Temporal and Spatial Aspects of the Colonization and Re-Colonization of Dragonflies in Lentic Habitats

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at George Mason University

by

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Dedication

This dissertation is dedicated to my wife Patricia A. Jackson

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My wife, Patti Jackson – the most influential environmental lobbyist in Virginia

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Abstract

TEMPORAL AND SPATIAL ASPECTS OF THE COLONIZATION AND RE-COLONIZATION OF DRAGONFLIES IN LENTIC HABITATS

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This dissertation describes dragonfly species of Hanover County, Virginia, which species are most likely to be first colonizers of a new or re-constructed impoundment, which species are never found as first colonizers, and which species are the dominant species three years after the impoundment fills with water. In this Piedmont region of Virginia, *Erythemis simplicicollis, Libellula incesta, Libellula luctuosa,* and *Perithemis tenera* were the first to colonize all sites researched. *Celithemis eponina* and *Pachydiplax longipennis* did appear as first colonizers, but not at all sites. Proximity to a source site appears to be a determinate for these six species, not any size or behavioral characteristics. Seventeen species, no matter what the proximity of a source site, never were first colonizer species for a new impoundment. During this research three species not previously noted on published species lists from government or organizations for this county were collected: *Anax junius*; *Libellula pulchella;* and *Pantala hymenaea*. Seven species found during this study are new additions for the Commonwealth of Virginia

official species list for Hanover County: *A. junius; A. longipes; Celithemis eponina; C. fasciata; Libellula vibrans; Pantala flavescens;* and *Tramea lacerate*.

Investigations regarding dominance after three years indicated that dominance did not change; whatever species arrived first, maintained dominance. Additional community structure in the lentic habitat was observed.

This dissertation investigated the impact of wind on dispersal direction. In a manipulated mark and observation experiment, findings indicate that wind velocity in excess of 5 km/hr. resulted in the dragonfly’s dispersal downwind. Less than 5 km/hr. results in varied direction of flight. Wind direction and velocity may impact direction of dispersal for adult dragonflies. Larval dragonflies were reared in an outdoor vivarium, the first of its kind, with documented survival of 74%, or greater, of the tenerals.

Chapter One

Introduction

Because dispersal is a fundamental component of life history, both vertebrate dispersal (Murray 1967, Gaines & McClenaghan 1980, Haas 1995, Paradis et al. 1998, Sutterland et al. 2000, Bowman et al. 2002) and invertebrate dispersal (MacArthur and Wilson 1963) were early foci of ecology investigations into community structure. Studies have focused on factors affecting dispersal (Angelibert and Giani 2003), types of dispersal (Corbet 1999, Bohonak and Jenkins 2003), causes and consequences of dispersal (McPeek and Holt 1992, Bohanak and Jenkins 2003, Langellotto and Denno 2001, Bowler and Benton 2005), limits of dispersal (Harabis and Dolny 2011,), and weather's impact on dispersal (McManus 1988, Srygley 2003). Winkler (2005), nonetheless, says that dispersal may be the "most pervasive and least understood" aspect of life history studies.

Dispersal has been described as a dichotomy between active or passive modes (Osborne et al. 2002). As strong, able fliers, for example, adults dragonflies (Odonata: Anisoptera) are considered active dispersers, and this group has been the focal taxon of many dispersal studies, including those studies listed above. Active dispersal implies that an organism controls the direction of dispersal. Specifically, actively dispersing individuals demonstrate searching and exploratory behavior until they locate suitable sites to breed, feed, or immigrate. Smaller insects that use wind or stream flow (Smock 1996), disperse when attached to hosts and are considered passive dispersers. This behavior is common in flightless insects (Bilton et al. 2001), particularly those incapable of living outside aquatic habitats. For insects exhibiting flight, storms and wind may push actively dispersing individuals to become passive participants. Depending on wind velocity and other conditions, adult odonate dispersal may be a combination of active and passive behavior with respect to direction. For example, damselfly (Odonata: Zygoptera) dispersal can be impacted by weather/wind. Mitchell (1962) reports that a 10-fold increase in dispersing damselflies occurred during a two-day wind storm. Angelibert and Giani (2003) conclude that weather conditions, including wind, determine when dispersal occurs and different species have different sensitivities to weather conditions. The degree to which many species of Odonata may switch between active and passive forms of dispersal or the amount that actively dispersing individuals may use wind or water movement to reduce the energetic costs of dispersal is not well understood, although Johnson (1969) does mention one example of the alteration of wing activity (continuous or not wing-flapping) by *Pantula flavescens*: when there is no wind this dragonfly glides, essentially saving energy. *P. flavescens* common name is Wandering Glider.

The stages of active dispersal, as Stamps (2001) describes, are: 1) searching; 2) settlement; and 3) residency. Motivations for dispersing are many, and Clobert et al. (2001), therefore, delineate several forms. Breeding dispersal, for instance, is any movement between successive breeding areas. Female anisopterans may store sperm for several weeks, breed with multiple partners (Corbet 1999), and disperse often in search of new mates. Natal dispersal (Clobert et al. 2001) is movement from the place of birth, and may occur to reduce competition between conspecifics, including parents and their offspring. It can be important in the maintenance of regional diversity of dragonflies and avoidance of inbreeding at more local levels. Research supports that natal dispersal by newly emerged adult dragonflies (tenerals) eventually terminates at aquatic sites that support breeding (Corbet 1999). Certain environmental cues may terminate searching and make sites attractive for settlement and residency. These cues include if sites contain water, are uninhabited or currently devoid of other conspecifics, and whether there is host preferred, high quality vegetation (Dingle and Drake 2007, Remsburg et al. 2008, Remsburg and Turner 2009). Despite the preference for sites not occupied by competitors, the range of searching for dragonflies may vary from less than one to several kilometers.

Dragonflies are top-tier predators as invertebrates, both larvae and adults at lentic systems. Additionally, adults are an important prey for birds and bats. Their trophic importance means that their presence in lentic environments is critical in habitats recovering from disturbance. While the studies described above do outline a few factors that influence settlement of dragonflies, few if any studies examine community assembly of Odonata in lentic habitats. Because the order or history of colonization is thought to influence succession (Suh and Samways 2005), it may be critically important to determine which species are first to settle in a habitat after a search period. Voshell and Simmons (1978) identified eight species of Anisoptera from aquatic habitats in the Piedmont section of Virginia that appeared at a new lake after it filled and were considered to be first colonizers. Their study was limited to a single site in Louisa County, Virginia. Moreover, the habitat they investigated, a new large reservoir, is atypical of the small ponds that might be created after a hurricane or similar weather disturbance. Some studies do mention early observed lentic species at other locations in other countries (Paterson and Fernando 1969, Fulan et al. 2010), as well as recolonization by larvae in Virginia (Braccia et al. 2007), but these studies did not identify which species settled first. In addition, studies of colonization by dragonflies have been largely descriptive, providing species lists rather than identifying the mechanisms that determine why some species arrive first.

McCauley (2006) studied factors that affected community structure of dragonflies in experimental cattle tanks. She determined that dispersal and recruitment limitations act as filters for richness of communities. In particular, the distance between tanks and community dissimilarity of larvae in the tanks were positively correlated (McCauley 2006) and adult dragonflies' richness decreased with increasing isolation of the tanks, suggesting that body size or other traits that influence a species upper dispersal limit may determine the similarity of assemblages in distributed lentic locations.

In addition to a lack of information on dragonfly colonization, few studies exist on successional changes in species identity in new communities after colonizing individuals settle. For dragonflies, changes in abundance have been documented by Johansson et al. (2006), who found that high fish predation in a pond reduces overall odonate abundance. Knight et al. (2005) took a much broader look at entire trophic levels, examining the impact of fish on dragonflies, pollinator insects, and plants in the littoral zone. This study concluded that fish predation in a pond reduced larval dragonflies abundance, which reduced the numbers of subsequent emerging adults.

Fewer adult odonates resulted in less predation pressure on pollinating insects; which increased shoreline plant species benefitting from those more abundant pollinators. However, fish predation is not a limiting factor on very young impoundments because some ponds often are too hypoxic for fish survival. This may be especially true for rebuilt ponds in which substantial terrestrial vegetation established before the pond was reformed. Fish may also have a difficult time dispersing into isolated rebuilt ponds. Large fish that might feed on dragonfly larvae also would be nonexistent or limited in number unless introduced by humans. Thus, in addition to factors that influence settlement, competitive interactions between dragonflies or between dragonflies and other early invertebrate colonizers may be more important in dictating patterns of residency or community assembly in these habitats.

Worthen and Patrick (2004) studied competitive interaction among various Odonata in a community. In their study, species differed in their preferences of perch height, which reinforced niche partitioning between species. Corbet (1999) describes combat behavior between *Aeshna cyanea* and *Sympetrum sanguineum* and similar activity between *Libellula quadrimaculata* and *S. striolatum* that exhibit partition of dragonfly niches or influence species in ways that would determine patterns of dominance. *Perithemis tenera* competitive behavior is researched by a study from Switzer and Eason (2003). Mating territories are noted, as patterns of response occur based on special determinants.

The focus of this dissertation research was to address shortcomings in the published literature with respect to each stage of dispersal. For the search phase of dispersal, I investigated the role of wind in active dispersal. In the second, or settlement, phase of dispersal, I determined the order in which species colonize newly constructed ponds. Finally, in the residency phase of dispersal, I investigated short term (three year) changes in community structure. Specifically, I investigated the following questions:

1. Does wind play a role in dispersal of adult dragonflies?
2. Which species are first colonizers for a lentic habitat in Hanover County, Virginia, and can we determine locally which species might first be consistent in colonizing a newly formed habitat?
3. Over three years, does the dominance of dragonfly species in the community change as succession occurs at a new impoundment? Is the community succession for anisopterans more of a stochastic process than a deterministic one?

Figure 1.1 provide a visual reference regarding the overall portions of the research conducted for this dissertation.

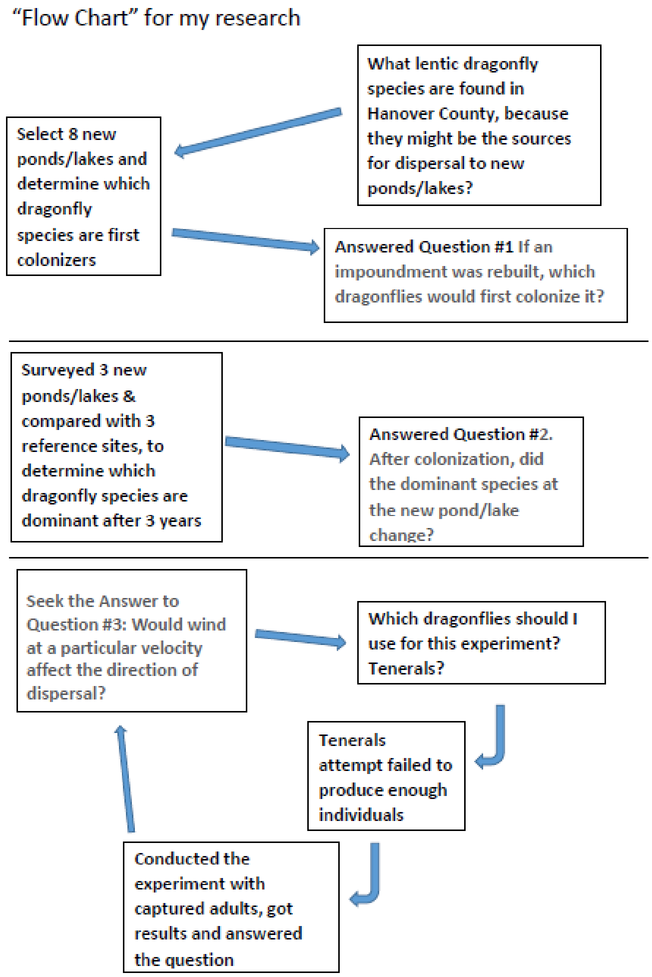

Figure 1.1. Flow Chart of the research conducted for this dissertation

Study System

This research was conducted in Hanover County, Virginia (the midpoint of the County being Latitude N 37.76, Longitude W 77.47). Hanover is located in the Central Piedmont section of Virginia, see Figure 1.2, and includes a variety of pond sizes and several lakes.

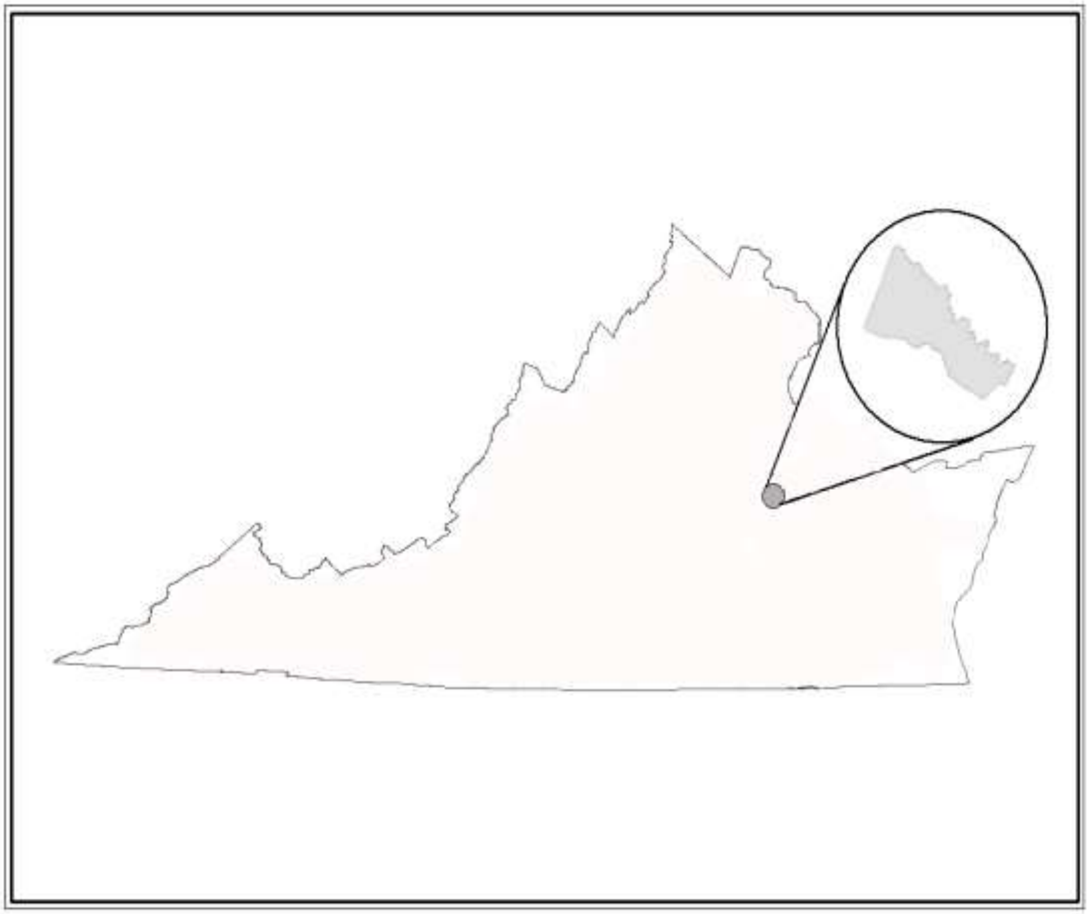

Figure 1.2. Map of Hanover County, Virginia

Dragonflies were selected as a focal study group because they are large and easily identifiable in field observations, are relatively easy to mark and observe in experiments, and are important predators in lentic communities. The aquatic larval stages do disperse to some extent, especially in lotic ecosystems. Adults on the other hand are capable of flight and will disperse into and colonize lentic locations (Johnson 1969, Corbet 1999).

Several families of dragonflies (Odonata: Anisoptera) occur locally, with Libellulidae being the most common family, based on lists from the Virginia Division of Natural Heritage. Migratory species that might occur in this area include *Anax junius*; *Celithemis elisa; Libellula pulchella; L. quadrimaculata; L. vibrans; Pachydiplax longipennis; Pantala flavescens; Tramea carolina;* and *T. lacerata* (Dunkle 2000). These species are also considered strong dispersers and potential residential species. Range maps of many other odonates were possible in this area.

In 2004, Hurricane Gaston remained over Central Virginia for four hours and eventually destroyed 54 lakes and ponds in Hanover County (Hanover County 2004). Most had earthen dams, and the excess water pressure from the torrential rains caused the dams to breech and the impoundments were drained. This event provided an ideal situation to research the recolonization of rebuilt impoundments by dragonflies. Available literature on recolonization of lentic sites is non-existent. Additionally, a study of colonization of new impoundments was undertaken.

Significance and Dissertation Research

This research in the context of natural history of Anisoptera behavior and conservation can provide new information on natural aquatic communities and the establishment of new/artificial impoundment habitats. Answering the questions of which dragonfly species first colonize a new impoundment, and studying if dominance of resident species change, can further add knowledge to this field. The study of the impact of wind on dispersal can reveal new data assisting in the understanding of how dragonflies might disperse in one direction versus another.

The approach addressing each of the three focal questions of this dissertation is presented below. First, in Chapter Two, I describe the results of observations on the identity of first colonizers, focusing on both species identity and on the specific order of colonization. In Chapter Three, I use three year data for each of three new sites and their corresponding, paired reference sites to describe local dragonfly community structure. Specifically, I address changes in the identity of resident species over time to determine if consistent patterns of dominance exist within the first three years after a new pond is established. In Chapter Four, I describe the results from an experiment in which larval dragonflies were reared to adulthood, for possible use in a wind experiment. Instead, in a manipulative experiment, captured *Libellula incesta* adults were released under different prevailing wind conditions (such as wind velocity and direction), and the direction of their dispersal recorded. Finally, I conclude in Chapter Five with a discussion of the implications of my findings for the restoration of lentic habitats and biodiversity conservation, including addressing the importance of dragonflies as indicator species of the local impacts of climate change.

Chapter Two

Which Species of Anisoptera will First Colonize or Recolonize a Lentic Habitat?

Introduction

Lentic habitats, such as ponds and lakes, are like islands in a terrestrial sea – independent environments of different sizes isolated by varying distances. Such spatial arrangement has consequences for the community structure of these aquatic habitats in that different members of the community may respond differently to the challenge of dispersing between locations. This is particularly true of aquatic insect communities, such as Anisoptera, in which adults may traverse terrestrial surroundings but larvae will not. Nearby populations of dragonfly species may act as sources of adult colonists. However, longer term community structure will be the outcome of both adult terrestrial dispersal and oviposition preferences and larval survival in aquatic habitats.

Superimposed upon this spatial structure are disturbance regimes of different spatial scales. For example, ponds and lakes in Hanover County, Virginia were destroyed by Hurricane Gastone in 2004. Determination should be made regarding which species are available from source sites to emigrate from those sites and immigrate to new sites such as a new pond.

Study System

Hanover County encompasses 122,765 hectares (474 square miles) in the Coastal Plain and Piedmont physiographic province draining to the Chesapeake Bay and Tidewater Virginia. Hanover County has approximately 70 lentic habitats with an undetermined number of wetlands. Size of non-ephemeral ponds and lakes vary from 0.1 ha to 37 ha. Annual rainfall is approximately 109.22 cm. Lacustrine, riverine, and forested wetlands exist in the variety of lentic habitats in Hanover.

Determination of Regional Species Pool

No published list of species or comprehensive species list is available specifically for Anisoptera in Hanover County, Virginia. Therefore, to determine the potential regional species pool of colonists in the study area, I conducted a literature survey of surrounding areas. For many locations within 100 miles of Hanover County, Virginia, publications noting verified voucher specimens of Anisoptera exist: Hagen 1877, Gloyd 1951, Layton and Voshell 1991, Roble and Stevenson 1994, Roble and Hobson 1996, Roble et al. 1997, Roble and Stevenson 1998, Roble 1999, Roble and Cuyler 2000, USGS 2005, and Braccia et al. 2007.

My literature review identified 38 species to be potential residents in this region (see Table 2.1). The United States Geological Survey (USGS) identified 55 possible species of Anisoptera for this county (USGS 2005). The 2006 Commonwealth of Virginia, Division of Natural Heritage (VDNH) official species list for Hanover County includes 30 species, with no details as to specific collecting locations (VDNH 2006). The

Odonata Central website (Odonata Central 2010), a joint project of the University of Texas and the Dragonfly Society of Americas, lists 27 species for Hanover County, but no actual global positioning system (GPS) location data within the County are provided. In fact the Odonata Central data report all species location at one point in the center of the County.

A review of F.L. Carle's (1982) doctoral dissertation and research reveals that he collected 13 species in Hanover County, VA. However, the data in the Carle report are incomplete and limited, actual collection records are not specific, and his dissertation was never published. Much of the Carle data were from Virginia Commonwealth University student collections, with questionable verification.

Geographically identified vouchers from two counties near Hanover County are published. In the first, Voshell and Simmons (1978) studied a new impoundment, Lake Anna, in the adjacent county of Louisa and they reported the sometimes lentic species and typical lentic species shown in Table 2.1.

Voshell and Simmons (1978) studied odonate species changes when the North Anna River was dammed and lentic species became established in the new Lake Anna, which is 5,261 hectares and just north of Hanover County. The reported lentic anisopteran species were limited in number, with only the lentic species *Erythemis simplicicollis*, *Pachydiplax longipennis*, and *Perithemis tenera* reported within the first year after the lake filled with water. One might consider this a published report of first colonizers, but the species number is very small and probably does not identify all first colonizers.

Layton and Voshell (1991) constructed 12 small artificial/experimental ponds (20 meters by 20 meters) in Nottoway County, Virginia, and for one year studied which macroinvertebrates would colonize the sites in 1988, the year/season after the ponds were filled. These ponds were filled by well water or rain water; thus, first colonizing anisopterans would have immigrated to these small sites via flight. This study states that some species in the anisopteran family Libellulidae were collected during the single year of study, but no specific colonizing species were identified. *Gomphus* (species unknown) is mentioned as being collected at most ponds. *Anax junius*, which could have been migratory, is noted. This study focused mostly on other macroinvertebrates and factors that might affect community structure. No data were provided about a second year, thus successful colonization may be in question.

In studying the 30,351 hectares of Fort A.P. Hill and some of surrounding Caroline County, VA, adjacent to Hanover, Roble and Hobson (1996) identified 35 species of lentic and lotic Anisoptera, the lentic species are noted in Table 2.1.

Braccia et al. (2007) was a follow-up study (after that reported in Layton and Voshell) which looked at six of the newly constructed ponds from the Layton and Voshell (1991) study to evaluate overall abundance of dragonflies at these ponds and to consider other factors affecting community structure at these sites. This study did identify 14 anisopterans that had colonized these ponds two years after construction of the ponds, listed in Table 2.1.

Table 2.1. Hanover County Regional Species List Reconstructed from Literature

Family	***Species***	***Reference***
Aeshnidae	*Aeshna umbrosa*	*O , R*
Aeshnidae	*Anax junius*	*O , R , B*
Aeshnidae	*Anax longipes*	*O , R*
Gomphidae	*Arigomphus villosipes*	*O , R*
Aeshnidae	*Basiaeschna janata*	*V , O , R*
Aeshnidae	*Boyeria grafiana*	*V*
Aeshnidae	*Boyeria vinosa*	*V , R*
Libellulidae	*Celithemis elisa*	*V , O , C , R , B*
Libellulidae	*Celithemis eponina*	*O , R , B*
Libellulidae	*Celithemis fasciata*	*O , R , B*
Cordulegastridae	*Cordulegaster obliqua*	*V , R*
Gomphidae	*Dromogomphus spinosus*	*V*
Aeshnidae	*Epiaeschna heros*	*O*
Corduliidae	*Epitheca cynosura*	*V , O*
Corduliidae	*Epitheca princeps*	*V , C*
Corduliidae	*Epitheca spinosa*	*R*
Libellulidae	*Erythemis simplicicollis*	*V , O , C , S , R*
Libellulidae	*Erythrodiplax minuscula*	*O , R , B*
Gomphidae	*Gomphus exilis*	*V , C , L , R , B*
Libellulidae	*Ladona deplanata*	*V , B*
Libellulidae	*Libellula auripennis*	*O , R*
Libellulidae	*Libellula axilena*	*O , R*
Libellulidae	*Libellula cyanea*	*V , O , C , R*
Libellulidae	*Libellula deplanata*	*V , O , C ,*
Libellulidae	*Libellula incesta*	*V , O , C , L , B*

Libellulidae	*Libellula luctuosa*	*V , O , C , R , B*
Libellulidae	*Libellula lydia*	*V , O , C , R*
Libellulidae	*Libellula pulchella*	*O , R*
Libellulidae	*Libellula semifasciata*	*O , R*
Libellulidae	*Libellula vibrans*	*O , R*
Libellulidae	*Pachydiplax longipennis*	*V , O , C , S , R*
Macromiidae	*Macromia illinoiensis georgina*	*O*
Libellulidae	*Pantala flavescens*	*V , O , R , B*
Libellulidae	*Pantala hymenea*	*B*
Libellulidae	*Perithemis tenera*	*O , C , S , R , B*
Gomphidae	*Progomphus obscurus*	*V , R*
Libellulidae	*Sympetrum ambiguum*	*O , R*
Libellulidae	*Sympetrum vicinum*	*V , O , C , R , B*
Petaluridae	*Tachopteryx thoreyi*	*V , O , R*
Libellulidae	*Tramea carolina*	*V , O , C , R*
Libellulidae	*Tramea lacerate*	*O , R*

Legend:

C is noted in Carle 1982

V is noted in Virginia Division of Natural Heritage 2006

O is noted in Odonata Central 2010

S is noted in Voshell and Simmons 1978

L is noted in Layton and Voshell 1991

R is noted in Roble and Hobson 1996

B is noted in Braccia et al. 2007

Thus a question asked in this dispersal research is: Which resident species in the area (the county) might be available to disperse to lentic habitats. Determining actual, field-verified species listed for the study area will establish a baseline for future comparisons if the ecosystem changes. In the second part of this chapter, the question of which anisopteran species in the studied lentic habitats are first colonizers is addressed. It is the preliminary hypothesis of this study that not every resident species of dragonfly in Hanover County, Virginia, will be a first colonizer. This study will attempt to determine which species are and which are not. Some consideration of why some species are first colonizers will be addressed.

