-developed fish fauna (FI). The symbols for species are as follows: *E. boreale* open squares, *E. cyathigerum* open triangles, *E. ebrium* ×, *E. geminatum* closed squares, *E. hageni* closed triangles. The number above each date is the number of adults collected to determine the relative abundances of species at that lake for that day.

Walsh were found exclusively at lakes supporting well-developed fish faunas, and both species were found at all of these lakes. *E. ebrium* was the only species of these five found at winterkill lakes. *E. ebrium* was also found at two lakes supporting well-developed fish faunas.

Dispersal between pairs of lakes

The relative frequencies of the five species at the six lakes are given in Fig. 1. I could detect no movement of adults between Deep Lake and Deep Lake Marsh. All *E. boreale* and *E. cyathigerum* adults died before the

Fig. 2. The calculated numbers of the three *Enallagma* adults flying at two pairs of ponds at the KBS Pond Laboratory. The numbers of *E. boreale*, *E. cyathigerum* and *E. ebrium* were calculated by multiplying the total number of *Enallagma* counted at a pond by the relative abundance of each species in the collections of adults made immediately after the counts. The triangles are the number at the fishless pond of the pair, and the squares are the number at the fish pond of the pair. The figures in the left column are for ponds A and B, the figures in the right column are for ponds 15 and 16.



second census date at Deep Lake Marsh, but I found no *E. hageni* or *E. geminatum* adults at Deep Lake Marsh on two subsequent census dates. Also, *E. ebrium* was essentially the only species captured at the two winterkill lakes on all census dates, indicating that substantial numbers of *E. boreale* and *E. cyathigerum* did not move between lakes. (One *E. boreale* was captured at Duck Lake out of 267 total *Enallagma* captured at the two winterkill lakes.)

However, the adult species composition changed dramatically over the two fishless lakes that were paired with winterkill lakes. Relative frequencies of *E. boreale* and *E. cyathigerum* steadily declined over their adult periods, and by the last census date *E. ebrium* constituted 95% of the adults captured at Marshfield Rd. Marsh ($G = 35.34$, $df = 2$, $P < 0.001$) and 85% at Turkey Marsh ($G = 27.54$, $df = 2$, $P < 0.001$).

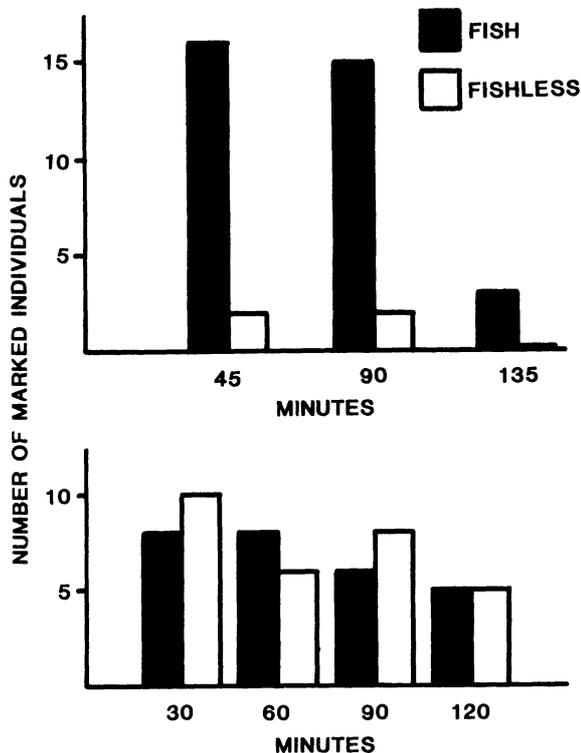


Fig. 3. The number of marked *E. boreale* and *E. cyathigerum* adults counted at the fish and fishless pond after release in the mark-release experiment. The upper figure is the release performed on 18 June, and the lower figure is the release performed on 20 June.

