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MACROPARASITE POPULATION DYNAMICS AMONG GEOGRAPHICAL LOCALITIES AND HOST LIFE CYCLE STAGES: EUGREGARINES IN *ISCHNURA VERTICALIS*

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ABSTRACT: Populations of several species of gregarine parasites within a single host species, the damselfly *Ischnura verticalis*, were examined over the course of 1 season at 4 geographic localities separated by a maximum distance of 9.7 km. Gregarines, having a life cycle with both exogenous and endogenous stages, are subject to a wide variety of selective pressures that may drive adaptation. Gregarine species showed some specificity for host life cycle stage, i.e., *Steganorhynchus dunwoodyi* and *Hoplorhynchus acanthatholius* were most prevalent in larval hosts while *Steganorhynchus dunwoodyi*, *Actinocephalus carrilynae*, and *Nubenocephalus nebraskensis* were most prevalent in adult hosts. Species prevalence and abundance differed by geographic locality. Gregarine prevalence was significantly higher in adult female damselflies than in males at 2 localities; sex differences in prevalence were insignificant for larval damselflies at all 4 localities. In larval hosts, gregarine abundance was independent of age (size). The present study, therefore, shows that pond characteristics, host life cycle stage, and adult host sex are the main factors that influence the prevalence and abundance of gregarine populations.

Gregarine parasites are perhaps the most diverse monophyletic group of eukaryotes (Levine, 1988). Gregarine species exhibit various degrees of host specificity; in some cases, a species may be restricted to a specific ontogenetic stage of the host, especially in holometabolic insects (Clopton, 2009). The existence of such specificity suggests that gregarine species and hosts have evolved in concert (Cielocha et al., 2011), although gregarine life cycles include both endogenous and exogenous phases; thus, both stages are subject to selective pressures that may drive adaptation. Furthermore, such pressures can easily vary over time and geographical space. The present study was intended to explore the effects of such temporal and spatial variation on populations of gregarine parasites in a host species, the damselfly *Ischnura verticalis*, which occupies 2 distinctly different habitats during its lifetime and occurs over a very wide geographical range in North America.

Population dynamics in a community of gregarine parasites reflect the successful transmission of exogenous stages to hosts and the subsequent compatibility between parasite endogenous stages and host. Thus, population dynamics reveal the overlap between the proper conditions for exogenous stage survival, host survival, and transmission from the environment to a susceptible host. These conditions represent at least some of the selective pressures that drive gregarine evolution. The present study focuses on those factors that are involved with distributing parasites among host populations, thereby affecting parasite fitness, a pre-requisite for understanding evolutionary change in such systems. Clopton (2004) suggested that host habitat fidelity contributes to isolation and subsequent speciation of gregarine populations, thereby producing high species diversity. In the present study, characteristics of geographic localities, as well as those of hosts, thus provide selective pressures.

Damselfly-gregarine systems are good ones for investigating the factors that affect gregarine reproductive success because hosts are abundant, geographically widespread, and occupy diverse environments; these hosts also are often heavily infected with several gregarine species. Gregarines (phylum Apicom-

plexa, class Conoidasida, suborder Septatorina) inhabit the host's gut in the endogenous trophont stage. Trophonts form pairs, in the process becoming gamonts, which then undergo syzygy and secrete a cyst wall, thus producing gametocysts which are expelled with the host's feces. Gametocysts undergo sporulation to produce oocysts, the infective stages that are subsequently scattered into the environment and ingested by hosts, thus completing the life cycle (Grell, 1973). Although the exact mode of transmission for damselflies is not known, it can be reasonably inferred that oocysts are ingested along with prey consumed by the host (Ábro, 1976). Adult damselflies and larvae occupy quite different environments, and thus can be expected to consume different types of prey. Accordingly, the gregarine fauna of the 2 life cycle stages are potentially different.

In the present study, gregarine infrapopulations were examined within a single host species, the damselfly *Ischnura verticalis* (Say, 1839), at 4 geographic localities and over the course of 1 season. Our objectives were to determine the relationships between host ontogenetic stage, host sex, geographic locality, and time. Accordingly, several hypotheses were tested, namely, whether gregarine prevalence and abundance are independent of (1) host ontogenetic stage, (2) host sex, (3) geographic locality, and (4) time.

