Journal of Insect Conservation **6:** 47–55, 2002.

Habitat requirements and local persistence of three damselfly species (odonata: coenagrionidae)

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Received 12 June 2001; accepted in revised form 15 October 2001

Key words: Damselfly, *Enallagma*, Extinction, Habitat requirements, Population persistence

Abstract

Habitat requirements and population persistence were investigated in three damselfly species, all coastal plain pond specialists: *Enallagma recurvatum, E. laterale*, and *E. pictum*. Because of geographic restriction, two are of special concern to conservation, *E. recurvatum* and *E. laterale*. We surveyed more than 70 ponds on Cape Cod, Massachusetts, and collected adult presence-absence data during the summers of 1999 and 2000. We achieved a detection rate approaching 100% for each species by visiting each pond up to three times. We looked for relationships between the presence of each damselfly species and presence of specific aquatic vegetation, the presence of the other *Enallagma* species, and the number of ponds within various distances of the 72 surveyed ponds. Using stepwise logistic regression, we found the following significant associations: *E. recurvatum* with the rush *Juncus militaris*; *E. laterale* with water lilies (*Nuphar variegatum* and *Brasenia schreberi*) the damselfly *E. pictum*, and the number of ponds within 2 km; and *E. pictum* with the water lily *Nymphaea odorata*, the damselfly *E. laterale*, and the number of ponds within 1.5 km and 2.5 km. Presence-absence data were used to calculate turnover and local extinction rates for each species between the two years. *E. recurvatum*'s turnover and local extinction rates (33.3% and 41% respectively) were much higher than either *E. laterale* (9.8%, 11.5%) or *E. pictum* (7.7%, 10%). These results suggest that *E. recurvatum* occurs in a metapopulation, and that patch colonization rates might be important to local population persistence.

Introduction

In general, species possess certain habitat requirements that contribute to site occupancy, and the frequency of occurrence of these specific habitats contributes to the distribution of a species (MacArthur 1972). Consequently, if the required habitat type is uncommon, then a species depending on that habitat also will be uncommon. Rabinowitz (1981) used three characteristics of a species to define its rarity: geographic range, habitat specificity, and local population size. She considered all species except those with a large geographic range, that are habitat generalists, and have relatively large local population size to be rare in one way or another (Rabinowitz 1981). A species' vulnerability to extinction depends, in part, on how a species is rare (Rabinowitz 1981; Reed 1992). Species that depend on uncommon, patchily distributed habitat are at risk from isolation and local extinction, particularly when habitat is being lost (Brown and Kodric-Brown 1977; Tilman et al. 1994; Tischendorf and Fahrig 2000). If patches occur in close proximity, it is possible for individuals to move among patches, decreasing isolation and reducing the risk of permanent extinction from a habitat. Such an arrangement of populations is termed a metapopulation (Hanski and Gilpin 1991), and dispersal among populations is important to persistence (Harrison 1991).

If a species occurs as a metapopulation, local extinction can be offset by colonization from neighboring populations. This allows metapopulation persistence although individual patches experience turnover. To identify a metapopulation, several conditions must be met: habitat patches must be able to support individuals, each population must be small enough to have a finite risk of extinction, dispersal between neighboring habitats must exist, and local dynamics are asynchronous (Hanski et al. 1995). Information on extinction risk and dispersal abilities of a species can help guide land management decisions to increase species persistence (Hanski and Gilpin 1991). Also, if a species exists as a metapopulation, it would require managing for a suite of sites connected by dispersal, rather than for a single isolated site, to ensure long-term persistence of that population (Harrison 1993).

We studied habitat requirements and population persistence of three *Enallagma* damselflies: *E. recurvatum* Davis, *E. laterale* Morse, and *E. pictum* Morse. Our goals for this study were to determine the type of aquatic vegetation associated with each damselfly species, to document local turnover and extinction rates from ponds, and to determine whether or not these species occur as metapopulations. Results from this work will be important for developing successful conservation plans, particularly because coastal plain ponds are threatened by human activities (Barbour et al. 1998; Sorrie 1994; Swain 1996).

Characteristics of the study system

Our study species, *Enallagma recurvatum* Davis, *E. laterale* Morse, and *E. pictum* Morse belong to the family Coenagrionidae, the largest and most diverse damselfly family, and inhabit ponds containing floating and emergent aquatic vegetation (Carpenter 1991; Westfall and May 1996). We chose them for study because they are geographically restricted to the northeastern United States and they are strict habitat specialists to coastal plain ponds. Two of the three species have been designated as being of conservation concern in Massachusetts. *E. recurvatum* (Pine Barrens Bluet) was considered to be state extirpated until 1986, when several populations were discovered on Cape Cod (Carpenter 1986). This species and *E. laterale* (New England Bluet) are threatened with a state rarity status of S2/S3 (Kearsley 1999). Both species are state listed because of their limited geographic distribution (Natural Heritage and Endangered Species Program 1995). *E. pictum* (Scarlet Bluet) is not state-listed, but was included in this study because it shares the same general habitat specificity as *E. recurvatum* and *E. laterale*, while experiencing a more limited geographic range.