Experiments on dispersal

The distributions of the three *Enallagma* species at the two pairs of experimental ponds were similar to the distribution observed at natural lakes (Fig. 2). Both *E. boreale* and *E. cyathigerum* were consistently more abundant at the fishless pond of each pair on every date (*E. boreale* – ponds A and B, $G = 115.04$, $df = 3$, $P < 0.001$; ponds 15 and 16, $G = 61.44$, $df = 3$, $P < 0.001$; *E. cyathigerum* – ponds A and B, $G = 85.42$, $df = 3$, $P < 0.001$; ponds 15 and 16, $G = 32.88$, $df = 3$, $P < 0.001$). Although *E. ebrium* showed significant differences in the numbers of adults at ponds in a pair (ponds A and B, $G = 16.88$, $df = 3$, $P < 0.001$; ponds 15 and 16, $G = 19.14$, $df = 3$, $P < 0.001$), *E. ebrium* was not consistently more abundant at one of the ponds.

The results of the mark-release experiments did not support the hypothesis that *E. boreale* and *E. cyathigerum* can distinguish between ponds with and without fish (Fig. 3) During the first experiment, a consistent breeze was blowing toward the pond containing fish and most adults flew toward this pond when released. However, the number of marked adults at each pond was consistent through the rest of the day (a Fisher's Exact Test for differences in the number at the two ponds in the first two observation times gives $P = 0.64$). Individ-

uals which had settled at the pond containing fish showed no tendency to move to the fishless pond. The day after the first release I saw two marked adults at the pond with fish, and no marked adults at the fishless pond. During the second experiment, no wind blew for the first 4 min after release. The number of adults at each pond was nearly equal throughout the entire count period ($G = 0.62$, $df = 3$, $P > 0.80$). The day after the second release I saw no marked adults at the pond with fish, and one marked adult at the fishless pond.

Discussion

Larvae of the five species considered in this study are able to survive only in the presence or absence of fish: *Enallagma boreale* and *E. cyathigerum* in the absence of fish, and *E. hageni*, *E. geminatum* and *E. ebrium* in the presence of fish. Predation by large dragonflies in fishless lakes and predation by fish in lakes containing fish are two major factors maintaining the *Enallagma* larval distributions (McPeck, in press): When simultaneously offered larvae of two *Enallagma* species in the laboratory, one from the fishless lake group and one from the fish-containing lake group, dragonflies consumed more individuals of the species from the fish-containing lake group, but fish consumed more individuals of species from the fishless lake group. The results of field experiments in which I transplanted *Enallagma* species between the lake types showed that fish and large dragonflies impose much greater mortality on species with which they do not coexist than on coexisting species. Therefore, the fitness of *Enallagma* individuals will be strongly influenced by mechanisms determining the lakes in which they oviposit.

Both the species found as larvae in fishless lakes and the species found as larvae in lakes with well-developed fish faunas appear to be strongly philopatric. During this study, I found only one *E. boreale* male at a lake containing fish, and no *E. cyathigerum*, *E. hageni* or *E. geminatum* at the lake type in which their larvae cannot survive. Moreover, only limited exchange occurs between ponds less than 10 m apart (Fig. 2). The results of the mark-recapture experiments suggested that these species cannot distinguish between fish-containing and fishless lakes. Individuals of these species apparently limit their dispersal between lakes by simply remaining at their natal lakes. This mechanism of limiting dispersal has also been observed in other damselfly species (Johnson 1966, Utizeri et al. 1976, Banks and Thompson 1985).

Both lakes supporting well-developed fish faunas and fishless lakes are constant in general ecological conditions through time in the absence of human intervention. Fishless lakes in southwestern Michigan are primarily those which do not have stream inlets or outlets to serve as channels of colonization for fish (M. A. McPeck, pers. obs.), and fish populations in lakes supporting well-developed fish faunas remain relatively sta-

ble through time (Mittelbach 1984). Dispersal away from those lakes may come at a high cost. Mortality of *Enallagma* adults is much higher for adults that move away from a lake to forage than for adults remaining at the lake (Anholt 1988), suggesting that adults dispersing between lakes may have a much lower probability of surviving to reproduction than nondispersers. In addition, because adults cannot distinguish fish-containing from fishless lakes, adults surviving dispersal will often settle at lakes of the wrong type. Therefore, remaining at natal lakes where ecological conditions will probably not change dramatically should be favored by natural selection in the face of the potentially high costs of dispersal (Hastings 1983, Levin et al. 1984, Holt 1985).