Additionally, the resulting extensive data set provides a basis for theoretical models that explain the stability of host-macroparasite population dynamics (e.g., Logan et al., 2012), as motivated by the earlier paradigms proposed by Anderson and May (1978). Ultimately, our goal was to identify which biological factors are the drivers of gregarine fitness and population stability in a field study.

MATERIALS AND METHODS

Gregarine species infecting *I. verticalis* hosts in the present study included *Actinocephalus carrilynae* Richardson and Janovy, 1990, *Steganorhynchus dunwoodyi* Percival, Clopton, and Janovy, 1995, *Nubenocephalus nebraskensis* Clopton, Percival, and Janovy, 1993, and *Hoplorhynchus acanthatholius* Percival, Clopton, and Janovy, 1995. Species were distinguished using morphological criteria provided in the original descriptions.

Data were collected over a 12-wk period from late May to early August 2010. Larval and adult-stage *Ischnura verticalis* damselflies were collected from 4 sites in the vicinity of Cedar Point Biological Station in

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TABLE I. Mean values of ranks in rank-sorted infrapopulations of gregarines in larval *Ischnura verticalis*, along with *F*-values and degrees of freedom in ANOVA of rank-sorted values and raw mean values (mean rank/raw mean). All *F*-values are high enough to reject the null hypothesis of no difference in mean infrapopulations among collection sites.

	Game and Parks Pond	Dunwoody Ditch	Dunwoody Pond	Little Beckius Pond	<i>F</i>	df
May	139.00/2.43	98.40/0.28	102.91/0.58	not applicable	13.46	2, 225
June	97.50/5.54	137.24/1.97	184.83/4.56	151.83/1.83	17.86	3, 247
July	111.38/5.88	131.01/1.33	237.77/3.29	200.45/5/41	36.19	3, 265

Keith County, Nebraska. The sites were: Game and Parks Pond (41°12'3.63''N, 101°39'55.83''W), Little Beckius Pond (41°12'29.73''N, 101°37'4.00''W), Dunwoody Pond (41°13'58.54''N, 101°34'46.63''W), and Dunwoody Ditch (41°13'36.08''N, 101°35'49.12''W). The shortest straight-line distance between these sites was 2.34 km; the longest straight-line distance was 9.68 km (see Table I). Odonates are not known to migrate great distances, normally traveling no more than approximately 200 m from water (Bried and Ervin, 2006). These collecting sites are distributed mainly east-to-west and the prevailing winds during the summer are south to north. Thus, migration of adult hosts between sites was considered minimal, an assertion supported by the parasite population data.

Specimens were collected from each site at least once every 2 wk throughout the season; collections were made weekly at the most abundant source of data, Game and Parks Pond. Larval damselflies were collected from pond vegetation using an aquatic dip net and a white pan and then placed into an 18.9-L bucket to be transported to the lab for necropsy. Adult *I. verticalis* were caught using an insect net, placed into 3.8-L plastic containers, and cooled in an ice chest during transport. Upon returning to the lab, adults were placed in a refrigerator to slow movement enough to collect body measurements and to necropsy.

The following data were recorded for all damselfly hosts: life cycle stage (larva, teneral, or adult), body length (without gills in the case of larvae), head width, and sex. Sexes were distinguished according to morphological criteria of Westfall and May (2006). Larvae were necropsied using forceps to hold the body and carefully remove the head. The gut was then extracted, teased apart in water, and examined for gregarines using a compound microscope. Adults were similarly necropsied by first removing the abdomen with a pair of forceps and then peeling off the ventral abdominal plate and extracting the gut. Any gregarines present were recorded using a microscope camera (Microimage Video Systems YC/NTSC, Boyertown, Pennsylvania and Nikon Alphaphot, Melville, New York) and VHS tape for further measurements and species identification. Each gregarine was measured and identified using criteria from the original species descriptions. Our data set includes observations from 2,135 damselfly hosts and 23,755 gregarines.