The three damselfly species studied here are coastal plain pond specialists. Coastal plain ponds are shallow, acidic glacial outwash ponds, usually with no inlet or outlet (Sorrie 1994). These ponds are typically linked directly to the underlying groundwater that maintains the pond (Sorrie 1994; Kearsley 1999). As a result, water levels drop during the summer and fall, and rise during the winter and spring, seasonally flooding the pond shore (Sorrie 1994; Whitelaw et al. 1989). Many plants are adapted to this seasonal change in water level (Theall 1983; Swain 1996; Schneider 1994) and the seasonal flooding of the pond shore maintains the plant community (Swain 1996). If groundwater is removed, pond water levels cannot recover during the winter, and the pond shore will experience an extended drought. This drought allows invasive plant species to colonize the pond shore habitat and push out native, coastal plain pond specialists (Keddy and Reznicek 1982, 1986). Alteration of the plant community by changing the natural flood regime of a pond would affect the ability of the damselflies to inhabit a site because aquatic vegetation is necessary for oviposition (Carpenter 1991). Thus, altering the plant community structure of a pond is analogous to habitat loss for *Enallagma* damselflies. Coastal plain pond habitat is limited to the Atlantic Coastal Plain (Carpenter 1991). New England contains a large number of these habitats, with the greatest concentration occurring in southeastern Massachusetts and southern Rhode Island (Sorrie 1994). We selected Cape Cod as our study area because of the abundance of habitats suitable for *E. recurvatum, E. laterale*, and *E. pictum*. The main threat to these damselflies is habitat loss (Rawinski and Price 1994), which on Cape Cod occurs through the removal of groundwater via wells (Barbour et al. 1998).

Methods

In 1999 and 2000 we surveyed 72 ponds throughout Cape Cod to identify sites used by *E. recurvatum* and *E. laterale*. Surveys were done in June, which corresponds to the flight season for these species (Carpenter 1991). After consulting topographical maps of the region, these ponds were selected from over 150 on the Cape based on proximity to other ponds and accessibility to the investigators. We documented presence or absence for each damselfly species in each of two years as well as aquatic vegetation species presence or absence at each pond. In July, during the flight season of *E. pictum*, we resurveyed the same 72 ponds as well as four additional ponds. To minimize detection error, each pond was visited up to three times each month with visits stopped once the target species were recorded. Both *E. recurvatum* and *E. laterale* are fairly abundant where they occur (Carpenter 1991), and therefore have high probabilities of detection. *E. pictum*, while not as abundant, is easily distinguishable due to its red coloration. Therefore, we assumed, and observed, that all three species have high probabilities of detection. Visiting each pond up to three times lowered the probability of making a Type I error (concluding a species is absent when it is not) (Reed 1996).

Sampling generally occurred between 0900 and 1700, which corresponds to the daily activity times for these damselflies (LKG, personal observation). Searches for adults were conducted along the pond shore vegetation and in vegetation within the pond. Adult males were captured using an aerial insect net and identified by examining the terminal appendages through a hand lens (Westfall and May 1996). It has been suggested that the minimum amount of time needed to survey for *E. recurvatum* and *E. laterale* where these species are not common is 37 minutes (deMaynadier and Hodgman 1998). On average, 45 min (range 10 – 90 min) was spent surveying a site. Since detection of one of these species usually occurred within 30 min if the species was present, this seemed a sufficient amount of time to spend at a pond.

While surveying ponds for *E. pictum* in July, the aquatic and pond shore vegetation of the pond was recorded. Aquatic vegetation is the flora found in the water of the pond, either floating (e.g. water lilies) or emerging from the water (e.g. rushes, reeds) (Sculthorpe 1967). These plants typically have their roots constantly submerged. Plants were identified to species, and visual estimates of cover area of aquatic vegetation were made.