In contrast, *E. ebrium*, which disperses substantial numbers of adults away from natal lakes, inhabits a lake type in which dramatic ecological changes occur periodically. In winterkill lakes, fish populations are periodically reduced to very low numbers or go extinct, because of low winter oxygen concentrations (Tonn and Magnuson 1982, Rahel 1984, Hall and Ehlinger 1990). Little is known about the changes in the invertebrate community caused by these reductions in the fish densities, but we can speculate about how ecological conditions may quickly change to the "fishless" condition. Large dragonflies characteristic of fishless lakes, such as *Anax*, *Aeshna* and *Tramea* species, oviposited in all lakes included in this study regardless of the presence or absence of fish (M. A. McPeck, unpubl. data). In years when fish populations are greatly reduced due to low winter oxygen concentrations, these dragonflies may survive and build up large populations, similar to those in fishless lakes. As the fish populations recover in subsequent years, these dragonfly species will be greatly reduced or eliminated from the lake (Hall et al. 1970, Crowder and Cooper 1982), restoring the ecological conditions normally associated with a lake containing fish.

If winterkill lakes do periodically cycle between the fishless condition in which large dragonfly predators dominate and fish-containing conditions in which fish predators dominate, natural selection should favor individuals of *E. ebrium* that disperse a fraction of their offspring away from natal lakes each generation. *E. ebrium* larvae, like the larvae of *Enallagma* species inhabiting lakes with well-developed fish faunas, appear to be unable to coexist with large dragonflies characteristic of the fishless condition. *E. ebrium* larvae do coexist with fish in winterkill lakes (M. A. McPeck, pers. obs.). Moreover, although I saw many *E. ebrium* females oviposit in Marshfield Rd. Marsh and Turkey Marsh during this study, I have not found *E. ebrium* larvae in these fishless marshes. Some non-zero rate of dispersal away from natal lakes may be favored for *E. ebrium*, because some dispersers may recolonize lakes in which *E. ebrium* populations have been greatly reduced or become extinct, and because some dispersing offspring of individuals may survive to reproduce when winterkill of

fish populations changes a lake to the fishless condition (Van Valen 1971, Roff 1974a,b, Comins et al. 1980). The fraction of offspring dispersed each generation should be proportional to the frequency with which winterkill lakes in a region cycle between the fishless and fish-containing condition (Levin et al. 1984).

Differences in the propensity to disperse may help explain species compositional differences between winterkill lakes and lakes supporting well-developed fish faunas (Tab. 1). *E. geminatum* and *E. hageni* were not found at winterkill lakes, although their larvae survive in the presence of fish. Because of their low propensity to disperse, they would have difficulty recolonizing these lakes after becoming extinct. Usually only 1–2 of the eight *Enallagma* species that inhabit lakes supporting well-developed fish faunas (see McPeck, in press, for a complete list) are found along with *E. ebrium* in winterkill lakes, while all eight species can usually be found in any given lake supporting a well-developed fish fauna (M. A. McPeck, unpubl. data). On the other hand, *E. ebrium* was found at only two of the seven lakes supporting well-developed fish faunas. Once *E. ebrium* colonizes one of these lakes, its relative abundance may continually decline because it disperses a large fraction of its population each generation, while the other species do not.

Variation in ecological conditions also appears to play a key role in affecting the dispersal tendencies of other insect groups. Species in many orders of insects have two wing morphs, a macropterous morph with large, functional wings, and a brachypterous morph with greatly reduced wings and associated muscles (see Harrison 1980 and Roff 1986 for reviews). The frequency of the two morphs in populations is thought to reflect the stability of the habitat, with the frequency of the macropterous morph being higher in temporally variable habitats because of its greater dispersal abilities, and the frequency of the brachypterous morph being higher in temporally constant habitats because of its greater reproductive output (Harrison 1980, Roff 1986, Kaitala 1988). Brachypterous morphs are probably not found in *Enallagma* species exhibiting limited dispersal, because flight is an integral part of courtship and mating in the Odonata (Corbet 1962, 1980): modification of morphological structures associated with flight is apparently not required to alter the rate of dispersal between habitats (cf. Fairbairn 1986). However, the key role that variation in ecological conditions may play in influencing the behavioral characters affecting the propensity of *Enallagma* adults to disperse from their natal lake warrants further study.