Negative binomial parameter values were calculated according to the methods of Bliss and Fisher (1953) using MATLAB (MathWorks, Inc., Natick, Massachusetts). The goodness-of-fit to expected values for negative binomial distributions was analyzed using a chi square (χ^2) test and Microsoft Excel (Microsoft Corporation, Redmond, Washington). A one-way ANOVA on rank-sorted infrapopulations (Conover and Iman, 1981) was used to test for equality of mean abundance values between sites using FieldStat software (Clopton and Janovy, 1996). Two- and 3-way ANOVAs were done with MATLAB. These ANOVAs were done separately for each host life cycle stage and each parasite species. Terminology is according to Bush et al. (1997); "abundance" equals the

number of parasites of a species in an individual host and can take the value of 0.

RESULTS

Frequency distribution of gregarines within hosts

Gregarines exhibited over-dispersed frequency distributions among host populations. Further, the negative binomial distribution was found to be a good fit for gregarine populations within both larval and adult hosts at Game and Parks Pond. Average goodness-of-fit and range of *P*-values for all collections were: 0.42 (0.00034–0.92) for *S. dunwoodyi* in larvae, 0.55 (0.092–0.994) for *S. dunwoodyi* in adults, and 0.46 (0.059–0.999) for *A. carrilynae* in adults. Only 1 collection, *S. dunwoodyi* in larvae on 23 June, failed to fit the negative binomial ($P = 0.00034$).

Relationship between larval length and gregarine infection

Body length of larvae, assumed to be proportional to host age, was insignificantly correlated with parasite abundance in most cases. Of 25 total collections, 3 *S. dunwoodyi* abundances showed significant positive correlations (28 May, $n = 82$, $r = 0.33$; 28 July, $n = 33$, $r = 0.48$, both at Game and Parks Pond; 7 June, $n = 18$, $r = 0.46$, at Dunwoody Ditch). The only other significant correlation was observed on 8 July with *H. acanthatholius* at Game and Parks Pond ($n = 45$, $r = -0.50$).

Seasonal abundance changes by geographical locality

ANOVA revealed that mean abundances differed significantly from equal among the 4 geographical localities during each study month for both larvae (Table I) and adults (Table II). In particular, mean *A. carrilynae* abundances in adult hosts often exceeded 50 gregarines at Game and Parks Pond whereas the mean rarely exceeded 10 for species at other sites (Fig. 4, Table II). Prevalence of gregarine species also varied greatly by geographic locality. For example, prevalence of *S. dunwoodyi* in larvae was high throughout the season at Game and Parks but exhibited very low prevalence at Little Beckius Pond (Fig. 1). In contrast, *H. acanthatholius* had high prevalence at Little Beckius Pond and a low prevalence at Game and Parks (Fig. 1).

TABLE II. Mean values of ranks in rank-sorted infrapopulations of gregarines in adult *Ischnura verticalis*, along with *F*-values and degrees of freedom in ANOVA of rank-sorted values and raw mean values (mean rank/raw mean). All *F*-values are high enough to reject the null hypothesis of no difference in mean infrapopulations among collection sites.

	Game and Parks Pond	Dunwoody Ditch	Dunwoody Pond	Little Beckius Pond	<i>F</i>	df
June	95.08/61.17	67.48/13.19	76.65/9.30	49.73/2.30	7.38	3, 161
July	127.79/111.94	55.36/6.10	70.84/11.86	98.53/10.98	18.16	3, 173