Data were analyzed using contingency χ^2 and logistic regression. Three 5×2 contingency tables were set up, one for each damselfly species, to examine the association between damselfly and aquatic vegetation presence. The columns represented either the presence or absence of the damselfly species, and the rows were categories of aquatic vegetation: emergent vegetation (e.g. *Juncus militaris*) only, floating vegetation (e.g. water lilies) only, emergent and floating vegetation, other kinds of emergent vegetation (not *J. militaris*), and no emergent vegetation. Stepwise logistic regressions (SAS 1990) also were performed to compare the presence of one damselfly species to several variables. This was done to determine whether a particular variable could be used as a diagnostic indicator for predicting the presence of a damselfly species at a pond. Variables included in the analysis were presence of specific aquatic vegetation (both emergent and floating vegetation), presence of the other two damselfly species, pond area, approximate cover of aquatic vegetation, distance to the closest pond, distance to the closest surveyed pond, and number of ponds within certain distances of a site. For this final variable, using only those ponds with emergent and/or floating vegetation, the number of ponds within concentric rings at 0.5 km intervals from 0.5 km – 5 km of a site was determined. An association with the number of ponds within a certain distance might suggest that some factor is influencing damselfly distributions at that spatial scale. Presence data from both years of the survey were used so that all occupied ponds in either year could be included in the analyses. Once significant ($p < 0.1$) variables were identified, a correlation analysis was performed to determine the direction of the relationship (whether there is a positive or negative association) between the presence of the damselfly and the significant variable (SAS 1990).

Results

E. recurvatum was detected at a total of 26 of 72 ponds (36.1%), *E. laterale* at 28 of 72 ponds (38.9%), and *E. pictum* at 21 of 76 ponds (27.6%). No new sites of *E. laterale* were detected after the second visit in either 1999 or 2000 (Figure 1). Only one new site was detected on the third visit for *E. recurvatum* in 2000 and for *E. pictum* in 1999 (Figure 1). By the second visit, detection rates were near 100% for all three species. *E. recurvatum* and *E. laterale* co-occurred at 11 ponds (42.3% of *E. recurvatum*-occupied ponds). *E. pictum* was found at 17 of the 72 ponds surveyed for all three species, and shared 14 of those ponds with *E. laterale* (82.3%).

Using contingency table analyses, we found the presence of aquatic vegetation to be significantly associated with the presence of *Enallagma recurvatum* $\chi^2 = 30.01$, df = 4, $p < 0.001$), *E. laterale* ($\chi^2 = 14.11$, df = 4, $p < 0.01$), and *E. pictum* ($\chi^2 = 12.82$, df = 4, $p < 0.025$) at a pond. The most common aquatic veg-

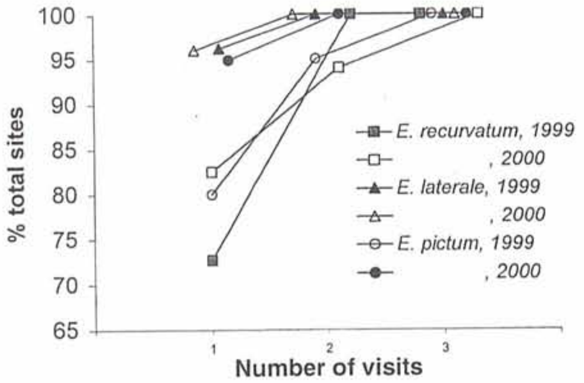

Figure 1. Cumulative percentage of new damselfly sites found from an assemblage of 72 ponds for *E. recurvatum* and *E. laterale* and 76 ponds for *E. pictum* as a function of sampling effort. Each site was surveyed up to three times to minimize detection error.

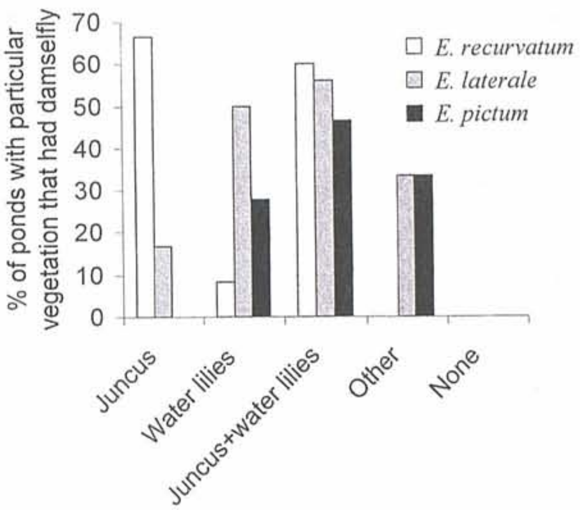

Figure 2. Emergent vegetation vs. damselfly presence. The percentage of ponds containing a specific type of emergent vegetation, which also contained a specific damselfly species. For example, of six ponds containing *Juncus* only, four (66.7%) contained *Enallagma recurvatum* and one (17%) contained *E. laterale*. It was determined that *E. recurvatum* is significantly associated with *Juncus militaris* (χ^2=17.5, df = 1, p < 0.0001).

etation encountered at these ponds were the emergent rush *Juncus militaris* Bigelow (Juncaceae), occurring at 34 ponds, and the water lilies *Nymphaea odorata* Aiton (Nymphaeaceae), *Brasenia schreberi* J.F. Gmelin (Nymphaeaceae), and *Nuphar variegatum* Engelmann (Nymphaeaceae). *N. odorata* was the most common of these water lilies, occurring at 41 of the 76 sites. While 10 ponds contained *B. schreberi*, this water lily species usually co-occurred with *Nymphaea odorata*. *N. variegatum* was the least common and was found at 9 ponds.