Acknowledgments – The research presented in this paper was submitted as part of a dissertation in partial fulfillment of the degree of Doctor of Philosophy at the Dept of Zoology, Michigan State Univ. I want to thank the members of my doctoral committee, D. Hall, S. Kalisz, R. Merritt, G. Mittelbach, D. Wilson, and especially E. Werner, for guidance during all phases of this research. This paper was greatly improved by the

comments of D. Hall, S. Kalisz, G. Mittelbach, K. Vepsäläinen, E. Werner and C. Wiklund. I want to especially thank Gail McPeck for assistance during the entire project. I was supported by a National Science Foundation Graduate Fellowship, a Barnett Rosenberg Fellowship (MSU), a College of

Natural Sciences Continuing Fellowship (MSU), and Grants-in-Aid of Research from Sigma Xi, The Scientific Society, and the Theodore Roosevelt Memorial Fund of the American Museum of Natural History. This is contribution #659 of the W. K. Kellogg Biological Station.

Appendix. Locations of water bodies and major fish species inhabiting each.

	County	Location*	Major fish species ⁺
<i>Fishless</i>			
Turkey Marsh	Kalamazoo	T.1S: R.9W: S.6	None
Yorkshire Rd. Pond	Kalamazoo	T.1S: R.9W: S.30	None
Marshfield Rd. Marsh	Barry	T.1N: R.9W: S.31	None
Long Woods Pond	Kalamazoo	T.1S: R.9W: S.8	None
Manning Rd. Marsh	Barry	T.1N: R.8W: S.6	None
Deep Lake Marsh	Barry	T.3N: R.10W: S.23	None
Duck Marsh	Barry	T.3N: R.10W: S.34	None
Otis Lake Marsh	Barry	T.3N: R.10W: S.6	None
<i>Winterkill</i>			
Duck Lake	Kalamazoo	T.1S: R.9W: S.5	Lm, Lc, Ul
Sheffield Rd. Marsh	Barry	T.1N: R.9W: S.31	Lm, Ul
Wintergreen Lake	Kalamazoo	T.1S: R.9W: S.8	Lg, Nc, Pf
Long Swale Pond	Kalamazoo	T.1S: R.9W: S.8	Lg, Nc
Pond Lily Pond	Kalamazoo	T.1S: R.9W: S.32	Pp
Otis Lake	Barry	T.3N: R.9W: S.31	Lg, Ul, Pp, Nc
<i>Fish</i>			
3 Lakes II	Kalamazoo	T.1S: R.9W: S.25	Lm, Lg, Ms
3 Lakes III	Kalamazoo	T.1S: R.9W: S.25	Lm, Lg, Ms
Lawrence Lake	Barry	T.1N: R.9W: S.27	Lm, Lg, Ms
Palmatier Lake	Barry	T.2N: R.10W: S.12	Lm, Lg, Ms
Dunn Lake	Barry	T.1N: R.8W: S.23	Lm, Lg, Ms
Hamilton Lake	Kalamazoo	T.1S: R.9W: S.1	Lm, Lg, Ms
Deep Lake	Barry	T.3N: R.10W: S.26	Lm, Lg, Ms

* Michigan township range section designation.

⁺ Abbreviations for major fish species found in each lake are as follows: Lm *Lepomis macrochirus*, Lg *L. gibbosus* (L.), Ms *Micropterus salmoides* (Lacépède), Ul *Umbra limi* (Kirtland), Nc *Notemigonus crysoleucas* (Mitchill), Pf *Perca flavescens* (Mitchill), Pp *Pimephales promelas* Raf.

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