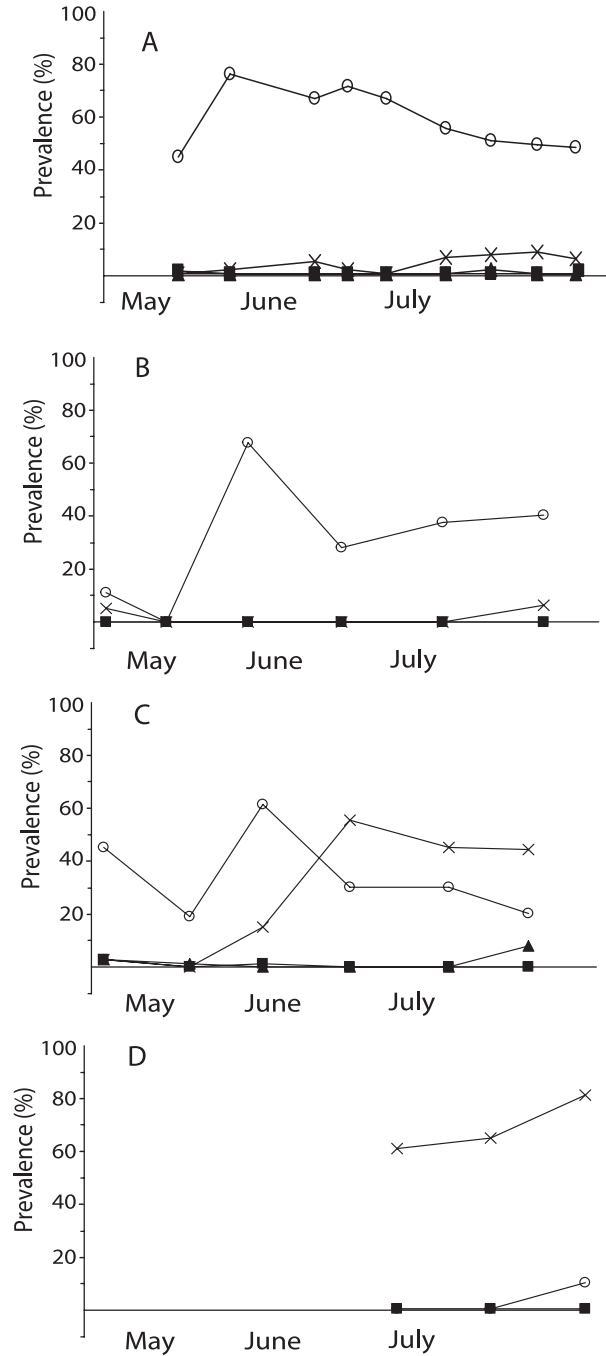


FIGURE 1. Prevalence of infection in larval hosts: *Steganorhynchus dunwoodyi* (circle marker), *Actinocephalus carrilynnae* (triangle), *Hoplorhynchus acanthatholius* (X), and *Nubenocephalus nebraskensis* (square) in (A) Game and Parks Pond, (B) Dunwoody Ditch, (C) Dunwoody Pond, (D) Little Beckius Pond.

Differences in species composition and abundance between host life cycle stages

It was evident that the composition of gregarine species differed substantially between adult and larval host stages at each locality (Figs. 1, 3). Specifically, *S. dunwoodyi* and *H. acanthatholius* infected both larvae and adults whereas *A. carrilynnae* and *N. nebraskensis* occurred in adult hosts almost exclusively. Adults