Methods and Materials

Field collections

The number of sites to be surveyed was decided on the basis of similar published studies (Lasswell and Mitchell 1997, Fulan et al 2010, Lund and Myrup 2011,). Fulan et al. (2010) studied the Alqueva Reservoir, an area in excess of 26,000 hectares, sampling 21 sites for five years, resulting in 10 Anisoptera species. Lund and Myrup (2011) studied lentic species in the Muddy River area of Clarke County, Nevada, an area of ~75,890 hectares. In the Muddy River study, the watershed covers about 40% of the county. The Lund and Myrup study sampled six sites and identified 24 dragonfly species. Lasswell and Mitchell (1997) surveyed Erath County, TX for one year, in which they collected 2253 individuals from 12 lentic sites, and reported 36 different dragonfly species. Based on these studies, I estimated that 26 lentic sites were adequate in number and distribution across the County to provide a complete or nearly complete inventory of lentic anisopteran species. The actual total number of lentic sites in Hanover is not known, but a survey of topographic maps indicated approximately 70 ponds and lakes in in Hanover County in 2005. Survey sites were selected haphazardly from those 70 based on spatial distribution to cover the width and length of the County and to provide an accurate representation of the lentic habitats in the County. Figure 2.1 shows the location of all sites surveyed. Thirty-seven lotic and lentic sites were sampled. Of the 26 lentic sites, twenty were freshwater ponds, five were lakes, and one wetland, considered as lotic habitat because of the hydrology, where standing water was apparent, was sampled.

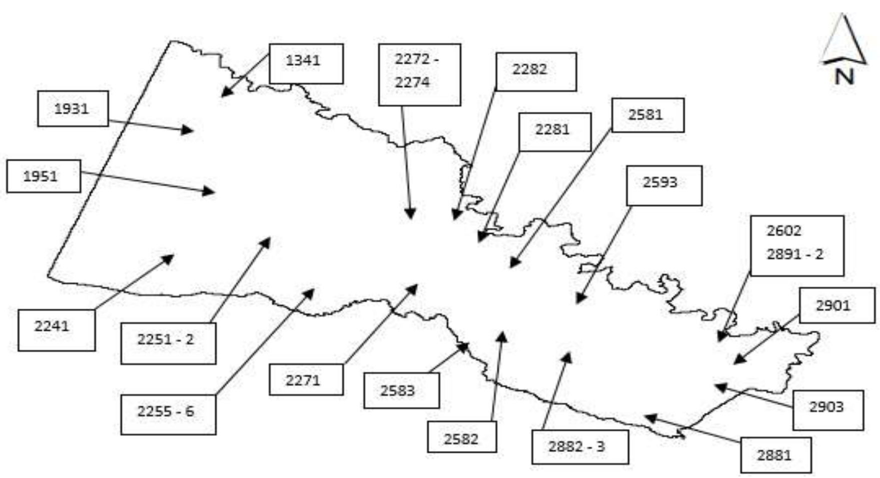

Figure 2.1. Hanover County, VA Lotic locations surveyed from 2005 – 2012 for dragonfly adults. Numbers correspond to location sites, arrows point to approximate site locations.

Impoundments ranged in size from 0.2 hectares to 8 hectares, and varied in age. A brief description of each surveyed site, with GPS data on each, is provided in Table 2.2.

Table 2.2 Hanover County VA Lentic Collection Locations, 2005 – 2012

Site #	Site Name	Size (in ha.)& Characteristics	GPS location
1341	Dragonfly Farm Pond	3 surrounded by pasture/ forest	N37 56.470 WO77 39.842
1931	Jones Pond	0.8 surrounded by fields	N37 49.165 WO77 41.199
1951	Hollows Club Lake	6 surrounded by golf course	N37 47.233 WO77 35.737
2241	Thomasson Pond	0.6 surrounded by grass bank	N37 43.612 WO77 40.185
2251	Federal Club Lake	7.6 on a golf course & forest	N37 45.860 WO77 36.030
2252	Federal Club Pond	0.2 surrounded by golf course	N37 45.901 WO77 36.083
2255	Sears Farm Pond (small)	0.8 surrounded by pasture/forest	N37 44.400 WO77 34.770
2256	Sears Farm Pond (large)	2 surrounded by meadow	N37 44.290 WO77 34.760
2271	Brooke Spring Pond	2.4 surrounded by forest	N37 42.433 WO77 27.450
2272	Pro Bass Pond	0.8 surrounded by grass banks	N37 42.98 WO77 27.00
2273	Northlake Stormwater Pond- Big	1.2 surrounded by grass banks	N37 43.378 WO77 27.447
2274	Northlake Stormwater Pond- Small	0.4 surrounded by grass banks	N37 43.560 WO77 27.416
2281	Courthouse Park Lake	2.4 surrounded by fields	N37 45.06 WO 77 21.48
2282	Snead Farm Pond	2.8 surrounded by forest\dam	N37 43.905 WO77 24.691
2581	Wayside Park	1 surrounded by forest	N37 42.102 WO77 22.890
2582	Rutland Stormwater Pond	0.2 with forest on one side	N37 39.185 WO77 23.874
2583	Summerduck Farm Meadows	meadows along a river basin	N37 40.088 WO 77 5.466
2593	Vitale Farm Pond	1.6 surrounded by fields & forest	N37 41.397 WO77 17.724
2602	West Lake	37 surrounded by forest & yards	N37 37.933 WO77 13.462
2881	Powhite Farm Pond	2.8 surrounded by forest	N37 34.689 WO77 18.322
2882	Creekside Stormwater Pond	0.8 surrounded by field	N37 37.192 WO 77 19.154
2883	Pebble Lake Stormwater Pond	0.2 surrounded by development	N37 36.794 WO77 19.061

2891	Woodlawn Pond	1.2 surrounded by forest	N37 37.495 WO77 14.038
2892	Lowe Farm Pond	0.4 surrounded by trees/fields	N37 37.089 WO77 13.610
2901	Hall Farm Pond (large)	2.8 surrounded by forest/fields	N37 37.171 WO77 12.335
2903	Camp Hanover Lake	4 surrounded by forest	N37 36.447 WO77 12.340

Survey sites were sampled for adult dragonflies from 2005 - 2012. Visits to the sites occurred on sunny to cloudy days, shade-recorded temperatures were between 20 and 35 degrees Celsius; barometric pressure varied from 29 to 31mm Hg; wind velocity was under 10 km/hr.; and collecting times occurred during daytime from 1000 hours to 1600 hours. Sampling occurred in three seasons per site: late spring (May 1 – June 15); summer (June 16 – August 1); and early fall (August 2 – September 15). Each site was visited three to eight times over the eight years. Adult dragonflies only were collected by the author and some assistants using hand nets. One voucher specimen of each species collected per site was retained; care was taken to avoid collecting duplicates of species at each site. Written permission to collect at each site was obtained from property owners or appropriate authorities, and copies are available for review.

When collected, each specimen was frozen within six hours of capture; and after thawing, each was preserved by soaking in a mixture of five-parts of acetone to one-part glycerin. The glycerin addition, a lesser known technique, helps keep the specimens less brittle. This method of preservation was recommended verbally from several Odonatologists, no published description of the addition of glycerin can be found. Voucher specimens were permanently stored and labeled using the recommended method in Needham et al. (2000). A site and specimen numbering system was devised; the first three digits represent pages of the site's location in the Alexandria Drafting Company map book (2002), the next digit is the site on that page (1 for site one, 2 for site two, etc.), and the last two numbers represent the specific specimen collected at that site. These vouchers are available from the author, but will eventually be stored at the Virginia Natural History Museum in Martinsville, VA.

Adherence to the Dragonfly Society of America Collecting Guidelines (Orr 1994) was observed, which recommend avoidance of duplication if the collector knows that species have to be collected at that location. Preliminary identifications were made using Needham et al. (2000), Dunkle (2000), and Merritt et al. (2008). For additional verification of identifications, an example of each collected species was reviewed by Dr. Hal White of the University of Delaware and Dr. Steve Roble of the Virginia Division of Natural Heritage, Department of Conservation and Recreation. Lotic species were not included in this report, although several were collected.

First Colonizers

To determine which dragonflies became first colonizers at the studied ponds, I conducted additional field surveys at newly established lentic location. I defined first colonizers as "species present one year after a new or reconstructed lentic habitat is filled with water and survive beyond that year." Thus, to qualify as a first colonizer, a dragonfly species had to meet the following criteria:

1. Be able to immigrate by flight into a new location, and
2. Establish residency and survive at the new location for a subsequent year

For one year following the filling of one new lake and two reconstructed impoundments (2007), adult dragonflies, assumed to be first colonizing adult species, were collected by hand netting at the surveyed locations. Samplings were at first taken from three impoundments: the new seven-hectare lake at The Federal Club golf course in western Hanover, and two rebuilt impoundments previously destroyed, Hall Pond (2.8 hectares) and Camp Hanover Lake (4 hectares), both located in the eastern end of the county. It should be noted that the last two were rebuilt impoundments that are typically identified as ponds; the Camp Hanover Lake should be more correctly called a pond because of its small size and lack of wind-induced mixing (Bronmark and Hansson 2005). The damaged impoundments and the new lake were grass-covered meadows with only a 1st order stream and no ponded water for at least two to three years prior to the impoundments filling with water. After the first year of re-establishment of the rebuilt impoundments during which the sites were filled with water, the specific adult species were collected and identified as potential first colonizers. Each new impoundment considered for this study was revisited a second and third year to verify the first colonizing species were still present. The same permission, collection, preservation, and identification procedures mentioned earlier in this chapter were followed. At least 5 visits per site were made during the summer season. These species were compared to the potential list of Hanover species that might be present at these sites. A second year of sampling was made to eliminate any species that may have been caught the first year, then never again; although that never happened.

With the first three impoundments, further investigations were made to see if the identified first colonizers from these sites might lead to a prediction of first colonizers at other new impoundments. As several new ponds in this region were constructed in 2009, 2010, 2011 and 2012, investigations were made one year after their filling with water to determine which dragonflies might be characterized as first colonizing anisopteran species.

These additional new sites were:

North Lake Ridge Stormwater Pond, Ashland, VA
Reynolds Stormwater Pond #1, Henrico, VA
Rutland Commons Stormwater Pond, Mechanicsville, VA
Pebble Lake Stormwater Pond, Mechanicsville, VA
Reynolds Stormwater Pond # 2, Henrico, VA

In total, eight new or reconstructed, filled impoundments were sampled for first colonizer species. These included the original three (the Federal Club Lake, Hall Pond, and Camp Hanover Lake) and the five noted above.

To establish the degree to which dragonflies were present before impoundment filling was initiated, samples of typical hurricane damaged former lentic sites were made. Each hurricane damaged location did have a small stream running through the site, and some lentic/lotic species might have been present before the impoundments were constructed; thus, actual resident species that became resident in ponds may not have immigrated as first colonizers. Other than simple probability measurements, no other statistical analysis was undertaken.

Results

Field Collections

The twenty-three lentic species of Anisoptera collected in this study in Hanover County, Virginia, at specific locations, from 2005 – 2012, are listed Appendix 1, including at which site (s) each species was collected. Four families of Anisoptera were collected. Approximately 300 individual dragonflies were collected in the Hanover research. If duplicates were caught in subsequent years at various sites, those were not reflected in any quantitative summaries. This represents more complete documentation than any previous Hanover County summaries. Noting Appendix 1, the actual GIS data for each location are provided, a first for this kind of study in Hanover County, Virginia. Table 2.3 summaries the numbers of Anisoptera families collected at the surveyed locations

Table 2.3 Anisoptera families collected from 2005-2012 in Hanover County, VA

FAMILY	NUMBER of SPECIES COLLECTED	NUMBER of LOCATIONS
Family Aeshnidae	2	2
Family Gomphidae	2	2
Family Cordulidae	1	3
Family Libellulidae	18	26
Family Petaluridae	1	2
Total Species Caught	24	

Collected individuals in this study include species in twelve genera, with three species not previously noted on published species lists from the federal government for this county (USGS 2005): *Anax junius*, *Libellula pulchella*, and *Pantala hymenaea*. Seven species found during this study are new additions for the 2006 Commonwealth of Virginia, Division of Natural Heritage official species list for Hanover County: *A. junius; A. longipes; Celithemis eponina; C. fasciata; Libellula vibrans; Pantala flavescens;* and *Tramea lacerate* (Commonwealth of Virginia 2006).

A species accumulation curve might be used to determine the degree to which a sampling regime has captured the species of a community, this county. Figure 2.2 summarizes the collections made from 2005 to 2012, eight years. With 26 random sites sampled, an asymptote is not reached, but from 2011 to 2012, the number of new species increased by only one new species collected. I am satisfied that the sampling of 26 lentic sites, and identification of over 300 specimens collected from 2005 – 2012, did result in a determination of the majority of anisopteran species currently found in Hanover County, Virginia.

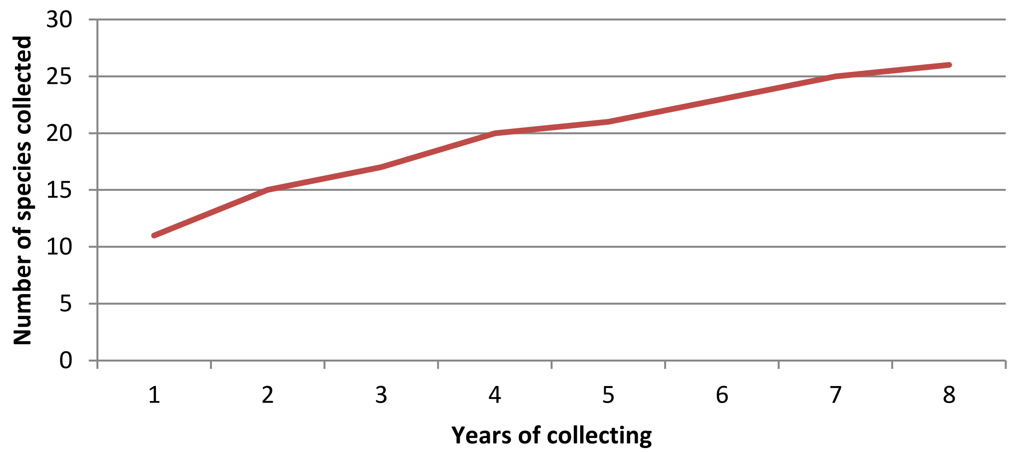

Figure 2.2 Cummulative Dragonfly Species Accumlation for Hanover County VA, Collected from 2005 - 2012

Although the rarest species may not have been found, the list of majority species obtained is sufficient to determine which species might be first colonizers.

First Colonizers

The first three new or reconstructed impoundments that I researched in 2008 (Hall Pond, Camp Hanover Lake, and the Federal Club Lake) did reveal that *Erythemis simplicicollis, Libellula incesta*, *Libellula luctuosa,* and *Perithemis tenera* were the first to colonize all sites. *Celithemis eponina* and *Pachydiplax longipennis* did also appear as first colonizers, but not at all three sites.

In 2010 three more sites, North Lake Ridge Stormwater Pond, Reynolds Stormwater Pond #1, and Rutland Commons Stormwater Pond, were sampled in their first year and similar results occurred, Table 2.3. It is noted that some of the original group of six species did not first colonize all of the additional three impoundments in the first year after the site filled with water. Eventually they did colonize at a slower rate, by the second year (2011) after complete filling with water.

Three more new sites became available in 2012, and further surveys were made. Pebble Lake Stormwater Pond, Reynolds Stormwater Pond # 2, and Reynolds Stormwater Pond #3 were sampled, with the original protocols regarding water filling, frequency of visits and times of season. Reynolds Stormwater Pond #3 turned out to be ephemeral, but it did have first colonizers *Libellula incesta* and *L. lydia* before it dried up.

The total number of ponds tested fully for first colonizer dragonflies was eight. Table 2.4 presents the results for all ponds sampled for first colonizer dragonflies from 2008 to 2012.

Table 2.4 Results from the field investigations (of eight sites) of first colonizers, dragonfly species sampled one year after the impoundment filled. These are the species found at most sites.

LOCATIONS

SPECIES	HFP 2901	CHP 2903	FCL 2251	RSP 2582	NSP 2274	JSP 2571	JSP 2 2572	PLP 2883
Year Sampled	2008	2008	2008	2010	2010	2010	2012	2012
Celithemis eponina		X	X		X	X	X	X
Erythemis simplicicollis	X	X	X	X			X	X
Libellula incesta	X	X	X	X	X	X	X	X
Libellula luctuosa	X	X	X	X	X	X	X	X
Pachydiplax longipennis	X	X		X	X	X	X	X
Perithemis tenera	X	X	X	X	X		X	X

HFP = Hall Farm Pond (2901)

CHP =Camp Hanover Pond (2903)

FCL= Federal Club Lake (2251)

RSP =Rutland Stormwater Pond (2582)

NSP = North Lakeridge Stormwater Pond (2274)

JSP = Reynolds Stormwater Pond #1 (2571)

JSP 2 = Reynolds Stormwater Pond #2 (2572)

PLP = Pebble Lake Stormwater Pond (2883)

Figure 2.3 provides images of the six species of first colonizers, determined in this research, for Hanover County, VA

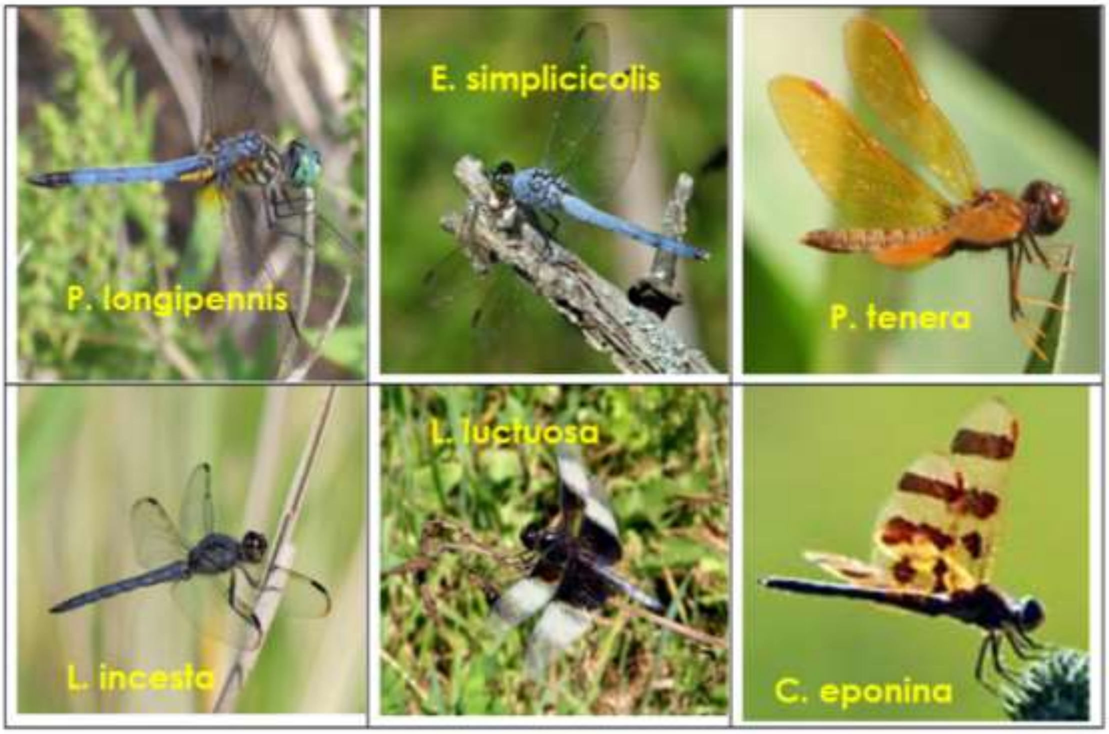

Figure 2.3 Anisoptera first colonizer species for lentic habitats in Hanover County, VA

In Figure 2.3, several additional first colonizer species appeared at some new sites. At Reynolds Stormwater Pond # 2, *Libellula lydia* and *Anax junius* appeared as first colonizers, but may have occurred for a reason to be covered later in this document. At Pebble Lake Stormwater Pond, *L. lydia* also appeared as a first colonizer, along with *Tramea carolina* and *T. lacerate*. It is noted that they became first colonizers at only these two sites, and this may vary at other new sites, which makes conclusions and absolute statements difficult.

What may be noted from my research is that as many as 17 Hanover County species are normally not first colonizers, but later immigrate to a new pond as succession of the lentic sites continues. Significant in this research is which species never appeared to be first colonizers. Table 2.5 lists anisopteran species that appear not to be consistent first colonizers in Hanover County, VA.

Table 2.5 Hanover Dragonfly Lentic Species Consistently Not First Colonizers

Anax junius	*Libellula pulchella*
Anax longipes	*Libellula vibrans*
Celithemis elisa	*Pantala flavescens*
Celithemis fasciata	*Pantala hymenaea*
Epitheca cynosura	*Sympetrum vicinum*
Gomphus exilis	*Tachopteryx thoreyi*
Libellula cyanea	*Tramea carolina*
Libellula deplanata	*Tramea lacerate*
Libellula lydia	

It might be noted that *Anax junius, Libellula lydia, Tramea carolina,* and *T. lacerata* were left in this "not first colonizer list," even though they were discovered as first colonizers at some sites. *Anax junius* is rare at most lentic sites at any time. Because it is known to range great distances because of its size, this might result in appearances in unexpected places. *Libellula lydia's* appearance as a first colonizer is an anomaly. *Tramea carolina* and *T. lacerata* were only found once as first colonizers, likely because they may have explored this new, close pond which is only 0.5 kilometers from what is probably their natal pond, and remained at this location. These indicate what may be good examples of dispersal, but not probable first colonizer behavior.

Discussion

Twenty-four lentic species of dragonflies were collected from Hanover County, Virginia. Results from this research indicated that a subset of six species are typical first colonizers for a lentic habitat in central Virginia. These are: *Celithemis eponina, Erythemis simplicicollis, Libellula incesta, Libellula luctuosa, Pachydiplax longipennis,* and *Perithemis tenera.*

In this study twenty-six sites spread across the 474 square mile county were sampled with the number of total samples being over 300. Several lentic species were found more commonly at the sampled Hanover sites, including: *Erythemis simplicicollis; Libellula incesta; L. luctuosa*; *L. lydia; Pachydiplax longipennis;* and *Perithemis tenera*. This may be a result of their behavior of remaining close to the lentic habitat more frequently, and being less prone to move away from the impoundments, especially for territorial males. Once they find a suitable habitat they settle in and become resident. One might consider these as “sedentary” individuals (or species) verses “nomadic” in their daily behavior. These two categories were first suggested by Wiens, et al. (1986).

The 2005 United States Geological Survey (USGS) published species list for Hanover County, VA, is based on range maps, and may be interpreted as a possible or “expected” list of county species (USGS 2005). The USGS data are not based on actual verified, collected specimens. Comparing the presented list herein with data from those on the USGS list, 68 % of the “expected” lentic species of Hanover County were collected during my research, while ten species on the USGS list were not found in my study. Similarly, the Odonata Central (OC) database, supported by the Dragonfly Society of America and the University of Texas at Austin, is primarily based on range maps versus actual published records. The OC list of species differs from the collected species of this study; they list 27 lentic species and this study collected 23 species. Some of the OC listed species are not on this study's list and some of the collected species in this study are not on the OC range list. This information presents some questions to be addressed: were the missing species not found by my research still living in Hanover and I just did not encounter them? Were they ever there, or are they now locally extinct?

Some of the missing lentic species have been found in neighboring Caroline County to the north, and may be expected to be found eventually in Hanover with further investigations. The species not found which were on the USGS list include: *Arigomphus villosipes; Epitheca princeps; Erythrodiplax minuscula; Libellula semifasciata;* and *Sympetrum ambiguum.* Further field work in more specialized habitats may result in collection of these and additional species, such as *Celithemis martha, C. verna, Epiaeschna heros*, and *Libellula auripennis.*

As global climate change continues, it may be determined that resident dragonfly species are changing in Hanover County. The range of some lentic species may shift further north. Such southern species moving north, and not currently found in Hanover, might include *Coryphaeschna ingens*, *Celithemis bertha*, and *C. amanda*. The decrease in farm ponds and wetlands in the county may also decrease the resident species. The increase of stormwater retention ponds may increase the abundance of Hanover lentic species, but may not increase richness.

It is important to recognize that the placement of, and presence locally of, other impoundments may affect first and subsequent colonization. If an older, source pond exists near the new pond, it may serve as a location to provide immigrating species at a new lentic site. In my investigation of possible source ponds near new ponds (see Table 2.6), of the six first colonizer species, at the nearby possible source ponds, # 2273 (close to 2274), #2882 (close to 2883), and Reynolds # 1 (close to Reynolds #2) I noted that all hypothesized first colonizer species except *Libellula luctuosa* were present for possible immigration to the new pond.

The close proximity of a source location may result in non-typical first colonizers. Noted from this research, if a source site is less than a kilometer away, atypical colonizers may appear in the first year. This was demonstrated at Reynolds Stormwater Pond # 2 (RSP#2) and # 2883 Pebble Lake Stormwater Pond (PLSP). As probable source sites, Reynolds Stormwater Pond # 1 (near RSP#2) and Creekside Stormwater Pond (# 2882 near # 2883 PLSP) were each less than 1 kilometer from the new ponds noted above. This may account for the presence of the non-typical colonizers, *Anax junius, Libellula lydia, Tramea carolina,* and *T. lacerata,* at the two new ponds.