Stepwise logistic regression revealed that the only variable significantly associated with *Enallagma recurvatum* presence was *Juncus militaris* presence (χ^2= 17.5, p < 0.0001) (Figure 2), and they were positively correlated (Table 1).

E. laterale was positively associated with the presence of the water lilies *N. variegatum* (χ^2= 5.17, df = 1, p = 0.023) and *B. schreberi* (χ^2= 6.04, df = 1, p = 0.014) (Figure 3), the damselfly *E. pictum* (χ^2= 4.32, df = 1, p = 0.038), pond area (χ^2= 4.47, df = 1, p = 0.035), and the number of ponds within 2 km of a habitat site (χ^2= 7.33, df = 1, p = 0.007) (Table 1). The significant association of *E. laterale* and *E. pictum* is illustrated by the fact that *E. laterale* was present at 82.3% (14 out of 17 ponds) of the *E. pictum* sites. *E. laterale* was not associated with *E. recurvatum* (logistic regression χ^2 = 2.60, df = 1, p = 0.107). Of the 26 sites observed to have *E. recurvatum* in both 1999 and 2000, *E. laterale* was present at 42.3% of these sites (11 ponds). According to the correlation analysis, *E. laterale* has a positive association with *Brasenia schreberi* (r = 0.344, p = 0.009), and with *E. pictum* (r = 0.433, p = 0.001). However, *E. laterale* was negatively associated with the number of ponds within 2 km of a site (r = –0.363, p = 0.006) (Table 1). This implies that the more ponds within 2 km of a site, the less likely the occurrence of *E. laterale*. However, this association was not found at other spatial scales.

Coastal plain ponds that support emergent and floating vegetation tend to be small and relatively shallow (Theall 1983). Large, deep ponds have steep pond shores that are unable to support typical coastal plain pond flora (Swain 1996). The largest ponds surveyed (largest pond = 128 ha) lacked any form of aquatic vegetation. Of the ponds with aquatic vegetation, the larger ponds (larges pond = 16 ha) generally had less vegetation (small area) compared to the smaller ponds (smallest pond = 0.05 ha). The largest pond containing *E. laterale* was approximately 16 ha and the smallest was around 0.7 ha, and the populations of *E. laterale* were present in both years of the survey at these sites. Both of these ponds had floating vegetation, suggesting that perhaps the primary factor necessary for this species to view a site as suitable is the presence of the appropriate vegetation. Similarly, pond area ranged from 0.05 ha to 16 ha for *E. recurvatum* and from 0.7 to approximately 11 ha for *E. pictum*, and again, both the largest and smallest occupied ponds supported the required vegetation. However, smaller ponds are more prone to com-

Table 1. Significant variables ($p < 0.01$) from logistic regression analysis and direction of relationship (from correlation analysis). For each variable, df = 1.

Species	Variable	p-value	Direction of association	Model concordance
E. recurvatum	*J. militaris*	< 0.0001	+	65.6
E. laterale	*N. variegatum*	0.023	+	87.9
	B. schreberi	0.014	+	
	E. pictum	0.038	+	
	Pond area	0.034	+	
	# ponds within 2 km	0.007	−	
E. pictum	*N. odorata*	0.065	+	96.0
	E. laterale	0.015	+	
	# ponds within 1.5 km	0.034	−	
	# ponds within 2.5 km	0.032	−	

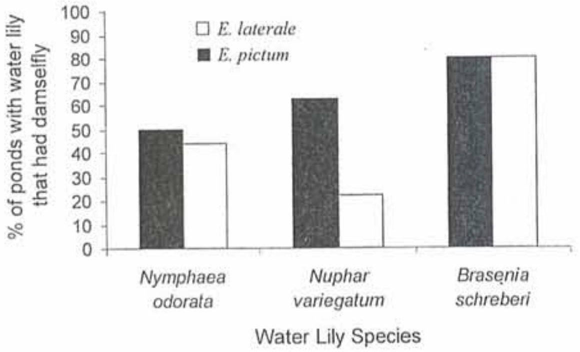

Figure 3. Comparison of *Enallagma laterale* and *E. pictum* occurrence with specific water lily occurrence. These water lily species were the only water lily species encountered among the sites surveyed. It was determined that *E. laterale* is significantly associated with *N. variegatum* ($\chi^2 = 5.17$, df = 1, $p = 0.023$) and *B. schreberi* ($\chi^2 = 6.04$, df = 1, $p = 0.014$) and *E. pictum* is associated with *N. odorata* ($\chi^2 = 3.41$, df = 1, $p = 0.065$).

pletely drying up during drought conditions, which would interfere with population persistence at the site. In fact, the smallest *E. recurvatum* site (0.05 ha) dried up between the two years of the survey, and as a consequence, *E. recurvatum* was not found at that location in 2000.