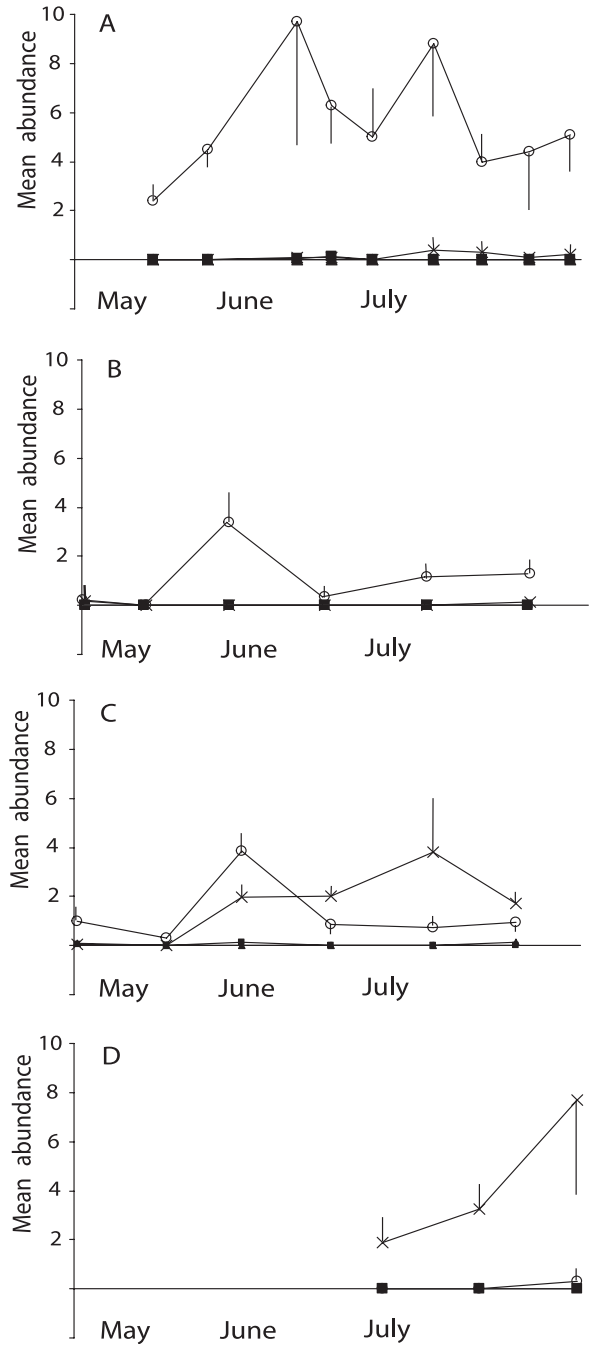


FIGURE 2. Mean gregarine abundances in larval hosts: *Steganorhynchus dunwoodyi* (circle marker), *Actinocephalus carrilynnae* (triangle), *Hoplorhynchus acanthatholius* (X), and *Nubenocephalus nebraskensis* (square) in (A) Game and Parks Pond, (B) Dunwoody Ditch, (C) Dunwoody Pond, (D) Little Beckius Pond.

also exhibited higher mean abundances of these 2 species than did larvae (Fig. 2, 4).

Prevalence differences between host sexes

Gregarine prevalence was independent of host sex in larvae at Game and Parks Pond, Dunwoody Ditch, Dunwoody Pond, and Little Beckius Pond ($\chi^2 = 0.003, 0.9148, 1.5110, \text{ and } 1.0154, \text{ df} =$

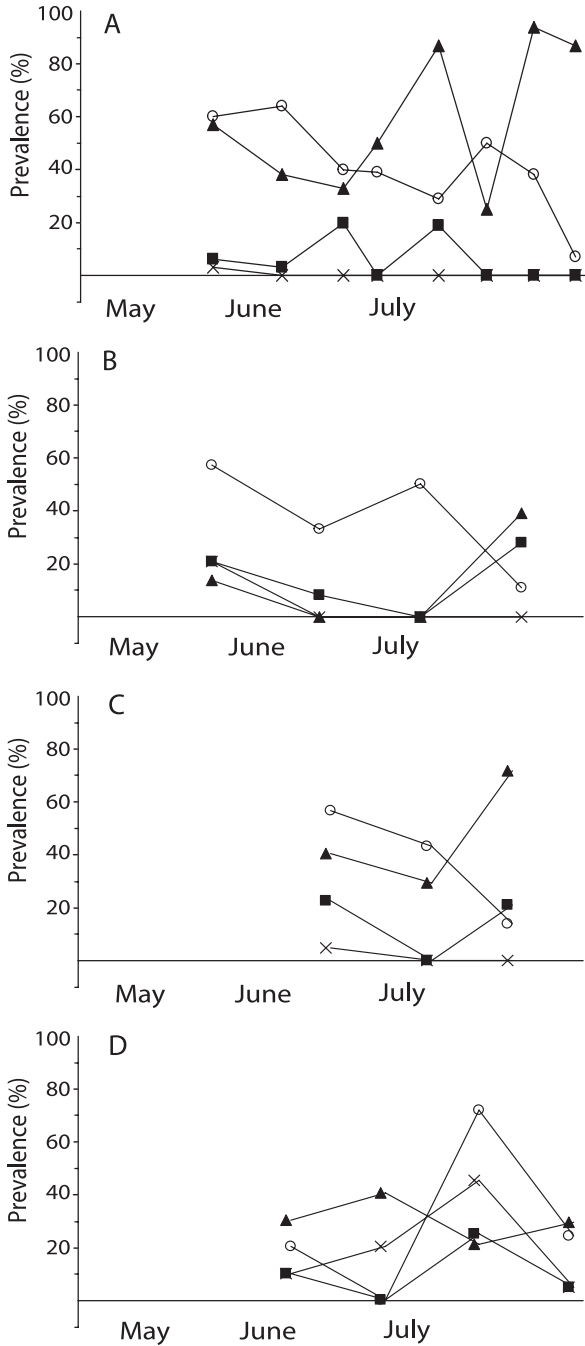


FIGURE 3. Prevalence of infection in adult hosts: *Steganorhynchus dunwoodyi* (circle marker), *Actinocephalus carrilynnae* (triangle), *Hoplorhynchus acanthatholius* (X), and *Nubenocephalus nebraskensis* (square) in (A) Game and Parks Pond, (B) Dunwoody Ditch, (C) Dunwoody Pond, (D) Little Beckius Pond.