The original three damaged impoundments (Hall Pond, Camp Hanover Lake, and the Federal Club Lake) were grass-covered meadows with a 1st order stream for two to three years prior to the impoundments refilling with water. This research considered the question of whether existing resident lentic odonates, along these streams or in the adjoining meadows, resided in the area before the ponds were built and just continued residency after the impoundments were constructed. Although pre-impoundment sampling of all sites was not done, I did sample similar sites in the county; specifically, two sites that had been destroyed by Hurricane Gaston. One site was Lake Rainer, formerly a 2.8 hectare pond, and the other was Parsley Mill Pond, formerly a four hectare pond; both were never rebuilt and both have a remaining small (one meter wide) stream. The lentic species, *Libellula incesta, L. lydia, Erythemis simplicicollis* and *Pachydiplax longipennis,* were found at these former lentic sites; but they are also found at some county lotic sites. This raises certain questions: Were they leftover species after the ponds were destroyed? Did they immigrate to the small creeks that remained after the ponds were destroyed? While these questions cannot be resolved definitively, I postulate that *Libellula incesta*, *Erythemis simplicicollis* and *Pachydiplax longipennis* should be considered first colonizing anisopteran species regardless, since they were found at most new impoundments that were surveyed.

Results support the designation of *Celithemis eponina, Erythemis simplicicollis, Libellula incesta*, *Libellula luctuosa, Pachydiplax longipennis*, and *Perithemis tenera* as typical first colonizer species in Hanover County, Virginia. The two *Libellula* species first colonized 100% of the sites sampled. *Pachydiplax longipennis* and *Perithemis tenera* first colonized 86% of the sites sampled. *Celithemis eponina* and *Erythemis simplicicollis* first colonized 75 % of the sites sampled.

Characteristics or life history factors which might be present in a first colonizer dragonfly, but might not be present in non-first colonizers include being a weak competitor. Begon (2006) states that the poor competitor is a better colonizer. Rockwood (2006) says that a trade-off between competitive ability and colonization ability may exist in some cases. I considered that weaker combat species might be more prone to emigrate. Curry and Kennedy (2010) state that aggressive interactions can affect local spatial distribution of species. I could not support any hypothesis other than the proximity of sources locations to new sites as a determinate of first colonizer status.

Many dragonfly species are prone to wander from the natal site (Corbet 1980). Corbet (1999) lists a number of species, such as *Erythemis simplicicollis* and *Pachydiplax longipennis*, which were also noted in this study. This can result in increased search behavior, as Stamps (2001) mentions, and increase their chance of finding an attractive immigration site to colonize, and thus disperse. The less common species at a typical pond did not appear as first colonizers at new sites.

In summary the existence of a natal site close to a new site could increase the chances that species from that natal site will immigrate to the new site. This may be an important factor, as observed at three of the sites I studied when a natal (source) pond was very close; these being North Lakeridge Stormwater Pond (2274), Reynolds Stormwater Pond #2, and Pebble Lake Stormwater Pond (2883).

Another determinant for the best colonizers may be abundance, since the more abundant species/individuals may be pushed from the natal site by conspecifics. First colonizer studied sites had species that were some of the most frequently encountered in the county. Considering the species list of the 26 studied County sites, and with the exception of *Celithemis eponina,* I noted that *Erythemis simplicicollis, Libellula incesta,* *Libellula luctuosa, Pachydiplax longipennis,* and *Perithemis tenera* are among the most frequently encountered species in Hanover County. The other species, *L. lydia,* may be a first colonizer species, and it is a very abundant species found at nearly all lentic sites eventually. The excess abundance of individual species of odonates in the county is consistent with my observation of first colonizers. It is my conclusion that greatest abundance is a strong determinant for which species is a first colonizer.

Using more advanced genetic data from first colonizers may provide more data regarding source locations, species that disperse, and species that are first colonizers.

Chapter Three

Dragonfly Community Structure at New Lentic Habitats

Introduction

The process of dispersal and immigration to new habitats by Anisoptera has three stages: 1) searching; 2) settlement; and 3) residency (Stamps 2001). After settlement and establishment of residency at a new location, some species may better assimilate into the community structure of that site than other species. If a species is observed more often or in greater numbers than other species, it may be considered the dominant species at that site.

The hypothesis of this research is that the dominance of dragonfly species at a new impoundment will change over time, especially as the habitat goes through natural succession and as species interactions are sorted out. To address this hypothesis, investigations were made of three new impoundments, beginning one year after the filling of water at each site, and of three established and similar impoundments to serve as reference sites.

Dominance in the context of this research is a description of greater abundance. The species identified as dominant are the species that are numerically superior at that location at a given point in time (Smith and Smith 2001). Obtaining accurate abundances of dragonflies in a particular location at a given time poses significant problems if individuals are constantly flying in and out of an area and returning some time after the first counting, which can lead to double counting, even if precautions are taken to avoid this artifact. A "frequency of observation count," rather than abundance count, is more practical as a measure of dominance. Such a method has been used in Christmas Bird Counts, and more specifically for dragonflies by Bried and Ervin (2006).The species which is observed most often is assumed to be the dominant species (Corbet 1999).

Some species of dragonflies are observed more frequently and more persistently at an impoundment because they tend to remain closer to the impoundment and may be more territorial; thus they are observed more often at the impoundment than some other species. Persistence of a species does contribute to stability of the dragonfly assemblage (Crowley and Johnson 1992). Other species might have different behaviors and return to the impoundment only to mate, and thus they are not of high abundance at the impoundment on a continual basis. Considering the community structure in a particular lentic habitat, species that are most abundant, or more often observed, may have significant effects on other species, but all, dominant or not, make up the community.

As the odonate community exploits a new habitat, competition may have an impact on dominance. All adult dragonflies generally compete for the same food (flying insects) at a lentic site, and there is evidence that they compete for perching sites (Switzer 2002). First colonizers could be displaced (for behavioral reasons) despite their early arrival. Perhaps being more prone to disperse or having less success in combat with other species might result in a species declining in numbers over time at a new site. Studies have supported that some species' aggressive interactions with others for territory may result in their increased abundance at the lentic site (Corbet 1980, Curry and Kennedy

2010). This is part of the theoretical basis for the hypothesis of this study: first colonizers will not remain the most abundant because they will be displaced by later arrivals. If the later arriving species is a better competitor, the competition-colonization trade-off theory (Levins and Culver 1971, Hastings 1980, Tilman 1994, Yu and Wilson 2001 and Calcagno et al. 2006) would allow a better competitor and a better colonizer to both occupy the same habitat: but what if an equilibrium can not be reached between the two, could the better colonizer/poor competitor become extinct in that habitat?

Dragonfly assemblages in a lentic habitat have an identifiable community composition. It may reach some stability, but can at times be stochastic. Stochastic communities would result in some variability of census numbers, i.e. one year a species may be the most abundant and the next year it might be counted as the second most abundant, only to be most abundant again the following year. Chase (2010) states that stochastic (highly variable) lentic communities can result in higher biodiversity. Sampling variability may also explain some of the variations in census numbers.

Several measures may be used to capture elements of community structure. Richness, the number of species in a community, may be considered a measure of community structure. Evenness, the relative abundance of individuals among species, may also be considered. The Shannon-Weaver Index of diversity measures numbers of individuals in species groups and the proportion of each species in the whole population, and thus includes components of both richness and evenness (Smith and Smith 2001).

Various factors may affect richness, evenness, dominance and community structure. After emergence from the larval stage, immature adults (tenerals) will leave the natal site to complete reproductive maturation (Corbet 1980). Waser (1985), in his study of avian and mammalian data, says that competition for mates is a primary factor for dispersal. In the case of dragonflies this may be one of the factors affecting abundance, and displaced individuals will no longer be part of the assemblage at a particular lentic site. Newly resident dragonflies may remain at this new site or they may disperse to another site. Corbet additionally says that this dispersal is frequent, and that mature adults will respond to cues as they select their reproduction sites, which may be other than the natal site.

Site cues and special characteristics of a site may cause a dispersing odonate to select a site for residency and increase its numbers at that site. Corbet (1980) states that trees and other littoral zone plants are important habitat selection factors. He also states that vegetation provides important shelter for immature adults while they mature. The importance of trees along a pond edge as a habitat element is also supported by Remsburg et al. (2008).

Suh and Samways (2005) studied dragonfly assemblages at a small reservoir (about 40 hectares) for 13 years. They reported that vegetation, whether submerged or floating in the pond or in adjacent shrub or forest, had a positive impact on dragonfly abundance. High vegetation diversity correlated with high odonate species richness and diversity at the studied site. Remsburg and Turner (2009) looked at the physical structure of littoral zone vegetation as a factor for lake odonate assemblages. They stated that *Libellula* spp. and Gomphidae had lower abundance at the studied lakes with less shrub and tree vegetation. However, a pond surface completely covered by a plant like duckweed, *Lemna minor,* has been shown to inhibit *Perithemis tenera* (Groover 2008).

Distance between lentic habitats can affect abundance and richness of species (Chase et al. 2010). Considering that dispersal from other lentic habitats could affect the eventual residents of a site, the farther away a source of immigrants is the less it may impact the potential immigration site. This may be a non-linear distance-decay effect, but no studies on dragonflies exist.

Abiotic factors may cause the colonizing dragonfly to stay or not stay at the new site. Samaika and Samways (2011) have noted that environmental variables might impact richness. For example, pH, water temperature, dissolved oxygen and conductivity were important variables.

Competition is a site selection factor and a stimulus to disperse. Even in a large pond dragonflies display combat with conspecifics and other species of dragonflies. Combat avoidance has been observed in which one individual departed the pond after visual contact with an individual of another species; males have the most frequent non-mating interactions (Lutz and Pittman 1970). Combat-winning males of *Perithemis tenera* appear to be abundant at some studied ponds observed by this researcher. Mating success affects what Switzer (2002) describes as “tenure” (a particular defended territory within a 24-hour period) at a pond for this species. Switzer also showed that later arriving males of this species have shorter tenure.

Dominance in the context of this study will be measured by numerical data, indicating abundance of species. My hypothesis is that species that were dominant in the first year that a new pond was available will be displaced by other, presumably competitively superior species in subsequent years. A second hypothesis is that: the dragonfly communities at these new impoundments will demonstrate changes in community structure that will be greater than that of the reference ponds. To test these two hypotheses, a survey of three new lentic sites paired with three established sites was undertaken for three years after the new impoundments had filled with water. Following the three established sites allows variability in dominance in a mature pond ecosystem to be determined and compared to changes at newly established ponds.

Methods

Study System

To assess changes in dominant species during the initial period of pond colonization, three new ponds and three established "reference" ponds were monitored and data collected from 2008 to 2010, from June 1 – August 31, the most active season for the adult dragonflies. Adult dragonfly species' censuses were taken at each impoundment. The three new ponds were: Hall Farm Pond, Camp Hanover Pond and Federal Club Golf Course Lake (see Chapter 2, Figure 2.1). As reference ponds, Vitale Farm Pond, Snead Farm Pond and Hollows Golf Course Lake were surveyed (also in Chapter 2). Hall was paired with Vitale, Camp Hanover was paired with Snead, and Federal was paired with Hollows.

The new ponds were selected because of their availability in the study county, their age (less than two years after filling with water), and the expected appearance of good dragonfly lentic habitats. The reference impoundments were selected because of their availability in the study county, similarities to the new impoundments, and the observed presence of lentic dragonfly species.

Upon first inspection, Camp Hanover Lake appeared to be a pond, but it was later determined to be a lake because of prevailing wind actions. The Snead Farm Pond is smaller and shallower and is not principally affected by wind currents, as occurs in lakes.

Despite these differences, a pairing of Camp Hanover Lake with Snead Pond seemed reasonable because of its adjacent topography and surrounding vegetation but was not expected to influence diversity due to size.

All impoundments had sufficient amounts of water during the observation periods, except for some water level reduction, and typical dragonfly foraging, mating and ovipositing was observed. Table 3.1 identifies some physical details regarding these compared impoundments.

Table 3.1 Hanover County impoundments compared for three years (2008 – 2010)

Site ID #	Site Name	Site Location	Role	Characteristics
1951	Hollows Lake	West Hanover County	Reference / Federal	6 ha. surrounded by golf course *
2251	Federal Club Lake	West Hanover County	New Lake	7 ha. on golf course & forest **
2282	Snead Farm Pond	Central/East Hanover County	Reference / Camp Hanover	2 ha. surrounded by forest & 2 dams
2903	Camp Hanover Lake	East Hanover County	New pond (lake)	4 ha. surrounded by forest
2593	Vitale Farm Pond	Central/East Hanover County	Reference/ Hall	1 ha. 40 year old farm pond
2901	Hall Farm Pond	East Hanover County	New pond	2 ha. surrounded by forest/fields

All but one (Site 1951) impoundment has abundant shoreline vegetation.
* cut grass only along shoreline and beyond
** subject to large (1-2 meter) fluctuation in lake water levels for weekly course watering

Data Collection

Water temperature, pH, dissolved oxygen and conductivity measurements were taken in 2009 at each impoundment studied (Table 3.1). All data were collected between the hours of 1000 and 1300 Daylight Savings Time (DST). The pH data were collected from grab samples one meter off shore and 0.5 meters below the surface; temperature (ºC) and conductivity (µSiemens/cm) samples were collected one meter off shore and 0.5 meters below the surface of the impoundment; dissolved oxygen (DO) was collected similar to the methods of Patterson and Fernando (1969) who collected data from 0.5 meters above the substrate and one meter off shore. Equipment used for each analysis is given in Table 3.2.

Protocols were established for dragonfly data collection and consistency of effort. For three years, the same three stations at each impoundment were surveyed. For consistency at each studied survey station, one survey location at each impoundment was on the earthen dam that formed the impoundment; another station was on the left side (while standing on the dam) of the impoundment 100 meters from its dam; and the final station was on the right side 100 meters from the dam. Global positioning data were taken on every plot and small stakes were placed at each survey station to demarcate the exact location per station during each visit for the three year study. At each sampling period the same locations were used for data collection at each studied impoundment.

Because dragonfly adults are most active at a lentic habitat during June, July, and August, the data collection occurred during those months. Dragonfly counts occurred during optimal conditions and times. Optimal time-of-day at the studied ponds was from 1000 to 1500 (DST- summer) hours. Observations were made only when all of the following optimal weather conditions were present: 22 - 35 °C (in the shade), clear or partly cloudy sky conditions, barometric pressure from 29-31 mm, and wind velocity under 10 km/hr. This selection of wind velocity threshold was based on personal field observations; when wind velocity exceeds 10 km/hr the adult dragonflies' presence appears to decline. Equipment used for these measures are noted in Table 3.2.

Table 3.2 Equipment used in the R.S. Groover field research

Equipment	Brand	Model	
GPS unit	Garmin	GPS map 765	And Barometric Pressure & Temperature
pH meter	Eutech/Oakton	3564-10	Waterproof pH Tester 10
Conductivity meter	Hanna	EC/TDS	HI 98312
Dissolved Oxygen	Extech	407510	Heavy Duty Dissolved Oxygen Meter
Anemometer	Lutron	LM-81AT	With Thermometer
Thermometer	Zoro	G1710581	Analog Thermometer

Methods for observations and counts from other studies were reviewed including those of Bried and Ervin (2006). In their research to determine abundance of dragonflies with respect to distance from a Mississippi wetland, these researchers made one circuit along transects during six sampling events for one year. Three distance intervals from the water's edge were covered: 10-40 meters, 70-100 meters, and 130-160 meters from the water's edge, respectively. The length of transects was not identified, but they walked slowly for 50 minutes, that constituted a transect. Only perching adult dragonflies were recorded for their study, which may have resulted in underestimates as many dragonflies remain flight active for long periods. Seven different species of dragonflies were recorded in their study.

Suh and Samways (2005) used "sampling units" for their assemblage study of a small reservoir, "with a 550 meter circumference." Their 31 sampling areas/units were 20 meters by 20 meters along the water's edge. The sampling units were sampled twice a month in active summer flight season. The researchers walked for six minutes in each sampling unit and recorded only male dragonflies. Only six minutes of observation in each area may have resulted in underestimation of individuals that had momentarily flown out of the surveyed areas. Females not counted might have increased their taxa list. They recorded 30 different species of Anisoptera.

The approach of Suh and Samways seemed well suited for my research with some modifications, and was adapted for my study. During all data collection events, a modified Pollard Walk technique was used. This technique has been validated for flying insect studies (Pollard 1977, Brooks 1993). At the defined stations, each census consisted of a slow walk through each station, at least 5 loops for a one hour per census per station per visit. Each walk involved using an established rectangular area (station) which was 20 meters in length along the pond's shoreline and 10 meters along the shorter sides of the rectangle (with 5 meters into the water and 5 meters back from the water's edge). Fulan et al. (2010) also used the 20 meters along the shoreline method, with three surveys per season.

During the counts, each dragonfly adult (male or female) that flew or perched in the rectangular area (station) within a one hour observation period was identified. Identification had to be made quickly and accurately. Recording the observed numbers of all dragonfly species was made using a Field Observation Data Sheet (Appendix 2), which was completed for each census at each station on the date of each visit. Time, wind velocity, temperature, and cloud cover data were recorded during each census to demonstrate consistency of effort within the established protocols. Wind direction was not an issue for these surveys.

At each location, three stations were sampled per impoundment site for three times per summer over three years. In summary, these data sets per impoundment totaled 27 censuses or samples (3 stations per pond X 3 times per summer X 3 years = 27). The only exceptions were for the two reference impoundments added after 2008, which were limited to 18 censuses.

Richness, Shannon-Wiener Diversity Index (also known as Shannon Diversity Index) and evenness values for each impoundment were calculated (Green River Community College 2013, University of Hawaii 2013).

Data were compiled in two ways. First, average abundances over all samples in a given year at a given site were compiled into a summary table for each impoundment. Second, each individual sample was used in a multivariate analysis. Samples from the paired impoundments were ordinated together and separately, and resulting sample patterns were examined in two dimensions, with data for each of the new sites being compared directly to the data from its corresponding reference site. In addition, an overall ordination incorporating all sites using total abundance for each year per site was done to obtain a comprehensive test of the hypotheses.

The observed communities were compared using multivariate analysis (MA). Since the underlying statistical distributions of the species abundances were not known to be normally distributed, a nonparametric ordination method was utilized: Nonmetric Multidimensional Scaling (NMS). In addition to being robust with respect to underlying data distributions, NMS allows the utilization of distance measures like the Sorensen (Bray-Curtis) distance which have proven more useful in the study of ecological communities that Euclidean Distance used in parameteric ordination methods like Principal Components Analysis (McCune and Grace 2002)

Samples from the paired impoundments were ordinated together and resulting sample patterns were examined in two dimensions, with changes in community composition at the new pond site compared to the data from a companion reference sites. In addition, an NMS was conducted combining total observed numbers of individuals for each pond by year. These analyses directly addressed the main hypothesis of the study: that dragonfly communities change over the early years of colonization more than in later periods.

The multivariate analysis package PC-ORD™ was used (MJM 2002). Ordination techniques included Nonmetric Multidimensional Scaling (NMS), with distance measurements using the Sorensen (Bray-Curtis) similarity matrix. A minimum of 250 iterations per run was used. Stress per iteration number was plotted with two dimensional solutions. The NMS analyses per year for co-plots in the new impoundments were significant when tau values exceeded 0.05 threshold for α.

Results

Water Quality Characteristics

Water temperature, pH, dissolved oxygen and conductivity measurements indicated that each studied impoundment was within acceptable levels to support a healthy odonate fauna (Bromark and Hanson 1998), as noted in Table 3.3.

Table 3.3 Water data for impoundments in Hanover County, Virginia, July 2009

Site ID #	Site Name	pH	Temperature (C°)	Dissolved O	Conductivity
1951	Hollows C.Club Lake	6.8 - 7.0	26.0 - 27.4	9.2 - 9.5	208 - 211
2251	Federal Club Lake	7.0 - 7.2	26.2 - 27.4	8.3 - 8.8	197 - 203
2282	Snead Farm Pond	7.5 – 7.8	24. 8 - 25.9	6.7 - 7.3	211 - 218
2903	Camp Hanover Lake	6.8 - 7.1	24.7 - 26.0	9.3 - 10.8	183 - 203
2593	Vitale Farm Pond	7.6 - 7.9	24.8 - 25.2	8.8 - 9.1	203 - 220
2901	Hall Farm Pond	6.9 - 7.4	24.4 - 25.8	8.7 - 9.6	210 - 218

Dragonfly Communities

Results were assembled for the six lentic habitats: three new and three established reference impoundments. The order of listed species in the tables has no specific relevance except in some cases the more numerous species are listed near the top of the tables. To be consistent the order of listing was maintained in subsequent tables. This presentation is organized using the predetermined pairing of new ponds and reference ponds with emphasis on the new ponds in the context of the reference ponds.

Hall and Vitale Data

Table 3.4 provides a summary of survey results for Hall Farm Pond, the new pond in the first pairing, over the three years of this study. This pond was reconstructed in 2007 and filled with water by 2008.

Table 3.4 Comparison of three years data for Hall Farm Pond - mean values and rank per year

SPECIES	2008*	2009*	2010*	Mean for 3 Years	rank in 08	rank in 09	rank in 10
Libellula incesta	24.22	22.00	10.11	18.78	2	1	1
Libellula lydia	6.22	4.22	1.11	3.85			
Libellula luctuosa	20.00	10.44	8.07	12.84	3	4	3
Erythemis simplicicollis	9.00	11.33	5.67	8.67	4	3	4
Celithemis eponina	1.00	0.22	0.07	0.43			
Perithemis tenera	0.00	3.33	1.11	1.48			
Pachydiplax longipennis	41.78	14.22	8.63	21.54	1	2	2
Tramea lacerata	0.00	0.67	0.67	0.45			
Sympetrum vicinum	0.00	0.00	0.07	0.02			
Celithemis elisa	0.00	0.00	0.04	0.01			
Anax junius	1.00	0.00	0.19	0.40			
Gomphus lineatifrons	0.00	1.00	0.00	0.33			
Celithemis fasciata	0.00	0.67	0.00	0.22			

*** Mean value per year. Value is abundance per unit effort where effort is counts of species at three stations surveyed per year.** Rank is highest to lowest for top 4 species for 2008, 2009, and 2010

Based on the survey methods used, dominant species represented by the four most abundant taxa were identified. The four most abundant taxa were consistent from year to year, varying slightly in order of abundance. Using a mean value for the three years, the top two species were *Pachydiplax longipennis* and *Libellula incesta.* Also of note in the first year of the pond, these two species were the most abundant and stayed that way for three years; and there were two species that consistently remained subdominant. The hypothesis, that a change in dominance would occur, was not supported by the data for this pond.

The forty-year old Vitale Farm Pond was paired with the Hall Farm Pond and served as a reference. As a reason for this paring, both impoundments are surrounded by similar forests, pasture, and cropland. They are close to the same size. Summary data for this pond are provided in Table 3.5

Table 3.5 Comparison of three years data for Vitale Farm Pond - mean values & rank per year

SPECIES	2008*	2009*	2010*	Mean for 3 Years	rank in 08	rank in 09	rank in 10
Libellula incesta	34.70	28.89	23.11	28.90	1	2	1
Libellula lydia	3.37	23.78	22.22	16.46	4	3	2
Libellula luctuosa	3.83	14.44	18.67	12.31	3		3
Erythemis simplicicollis	1.00	2.44	2.89	2.11			
Celithemis eponina	0.00	1.00	0.33	0.44			
Perithemis tenera	10.00	30.89	15.67	18.85	2	1	4
Pachydiplax longipennis	2.67	16.78	8.67	9.37		4	
Tramea lacerata	0.00	0.67	0.56	0.41			
Sympetrum vicinum	0.00	0.00	0.00	0.00			
Tramea carolina	0.00	0.00	0.67	0.22			
Celithemis fasciata	0.00	0.33	0.56	0.30			
Libellula cyanea	0.00	1.33	0.00	0.44			

*** Mean value per year. Value is abundance per unit effort where effort is counts of species at three stations surveyed per year.** Rank is highest to lowest for top 4 species for 2008, 2009, and 2010

This existing reference pond demonstrated some variability, with greater changes in dominant species from year to year. However, during the survey period only five species ever entered the annual top four ranking. Based on the mean value over the three years *Libellula incesta* and *Perithemis tenera* were the most abundant species. Note that *L. incesta* was very abundant in both ponds. However, while *Pachydiplax longipennis* was usually in the top two species in Hall Farm Pond, *P. tenera* was typically in the top two in the Vitale Pond.

Multivariate Analysis (MA) of the site data provides a comprehensive look at the community structures for these impoundments. Using the Nonmetric Multidimensional Scaling (NMS), dragonfly assemblages in Hall Farm Pond and its reference impoundment Vitale Farm Pond were examined. Figure 3.1 provides graphic results from the NMS of these two communities, with points coded by pond. The red triangles (#1, **Δ**) depict Hall Farm Pond data points, and the green triangles (#2, **Δ**) represent Vitale Farm Pond data points. The color-coded lines form convex hulls, essentially a polygon encompassing all samples from a certain pond. Interestingly, the established Vitale Farm Pond exhibits a greater spread in the community composition than the new pond.