Stepwise logistic regression showed an association between *E. pictum* presence and the presence of *Nymphaea odorata* ($\chi^2 = 3.41$, df = 1, $p = 0.065$) (Figure 3), *E. laterale* ($\chi^2 = 5.87$, df = 1, $p = 0.015$), other forms of emergent vegetation ($\chi^2 = 3.67$, df = 1, $p = 0.055$), and the number of ponds within 1.5 and 2.5 kilometers of a site ($\chi^2 = 4.47$, df = 1, $p = 0.034$ and $\chi^2 = 4.59$, df = 1, $p = 0.032$, respectively) (Table 1). There was a significant positive association of *E. pictum* with the presence of *N. odorata* ($r = 0.319$, $p = 0.016$) and *E. laterale* ($r = 0.433$, $p = 0.001$). However, there was a negative association with the number of ponds within 2.5 km ($r = -0.316$, $p = 0.017$) (Table 1).

Between the two years of this study, *E. recurvatum* experienced extirpations at 41% of the surveyed ponds (i.e., of 22 ponds where *E. recurvatum* occurred in 1999, 9 of those ponds did not have the damselfly in 2000) (Table 2). *E. laterale* and *E. pictum* experienced much lower extirpation rates of 11.5% (3 out of 26 ponds) and 10% (2 out of 20 ponds), respectively (Table 2). Colonization for *E. recurvatum* was also relatively high, with 23.5% of the ponds occupied in 2000 not occupied in 1999 (i.e., *E. recurvatum* occurred at 17 ponds in 2000, 4 of these ponds were not occupied in 1999) (Table 2). For *E. laterale*, 8% of the 2000 records were at formerly unoccupied ponds (2 out of 25 ponds), and 5% of *E. pictum* sites in 2000 were at formerly unoccupied ponds (1 out of 19 ponds).

From these data, we calculated turnover as $(c + e/a + b)*100$, where c is the number of ponds newly colonized in 2000, e is the number of ponds occupied in 1999 that were no longer occupied in 2000, a is the total number of ponds occupied in 1999, and b is the number of ponds occupied in 2000 (Diamond 1969) (Table 2). Faunal extinction rates, or the probability of a species becoming locally extinct (i.e., disappearing from a pond), were estimated as $2E/t(A + B)$,where E = the number of local extinctions, t = the number of intervening years between surveys, A = number of ponds occupied in the first year of the survey, and B = number of ponds occupied in the second year (Diamond 1971). The local extinction rate for *E. recurvatum* was higher than for the other two species (Table 2).

Table 2. Percent turnover (calculated using Diamond (1969)), faunal extinction rate (Diamond 1971) (see text for equations), and local extinction rate (# extinct sites/ # occupied sites in first year of study) of the three target damselfly species in our study.

Species	Turnover	Faunal Extinction Rate	Local Extinction Rate
Enallagma recurvatum	33.3	0.462	41%
E. laterale	9.8	0.118	11.5%
E. pictum	7.7	0.103	10%

Discussion

We found *Juncus militaris* to be the type of emergent vegetation most predictive of *Enallagma recurvatum* presence. Of the 26 sites with this damselfly, 23 had *J. militaris*. However, 12 ponds in 1999 and 14 in 2000 with *J. militaris* did not have *E. recurvatum* present. This damselfly oviposits inside the plant stem (Carpenter 1990, 1991). When we observed mating and ovipositing *E. recurvatum*, the female would crawl down the stem of the rush and use her sharp ovipositor to insert eggs directly into the stem of the plant. The habitats of *E. recurvatum* and *E. laterale* have been described previously and our results are consistent with earlier reports that aquatic vegetation is necessary for successful breeding (Carpenter 1990, 1991; deMaynadier and Hodgman 1998; Pucci and Mello 1993). We found *E. laterale* primarily at sites with water lilies: this damselfly occurred at 28 ponds total, with 26 of these possessing this type of vegetation. More specifically, *Nuphar variegatum* and *Brasenia schreberi* were significantly associated with this damselfly. Although there was no statistically significant association with the water lily *Nymphaea odorata*, it appeared to frequently co-occur with *E. laterale* (occurring at 12 of the 28 sites). Although the association between *E. laterale* and *B. schreberi* has been reported (deMaynadier and Hodgman 1998), the association between *N. variegatum* and *E. laterale* has not.