1, respectively). However, a significant difference was observed between adult male and female hosts at Game and Parks Pond ($\chi^2 = 26.07$, $df = 1$, $P = 3 \times 10^{-7}$) and at Dunwoody Ditch ($\chi^2 = 4.2177$, $df = 1$, $P = 0.04$). Prevalence differences were not significant in adults at Dunwoody Pond and Little Beckius Pond ($\chi^2 = 0.0037$ and 0.6871 , $df = 1$, respectively).

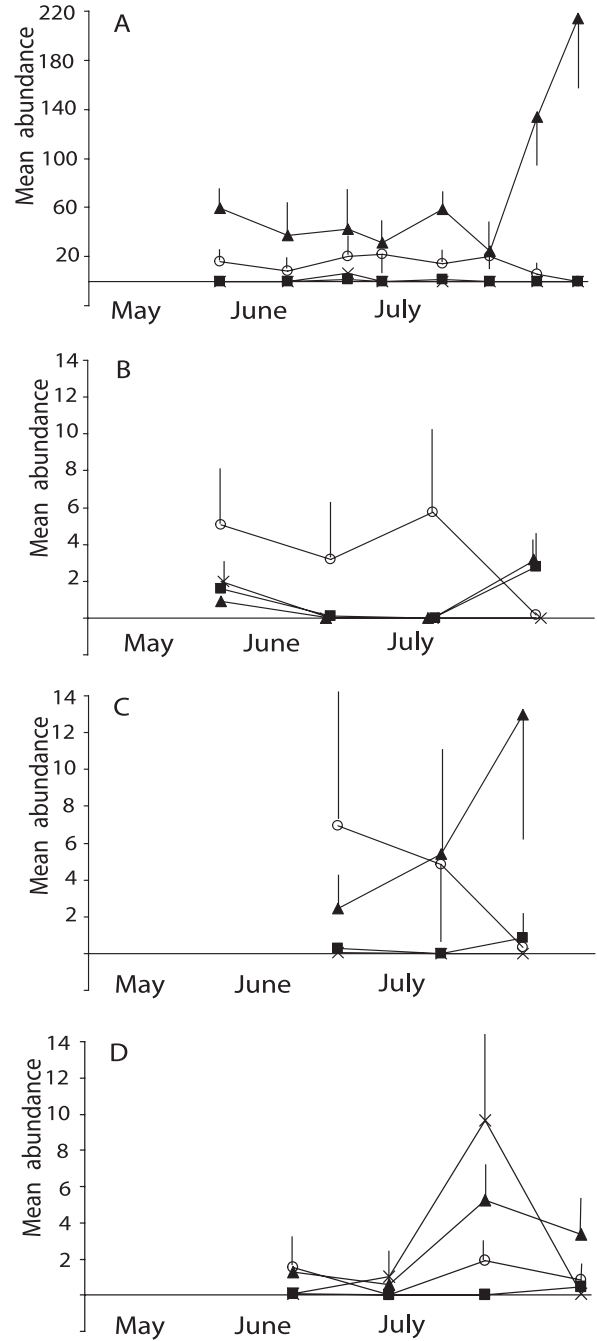


FIGURE 4. Mean gregarine abundances in adult hosts: *Steganorhynchus dunwoodyi* (circle marker), *Actinocephalus carrilynnae* (triangle), *Hoplorhynchus acanthatholius* (X), and *Nubenocephalus nebraskensis* (square) in (A) Game and Parks Pond, (B) Dunwoody Ditch, (C) Dunwoody Pond, (D) Little Beckius Pond.

Interactions between site, sex, and collection date

In larvae, ANOVA results showed no significant 2-way interactions between site, sex, and month for any species of parasite. In adults, significant 2-way, site \times sex interactions were observed only with *A. carrilynnae* ($P = 0.01$).