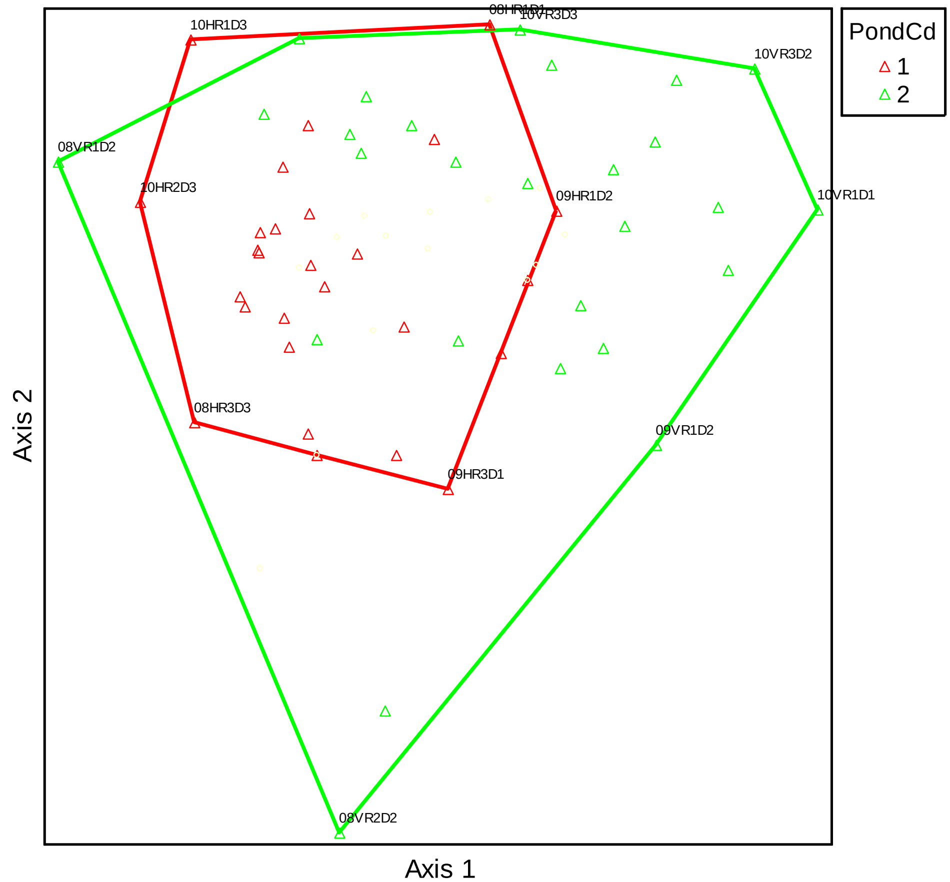

Figure 3.1 Scatterplot of the nonmetric multidimensional scaling results comparing dragonfly community data (2008 – 2010) for Hall Farm Pond (Pond CD 1) and Vitale Farm Pond (Pond CD 2). Final stress of 16.93 (fair), n = 55.

Key to labelled points in Figure 3.1 and subsequent figures. To explain what the codes mean, the example of **08VR1D2** is used:

08 is the year of the sample (2008)
VR is the impoundment code (Vitale Farm Pond)
1 is the location at the impoundment (one of three stations at the pond)
D2 is the second survey date (one of three surveys done that year at that station)

composition of the two sites. Hall Farm Pond was the new pond in the pairing with reference to Vitale Pond. The multivariate analysis reveals very little systematic difference in the community composition. Tight clusters represents similarity data. There is some separation on Axis 1 and Hall Farm pond samples are somewhat more tightly clustered, but there is very strong overlap in assemblages found in the two ponds over these three years. The lack of variability or directionality in community composition over the three years in the new pond is another indication that the results fail to support the hypothesis of odonate community change during the new pond's establishment.

NMS were coded to show year codes for both ponds together. These results are presented in Figure 3.2 with points labelled for each sample by year.

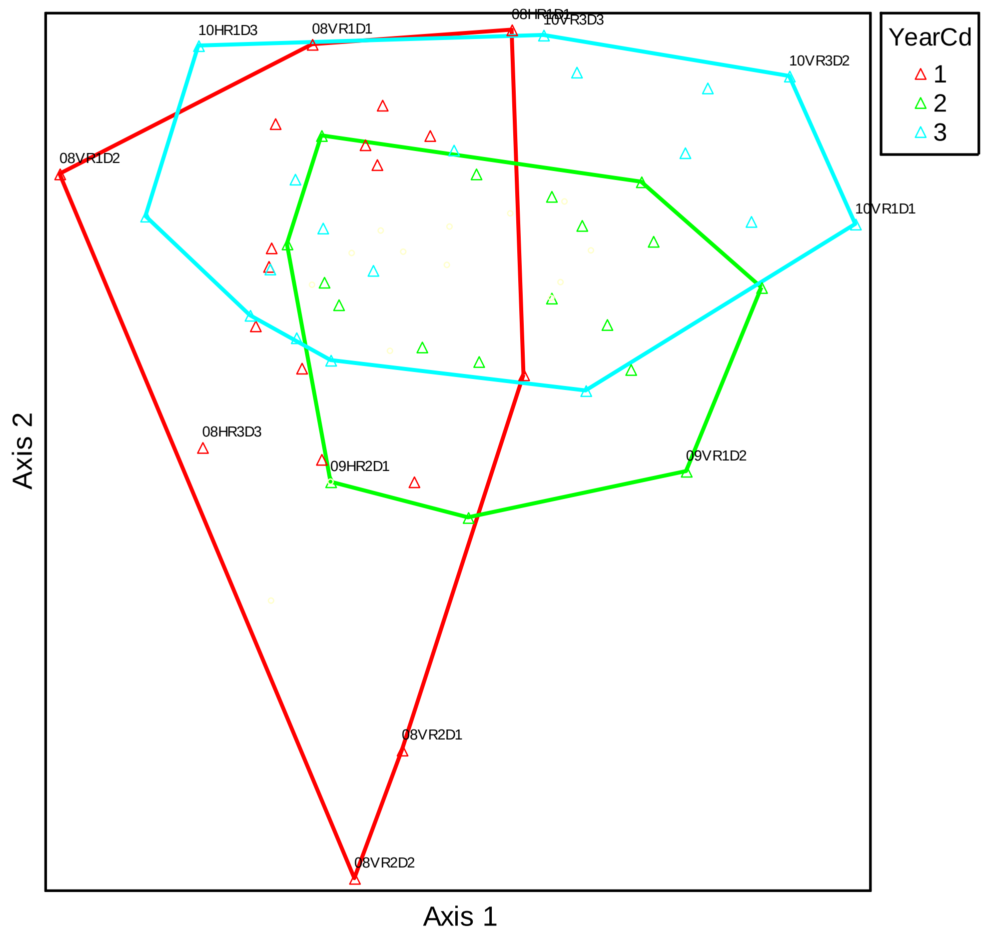

Figure 3.2 Scatterplot of the nonmetric multidimensional scaling results comparing three years 2008 (1), 2009 (2) and 2010 (3) of dragonfly community data for both Hall Farm Pond and Vitale Pond.

The first year (2008) resulted in a more expanded polygon, primarily because of the two data points near the bottom of the graph both being from station 2 of the Vitale Pond. If these were disregarded the polygons would be much more similar, but no explanation is offered for this possible anomaly. Considering year comparisons of both ponds, much overlap does exist, suggesting that there was substantial similarity among the dragonfly communities in the two ponds over the three years.

A major research question was to determine if there was a progression of community structure in the new pond and what was the level of variability in the established reference pond? A look at the year-to-year changes of each pond separately reveals more about their community structure. In Figures 3.3 (for Hall) and 3.4 (for Vitale) the three years for each pond is shown separately.

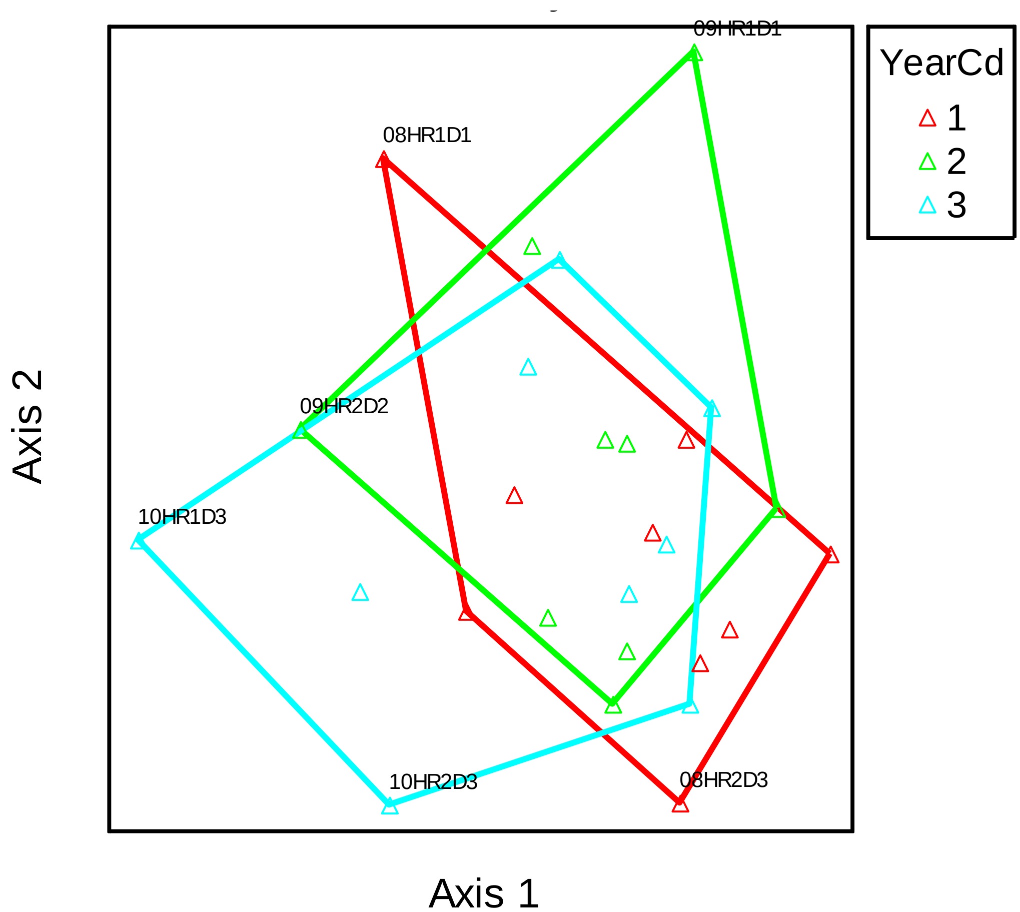

Figure 3.3 Scatterplot of the nonmetric multidimensional scaling results comparing three years 2008 (1), 2009 (2) and 2010 (3) of dragonfly community data for Hall Farm Pond. Final stress is 20.44, n = 28, which is poor. Poor was noted by the NMS run results.

From 2008 to 2010 the community structure of Hall Pond might be expected to change as the new pond ages. Each year did reveal outliers, with stations one and two most prominent and no apparent outliers from station number three. It can be noted that for the three years the data points did cluster more so in the right half of the scatterplot and more so in the lower right quadrant. This would indicate that the pond's dragonfly community remained fairly constant and nondirectional even though some changes did occur per year.

Consideration could be made as to how the dragonfly community changed in this new impoundment per species. From an NMS run for Hall Pond, noted in Figure 3.3, individual co-plots correlation coefficients for the top four species are provided in Table 3.6. Any tau values greater than 0.360 would be significant at the 0.05 level, as noted for *Pachydiplax longipennis* both axes, and *Erythemis simplicicollis* for Axis 2. Since no groupings were observed by year, the variations in species composition associated with these axes could not be assigned to consistent or directional change through time.

Table 3.6 Correlation Coefficients (tau) between NMS Axes and dominant species. Hall Farm Pond only NMS (n = 26), significant values indicated by *

Species	NMS Axis 1	NMS Axis 2
Libellula incesta	-0.003	-0.055
Libellula luctuosa	0.321	0.189
Pachydiplax longipennis	0.576 *	-0.397 *
Erythemis simplicicollis	-0.145	-0.509 *

\

The Vitale Farm Pond, the 40-year old reference pond, exhibited more variability among years than did the new pond (Figure 3.4). Data for 2009 and 2010 overlapped strongly, but 2008 showed distinct systematic differences from the two later years and two outliers. Thus, the existing pond in this pair showed more inter-annual variability than the new pond.

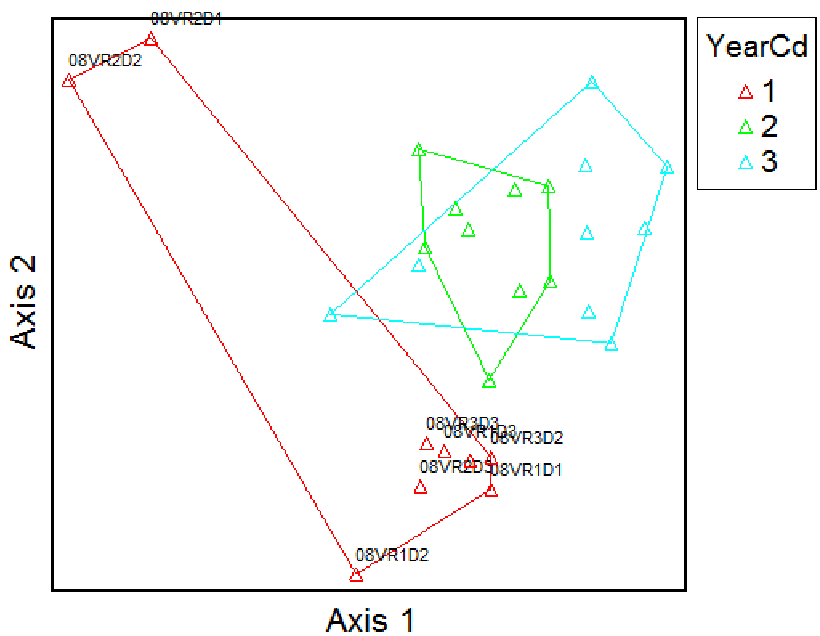

Figure 3.4 Scatterplot of the nonmetric multidimensional scaling results comparing three years 2008 (1), 2009 (2) and 2010 (3) of dragonfly community data for Vitale Farm Pond. Final stress is 14.95, n=27, which is fair.

Camp Hanover and Snead Data

The next paired impoundments are Camp Hanover Lake and its reference, Snead Farm Pond. Table 3.7 provides the summary data for Camp Hanover for three years after its reformation.

Table 3.7 Comparison of three years data for Camp Hanover Lake - mean values & rank per year

SPECIES	2008*	2009*	2010*	Mean for 3 years	rank in 08	rank in 09	rank in 10
Libellula incesta	27.57	28.56	30.78	28.97	1	2	1
Libellula lydia	0.43	2.67	0.44	1.18			
Libellula luctuosa	7.53	12.00	7.78	9.10	3	3	4
Erythemis simplicicollis	3.77	2.67	9.22	5.22			3
Pachydiplax longipennis	19.90	29.44	12.11	20.48	2	1	2
Perithemis tenera	4.80	8.33	4.00	5.71	4	4	
Celithemis fasciata	2.57	4.89	2.56	3.34			
Celithemis eponina	1.53	0.56	1.22	1.10			
Anax junius	0.10	0.03	0.78	0.30			
Libellula cyanea	0.33	0.00	0.44	0.26			
Celithemis elisa	0.00	0.11	0.00	0.04			
Sympetrum vicinum	0.00	0.22	0.00	0.07			
Tramea carolina	0.00	0.00	0.33	0.11			

*** Mean value per year. Value is abundance per unit effort where effort is counts of species at three stations surveyed per year. Rank is highest to lowest for top 4 species for 2008, 2009, and 2010**

Camp Hanover Lake, a new impoundment, had a richness of 13 species when all three years were considered. Dominance varied only slightly among the three years, with two species being most abundant in all three years: *Libellula incesta* and *Pachydiplax longipennis*. These two species were the most abundant first colonizers the first year, and their mean values for the three years continued to place them as the two most abundant species. Three other species were in the top 4 in some of the years, but never the top two: *Libellula luctuosa*, *Erythemis simplicicollis*, and *Perithemis tenera*. Again, note that dominance did not greatly change after the first year, and thus does not support my hypothesis that dominance would change within three years.

The reference impoundment for Camp Hanover Lake was Snead Farm Pond (Table 3.8). In 2008, only one reference pond for the entire research was planned for this portion of the dissertation research with no specific reference pond for Camp Hanover's impoundment. Then for 2009 and 2010, Snead Farm Pond was added to provide a reference for Camp Hanover Lake. While taxa patterns were not identical, the reference site did have the same two top species, *Libellula incesta* and *Pachydiplax longipennis*. The former species was in the top two for both years; the latter dropped from 1st to 4th place, but remained very abundant in 2010. The two other species in the top four (*L. luctuosa* and E. *simplicicollis*) in Snead Farm Pond were also the subdominants in Camp Hanover Lake and were similar in abundance between the two ponds.

Table 3.8 Comparison of two years data for Snead Farm Pond - mean values & rank per year

SPECIES	2009*	2010*	Mean for 2 years	rank in 09	rank in 10
Libellula incesta	22.11	24.56	23.34	2	1
Libellula lydia	0.89	3.11	2.00		
Libellula luctuosa	6.78	16.44	11.61	4	2
Erythemis simplicicollis	8.00	15.78	11.89	3	3
Pachydiplax longipennis	32.89	14.78	23.84	1	4
Perithemis tenera	0.67	0.00	0.34		
Celithemis fasciata	2.56	2.22	2.39		
Celithemis eponina	4.11	6.00	5.06		
Anax junius	0.22	0.00	0.11		
Libellula cyanea	0.33	3.56	1.95		
Anax longipes	0.11	0.00	0.06		
Tramea carolina	0.00	2.22	1.11		
Tramea lacerata	0.00	0.22	0.11		

*** Mean value per year. Value is abundance per unit effort where effort is counts of species at three stations surveyed per year. Rank is highest to lowest for top 4 species for 2009 and 2010, no data exists for 2008.**

Multivariate analysis using NMS for these two ponds reveals expected overlap and some differences. Figure 3.5 indicates the relationships among the samples based on their taxa composition for the combined impoundments coded by pond. The red triangles (#1, **Δ**) indicate Camp Hanover Lake data points, and the green triangles (#2, **Δ**) represent Snead Farm Pond data points. Along Axis 2 there is some tendency for Camp Hanover samples to cluster on the right and Snead Farm Pond samples to cluster on the left, although there is a zone of considerable overlap in the middle for both impoundments. If you disregard the one outlier (08CH1D2) for Camp Hanover Lake, its scatterplot is more compact.

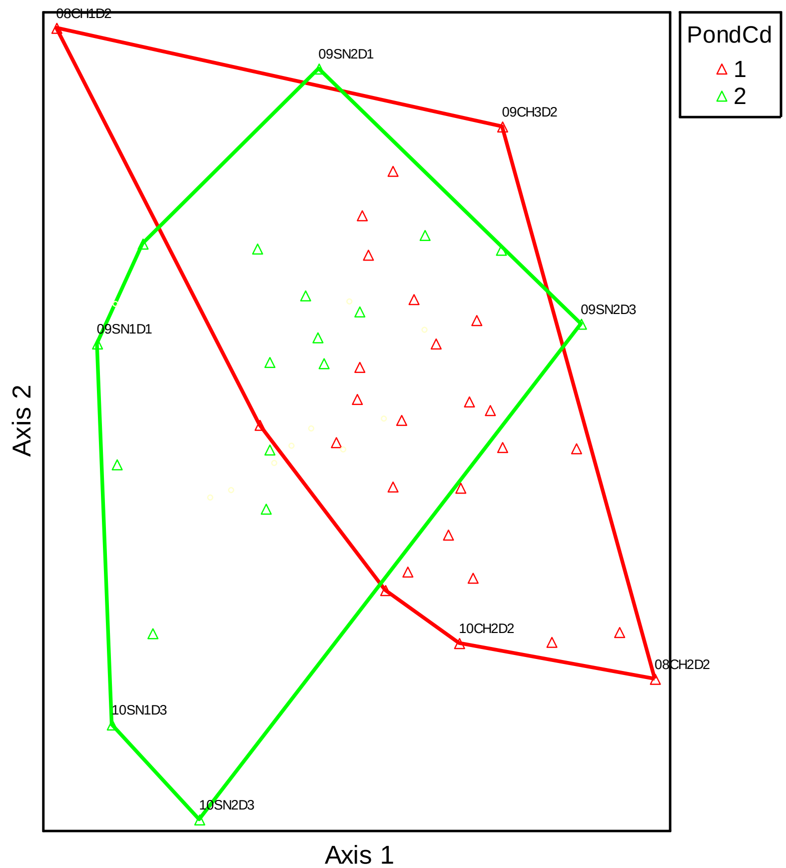

Figure 3.5 Scatterplot of the nonmetric multidimensional scaling results comparing dragonfly community data for 2008 – 2010 for both Camp Hanover Lake (Pond Cd 1) and 2009-2010 for Snead Farm Pond (Pond Cd 2).

Coding the points in this two dimensional NMS by year (Figure 3.6) revealed that there were some differences among the years when looking at the combined data set of the two lakes. All three years tended to cluster in the center, and there is overlap among all three years. Years 1 and 2 are perhaps the most dissimilar, but it is important to remember that one of these years (2008) had no data from Snead.

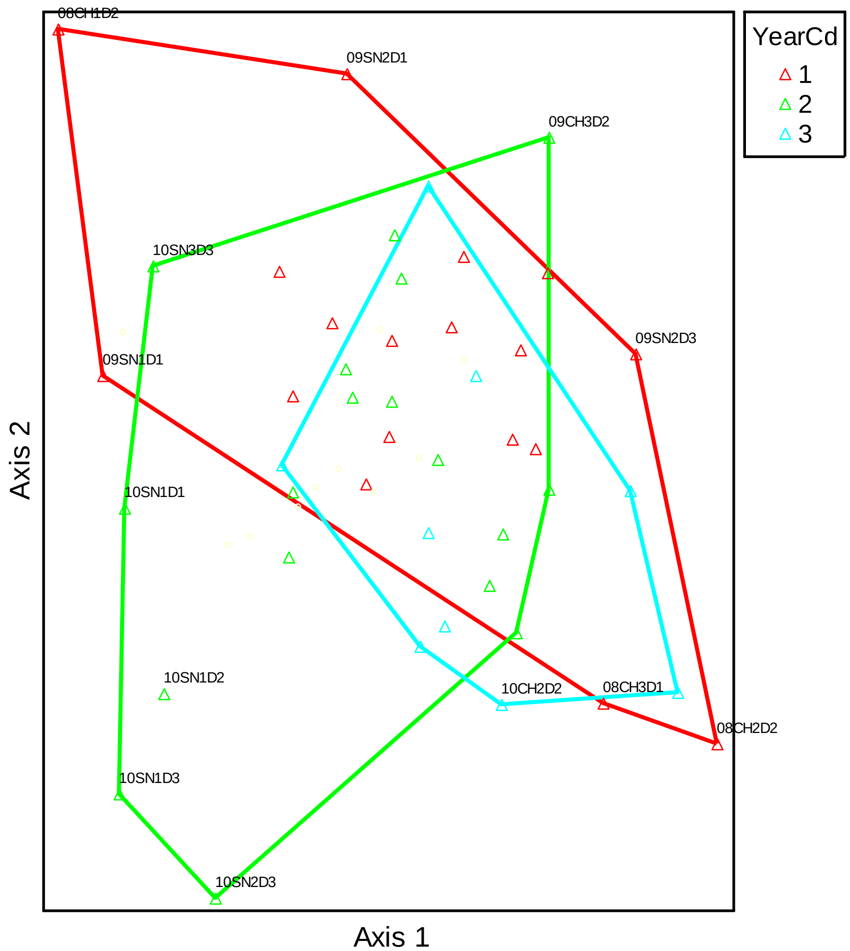

Figure 3.66 Scatterplot of the nonmetric multidimensional scaling results comparing years of dragonfly community data for both Camp Hanover Lake 2008 (1), 2009 (2) and 2010 (3) and Snead Farm Pond 2009 (1) and 2010 (2).

Examining year effects separately for each pond was important since pooling the data could obscure the time course in each pond. In the first year (2008) Camp Hanover

Lake did display an elongated polygon of data points with 08CH1D2 and 08CH2D2 noted (Figure 3.7). Examination of the field data notes and a comparison of all observations for Stations 1 and 2 at the second survey date revealed that very few species were present, with only two having large abundance: *Pachydiplax longipennis* and *Libellula cyanea*. This lake was in its first year after filling and many future resident species were not yet present.