There are no published reports documenting the habitat requirements of *Enallagma pictum*. Anecdotal accounts describe *E. pictum* habitat as similar to that of both *E. recurvatum* and *E. laterale*, including both *Juncus militaris* and some form of water lily (V. Carpenter, personal communication). Our analyses showed that this damselfly is associated primarily with *Nymphaea odorata*. Although the level of significance for this association was marginal, we believe there is a biologically significant association. This damselfly has similar breeding habits as *E. laterale,* choosing the lower surface of a water lily leaf for oviposition (personal observation). Due to the prevalence of *N. odorata* on Cape Cod, this plant cannot serve as a diagnostic predictor for the presence of *E. pictum* at a pond. However, this water lily is a critical element of the pond habitat because *E. pictum* requires it for breeding.

In general, habitat size is associated with population persistence, since a larger habitat would be able to house a larger population, reducing the risk of local extinction (Hill et al. 1996). In our study, pond area was significantly associated with only *Enallagma laterale*. It has been proposed that habitat selection by damselflies is a visual process (Corbet 1999), and our results suggest that pond size is not a major factor in this process. This result might not be surprising for our study system because larger ponds did not have proportionately more emergent vegetation, possibly because the pond profile left little area for emergent vegetation. However, smaller ponds are more prone to completely drying up during drought conditions. Consequently, larger ponds with the appropriate vegetation might provide a more stable environment for these species despite the more confined breeding area, by holding water longer.

An interesting result was the lack of association between *Enallagma recurvatum* and *E. laterale*. This contradicts previous assertions that these two species typically coexist (Carpenter 1991). This lack of association may indicate competition between these two species. If competition is driving the occupancy patterns of these species, however, it is unlikely over oviposition sites: these two species do not share vegetation requirements. *E. recurvatum* appears to require emergent vegetation, whereas *E. laterale* is associated with floating vegetation. However, their lack of association could result from plant-plant competition. *E. laterale* and *E. pictum*, on the other hand, were associated. This may be related to their breeding habits and similar oviposition sites. Both species use the underside of water lily leaves for oviposition, and these two species were most often found at ponds with abundant floating vegetation.

One major finding of this investigation is the apparent transient nature of local *Enallagma recurvatum* populations. Compared to *E. laterale* and *E. pictum* populations, this species exhibits a much higher turnover rate and experienced a higher extinction rate. Faunal extinction rate was over four times greater for this species than the other two, meaning it is much more likely to go extinct. Looking at the turnover rates for these three species may afford an understanding of their dispersal patterns. Ponds are discrete habitats surrounded by hostile territory that must be traversed by dispersing individuals. Dispersal is one of the key components of metapopulation dynamics (Hanski and Gilpin 1991; Harrison 1991; Brown and Kodric-Brown 1977) and the ability of a species to survive dispersal and occupy appropriate sites is fundamental to metapopulation persistence (Nève et al. 1996; Drechsler and Wissel 1998; Moilanen and Hanski 1998).

The differences in turnover may reflect differential dispersal capabilities of each damselfly species. There have been reports of *Enallagma* adults being found up to 2.7 km from source populations (Moore 1954 cited in McPeek (1989)). Higher dispersal rates may influcence colonization rates. If individuals tend to disperse away from ponds, this may exact a cost in the form of increased predation or inability to locate suitable habitat, yielding low colonization rates. However, longer dispersal distances can lead to higher colonization rates, since dispersing individuals could establish new populations. *E. recurvatum* may have a greater tendency to disperse than either *E. laterale* or *E. pictum*, which could explain the higher turnover rates.

Enallagma laterale and *E. pictum* may not disperse as widely as *E. recurvatum*. McPeek (1989) demonstrated that several *Enallagma* damselflies tend to remain at their natal pond, displaying strong philopatry. Other genera of damselflies belonging to the same family also exhibit limited dispersal (Garrison and Hafernik 1981). Individual damselflies were shown to have low daily movement rates (6 m/day), and only traveled 150 m from the natal site (Garrison and Hafernik 1981). Dispersal away from natal ponds might increase adult mortality, yielding reduced expected reproductive success for dispersing adults than for non-dispersers (McPeek 1989). By limiting dispersal and remaining at natal sites, these species may be able to reduce the risk of mortality, hence the lower turnover rates demonstrated by these two species.