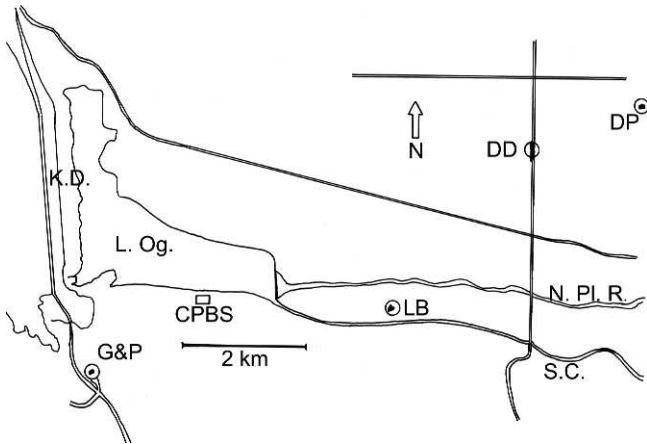


FIGURE 5. Map of the study area. CPBS, Cedar Point Biological Station; DD, Dunwoody Ditch; DP, Dunwoody Pond; G&P, Game and Parks Pond; K.D., Kingsley Dam (impounds Lake McConaughy to the west); LB, Little Beckius Pond; L. Og., Lake Ogallala; N. Pl. R., North Platte River; S.C., Southerland Irrigation Canal.

DISCUSSION

The major contribution of this study is the demonstration that host sex, life cycle stage, and geographic locality are the major factors associated with parasite prevalence and abundance over relatively small geographic distances (Fig. 5). In addition, in the case of larval hosts, gregarine abundance is independent of age (size). Moreover, as indicated by varying levels of prevalence and abundance, eugregarine adaptation must respond not only to ecological differences in the geographical localities in which hosts reside but also to host developmental stages and sexes.

Conclusions from previously published works are mixed with respect to the importance of gregarine virulence. Gregarines may present a barrier between the host's gut epithelium and food, interfering with digestion and absorption, and have been credited with reducing a host's longevity and ability to survive (Åbro, 1971). However, within the context of those factors that affect odonate population dynamics, gregarine-induced mortality is likely a minimal regulatory agent (Åbro, 1986). For example, Hecker et al. (2002) found a positive relationship between the number of gregarines and survivorship of the damselfly *Enallagma boreale*. If gregarines do harm their hosts, the effects are likely subtle and masked by other factors such as age of host, predation on hosts, and seasonal or environmental factors.

As is characteristic of most host–parasite systems, gregarines infecting *I. verticalis* exhibit an aggregated frequency distribution best described by the negative binomial model, with most hosts having 0 or few parasites and a few hosts being heavily infected (Janovy and Hardin, 1987; Gregory, 1992; Rekasi et al., 1997; Knudsen et al., 2004; MacIntosh et al., 2010). Biologically, an aggregated distribution may indicate unequal host susceptibility or temporal or spatial variation in dispersion of infective stages. Because of previous research showing little significant virulence of these parasites (Hecker et al., 2002; Rodriguez et al., 2007; Honkavaara et al., 2009), we can most reasonably infer from our data that the observed distributions of gregarines in *I. verticalis*

likely result from clumped dispersion patterns of infective oocysts in the environment.

The lack of correlation between host body length or age and abundance suggests that, at least in the case of larvae, hosts do not accumulate parasites over time at a constant rate; young host are as likely to be heavily infected as are older hosts. This phenomenon could be related to either the timing of parasite development or host–parasite encounter dynamics (or both), the latter likely involving both physical distribution of infective stages in the aquatic environment and the nature of potential transport hosts. Should this system be used as a model for macroparasite population dynamics, this lack of correlation will be a major factor influencing the formation of accurate theoretical models (Logan et al., 2012).

The prevalence and abundance of gregarine species varied drastically among geographic localities. Such complex population dynamics reflect a combination of stochastic events and deterministic biological processes (Benton et al., 2006). Thus, a gregarine population must first become established in a geographic locality as a matter of chance; then, there must be suitable conditions for exogenous stage development, survival, and transmission to a compatible type of host. External factors may be just as important in this regard as are interactions between host and parasite in terms of gregarine adaptation. Mylnarek et al. (2011) concluded that gregarine parasitism is likely to be associated with landscape characteristics. Differences in oocyst morphology or opportunity for dispersal may have played a role in the observed variation among localities. In a study of gregarines in dragonflies, Locklin and Vodopich (2010) suggested that geographical variation in parasite prevalence and intensity may be a function of abiotic factors that affect distribution, availability, and viability of oocysts. Data from the present study strongly support the importance of such variables, as populations were from a single host species at multiple geographical localities.