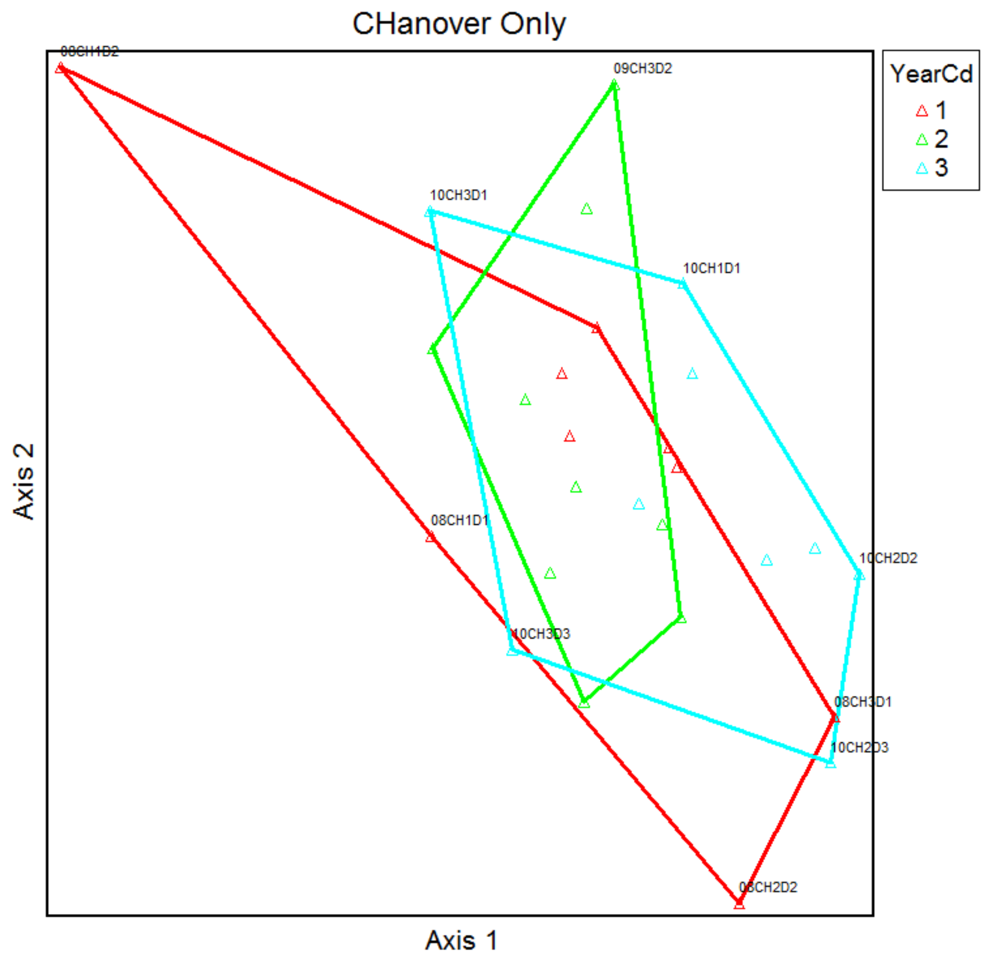

Figure 3.7 Scatterplot of the nonmetric multidimensional scaling results comparing three years 2008 (1), 2009 (2) and 2010 (3) of dragonfly community data for Camp Hanover Lake.

Consideration is made as to how the dragonfly community changed at Camp Hanover Lake over the three years of the study. Table 3.9 reveals tau values for each of the top four species at the Camp Hanover Lake. Any tau values greater than 0.394 would be significant (0.05 α), as noted for *Libellula incesta* for Axis 1 and *Pachydiplax longipennis* for both axes. Since neither of the NMS axes corresponded to a temporal change in taxa composition, these species correlations cannot be related to yearly variations in the community.

Table 3.9 Correlation Coefficients (tau) between NMS Axes and dominant species. Camp Hanover Lake only NMS (n = 28), significant values indicated by *

Species	NMS Axis 1	NMS Axis 2
Libellula incesta	0.409 *	0.194
Libellula luctuosa	- 0.178	0.079
Pachydiplax longipennis	- 0.489 *	0.800 *
Erythemis simplicicollis	0.095	0.113

Figure 3.8 provides a graph for Snead Farm Pond over a two year comparison, as no data are recorded for 2008. The Snead Pond data demonstrates a greater difference between years than was found for most of the ponds. There is only small degree of overlap of the convex hulls for the two years indicating some fairly consistent inter-annual differences in taxon composition in this established pond.

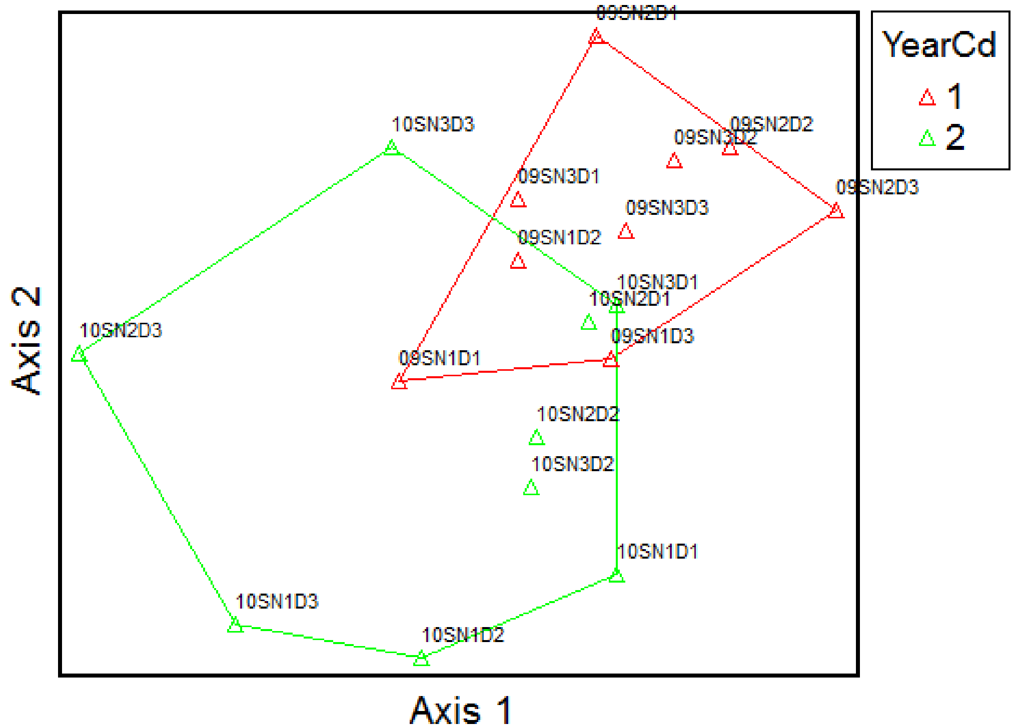

Figure 3.8 Scatterplot of the nonmetric multidimensional scaling results comparing three years 2009 (1) and 2010 (2) of dragonfly community data for Snead Pond.

Federal Club and Hollows Data

The final paired impoundments, Federal Club Golf Course Lake and Hollows Golf Course Lake, exhibited more inter-annual variation than most of the other ponds. Table 3.10 provides data for the new impoundment Federal Golf Club Course Lake. Numbers of individual dragonflies per survey were lower than found in most of the other impoundments in this study and lower than expected for this type of habitat.

Table 3.10 Comparison of three years data for Federal Club Lake - mean values & rank per year

SPECIES	2008*	2009*	2010*	Mean for 3 years	rank in 08	rank in 09	rank in 10
Libellula incesta	2.10	2.44	6.22	3.59	2	3	2
Libellula lydia	1.43	7.22	2.33	3.66	4	1	3
Libellula luctuosa	4.10	1.78	3.44	3.11	1	4	4
Erythemis simplicicollis	1.97	3.11	2.11	2.40	3	2	
Pachydiplax longipennis	0.00	0.33	0.33	0.22			
Perithemis tenera	0.47	0.44	1.22	0.71			
Celithemis fasciata	0.00	0.00	0.67	0.22			
Celithemis eponina	0.90	0.00	2.44	1.11			
Libellula vibrans	0.10	0.00	0.00	0.03			
Libellula cyanea	0.00	0.00	0.89	0.30			
Celithemis elisa	0.00	0.00	7.22	2.41			1
Tramea lacerata	0.00	0.33	1.78	0.70			
Tramea carolina	0.00	0.00	0.00	0.00			

*** Mean value per year. Value is abundance per unit effort where effort is counts of species at three stations surveyed per year.** Rank is highest to lowest for top 4 species for 2008, 2009, and 2010

Data reveal that the four species that were the most dominant for the three years of this impoundment were *Libellula incesta, L. Lydia, L. luctuosa*, and *Erythemis simplicicollis.* These four species were the most abundant the first year as first colonizers, and remained most dominant for the three years studied; thus, providing further evidence that does not support my hypothesis. In 2010, *Celithemis elisa* was the most abundant, but this was an anomaly because of a mating event occurring during one census, resulting in many more adults observed and which increased their overall mean numbers for that year.

At the reference impoundment, Hollows Golf Course Lake, data were collected for only two years, 2009 – 2010. As noted previously, this third reference location was not surveyed in 2008. It was assumed that another golf course lake would be an appropriate comparison for Federal Club Lake and this site was similar in function and size. However, as the study progressed it became clear that Hollows Golf Course Lake possessed dissimilar littoral zone characteristics. The summary odonate data for Hollows Golf Course Lake are found in Table 3.11.

Table 3.11 Comparison of three years data for Hollows Lake - mean values & rank per year

SPECIES	2009*	2010*	Mean for 3 years	rank in 09	rank in 10
Libellula incesta	1.89	5.11	3.50		4
Libellula lydia	3.67	3.56	3.62	2	
Libellula luctuosa	2.33	5.33	3.83	4	3
Erythemis simplicicollis	0.67	4.22	2.45		
Pachydiplax longipennis	1.56	1.44	1.50		
Perithemis tenera	22.56	16.11	19.34	1	1
Celithemis fasciata	0.00	0.22	0.11		
Celithemis eponina	3.00	8.56	5.78	3	2
Celithemis elisa	0.22	0.00	0.11		
Tramea lacerata	1.44	1.44	1.44		

*** Mean value per year. Value is abundance per unit effort where effort is counts of species at three stations surveyed per year.** Rank is highest to lowest for top 4 species for 2009 and 2010, no data exists for 2008.

Taxa abundances in Hollows Golf Course Lake were lower than expected for most species. The exception was *Perithemis tenera*, whose values were higher than at other studied impoundments. It was noted that the littoral zone of the lake is very sparse of vegetation tall enough to be favored by dragonflies, as the grasses was trimmed to only an couple of inches from the soil.

Ordination results for the combined data coded by pond shows a distinct separation in the communities of the two ponds (Figure 3.9); little overlap may be due to the lack of similarities of the two impoundments, both are located at golf courses and both are about the same size, but the similarity ends there. Federal Lake has much more vegetation around it, including a forest on one side, and has more abundant wildlife which might be predators of dragonfly adults. Hollows Lake data does shows less variation and more clustering in the upper quadrat and more positioning along Axis 2. Data for the Federal Lake is more dispersed in the entire scatterplot, but does not overlap with that for Hollows Lake.

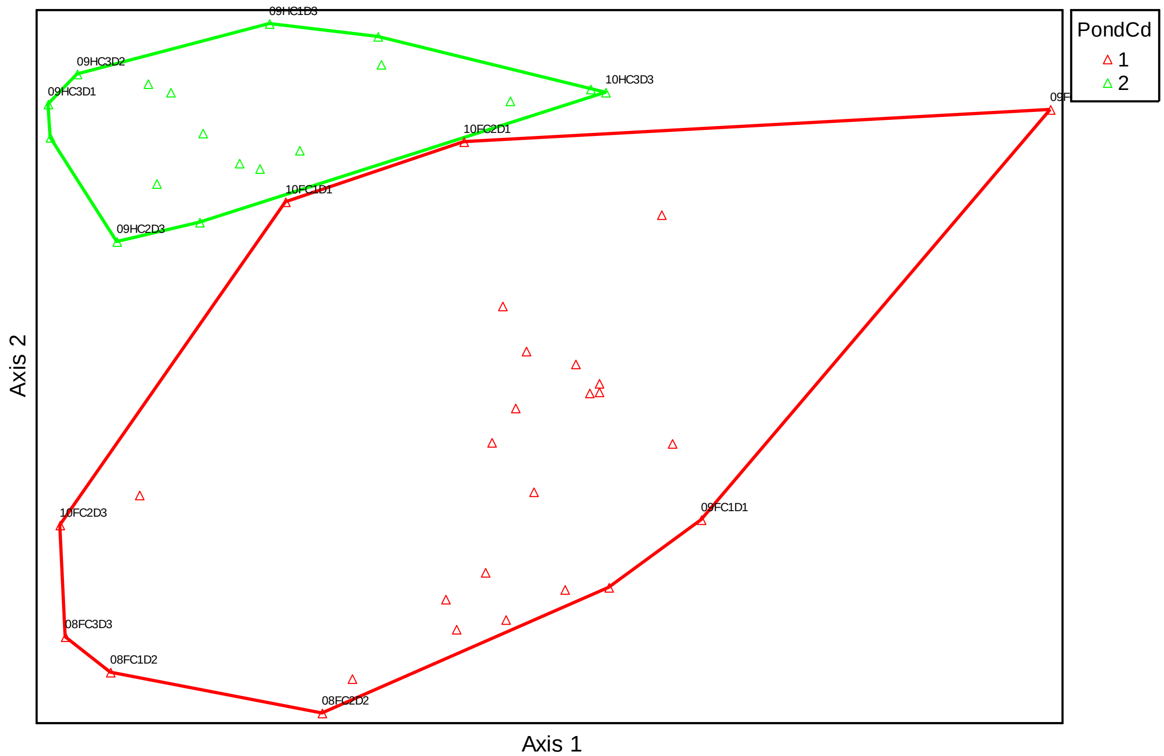

Figure 3.9 Scatterplot of the nonmetric multidimensional scaling results comparing dragonfly community data (2008 – 2010) for Federal Club Lake (Pond Cd 1) and (2009 – 2010) Hollows Course Lake (Pond Cd 2). Stress was higher than is generally acceptable, data problems may be interfering.

The year comparisons are equally not supporting correlations for these two locations, as seen in Figure 3.10. Much variability is demonstrated from the data, with no discernible pattern per year per impoundment. Although there are no data for 2008 for Hollows, considering 2009 and 2010 (the green and blue polygons) for both lakes minimal overlap exists. Any clustering of one year’s data compared to another is not present, and is surprising since both lakes experience the same temperature and weather factors, had generally the same dragonfly species present, and are both located within 8 kilometers of each other.

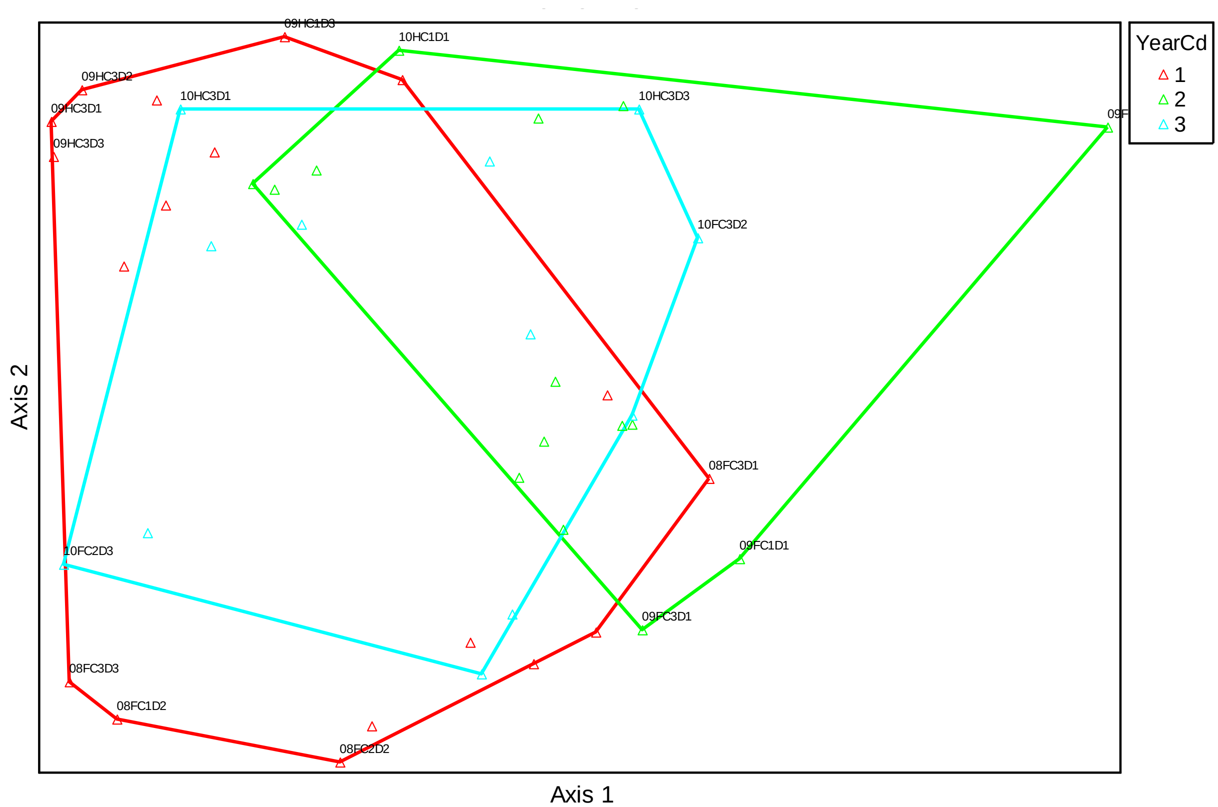

Figure 3.10 Scatterplot of the nonmetric multidimensional scaling results comparing dragonfly community data for 2008 (1), 2009 (2) and 2010 (3) at the Federal Club Lake and 2009 (1) and 2010 (2) Hollows Course Lake.

A scatterplot of the Federal Club Lake alone shows some differences among years, but no directionality and still a lot of overlap (Figure 3.11). No consistent patterns occur and there is greater variation in the scatterplots from year to year. Each year at this site had problematic and different issues that appear to have affected the data.

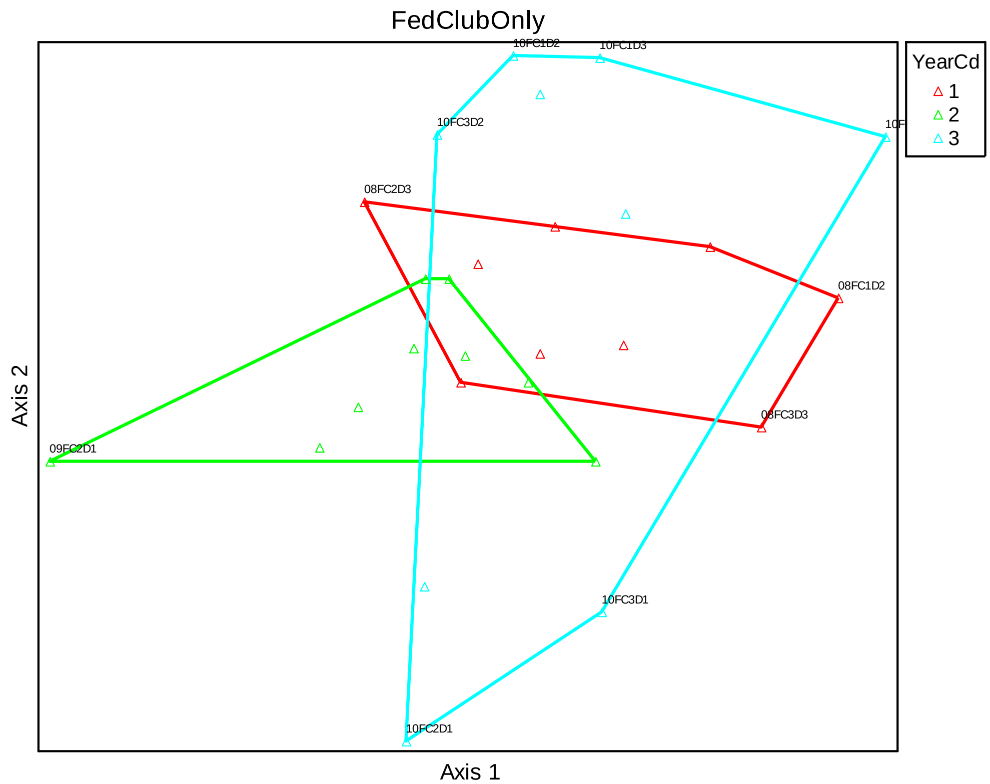

Figure 3.11 Scatterplot of the nonmetric multidimensional scaling results comparing dragonfly community data for 2008 (1), 2009 (2) and 2010 (3) at the Federal Club Lake.

Co-plots for four species at Federal Club Lake were run. Table 3.12 provides correlation coefficient values of tau, with 0.356 or higher being significant at 0.05 level. *Libellula incesta* was significant for Axis 2, and *Erythemis simplicicollis* did show a correlation with Axis 1. As with other ponds these taxa correlations did not correspond with a temporal progression in taxa composition.

Table 3.12 Correlation Coefficients (tau) between NMS Axes and dominant species. Federal Club Lake only NMS (n = 26)

Species	NMS Axis 1	NMS Axis 2
Libellula incesta	0.025	0.532
Libellula luctuosa	0.146	0.319
Pachydiplax longipennis	-0.005	0.060
Erythemis simplicicollis	0.475	-0.326

A scatterplot of the Hollows Lake alone shows a good deal of overlap between the two years (Figure 3.12). Year 1, 2009, had less variability in community composition than 2010. Data for 2009 also had more clustering in the upper half of Axis 2.

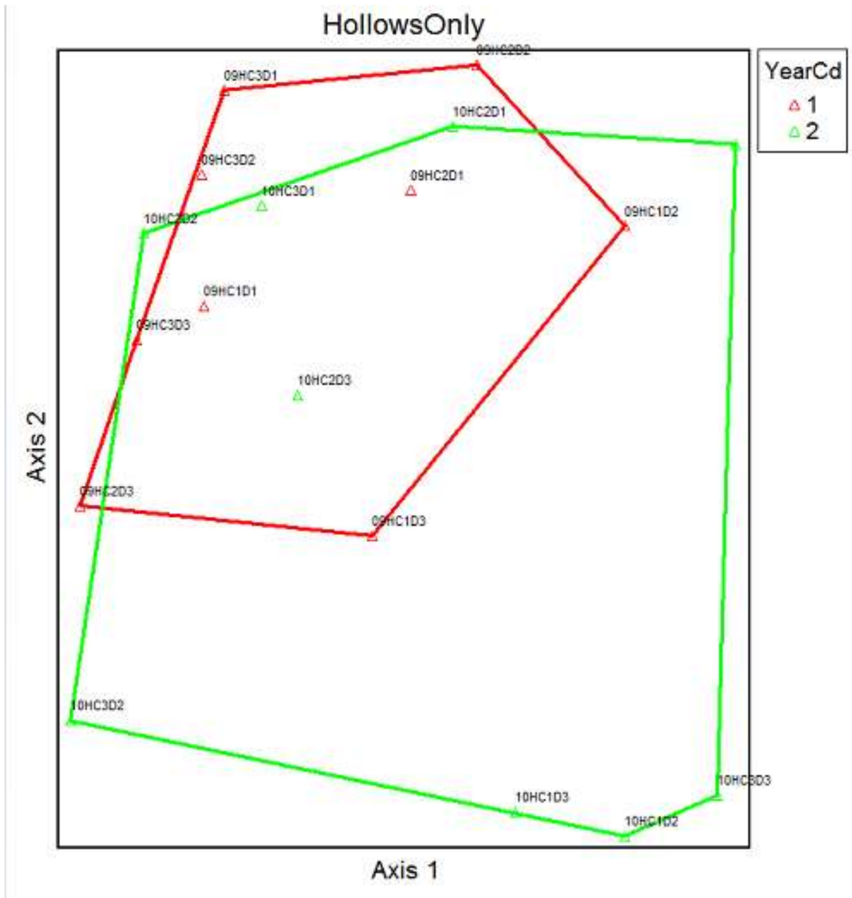

Figure 3.12 Scatterplot of the nonmetric multidimensional scaling results comparing dragonfly community data for 2009 (1) and 2010 (2) at the Hollows Lake.

Overall ordination comparing all ponds together

A single ordination was done including all ponds. In this ordination each combination of year and pond was represented by a single total abundance value, see Figure 3.13.

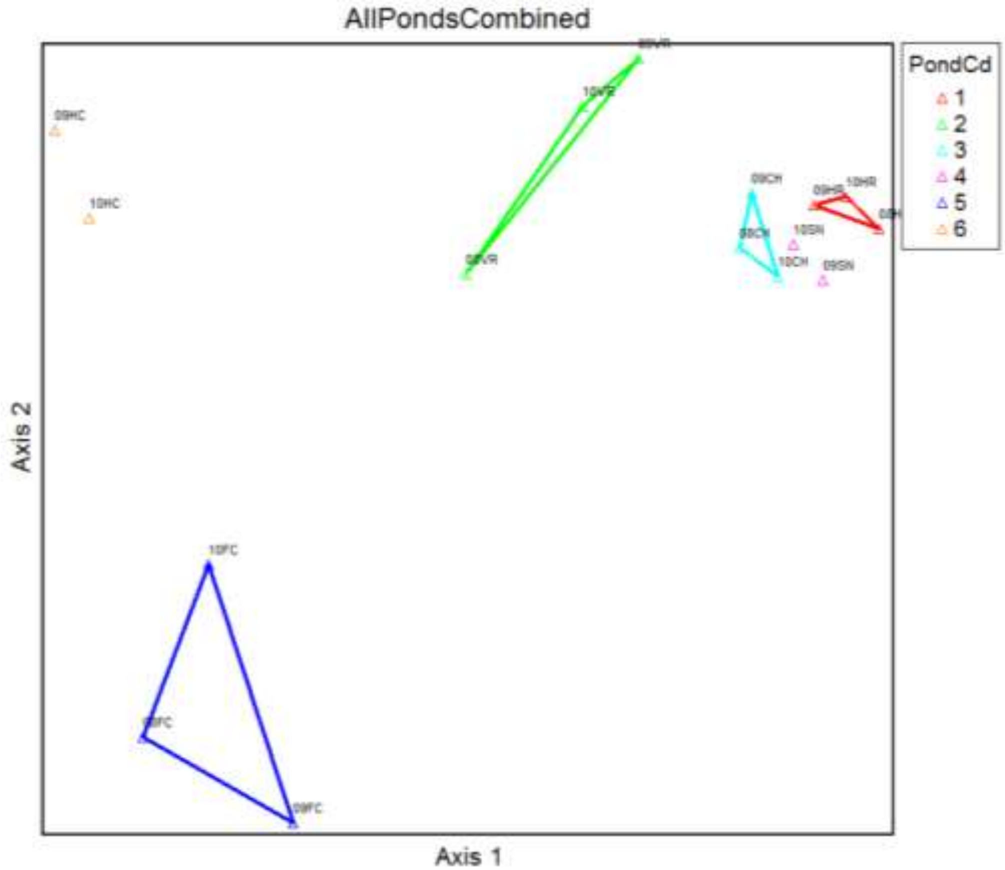

Figure 3.13 Data for all impoundments combined. The Pond Codes are #1 is Hall Pond, #2 is Vitale Pond, #3 is Camp Hanover Lake, #4 is Snead Pond, #5 is Federal Club Lake, and #6 is Hollows Club Lake. Data points per pond per year are summarily noted on the graph.