As well as demonstrating a higher turnover rate, the extinction rate for *Enallagma recurvatum* (41%) was also higher than the extinction rates of the other two species. Of the 22 ponds containing this species in 1999, nine lost this damselfly in 2000. Cape Cod experienced a drought during the summer of 1999, and pond water levels dropped substantially during the summer months (McHorney 2000). Droughts can have a marked effect on pond fauna, with permanent ponds losing many of the characteristic taxa to immigrants from temporary ponds (Jeffries 1994). *E. recurvatum* has a greater risk of local extinction, with the probability of extinction more than four times greater than either *E. laterale* or *E. pictum*. Despite the relative abundance of this damselfly species on Cape Cod in comparison to other locations, it appears that these populations experience more local extinctions and colonizations than populations of *E. laterale* and *E. pictum*. Therefore, *E. recurvatum* faces a greater local extinction risk due to its high turnover rate, but might persist well as a metapopulation if ponds are maintained.

Based on the turnover data and the patchy distribution of appropriate ponds, evidence supports the idea that *E. recurvatum* occurs as a metapopulation. The population structure of *E. laterale* and *E. pictum* cannot be easily surmised from the turnover data. These two species exhibited fewer instances of extinction and colonization, which may be attributed to sampling error. Further investigation is warranted for determining whether the patterns observed during this study are representative of normal population dynamics, or whether they are consequences of the drought of 1999. The damselflies we studied exist in patchy habitats: coastal plain ponds represent discrete habitat patches that are independent from similar ponds.

Knowledge of the population structure and breeding requirements is critical to the development of successful management plans for these damselfly species. However, there might be some other ecological processes driving the distribution of these species besides the processes discussed in this paper. *E. laterale* and *E. pictum* demonstrated an association with the number of ponds within specific distances of an occupied pond. Specifically, *E. laterale* was associated with the number of ponds within 2 km of an occupied pond, and *E. pictum* was associated with the number of ponds within 1.5 km and 2.5 km. The observation that the presence or absence of these species can be partially explained by distance indicates the influence of some ecological factor(s) operating at these spatial scales (Levin 1992). This study cannot determine what these processes might be; therefore future research on these damselflies should focus on identifying these factors. However, the associations of *E. laterale* and *E. pictum* with these specific distances should be used when considering management for these species.

One important outcome of this study is the acquired knowledge of the ecology of *Enallagma pictum*, a species that has not been the subject of many studies. Based on the amount of time needed to survey a pond for each species, it seemed like *E. pictum* was rarely dominant at a pond and appeared to have relatively small local population sizes compared to *E. recurvatum* and *E. laterale*. While all three species should qualify for high conservation priority due to their habitat specificity and narrow geographic distribution, *E. pictum* deserves a higher conservation priority based on the fact that it seems less abundant at ponds than either *E. recurvatum* or *E. laterale* (cf. Reed (1992)). *E. pictum* has not yet been state-listed in Massachusetts, but the results of this study reveal that it is as rare, if not rarer, as either *E. laterale* (state-listed as a species of special concern) or *E. recurvatum* (state-listed as threatened). Hopefully the results of this study will provide incentive to add *E. pictum* to the state list of species of concern and prompt more research into the ecology of this species.

Acknowledgements

This study was partially funded by the Massachusetts Chapter of The Nature Conservancy, the Draupner Ring Foundation, the Arabis Fund, and the Tufts University Biology Department. This study was undertaken with the permission and cooperation of the Massachusetts Natural Heritage and Endangered Species Program. We also thank the Cape Cod National Seashore for their permission to survey and collect damselflies at several of their ponds.

References

Barbour H., Simmons T., Swain P. and Woolsey H. 1998. *Our Irreplaceable Heritage: Protecting Biodiversity in Massachusetts*. Natural Heritage and Endangered Species Program of Division of Fisheries and Wildlife and The Massachusetts Chapter of The Nature Conservancy.

Brown J.H. and Kodric-Brown A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445–449.

Carpenter V. 1986. Notes on the status habitat and conservation of three state-listed odonates on Cape Cod Massachusetts. Cape Cod Dragonfly Inventory. Cape Cod Museum of Natural History, Brewster, Massachusetts, USA.

Carpenter V. 1990. An ecological and behavioral study of the Barrens Bluet damselfly (*Enallagma recurvatum*) including results of general odonate inventories. Cape Cod Museum of Natural History, Brewster, Massachusetts, USA.

Carpenter V. 1991. Dragonflies and Damselflies of Cape Cod. Cape Cod Museum of Natural History, Brewster, USA.

Corbet P.S. 1999. Dragonflies: Behavior and ecology of Odonata. Cornell University Press, Ithaca, USA.

deMaynadier P. and Hodgman T.P. 1998. A survey of rare threatened and endangered fauna in Maine: Central Interior Midcoast and Penobscot Bay regions. A collaborative project by the Maine Department of Fisheries and Wildlife and the Maine Natural Areas Program.

Diamond J.M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. Proc. Natl. Acad. Sci. 64: 57–63.