First, in the upper left quadrant only two data points (09HC, 10HC) are noted for reference impoundment Hollows Lake, as data was only collected for two years; and summarily noted for reference impoundment Snead Pond to the upper right (09SN, 10SN). The distance between the data points in both of these individually is small, which denotes minimal variability within each site during the two years data was collected. Reference pond Snead reveals the least variability.

For the co-plots for Federal Club Lake (lower left quadrant) exhibited the greatest variability for the three years of data, compared to other impoundments. The least variability for three years data analysis is noted for Camp Hanover Lake and Hall Pond as compared to all other impoundments surveyed for three years.

The dragonfly communities in three new impoundments (Hall, Camp Hanover, and Federal Club) are no more variable than those of the three reference sites (Vitale, Snead, and Hollows). This outcome is evidence that the hypothesis of substantial change in dragonfly communities during colonization is not valid. It appears that factors other than colonization dynamics are more important in determining community change in dragonfly communities.

Richness, Shannon-Weaver, and Evenness Data

The richness values for the six studied impoundments are provided in Table 3.13. Richness for individual ponds ranged from 10 species to 13 when all three years were pooled. There was a general pattern of increasing richness over the years at the new impoundments (Federal Club, Camp Hanover, and Hall). This trend suggests that there was an enrichment of species pool over time over the new impoundments. There was also an increase at one existing pond (Vitale) surveyed all three years.

Table 3.13 Richness values for six impoundment for this research, based on three years (2008-2010), with between 10 and 13 taxa at each impoundment

Site ID #	Site Name	Number of species from 2008 - 2010	2008	2009	2010
1951	Hollows Lake	10	na	9	9
2251	Federal Club Lake	12	7	7	11
2282	Snead Farm Pond	13	na	11	10
2903	Camp Hanover Lake	13	10	11	11
2593	Vitale Farm Pond	12	6	10	10
2901	Hall Farm Pond	13	8	10	11

The Shannon-Weaver diversity index and evenness values for all of the impoundments from 2008 (if available) to 2010 are provided Table 3.14. The progress for the three years does support an enrichment of the species pool and dragonfly community development especially for the new impoundments: Federal Club Lake, Camp Hanover Lake, and Hall Farm Pond. Except at Vitale Pond richness at older and reference ponds were constant. The increase at Vitale may demonstrate an anomaly the first year (2008).

Table 3.14 Shannon-Weaver (SW) diversity index & evenness (E) values for studied impoundments, 2008 – 2010

Site ID #	Impoundment Name	S-W values 2008-10	2008	2009	2010	E values 2008-2010	2008	2009	2010
1951	Hollows Lake	1.46	N/A	1.42	1.50	0.67	N/A	0.65	0.68
2251	Federal Lake	2.07	1.63	1.48	2.09	0.83	0.84	0.76	1.22
2282	Snead Farm Pond	1.81	N/A	1.57	1.90	0.71	N/A	0.65	0.86
2903	C. Hanover Lake	1.68	1.59	1.62	1.67	0.65	0.66	0.68	0.70
2593	Vitale Farm Pond	1.73	2.61	1.75	1.75	0.70	1.63	0.76	0.76
2901	Hall Farm Pond	1.69	1.19	1.76	1.64	0.71	0.61	0.77	0.75

Looking at the year-to-year values for the new impoundments, the SW index rose in Federal and Camp Hanover lakes, as might be expected for new impoundments. The Hall Pond SW index went up and then slightly down, but had a substantial net increase over three years. Evenness values for the new impoundments vacillated with no consistency, as might be expected as the dragonfly community changes for the early years. SW index values for existing impoundments were within 0.37 units of one another, in a given impoundment. Evenness values for existing impoundments were within 0.04.

Discussion

The original hypothesis stated that dragonfly dominance at new impoundments would change in three years; that the dominant dragonfly species at new impoundments would change, especially as the habitat went through natural succession. In general, my data do not support this hypothesis within the three years of this research. The ranking of most abundant dragonfly species per year at all impoundments sometimes changed annually, but there was no evidence of initially most abundant species declining and another species becoming dominant. Generally, dominance vacillated from year to year within sets of two to three species, in the new impoundments and in established reference ponds. The species which dominated for the first years continued to maintain dominance in the dragonfly communities over the three year study.

Likewise, little systematic or directional change was noted in community composition over the three years in new ponds or lakes using NMS. This is noted in the scatterplots per year for two new impoundments, Figures 3.3 (Hall Pond) and 3.7 (Camp Hanover), especially if a few outliers are disregarded. Figures 3.11 (Federal Club) demonstrated the most variation, but that was due to anomalies of that site, noted later in this discussion.

Ordination results for the combined data (Figure 3.13) coded by pond show a distinct separation in the communities of the six impoundments, variability comparing sites, but no more variability than when individual pairings are analyzed.

In colonization, new ponds or lakes do not appear to be more variable that the reference impoundments, as is evident when all impoundments are analyzed together. The combined analysis did support that there were five most abundant species as a collective group analysis of all six impoundments; those species were: *Pachydiplax longipennis, Libellula incesta, L. luctuosa, Erythemis simplicicollis,* and *Perithemis* *tenera*. Of note these are five of the typically most common six first colonizers noted in Chapter 2.

The pairing of new ponds with a specific reference pond provided a framework for determining if changes in dominance and community structure during the initial pond colonization period of three years were especially great or if they fell within typical inter-annual variations experienced by established ponds. For the Hall and Vitale pairing, four species at each pond shared the top four most dominant rankings. The pairing of Camp Hanover and Snead also demonstrated primarily four species sharing the top four dominant rankings. Finally, the pairing of Federal and Hollows Lakes again shared most abundance within a group of four each year at each specific lake, with the exception of the outliers such as *Celithemis elisa* at Federal Lake and *Libellula incesta* at Hollows Lake.

This study did not delve into factors that might affect residence selection or the outcomes of abundance at those sites. My research looked at who arrived one year after the new site filled with water and what abundance outcomes resulted over the first three years of residency.

This study did reveal much about the community structures at most of the impoundments. The multivariate analysis was conducted on each pairing and on each impoundment alone, especially with year-to-year considerations. Four factors might be noted in analysis of dragonfly community structure. They are:

1. Which species are in the group of early colonizers;
2. Did mating events present data differences;

3. Did predation on the dragonflies affect data; and
4. Were habitat alterations responsible for some data differences over the span of this study?

Which species are in the group of early colonizers?

Both Hall Farm Pond and Vitale Pond demonstrated consistent resident species. *Libellula incesta*, *L. luctuosa*, *Erythemis simplicicollis* and *Pachydiplax longipennis* were the most common early colonizers for the new pond. Hall Farm Pond, in 2008 for station 1, had high numbers of *Pachydiplax longipennis* and *Libellula incesta* and no other species. Most other species had atypical low individual numbers at this station. This is an early year in the life of this pond, as most other species had not yet gotten well established. This trend remained at other stations that year. Thus to a point, dragonfly community richness seems to increase as the impoundment ages.

In the second pairing, Camp Hanover Lake and Snead Pond, demonstrated consistent resident species. *Libellula incesta*, *L. luctuosa,* and *Pachydiplax longipennis* were the most common early colonizers at the new impoundment, Camp Hanover.

In the third pairing, the two golf course lakes, Federal Club and Hollows, presented more variability in resident species, especially at the Hollows Lake. The new lake at Federal Club was consistent with the most common early colonizers being *Libellula incesta*, *L. lydia*, *L. luctuosa,* and *Erythemis simplicicollis.* Then in 2010, *Celithemis elisa* appeared and had the highest abundance in 2010.

Did mating events present data differences?

For the Hall Pond in 2008, there was a very large number of *Pachydiplax longipennis* at station 2. The large individual counts suggests a mating event for this species was occurring. A closer inspection of data for 08HR3D3 also supports a mating event of the species *Pachydiplax longipennis* at that specific station during that census date.

In 2010 at Hall Pond, each of the third surveys was unique. For 10HR1D3 *P. longipennis* and *L. luctuosa* were in lower than usual numbers. Data set 10HR2D3 and 10HR3D3 also exhibited lower than usual numbers of *L. luctuosa*. It may be that the high numbers of *L. incesta* were mating and chased away the *P. longipennis* and *L. luctuosa* which are typically present in larger numbers in the littoral zone of the pond.

At Vitale Pond investigation of data indicate that these sites at Vitale Pond that year had uncharacteristically low numbers of *Erythemis simplicicollis,* and no individuals for *Libellula incesta*; perhaps both of the species are affected by the blue dye the owner placed in the pond. But for those data points *Pachydiplax longipennis* had very high numbers, probably indicative of mating events for that species on those survey dates. This species can get very aggressive even toward conspecifics in the pond edge area when they are mating, and may have chased most other species away on those survey dates, as was observed in this investigation.

Camp Hanover's polygon for 2008 has two outlier data points: in the first no typically-present *Libellula incesta* were observed at this station on that survey date, but they were present in considerable numbers at the other two stations. Then for 08CH2D2

Pachydiplax longipennis was completely absent but very abundant at the other two stations on that survey date. Effects of matings, drawing individuals to those locations where matings were occurring, and which were observed, may have resulted in dragonfly species shifting around the pond.

At Hollows Golf Course Lake, *Celithemis elisa* appeared and highest abundance in 2010 and this was probably due to observed mating during most of the surveys that year, at all stations.

Did predation on the dragonflies affect data?

The data from Federal Club Lake may be explained by factors associated with this impoundment. In 2008, data for individual dragonflies observed suddenly plunged in mid-season, possibly because a resident barn swallow (*Hirundo rustica*) population matured and increased predation on the resident dragonflies. In 2009, the adjacent barn was torn down, the *Hirundo rustica* population was noticeably smaller, but an American Bittern (*Botaurus lentiginosus*) took up residence and was observed eating adult dragonflies along the thick shoreline vegetation, from June to August. The population numbers were higher than 2008, but less than what might be expected from a good lentic habitat, as the Federal Club Lake appeared to be. In 2010, a confounding factor was the water level. That year was extremely dry and the golf course owners used their lake for increased irrigation. The lake surface level dropped as much as 2 meters at one point, making the water's edge further away from the shoreline vegetation and exposing a clay bottom, both of which are less attractive for lentic adult dragonflies.

Were habitat alterations responsible for some data differences over the span of this study?

The Vitale Farm Pond was selected as a reference pond in the Hall/Vitale pairing. The Vitale Pond is 40+ years old. As expected, the cluster of data points for years 2009 and 2010 are close together (see Figure 3.4), as one might expect for a stable dragonfly community impoundment. In 2008 the data for the dragonfly communities surveyed were skewed outside of data points for the next two years. Not until doing the multivariate analysis was this perceived anomaly noticed. It was recalled that in 2009, the property owner told me that she had a wedding hosted near the pond in 2008, and that "to make the pond look nicer," she had dumped an unknown quantity of blue dye into the small pond. It is my conclusion that this may have affected dragonfly numbers for 2008, and such would not have been recognized had the MA not been performed and revealed the skewed data in the graphs.

The pairing of the two golf course lakes (Federal and Hollows) considers both impoundments and notes both having issues that adversely affected the dragonfly communities. Their sizes are similar, but the littoral zone at each is very different. The Federal Club Lake littoral zone has increased shoreline vegetation. Hollows Lake does not and its vegetation along the shoreline is trimmed to the water's edge. The Hollows Golf Course management chose to cut all shoreline vegetation down to the water's edge, leaving only trimmed grasses. Shrubs and a nearby forested area do not exist at Hollow Club Lake. The lack of favorable shoreline vegetation at the Hollows Lake resulted in less attractive habitat for adult dragonflies. This condition would reduce richness of species and quantity of dragonflies at the lake. The littoral zone vegetation can affect speciation at an impoundment, and this was very evident at the Hollows Course Lake, that resulted in a non-typical dominant species, *Perithemis tenera*, at this lake.

Since the study ended in 2010, the owners have taken the advice from this study and are no longer cutting vegetation down to the water's edge at Hollows lake, but instead have a one meter strip of shrub and high grass vegetation along the water's edge, a much preferred habitat for dragonflies. Post 2010 observations indicate that a greater abundance of dragonflies are now present.

At Federal Club Lake the population numbers were higher for each subsequent year, but less than what might be expected from what appeared to be good lentic habitat. Water levels affected Federal Club Lake, as the levels dropped during the hot summer of 2010, requiring more irrigation of their golf course. The lake surface level dropped as much as 2 meters at one point, making the water's edge further away from the shoreline vegetation and exposing a clay bottom, both of which are less attractive for lentic adult dragonflies.

Choice of Studied Impoundments and other analysis

The three new sites used (Hall, Camp Hanover, and the Federal Club Lake) were appropriate as new impoundments to study. No two impoundments were exactly the same, as should be expected.

Noting Figure 3.1, the scatterplot of the nonmetric multidimensional scaling results comparing dragonfly community data, the pairing of Hall and Vitale ponds were appropriately matched. Both ponds are different from the other as might be expected, but the multivariate analysis (MA) does indicate some overlap, especially if the anomaly of data for Vitale in 2008 were disregarding.

The impoundments of Camp Hanover Lake and Snead Pond seemed a reasonable pairing for the study of dragonfly adult communities, but in comparison with each other, the aging Snead Pond's data revealed that it was less comparable as a reference pond for Camp Hanover. Considering characteristics of both; Camp Hanover is an elongated lake and Snead Farm Pond is a shallower pond. Their littoral zones and the forest beyond the impoundments have very similar vegetation, but the water depths turned out to be very different. Camp Hanover Lake was deeper and should have more fish predation, which could have affected the total number and variety of dragonflies. Dragonfly larvae may be found in over two meters deep areas of a pond, which would expose them to more predacious fish (Corbet 1999). The mean value of dragonfly numbers at the shallower Snead Pond's during the study period for all stations was 83.79. The mean value of individual dragonflies for the study period for all stations at Camp Hanover was 75.78. The species richness values of these two impoundments were equal.

The two golf course lakes, Federal Club and Hollows, presented a number of issues that confounded much comparison. Individually, they were suitable dragonfly community study sites. The Hollows Lake was perhaps too dissimilar in littoral zone characteristics for a solid comparison with the Federal Club Lake, but it was the best site possible within a 13,000 square hectare distance from the Federal Club Lake.

Richness values, Shannon-Weaver (SW) diversity index and evenness values have not often been reported in dragonfly community research (Shurin and Allen 2001, Kadoya et al. 2004, Suh and Samways 2005, Bried and Ervin 2006). Even the ten-year study by Shiffer and White (1995), of the dragonfly community at Ten Acre Pond in Central Pennsylvania does not report these numbers. As a comparison with the few studies richness, SW and evenness at locations that are larger, the Shannon values of this study are lower, but within expected values. Adu and Ogbogu (2013) studied the Aponmu Forest in Nigeria, including two rivers and one pond. One hundred and three species of Anisoptera and Zygoptera were recorded. They report a Shannon-Weaver Index value of 3.44, and an Evenness value 0.77. This was a much larger study area than the six ponds of my study. Fulan et al. (2010) studied abundance and diversity of part of a 250 sq. km. reservoir in Portugal. Their study reports only 10 dragonfly species. Their average Shannon Index value was 2.52. Evenness was not reported in their report.

Values in the current study are comparable with richness, Shannon-Weaver and evenness with those other studies. At Hollows Lake the absence of a preferential littoral zone for dragonflies limits its richness. The usual range of 12 – 13 species per impoundment is typical for an impoundment in Hanover County, Virginia, based on this study. For the impoundments in Hanover County, Virginia, the Shannon-Weaver Index and Evenness values are comparable for impoundments of their sizes and ages.

The data for the established impoundments exhibited some stability, as indicated that dominance did change slightly from year to year, but only within four to five species of dragonflies. Low variability at a pond does achieve stable assemblages, unless some other factor like drainage results as an extreme change. This study supports the hypothesis that most ponds do achieve some stability, as noted best in 2009 and 2010 at the Vitale pond, and the abundance of species at those impoundments and changes very little over time, as long as the pond was not affected by unusual human associated activity.

Yodzis (1986) examined post-colonization community structure. With respect to dominance, he found that competition can control community structure. "Founder control" species' richness increases until the entire area is occupied. As implied in this theory, no species has a competitive advantage at first; and whichever species got there first (colonized) in the greater number maintained greater abundance. My research results are consistent with Yodzis' observation.

Hubbell (2001 and 2010) suggested the "Neutral Theory" in connection to aspects of the Island Biogeography (MacArthur & Wilson Equilibrium Theory, 1967). Contrary to MacArthur and Wilson's explanation that local immigration and extinction have an equilibrium for species richness, Hubbell discounts extinction rates that are a part of the MacArthur-Wilson premise. Hubbell also states that ecological equivalence (or near equivalence) considers that any species that may have immigrated to a site and "won" the site because it was an effective competitor will hold its place in relative abundance.

A theoretical underpinning of this study was that first colonizers have some characteristics that make them more suited for colonization, but not necessarily to be able to maintain dominance as the site ages. This study did not provide any examples of this type; but the first colonizers remained dominant. Results of this study are more consistent with the view that dominance over ensuing years was a function of which species arrived first and not by strongly identifiable characteristics of one species being dominant over another unless of course these interactions all played out in the first year of colonization.

Chapter Four

Impact of Wind on Flight Dispersal of Dragonflies

Introduction

Numerous small impoundments were destroyed in Hanover County in 2004 due to hurricane-induced flooding and some were subsequently rebuilt. This presented an opportunity to compare the colonization dynamics of dragonfly species at the new or rebuilt lentic sites with those in existing sites. Changes in community structure during a period of three years post water-filling were presented in Chapter 3. A final consideration in this dissertation is the role of wind in dispersal. Lentic adult dragonflies are active, not passive dispersers (Rundle et al. 2007). Lentic adult dragonfly species disperse by flight, and this chapter examines flight dispersal with the influence of wind velocity and direction of flow. The hypothesis is that at some wind velocity, dispersing dragonflies will fly downwind with the direction of wind flow as opposed to attempting to fly in another direction. A manipulated field experiment was conducted to test this.

The teneral (defined as a non-sexually mature adult) stage in anisopterans usually lasts for 24 hours (Corbet 1999), and this stage or soon after may be most suited for local dispersal. For either gender, lentic tenerals' first flights are from their natal ponds and Corbet (1999) identifies these as "maiden flights." Females will disperse at a higher rate than most males (Corbet 1999). After emergence from larvae to adults, tenerals often leave the lentic site for several days, most likely hardening their exoskeleton. The period prior to reproduction, which might include dispersal, may last 14 days (Corbet 1999).

Some early emerging tenerals will return to the natal pond, but others will disperse to new locations (Corbet 1999).

Harabis and Dolny (2011) report that zygopterans have limited dispersal abilities, primarily because they are more at risk when they disperse, but this may not be true of other odonates such as anisopterans. These authors state that habitat specialists like zygopterans have fewer dispersal strategies, exhibiting more natal residency behavior, and thus are less prone to disperse. The authors add that within the suborder Anisoptera, "percher" dragonflies have less activity and are better conservers of energy than "fliers." The authors speculate that the percher species may be less prone to disperse. Perchers are species that spend most of their active period on a perch with short occasional flights, while fliers exhibit continuous flying (Corbet 1962, Henrich and Casey 1978).

Studies on dragonfly movement have considered sun orientation and weather events as the primary determinants of the direction of travel. Mikkola (1986) states that insect migration can be related to wind, but migration is different from local dispersal. Johnson (1969) supports the idea that dragonflies migrating long distances are impacted by weather and wind. Little is known about the connection between wind and local dispersal.

Rainey (1976) noted that down-wind displacement is exhibited in species like locusts, and theorized that insects are likely to be passively impacted. Compton (2002) states that small insects (smaller than dragonflies) lose direction control with wind supported dispersal. Most anisopteran species are medium to large size insects, with body sizes of 4 cm to 8 cm in length, and they are strong fliers compared to some other insects; thus they are unlikely to be victims of totally passive dispersal.

Most dispersal for anisopterans probably occurs in the flight boundary layer, as first described for insects by Taylor (1958), as the location where local dispersal of many insects occurs. Taylor describes aphid dispersal in a “boundary” layer, but no specific height (altitude) of the boundary layer is provided, only a mention of it having variability. Walker (1985) discusses the boundary layer in reference to migration of butterflies, and he defines it as “the layer of air near the ground where wind velocity is less than the insects’ air speed.” Taylor (1974) further describes the boundary layer as “a hypothetical layer of air near the ground” within which the insect’s flight velocity may exceed the wind speed and the insect is able to control its movements relative to the ground. Srygley and Oliveira (2001) point out that when wind speed remains below flight speed in the boundary layer, the insect can control its direction of flight. The boundary layer for each taxon may differ, and for Anisoptera the altitude has not been defined. The operational boundary layer for dispersal in this experiment was no higher than 50 meters, because these insects, while in close horizontal range, were still visible to an altitude of 50 meters above the surface.

Mikkola (1986) reports that odonates can migrate upwind, but few details are provided in his study. Corbet (1999) acknowledges that wind plays a role in “spatial displacement by flight,” but specifics are not provided. It is assumed that flight downwind saves energy and, thus is utilized by the adult dragonfly if the direction is not predetermined. In other words, flight is more successful in the direction of the wind movement, not into the wind. No evidence exists that local dispersal of dragonflies has a behaviorally predetermined direction.

The hypothesis for this study states that, at some wind velocity in the boundary layer, dispersing dragonflies will fly downwind with the direction of wind flow or at least end up downwind. A manipulated field experiment was conducted to study this.

Methods

Acquisition of Tenerals

The research in this chapter is divided into two parts. The first covers efforts to obtain enough tenerals for the second part which constitutes the experiment. Out of 400 + adult dragonflies captured by this researcher over six years, only one teneral was caught, probably because after emergence the young and immature dragonflies immediately escape to the trees for protection and are not seen until they have time to harden the exoskeleton and become sexually mature. Thus, efforts to raise tenerals were undertaken. The rearing of substantial numbers of odonate tenerals in an outdoor vivarium for experimental purposes has not been previously described in the literature. The goal of rearing tenerals in a vivarium was to provide enough individual dragonflies for a subsequent mark and recapture experiment to examine the wind's impact on dispersal.

The rearing protocol began by collecting larvae in late instars from a source pond and then raising them in an outdoor vivarium to produce enough tenerals at one time for a mark and recapture experiment in which the impact of wind on dispersal could be studied. The goal of the effort was to obtain three cohorts of tenerals, each having 20 individuals.

Limited studies of dragonflies raised in an outdoor vivarium structure exist. Michiels and Dhondt (1989) placed a structure over an area with a small pond and some vegetation. The structure into which the dragonfly adults emerged had a mesh covering of 10 meters X 20 meters X 5 meters high. Their “cage” was employed to study reproductive and flight activity of various dragonfly adults. No emergence data of tenerals were provided. Dunham (1994) constructed a “shadecloth”-covered “temporary cage,” 10 meters X 20 meters X 3 meters high, over a small stream. No data were provided as to the numbers of tenerals that emerged. From this author’s personal observation, Carl Cook, an amateur odonatologist in Kentucky, has converted a chicken coop into an “adults-from-larvae” harvesting structure, but again no data are available regarding operation or results for teneral harvesting. No structure like the one proposed here has been found in the literature.

After securing grant funding, the vivarium was designed, constructed, and placed outdoors to simulate the optimal lentic conditions for rearing. Figure 4.1 depicts the construction design of the vivarium (Groover 2007). The vivarium was built and installed in central eastern Hanover County, Virginia. This is the same area in which all other aspects of this chapter’s experiment were conducted.

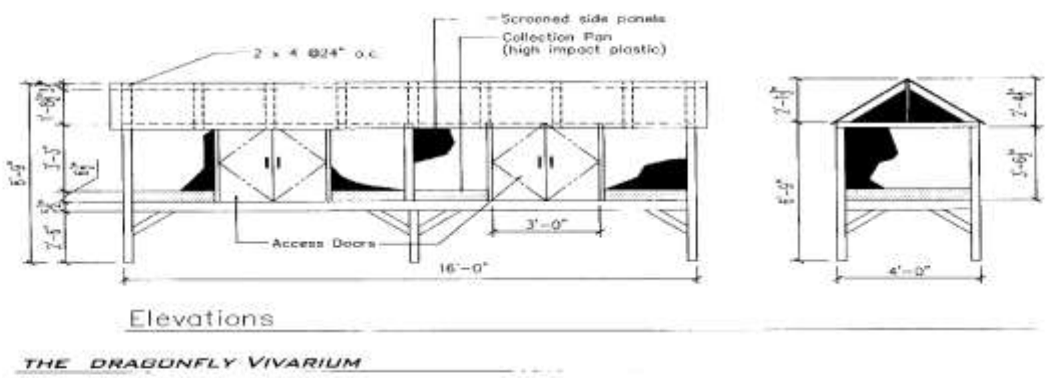

Figure 4.1 The Outdoor Dragonfly Vivarium

A photograph of the actual vivarium is provided in Figure 4.2

Figure 4.2 Dragonfly vivarium located in Hanover County, VA

Internally in the vivarium, individual chambers with mesh walls were formed to reduce cannibalism. Forty individual chambers (5 cm by 5 cm, 8 cm tall) were constructed inside and up from the floor of the vivarium, using stainless steel wire mesh (304 SS Woven Wire Cloth, 8 x 8 mesh, .032" wire dia., 0.093" opening 2.36 mm) to form the chamber walls. The bottom of the vivarium had a black plastic shower liner to provide water tightness. Water from the source pond was used to "fill" the vivarium up to 6 cm from the bottom, with approximately 0.5 - 1 cm of pond substrate placed in the bottom of each chamber. Inside each chamber, oak leaves from the source pond bottom were placed on the bottom of the chambers to provide cover and concealment for the larvae.