Diamond J.M. 1971. Comparison of faunal equilibrium turnover rates on a tropical island and a temperate island. Proc. Natl. Acad. Sci. 68: 2742–2745.

Drechsler M. and Wissel C. 1998. Trade-offs between local and regional scale management of metapopulations. Biol. Cons. 83: 31–41.

Garrison R.W. and Hafernik J.E. 1981. Population structure of the rare damselfly, *Ischnura gemina* Kennedy (Odonata: Coenagrionidae). Ecology 48: 377–384.

Hanski I. and Gilpin M. 1991. Metapopulation dynamics: brief history and conceptual domain. Biol. J. Linn. Soc. 42: 3–16.

Hanski I., Pakkala T., Kuussaari M. and Lei G. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos 72: 21–28.

Harrison S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biol. J. Linn. Soc. 42: 73–88.

Harrison S. 1993. Metapopulations and conservation. Large-scale ecology and conservation biology. : 111–128.

Hill J.K., Thomas C.D. and Lewis O.T. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. J. Animal Ecol. 65: 725–735.

Jeffries M. 1994. Invertebrate communities and turnover in wetland ponds affected by drought. Freshwater Biol. 32: 603–612.

Kearsley J. 1999. The natural communities of Massachusetts: Palustrine section. Unpublished draft Massachusetts Natural Heritage and Endangered Species Program., Westborough, Massachusetts, USA.

Keddy P.A. and Reznicek A.A. 1982. The role of seed banks in the persistence of Ontario's coastal plain flora. Amer. J. Bot. 69: 13–22.

Keddy P.A. and Reznicek A.A. 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. J. Great Lakes Res. 12: 25–36.

Levin S.A. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943–1967.

MacArthur R.H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. Harper and Row Publishers, New York, USA.

McHorney R. 2000. Report on Biological Monitoring at Mary Dunn and Nearby Ponds. The Nature Conservancy., Unpublished report.

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

Moilanen A. and Hanski I. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79: 2503–2515.

Nathan R., Safriel U.N. and Shirihai H. 1996. Extinction and vulnerability to extinction at distribution peripheries: an analysis of the Israeli breeding avifauna. Israel J. Zool. 42: 361–383.

Nève G., Barascud B., Hughes R., Aubert J., Descimon H., Lebrun P. et al. 1996. Dispersal colonization power and metapopulation structure in the vulnerable butterfly *Proclossiana eunomia* (Lepidoptera: Nymphalidae). J. Applied Ecol. 33: 14–22.

Pucci T.M. and Mello M.J. 1993. Survey of odonata at coastal plain ponds of southeastern Massachusetts. A report to the Massachusetts Natural Heritage and Endangered Species Program.

Rabinowitz D. 1981. Seven forms of rarity. In: Synge H. (ed.), The Biological Aspects of Rare Plant Conservation. Wiley, N.Y., USA, pp. 205–217.

Rawinski T.J. and Price S.D. 1994. Conclusion: an action plan for coastal plain wetland conservation. Toward a continental conservation strategy. Biol. Cons. 68: 281–284.

Reed J.M. 1992. A system for ranking conservation priorities for Neotropical migrant birds based on relative susceptibility to extinction. In: Hagen J.M. and Johnston D.W. (eds), Ecology conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA, pp. 524–536.

Reed J.M. 1996. Using statistical probability to increase confidence of inferring species extinction. Cons. Biol. 10: 1283–1285.

SAS 1990. SAS Institute Inc., SAS/STAT User's Guide, Version 6. 4th edn. Vol. 1. SAS Institute Inc, Cary, USA.

Schneider R. 1994. The role of hydrologic regime in maintaining rare plant communities of New York's coastal plain pondshores. Biol. Cons. 68: 253–260.

Sculthorpe C.D. 1967. The Biology of Aquatic Vascular Plants. Edward Arnold Ltd, London, UK.

Sorrie B.A. 1994. Coastal plain ponds in New England. Biol. Cons. 68: 225–233.

Swain P. 1996. Coastal plain pondshore communities. Massachusetts Wildlife 96: 2–11.

Theall O. 1983. An investigation into the hydrology of Massachusetts coastal plain ponds. Massachusetts Natural Heritage Program Division of Fisheries and Wildlife, November.

Tilman D., May R.M., Lehman C.L. and Nowak M.A. 1994. Habitat destruction and the extinction debt. Nature 371: 65–66.

Tischendorf L. and Fahrig L. 2000. On the usage and measurement of landscape connectivity. Oikos 90: 7–19.

Westfall M.J. and May M.L. 1996. *Damselflies of North America*. Scientific Publishers, Gainesville, USA.

Whitelaw G., Hubbard P. and Mulamoottil G. 1989. Restoration of swampland: planning guidelines and recommendations. Can. Water Resources J. 14: 1–9.