Lentic dragonfly larvae usually live in less than 1 meter of water (Corbet 1999), and thus water depth in the vivarium is of less concern. Additional source pond water was added every few days, as needed to maintain a water depth of 6 – 7 cm in the vivarium. Two Danner Pondmaster 1.9 magnetic driven utility pumps, with adjustable flow, were installed on the sides of the vivarium to reduce algae build-up and help maintain needed dissolved oxygen levels.

To sustain the larvae and maintain their robustness, they were provided/fed approximately 10 *Lumbriculus variegatus* per week per dragonfly larva. Previously an attempt was made to feed them *Daphnia pulex*, but not enough *D. pulex* could be harvested to sustain the number of dragonflies being reared. The *L. variegatus* were easily accessible from a local pet store and appeared to sustain the nutritional requirements for the dragonfly larvae, as they grew and eventually emerged as adults.

The sides of the vivarium were covered with standard screen door mesh so that emerging tenerals could not escape. The vivarium was placed in a shaded location, receiving no direct sunlight, to maintain optimal water temperature and minimal evaporation, and simulate a shaded pond condition.

To maximize available space in the vivarium, 3 to 4 larvae were placed in each chamber to complete their metamorphosis to become adults. Dragonfly larvae will exhibit cannibalism (Corbet 1999), but the like-sized individuals were not expected to consume each other. Therefore, individuals of similar size were placed in the chambers.

The source pond (Hall Farm Pond) for the dragonfly larvae used in this study provided water with abiotic conditions acceptable for this experiment. Dissolved oxygen (DO) is not an issue because a water pump was used in the vivarium and would have increased the DO in the vivarium operation. In the source pond, DO was recorded at 8.7 – 9.6 mg/liter. In the vivarium, conductivity was between 190 (in 2011) – 207 (in 2012) μSiemens/cm at 11 - 18 ^{o} C, when the vivarium was filled, with pH ranging from 6.8 – 7.2. These values are comparable to ponds found in other odonate studies in the Piedmont Region of Virginia (Woodson 1969, Layton and Voshell 1991, Braccia et al. 2007).

Difficulties were encountered with the attempt to rear enough larvae for the mark and recapture portion of this experiment. Therefore, an alternative method of supplying the needed dragonflies for the wind study was undertaken. Deciding not to use vivarium-reared tenerals in this experiment, approximately 80 captured adult *Libellula incesta* were obtained for the release. This species was selected because it is very abundant, easy to catch, large, easily seen at short distances (10 – 40 meters away) and dark in color, making them easy to use for this experiment. A Hanover County location, Summerduck Farm (site # 2583, in Chapter 2), has a very large concentration of *L. incesta*. On visits to Summerduck Farm I observed over 40 adult *L. incesta* per visit, so twenty individuals each time for four experiment trials would be easy to obtain and use.

On the morning of each wind experiment event, 20 – 21 *L. incesta* were caught and carefully secured in an air-conditioned environment (truck cab) for live transport to the release location. Heat above 35^{o} C can cause death for confined dragonflies, especially without water and freedom to conduct behaviors for cooling. Individuals were transported in modified 1.89 liter juice containers, with an internal paper-towel cushion to limit their movement while being held inside the transport container, see Figure 4.3.

Figure 4.3 Modified 1.89 liter juice container used to transport live dragonflies

Collection of dragonflies to be marked and released occurred between 1000 hours and 1100 hours on the mornings of the mark and recapture experiments. The trip to the release location took 15 minutes, and captured dragonflies rested for one hour before being released. The live transport containers with captive dragonflies were stored in an air conditioned environment (cab of a truck) until they were removed for marking and release. Truck temperature (inside area) was 24 ^{o}C - 25 ^{o}C.

Wind Experiment Location

The experimental (release) location was Powhite Farm in eastern Hanover County, Virginia. GPS of the release site is N 37^{o} 34.47 WO 77^{o} 18.43. This location is 130' above sea level (17% accurate with 5 satellites). This site's 2.8 ha pond had been sampled for dragonflies for the previous four years (Figure 4.4).

Over a two year period (2010 – 2011) before the experiments occurring in 2012, the site for the experiment was prepared. The 45-ha cow pasture was leased to build eight artificial ponds that could serve as potential receiving ponds for the released and marked dragonflies. As constructed, the ponds were 20 meters square by one meter deep, and arranged in a large circular arrangement in the pasture (see Figure 4.4). Each pond was 300 meters from the opposing side's pond, and thus 150 meters from the geometric center of the "circle of ponds." Each artificial pond was given a number, assigning #1 to the most northern pond, moving clockwise with subsequent assigned numbers, so that the most southern pond was #5 with the numbers continuing to #8 moving north again.

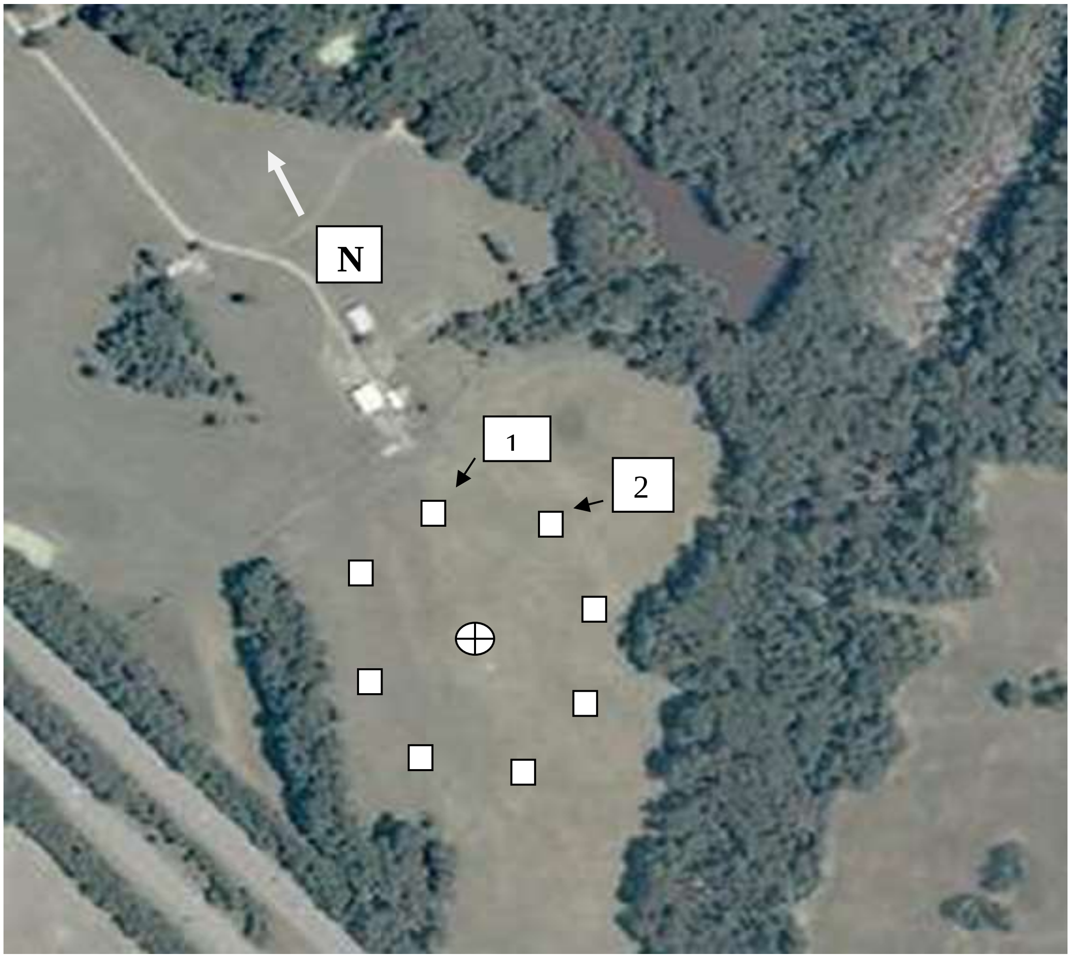

Figure 4.4 Mark and recapture experiment location and arrangement of artificial

Ponds' circular arrangement around the geo-center release location

Legend ⊕ is the center, where dragonflies were released

□ is an artificial receiving ponds, assigned numbers 1 - 8

Mark and Recapture Experiment

Mark and recapture studies of dragonflies have been successfully attempted previously (Hinnekint 1974, Michiels and Dhondt. 1991, Macagno et al. 2008), but a wind effects experiment like the one employed here has never been attempted. This experiment included four trials. The trials were conducted on June 23 and 24, 2012, and on July 14 and 15, 2012.

A pilot study was conducted the year the ponds filled with water in 2011 to address the concern that the released dragonflies would fly straight to the woods after release, an expected response when dragonflies wish to escape from some threat. In this pilot study, 10 *Libellula incesta* were released after they were transported from their source location to the experimental location. Upon release, the dragonflies did not fly directly toward the woods, instead all but one flew downwind; thus, the pilot study indicated that the actual wind experiment could proceed.

In the four trials (approximately 20 individuals each trial) adult dragonflies (*Libellula incesta*) were marked and released and then attempts were made to recapture them. The marking of dragonflies for such an experiment is explained in Hinnekint (1974) and Hagler and Jackson (2001). Released dragonflies for this experiment were marked with a white marking pen dot (< 4 mm round) on the dorsal side of the dragonfly's thorax, and a number placed over the white dot. Inks dried instantly and did not interfere with flight movements. Marking was applied a few seconds before the individuals were released.

The original study design included attempts to recapture marked and released dragonflies. Eight student assistants per release date were hired to capture or observe the released dragonflies; one person was assigned to each of the eight ponds. Each assistant was trained for several weeks prior to the experiments to insure adequate skill level in net-capturing of dragonflies, to avoid loss from escaping dragonflies, to avoid damaging caught dragonflies, and to address consistency of effort at each pond. The assistants were randomly rotated on each release date, from one pond to another pond, so that any bias per assistant's skills or observations would be minimized.

When the experimental day began, for one hour prior to release of the experimental *Libellula incesta*, each assistant captured every adult dragonfly he/she encountered, attempting to "sweep" the experiment field of all or most other dragonflies so that their existence at the site did not become a confounding factor when the release began. All of these resident caught dragonflies were collected and transported to a local pond one kilometer away.

Release procedures for the experiment trials were as follows:

1. Each *Libellula incesta* was carefully removed from the transportation container;

2. A white dot was placed on the dorsal thorax of each released dragonfly and a number was written on the dot;

3. Wind direction and velocity were recorded at the location and moment of release, using a flagging tape wind vane and a SPER Scientific Mini Environmental Quality Meter anemometer;

4. While holding the marked dragonfly, it was raised an arms-length by the releaser, while being held to about 3 meters altitude (i.e. within the Boundary Layer) and released facing into the wind;

5. At release the direction of flight traveled by the released dragonfly was observed, recorded, and confirmed when possible by the assistant at the pond in that flight direction;

6. Recaptured dragonflies were recorded by location of recapture and assigned number on the thorax. Release of the individuals occurred about every 5 minutes.

The daily experiment was terminated when all dragonflies had been released and all possible recaptures were completed.

Analyses of the wind experiment field data were performed. Chi-squared calculations were made on each set of data. Although there is some disagreement about situations in which it is appropriate to use the chi-square test (Baker and Lee 1975, Jelinski 1990), for this analysis these critiques were disregarded, and chi-square analysis was performed.

Data were analyzed by a directional statistic package, *Oriana* (Kovach 2011). The data were configured to work with the software. If at release, the wind was coming from the south compass direction, then flight to the north was recorded as 180^{O} and would be defined as downwind. If the wind shifted and was coming from the southeast, then 180^{O} would be to the northwest. As data are loaded into the software program, the wind direction, the degree direction the dragonfly flew and the wind velocity at release were recorded.

Results

An attempt was made to raise enough tenerals for the mark and recapture experiment. The vivarium was operated in the late spring – early summer of 2011 and 2012. Tables 4.1 and 4.2 provide results for these times.

The vivarium emergence data agree with field observations made in Hanover County, Virginia, and data from Wissinger (1988) in Indiana. In a natural case, Wissinger reports high rates of mortality for larvae, but making a comparison with my data was not possible because I did not determine the population numbers of these species while in the source pond.

Table 4.1 Dragonfly Vivarium Operation 2011
Results: larvae that emerged as tenerals

Date	Species	Gender	Quantity
6/1/2011	*Pachydiplax longipennis*	M	1
	Erythemis simplicicollis	F	2
		M	2
	Libellula lydia	F	3
6/3/2011	*Pachydiplax longipennis*	M	2
		F	1
	Libellula lydia	M	1
6/4/2011	*Libellula lydia*	M	3
		F	1
6/7/2011	*Pachydiplax longipennis*	M	1
6/11/2011	*Pachydiplax longipennis*	M	1
		F	1
	Libellula luctuosa	M	4
	Libellula incesta	F	2
6/13/2011	*Pachydiplax longipennis*	F	3
		M	3
	Libellula vibrans	M	2
		F	2
	Libellula luctuosa	M	3
	Libellula lydia	F	1
6/12/2011	*Erythemis simplicicollis*	F	2
	Libellula vibrans	M	4
	Libellula luctuosa	F	1
	Libellula lydia	F	3
6/16/2011	*Libellula incesta*	M	5
6/18/2011	*Pachydiplax longipennis*	M	1
6/20/2011	*Libellula incesta*	F	2
6/23/2011	*Erythemis simplicicollis*	M	1
	Libellula luctuosa	M	1
		F	2
Survivors/tenerals = 84 %			61

73 Original larvae were collected from Hall Farm Pond (#2901), May 21-22, 2011

Table 4.2 Dragonfly Vivarium Operation 2012 Results: larvae that emerged as tenerals

Date	Species	Gender	Quantity
6/9/2012	*Erythemis simplicicollis*	M	1
		F	2
	Libellula lydia	F	3
6/10/2012	*Pachydiplax longipennis*	M	2
		F	1
6/12/2012	*Libellula incesta*	M	2
		F	1
6/19/2012	*Libellula lydia*	M	3
6/20/2012	*Pachydiplax longipennis*	F	2
6/21/2012	*Pachydiplax longipennis*	M	3
		F	1
	Libellula incesta	M	2
	Libellula luctuosa	M	1
6/22/2012	*Pachydiplax longipennis*	F	1
		M	3
	Erythemis simplicicollis	M	2
6/23/2012	*Erythemis simplicicollis*	F	2
	Libellula incesta	M	2
		F	1
6/25/2012	*Erythemis simplicicollis*	M	3
6/26/2012	*Libellula lydia*	F	1
6/28/2012	*Pachydiplax longipennis*	M	2

Survivors/tenerals = 74%			41

55 larvae collected from Hall Farm Pond on May 26-27, 2012

The second year of the vivarium rearing experiment was conducted in 2012, and excessive amounts of algae grew in the vivarium. This occurred because we were not as careful about algal contamination from the source pond. Algae normally are not a problem for dragonfly larvae (Groover 1974), but they did restrict water flow from the water pumps.

For vivarium-raised adults to be a viable source of enough mature adults for the wind experiment, at least 20 individuals needed to be available at one time for each trial. This was not accomplished from the vivarium-reared population, and thus collections of *L. incesta* from Summerduck Farm were undertaken to provide enough adults for the wind experiment.

During the wind experiments, 20-21 remotely captured dragonflies were transported, marked and released during each trial. Their direction of flight, wind direction, and velocity were recorded; results for each experiment are provided in Tables 4.3 - 4.6. After transport to the release site, some individuals had damaged themselves during their brief captivity, and their condition is noted in these tables. Favorable temperature and wind conditions were recorded. The assigned assistants were noted for each day’s trials.

Table 4.3 Results from the Wind Experiment on June 23, 2012

Dragonfly # and Condition	Time of Release	Wind Direction and velocity @ Release (km/hr)	Direction Flew	Compass Degree Of Dragonfly Flight	Notes
1 – ok	1335	S – 5.2	S	180	
2 – ok	1339	S – 5.1	SE	135	
3 wing damaged	1343	S – 5.4	S	180	
4 - ok	1346	S – 1.3	E	90	
5 - weak	1350	S - 11.1	SW/S	202	
6 –weak	1352	S – 11.6	SE	135	
7 wing damaged	1356	S - 5.1	SW	225	
8 wing damaged					Not released
9 – ok	1358	0	SW	225	
10 - ok	1403	SE – 6.1	SW	270	
11 - ok	1405	S – 6.5	SW	225	
12 - ok	1408	S – 1.1	W	270	
13 - ok	1411	S – 6.8	SE	135	
14 - ok	1414	SW - 12	SW	180	
15 - ok	1418	S – 4.1	SW	225	
16 wing damaged					Not released
17 - ok	1421	S – 3.8	W	270	

Conditions of the day: Weather - Clear 29.9 BP TEMP 36 ^{o} C

Assistant Assignments
Pond 1 – Ryan Pond 2 – Jordan Pond 3 – Alyson Pond 4 – Justin Pond 5 – Jason
Pond 6 – Alex Pond 7 – Curt Pond 8 – Eric

Table 4.4 Results from the Wind Experiment on June 24, 2012

Dragonfly # and Condition	Time of Release	Wind Direction and velocity @ Release (km/hr)	Direction Flew	Compass Degree Of Dragonfly Flight	Notes
1 – wing damaged	1300	N – 7.9	NE	225	
2 - damaged					Not released
3 – ok	1305	NW – 3.5	N	225	
4 – ok	1308	N – 5.6	N	180	
5 – ok	1311	0 wind	E	270	
6 - weak	1315	N - 6.5	W	90	
7 – ok	1318	N – 8.0	N	180	
8 – ok	1321	N – 8.1	N	180	
9 – ok	1325	N – 8.5	N	180	
10 - ok	1329	N – 11.2	N	180	
11 - ok	1332	N – 8.6	NW	135	
12 - ok	1337	N – 9.3	N	180	
13 - ok	1340	N – 12.2	NW	135	
14 – wing damaged	1342	N – 13.1	W	90	
15 - ok	1350	N – 1.0	W	90	
16 - ok	1353	E – 5.9	NW	45	
17 – wing damaged					Not released
18 - ok	1358	N – 10.1	NE	225	
19 - ok	1403	N – 10.4	N	180	
20 - ok	1406	N – 10.0	NW	135	
21 - ok	1409	N – 14.7	NW	135	

Conditions of the day: Weather – partly cloudy 29.97 BP TEMP 34^{o} C

Assistant Assignments
Pond 1 –Eric Pond 2 – Alyson Pond 3 – Curt Pond 4 – Alex Pond 5 – Ryan
Pond 6 – Justin Pond 7 – Jason Pond 8 – Jordan

Table 4.5 Results from the Wind Experiment on July 14, 2012

Dragonfly # and Condition	Time of Release	Wind Direction and velocity @ Release (km/hr)	Direction Flew	Compass Degree Of Dragonfly Flight	Notes
1 - ok	1430	NW 7.0	NW	180	
2 - ok	1440	NW 3.0	E	315	
3 - ok	1445	NW 6.0	W	135	
4 - ok	1448	N 1.4	E	270	
5 - ok	1453	NW 3.3	W	135	
6 - ok	1458	N 6	NW	135	
7 - ok	1501	N 4.6	W	90	
8 - ok	1504	N 7.1	NW	135	
9 - ok	1509	N 6.2	N	180	
10 - ok	1512	N 2.9	E	270	
11 - ok	1518	NW 9.0	NW	180	
12 - ok	1522	N 3.6	SE	315	
13 - ok	1525	N 7.5	N	180	
14 - ok	1529	N 6.9	NE	225	
15 - ok	1532	N 3.3	W	90	
16 - ok	1536	N 10.1	N	180	
17 - ok	1539	N 11.1	NW	135	
18 - ok	1542	N 7.1	NW	135	
19 - ok	1546	N 11.2	NE	225	
20 wing damaged					Not released
21 - ok	1550	N 6.5	NW	135	

Conditions of the day: Weather - P. Sunny TEMP 29.9 BP=30

Assistant Assignments
Pond 1 – Curt Pond 2 – Wesley Pond 3 – Alex Pond 4 – Ryan Pond 5 – Eric
Pond 6 – Alyson Pond 7 – Justin Pond 8 – Jason

Table 4.6 Results from the Wind Experiment on July 15, 2012

Dragonfly # and Condition	Time of Release	Wind Direction and velocity @ Release (km/hr)	Direction Flew	Compass Degree Of Dragonfly Flight	Notes
1 - ok	1330	8.9 N	NW	135	
2 - ok	1333	7.8 N	NW	135	
3 - ok	1337	11.1 N	N	180	
4 - ok	1340	10.8 N	NW	135	
5 - ok	1342	6.2 N	N	180	
6 wing damaged					Not released
7 - ok	1349	3.9 N	W	90	
8 - ok	1352	8.4 N	NW	135	
9 - ok	1357	3.8 N	S	360	
10 got away					No results
11 - ok	1402	10.1 N	N	180	
12 - ok	1405	6.0 N	E	270	
13 - ok	1407	8.6 N	NW	135	
14 - ok	1410	9.4 N	N	180	
15 - ok	1414	3.6 N	NE	225	
16 - ok	1419	6.7 N	NW	135	
17 - ok	1423	7.2 N	N	180	
18 - ok	1426	8.5 N	N	180	
19 - ok	1430	7.9 N	NE	225	
20 wing damaged					Not released

Conditions of the day: W - Partly Sunny TEMP 30.5 C BP= 30.1

Assistant Assignments
Pond 1 –Justin Pond 2 – Curt Pond 3 – Ryan Pond 4 – Amy Pond 5 – Alyson
Pond 6 – Eric Pond 7 –Alex Pond 8 – Wesley

The total N value over all trials was 71. The direction that the dragonflies flew upon release is noted in the above tables. The released dragonflies were visible for 50 – 70 meters from the release site. The assistant at the pond in the direction of travel was alerted by voice command. Forty-five percent of released dragonflies were caught at the ponds or observed by the assistant at a pond.

Out of the 71 individuals only one flew into the wind (July 15, #9). Examination of the raw data suggests that the direction of flight generally corresponded with wind direction at above a certain velocity. Additional analysis supported this.

Chi-Squared analyses were used to test data collected on June 23, June 24, July 14 and July 15, as shown in Table 4.7. For the null hypothesis in this analysis, there is no significant difference between the observed distribution and a uniform distribution. The expected distribution under the null hypothesis is uniform (with no bias in any direction). For the directions under the null hypothesis, the distribution is uniform across all eight octants of the wind. Analysis indicates that dragonfly dispersal downwind was nonrandom at a high level of significance on all dates, meaning that downwind direction of flight is indicated. The null hypothesis is rejected, accepting the alternative hypothesis that wind has influenced the numbers and they are not uniform.

Table 4.7 Chi-square calculations for dragonfly dispersal experiment on June 23, 24, and July 14, 15 2012

DATES	Observed # of Dragonflies	Number Wind Directions	Degrees of Freedom	Observed Chi-squared Value*
23-Jun	15	8	7	18.294
24-Jun	18	8	7	28
14-Jul	20	8	7	17.882
15-Jul	17	8	7	20.176

*Statistical significance at 0.05 level (each larger than 14.067 [Zar 1999])

The data suggest that when the wind velocity was below 3 km/hr, the dragonflies were more likely to fly in random directions; when the wind velocity was greater than 5 km/hr they flew downwind.

Analysis using directional statistics provides further support for the impact of wind velocity on direction of dragonfly flight. Wind velocity of 5 km/per hour is a “cut-off” point: below 5 km/hr the flight direction is random, but over 5 the direction of flight is downwind. Figure 4.5 provides a visual depiction of the results from the wind experiment. This Rose Diagram demonstrates the number of release dragonflies that flew in various directions. Making adjustment as to the direction the wind blew, 180^o is always downwind. Directions between 135^o and 225^o may also be defined as downwind. It should be noted that most released dragonflies did fly downwind, but some flew in different directions, perhaps even 90^o from the direction the wind was blowing.

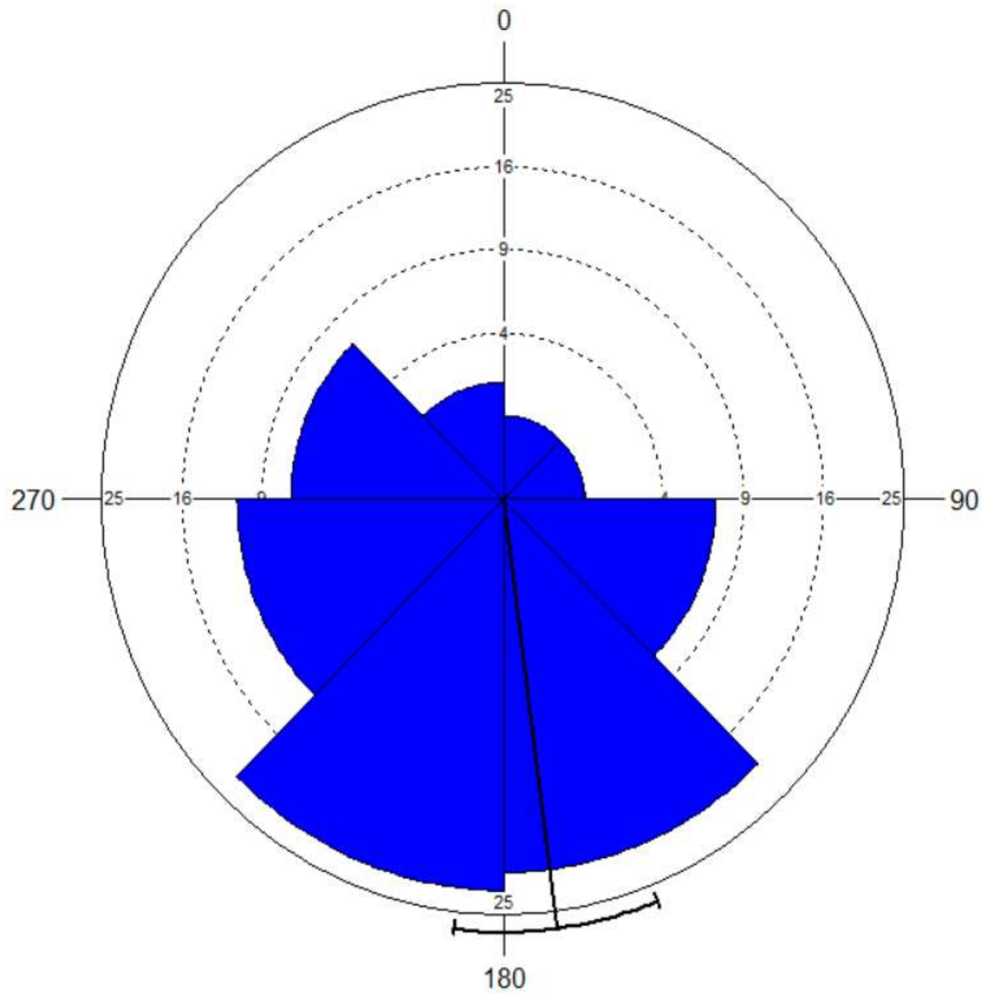

Figure 4.5 Rose diagram of the experiments' results on wind direction with dragonfly flight direction identified. Compass direction of 180^{O} is downwind from direction wind was blowing. The inner circle units are individuals in four trials that went that direction: 16 would be 16 individuals, 9 would be 9 individuals, etc.

Additional directional analysis providing a diagram of wind velocity and the frequency of individuals that flew in that direction is provided in Figure 4.6.

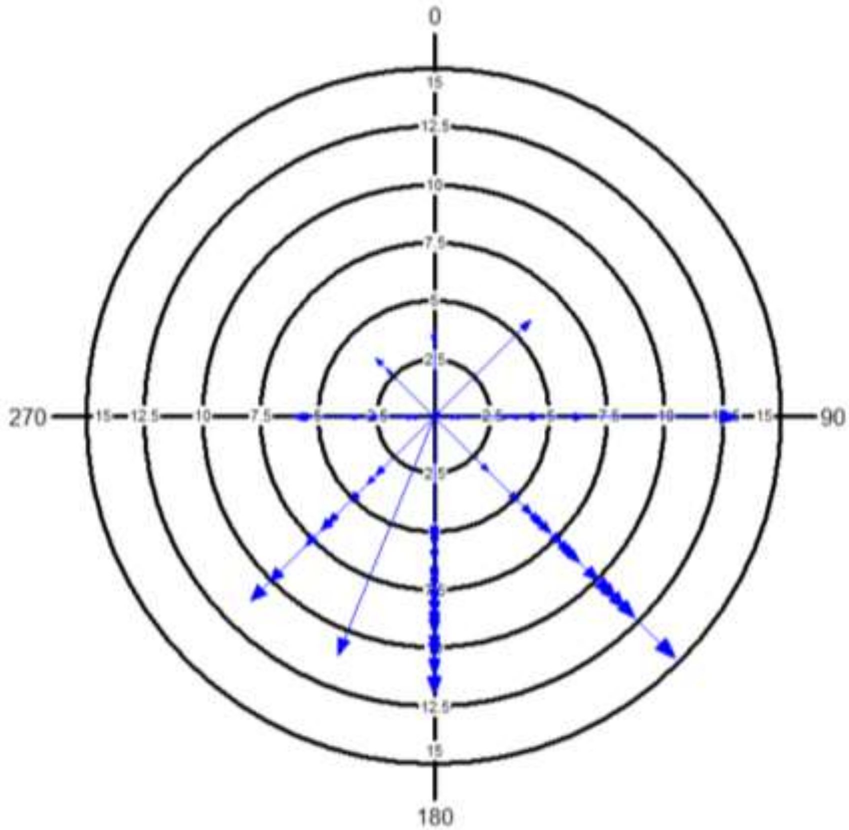

Figure 4.6 Results from wind direction and wind velocity for dragonfly flight. The inner circles are wind velocities (kilometers per hour) at the moment of release; five km/hr is indicated on the # 5 circle, 7.5 km/hr is indicated on the # 7.5 circle, etc. The arrows directions indicate direction of flight by the released dragonfly. Zero degrees represents the direction the wind was blowing at the moment of release, and 180o is downwind from the direction the wind was blowing at the time of release. The length of the arrows represents number of individual dragonflies that flew in that direction.

When wind velocities were greater than 5 km per hour, the released dragonflies usually flew downwind, in a compass direction between 135^o and 225^o, with most flying downwind toward 180^o (Figure 4.5). The more numerous arrows indicate flight in a down wind direction, or at least greater than 90^o from the direction the wind was blowing.

Figure 4.7 provides a summary of the "cut-off" wind velocity during which downwind flight may be expected. Between 5 and 7 km per hour downwind flight becomes 80 to 100% expected.

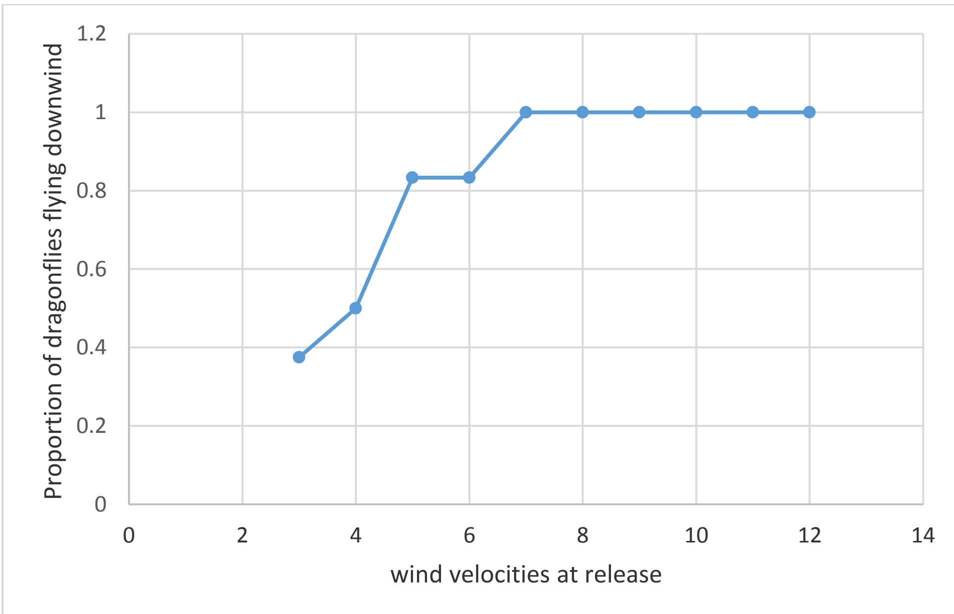

Figure 4.7 Proportion of dragonflies flying downwind at different wind velocities

Discussion and Conclusions

The hypothesis for this study was that at some wind velocity in the boundary layer, dispersing dragonflies will fly downwind with the direction of wind flow, and this experiment demonstrated that at 5 km per hour velocity downwind flight is expected 80% of the time or greater.

The original plan to use reared tenerals proved impractical due to difficulties in obtaining the large numbers of test organisms needed for the dispersal experiments. However, the vivarium designed and tested here was successful in rearing moderate numbers of tenerals and it was shown that *Lumbriculus variegatus* provides a suitable source of food that can sustain the larvae during this phase of their natural history. This is the first time that the harvesting of dragonfly larvae on this scale has been recorded.

During the vivarium operation, a new observation (never previously documented in the literature) was made concerning what happens when the larvae are about to molt and emerge into adults. While still underwater, they become lethargic, slow and minimally responsive to probing. Corbet (1999) reported that during the late instar stage, and before the final larval stage, larvae undergo physical changes. But this observed lethargic behavior has not been previously reported. The lethargic behavior was observed numerous times (no actual numbers were recorded) and is an atypical daily behavior in the larval stage; normally when probed the individual will squirt water from its abdomen to escape and work its legs for additional propulsion. Perhaps physiological events are occurring in the animal that restricts its escape response. Perhaps it is a preparatory response to save energy before the larvae ascend out of the water and molt from their larval exoskeleton. It may be noted that this places the larva in a dangerous situation, not being able to escape underwater predators.

As expected, the ascents by the larvae occur always at night. None were observed during daylight hours. Exuvia were discovered as much as one meter away from the water surfaces inside the vivarium; thus the individual crawled some distance before completing the emergence. When my team was collecting larvae at Hall Pond for this experiment, one exuvium was found three meters from the pond surface. This is unusual and would have placed that dragonfly far from frog predation, but at greater risk from other nocturnal predators like snakes and birds.

The vivarium experiment was successful in terms of raising dragonfly tenerals, but it did not work to produce the cohorts of twenty individuals available at one time, as needed for the dispersal experiment. Noting the results in Tables 4.1 and 4.2, I could get 20 tenerals in a two to four day period, but keeping the earlier emergers robust for the mark and recapture experiment was not possible. The tenerals in 2011 were placed in a 12' X 12' mosquito blocking enclosed "picnic tent," to prevent their escape and allow me to feed them in captivity and assemble the needed 20 individuals. But their conditions seemed to weaken because I could not provide enough food or proper conditions for them to mature and remain strong. Numerous food types, from mosquitos harvested from a trough to bot flies harvested from rotting meat, were attempted.

Use of tenerals for the wind experiment was questionable because tenerals remain immature for up to two weeks (Corbet 1999), a period of time that would have been impossible to sustain in captivity. After this experience, I decided to instead use mature adults (*Libellula incesta*) from one easily accessible location, easily captured and easily transported to the release site.

Methods for transporting the collected adult dragonflies were successful 91 % of the time. Initially 79 individual dragonflies were captured for this experiment; with 7 being so damaged during capture and transport that they could not be released for the wind experiment. The transport container was not of this researcher's original design, but it was modified by this researcher and improved, and this will be published for others' use and information.

Data from the manipulated wind impact experiment were collected, and the direction of flight/dispersal once released was noted. The original study design predicted that released dragonflies would fly a short distance to a pond and perhaps rest and be captured. Few dragonflies exhibited this behavior or were caught after release; many flew by the artificial ponds and continued their flight. Various theories can be suggested to explain this behavior. Perhaps dragonflies normally fly farther from their home area when they disperse before resting. Alternatively, stress levels induced by handling caused this "fly-by" to occur, and it became a confounding factor in this study. Stress hormones could be studied further for dragonflies to consider this theory, but very little is known about stress hormones in dragonflies.

The selection of an easily observable insect, and the "sweep" of the experiment site before implementing the mark and recapture, resulted in useful data despite the failure of many dragonflies to stop at the artificial ponds.

In summary, flight downwind occurred when wind velocity exceeded 5 km/hr. in 78% of the time (40 out of 51 individuals in the +5 km conditions). In the less than 5 km/hr. wind velocity conditions, direction of flight was in the downwind direction only 19% of the time (3 out of 16 individuals in the < 5 km conditions). This leads to a revised hypothesis: when wind velocity exceeds 5 km/hr., dispersal of adult dragonflies will be in a downwind direction.

Based on this experiment, upwind dispersal when wind exceeds 5 km/hr is unlikely to occur (uncommon at least). But wind direction is never constant either by velocity or direction, thus we can not predict that dispersal will always occur in one direction, based on wind’s influence. If winds during the daytime, when most dragonfly flight occurs, is more constant and frequent in one direction, then predictions could be made about dispersal occurring in a direction, based on these results. Said another way, prevailing wind direction, being more constant in one direction, may affect the direction of dispersal in a greater frequency.

Chapter Five

Conclusions and Future Research

Chapter Five discusses some implications of this research on dragonfly dispersal and colonization. Community structure in the lentic ecosystem and affecting factors are summarized. Relevant points on the restoration and conservation of dragonflies' habitat are discussed. The importance of dragonflies as indicator species of climate change is considered. A discussion of biochemistry in dragonflies is mentioned. Recommendations are made for future research.

Implications of this Research for Dragonfly Colonization & Dispersal

Corbet (1962) defines dispersal of dragonflies as "meaning the colonization of new breeding sites." Corbet states that dispersal is a movement "undertaken to satisfy a specific need." Improved opportunities for breeding are such needs as are the lessening of competition due to high population densities. The result may also be improved and expanded gene pools for breeding dragonflies. Dispersal may also help maintain distribution and abundance of local species and compensate for local extinctions as disruptive conditions occur.

Summary of Research

Chapter Two identifies the resident species of Hanover County. It was hypothesized that during dispersal to new ponds, local (closer) lentic habitats serve as sources from which many dragonflies emigrate. The proximity of source locations to new sites is supported as a determinant of first colonizers in lentic habitats, based on data from North Lakeridge Stormwater Pond (2274), Reynolds Stormwater Pond #2, and Pebble Lake Stormwater Pond (2883), see Chapter Two.

Additional research with genetic identification and/or marking of collected individual dragonflies can further support this. Species from potential source ponds (from where they emigrate) can have their DNA identified and compared with DNA from individuals at possible destination ponds. While useful, this may not yield clear results because a mated female could have more than one sperm donor: one from the source pond and one at the new pond where eggs are oviposited.

After colonization of a site by dragonflies, if conditions remain nearly the same, the relative abundance of resident species was found to remain rather stable, based on research reported in Chapter Three. But no habitat that goes through this succession remains static. Obvious changes will normally occur often with the littoral zone vegetation, especially during the first couple of years. Remsburg and Turner (2009) noted that vegetation is an important aspect in the lentic habitat for dragonflies and their residency. Shading along the littoral zone is an influencing factor for some adult dragonfly species' abundance (Remsburg and Olson 2008). Many dragonfly species do not like heavy shading, but some littoral zone shrub or grass vegetation is a positive factor for most dragonfly species.

Chase (2010) states that stochastic communities cause higher local biodiversity in more productive environments. The observed numbers noted in Chapter Three are not very different from year to year in most of the reference ponds, presumably the degree of stochasticity (which occurs in all lentic habitats) at these sites is less but they have some variability of resident species. Data in Chapter Three does support minor variability in dragonfly abundance numbers per species in all of the studied reference impoundments. This research also notes that one older (40 years) reference pond (Hollows Golf Course) with minimal littoral zone vegetation has less resident species. In this case excessive cutting of littoral zone vegetation (mostly grass) at the manicured golf course reduces the dragonfly assemblages. Dragonfly adults (especially perchers) prefer some vegetation along the pond's edges. Since dragonflies can be an effective predator of mosquitoes (Corbet 1999), managers of golf courses can improve the lentic habitat of this apex insect predator and reduce the use of chemicals for mosquito control by managing habitat more effectively. Future research comparing lakes with excessive cutting regimes versus those with more limited cutting of shoreline vegetation could test the validity of such a management approach.

New ponds, less than four years after their creation and having some vegetation succession, were expected to have greater variability in dragonfly communities, but results do not support this. What was originally hypothesized was a complete change in the most dominant species, but that did not occur and is unsupported by any field data.

Habitat decline means fewer dragonflies

On a grander scale, lentic habitats are declining in Hanover County, Virginia. Fewer ponds exist today, compared to 40 years ago. Based on a comparison of topographic maps, Hanover County had approximately 200 ponds countywide in the 1970s. Many of these small farm ponds no longer exist. More recent topographic maps (2015) reveal about 20% less ponds compared to 2004. In 2004, many impoundments were destroyed during Hurricane Gastone and were not rebuilt. Development of housing subdivisions, parking lots, shopping areas, etc. reduces the number of lentic sites as the ponds are filled and housing or commercial developments occur. In some cases stormwater management ponds, supporting land development, are not required and are not built. This reduces suitable aquatic habitats for anisopterans, and then the total numbers of dragonflies in the county drops. Not only have ponds and lakes declined in Hanover County, but so have wetland areas. Using statewide estimates the non-tidal wetland loss of 2500 acres (1011.714 ha.) per year (Chesapeake Bay Foundation 2006), means that Hanover County has lost a share of its freshwater areas, important sites where some dragonfly species are commonly found.

Locally, what role does climate change bring to lentic areas and abundance of dragonflies? As seen in the Federal Club Lake, the water level declines as observed in 2010, have had an impact resulting in the lower counts of dragonflies at that site. Climate change may impact Anisoptera density and distribution, especially if areas dry up then are refilled later or do not have any standing water at all. Lentic sites are impacted by local climate changes. Data support the presence and continuation of drought in Virginia that is specifically connected to climate change (Virginia Department of Environmental Quality 2016, Virginia Drought Monitoring Task Force 2016). Bates et al. (2008) predicts that water levels in lakes in the United States are projected to decline at mid-latitudes. Klos et al. (2009) state that older and denser forests are more susceptible to drought and have increased mortality. If drought causes some forest cover to disappear, or higher surface temperatures occur with greater evaporation, lakes and ponds may periodically dry-up or may cease to exist. Lentic Anisoptera may decline in abundance as water in these impoundments decrease, as was observed at the Federal Club Lake during this study.

Bates et al. (2008) further predict that inland freshwater wetlands will experience drying trends, as a result of local climate change. If this occurs, wetland dragonfly species may face further reductions.

Discussion of Improvements that will help local biodiversity

Can these potential losses of anisopterans from habitat decline be mitigated? They can with the construction of more lentic sites and incentives for the construction of wetlands. The cost of construction of ponds and lakes could be supported by state tax incentives for private land owners, as they were previously according to local farmers. If a farmer built a pond, the cost could be deducted from state income taxes. In the past the government paid some of the cost of pond constructions for farmers. For larger impoundments the state could acquire several large tracts and build state parks on those sites with new lakes included, as was done in the 1930s. If properly managed, new lakes and ponds may provide habitat for more dragonflies.

Further research can address the degree to which new lentic habitats sustain the richness and abundance of dragonfly species. Le Viol et al. (2009) report that stormwater retention ponds affect aquatic macroinvertebrate biodiversity. Odonata, noted in this report, do have increases in the local abundance and diversity in their studied stormwater ponds, and an increase in local abundance. This also occurred at several constructed stormwater sites studied for this dissertation's research; such as Site 2272 - Pro Bass Pond; 2273 – Northlake Stormwater Pond (large); 2274 – Northlake Stormwater Pond (small); 2281- Courthouse Park Lake; 2582 – Rutland Stormwater Pond; 2882 – Creekside Stormwater Pond; and 2883- Pebble Lake Stormwater Pond. Prior to 2008, none of these sites existed. Any lentic species previously found in these areas were only passing through the area as they foraged for food. When these ponds were created, dragonflies dispersed to them and colonized these impoundments. These new aquatic sites contributed to local richness and abundance in the hectares surrounding these sites, all of which had no lentic habitats within one to two kilometers. Since the stormwater ponds must be built for some county or state MS4 permits, if these sites exist as rainwater and stormwater keep them filled, these would attract dragonfly residents if they managed to attract dragonflies. New non-ephemeral sites may result in good habitat for lentic dragonfly species.

Currently wetland banking is a profitable enterprise as former wetlands are being reestablished. A land owner may rebuild a former wetland, give it a designated protection easement, and that value can be paid for to this land owner by someone who wants to destroy an existing wetland somewhere in the same watershed; this is considered an allowable mitigation for existing wetlands being destroyed. As these are established and the wetland is built, dragonflies find these sites and colonize them.

Dragonflies as bioindicators for climate change

Anisopterans are recognized as a "diversity indicator." Chovanec and Raba (1997) identify Odonata in a role as a "bioindicator" for wetlands monitoring, for constructed wetlands evaluation, and perhaps a suitable organism for landscape planning. These authors conclude that odonates can be studied to achieve appropriate management for artificial wetlands.

Dragonflies are cited by Kalkman, et al. (2008) as successful "indicators for environmental health and conservation management." Because dragonfly species respond to changes in biogeography and climate conditions, their presence, or lack of, can indicate over the long term, what the impact of change may be. Kalkman et al. state that dragonflies in Europe are expanding their ranges north as the temperatures in northern areas annually rise.

Richter et al. (2008) have developed a model to use dragonfly emergence data for comparison with changes in climate. Their model is used in the investigations of emergence predictions correlated with temperature rise. My investigations using contacts with the members of the Dragonfly Society has begun to provide some indication of the climate change impacts on dragonfly adult emergence (Groover 2012). Range changes are expected for the more specialist species, but which specific species would benefit can be further studied.

Odonata is identified to be a global assessment group for insects (Clausnitzer et al. 2009). These researchers report that one in 10 species of dragonflies (Anisoptera) and damselflies (Zygoptera) is threatened with extinction. They state that odonates have "above-average dispersal ability" which may help their survival in some regions. Habitat destruction will reduce sites to which they can disperse.

Dragonfly Stress Hormones

Concern was raised by this investigator, regarding dragonfly behavior during the stressful conditions of the wind experiment (Chapter Four). Handling of the dragonflies was expected to cause stress hormones in the dragonflies to rise. Their release was delayed in hopes that any stress hormones might have dissipated. During my experiment trials, their behavior did not appear to affect the directional flight results of this experiment; recall that not all of them tried to fly directly to the woods in the closest direction. Could the stress levels alter behavior in some other ways? During the experiment the dragonflies were kept at a cooler temperature to slow their respiration, and maybe reduce stress hormone release. Stress hormones in dragonflies are not well researched. A study on insect neurohormones and stress has probed this, but more detail could be examined (Peric-Mataruga et al. 2006). If a study of Anisoptera behavior and their stress hormones is undertaken, I suggest research could include: 1). determine exactly which stress hormones occur in dragonflies; 2). determine if these can be suppressed when conducting experiments so that stress response can be mitigated as a confounding factor. Perhaps a neutralizing chemical could be identified and administered during stress causing experiments, and completely mitigate any influences of stress on tested individuals. Much like smoke is used to calm honeybees, is there some way to calm dragonflies during a stressful experiment? This area of biochemistry of dragonfly hormones has many possible avenues to explore.

Appendix

Appendix 1   Lentic Species of Dragonflies Collected in Hanover County, Virginia, from 2005 – 2012

Species   Site Numbers   X = Species collected per site

	1341	**1931**	**1951**	**2241**	**2251**	**2252**	**2255**	**2256**	**2271**	**2272**	**2273**	**2274**	**2281**	**2282**	**2581**	**2582**	**2583**	**2593**	**2602**	**2881**	**2882**	**2883**	**2891**	**2892**	**2901**	**2903**
Family Aeshnidae						↓															↓					
Anax junius						X															X					
Anax longipes																					X					
Family Gomphidae														↓											↓	
Gomphus exilis														X											X	
Progomphus borealis																									X	
Family Corduliidae									↓									↓						↓		
Epitheca cynosura									X									X						X		
Family Libellulidae	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓
Celithemis elisa	X			X	X	X		X		X			X	X							X	X				X
Celithemis eponina	X	X	X		X						X										X				X	X

Celithemis fasciata			X										X	X				X					X		X	X
Erythemis simplicicollis	X	X	X	X	X		X	X	X	X	X	X		X	X		X	X		X	X	X	X	X	X	X
Libellula cyanea		X											X	X	X								X	X	X	X
Libellula deplanata																		X					X		X	X
Libellula incesta	X	X	X				X	X	X	X	X	X		X	X		X	X	X	X	X	X	X		X	X
Libellula luctuosa	X	X		X	X	X	X		X				X	X	X			X				X		X	X	
Libellula lydia	X		X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	
Libellula pulchella				X																X						
Libellula vibrans														X	X		X		X	X			X		X	
Pachydiplax longipennis	X	X	X		X	X	X	X	X		X	X		X		X		X	X	X	X	X	X		X	X
Pantala flavescens											X							X		X					X	X
Pantala hymenaea				X																						
Perithemis tenera	X	X	X	X	X		X	X			X			X		X		X	X	X		X		X	X	X
Sympetrum vicinum														X											X	
Tramea carolina												X									X	X				
Tramea lacerata						X					X											X			X	
Family Petaluridae															↓		↓									
Tachopteryx thoreyi															X		X									

FIELD DATA SHEET Appendix 2

SITE: Survey Station Number:

Date:

Time: Weather: Barometeric P.: Temperature: Wind:

SPECIES	COUNTS of INDIVIDUALS			
	Column1	Column2	Column3	Column4
Ashy Clubtail				
Autumn Meadowhawk				
Blackshouldered Spinyleg				
Brown Spiketail				
Blue Corporal				
Blue Dasher				
Calico Pennant				
Carolina Saddlebags				
Clamp-tipped Emerald				
Cobra Clubtail				
Common baskettail				
Eastern Pondhawk				
Common Whitetail				
Common Sanddragon				
Eastern Amberwing				
Eastern Ringtail				
Fawn Daner				
Gray Petaltail				
Great Blue Skimmer				

Harlequin Darner				
Halloween Pennant				
Lancet Clubtail				
Little Blue Dragonlet				
Ocellated Darner				
Prince Baskettail				
Slaty Skimmer				
Splendid Clubtail				
Spot-winged Glider				
Twelve Spotted Skimmer				
Widow Skimmer				
Spangled Skimmer				
Common Green Darner				
Banded Pennant				

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Biography

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