Differences in gregarine species composition between larval and adult hosts indicate different modes of transmission for gregarines infecting either life cycle stage. Stadium specificity occurs when different host life cycle stages function as separate, distinct parasite habitats. Such specificity has been reported for gregarines in the beetle *Tenebrio molitor* in which adults and larvae have different gregarine faunas that are not cross-infective (Clopton et al., 1992). In damselfly hosts, these differences presumably arise from ingestion of oocysts within, or attached to, different types of prey. However, it is unclear how some populations, e.g., *A. carrilynnae*, have established exclusively in adult hosts. This question could be resolved with a thorough understanding of the mechanism by which oocysts that require water to develop, and thus are constrained to the aquatic environment, are then dispersed and ingested by terrestrial hosts. Dispersal to adult odonates may be accomplished by terrestrial carriers such as midges (Åbro, 1976). Such ecological transport is common in parasites of vertebrates, e.g., in the case of trematodes, and has been demonstrated experimentally for insect carriers of nematormorphs, or horsehair worms (see Hanelt and Janovy, 2003). Additionally, Wise et al. (2000) demonstrated that freshwater snails act as mechanical vectors for transport of gregarine oocysts to leech (*Helobdella triserialis*) hosts. In the case of adult *I. verticalis*, if an oocyst carrier is involved, heavy infections imply that the carrier functions very effectively as a transport host.

The gregarine population differences between host sexes can be explained at least in part by behavioral differences. In the present study, teneral (newly-emerged) damselflies were analyzed separately from adult damselflies in order to avoid bias in sampling procedures, as described by Locklin and Vodopich (2010). Behavior is more likely than immunity to account for sex differences; Córdoba-Aguilar et al. (2006) found greater immune response in female adult damselflies of 2 species (*Hetaerina americana* and *Argia tezpi*) but insignificant differences in parasite prevalence and intensity between sexes. Consequently, the prevalence and intensity of gregarine infection may not be a good indicator of immune response. Male and female larvae exhibit similar foraging ecology; however, adult female damselflies are known to ingest more food than do males, thereby increasing the probability of oocyst ingestion. This finding is in accordance with Hecker et al. (2002), who found significantly greater prevalence and intensity of gregarine infections in female *Enallagma boreale* damselflies but insignificant sex differences in larval damselflies. Similarly, Åbro (1996) reported that adult female *Calopteryx virgo* damselflies had greater intensities of gregarine infection than did adult males.

Host ontogenetic stage, sex, and geographic locality are factors that characterize the distinct habitats in which gregarine evolution occurs in this multi-species system. Apicomplexans in general, and gregarines in particular, comprise perhaps the most diverse monophyletic group of eukaryotes, in part because of the diversity of their hosts (Levine, 1988; Clopton, 2009). Traditionally, host specificity has been assumed to reflect phylogenetic history. However, the case of gregarine populations may reflect an ecotypic assemblage rather than a vicariant one (Cielocha et al., 2011), in which a parasite species is adapted to a particular set of environmental conditions. Clopton (2009) makes a convincing case that gregarine phylogeny “track(s) niche resources along lines of transmission” instead of host phylogeny, suggesting that studies such as this one have potential for revealing evolutionary events and mechanisms that drive speciation in this hyperdiverse group of eukaryotes.

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ERRATUM

In Vieira et al., **99**: 327–331, Figures 14 and 15 are mentioned, but there are no Figures 14 and 15; and Table I below was omitted from the article.

TABLE I. Comparative measurements* of *Angiostrongylus vasorum* (Bailliet, 1866), *Angiostrongylus chabaudi* Biocca, 1957, and *Angiostrongylus felineus* n. sp.

	<i>A. vasorum</i> Bailliet (1866)		<i>A. vasorum</i> Rosen et al. (1970)		<i>A. vasorum</i> Guilhon and Cens (1971)		<i>A. chabaudi</i> Biocca (1957)		<i>A. felineus</i> n. sp.	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Total body length	14–15	18–21	13.67–14.99	18.56–21.30	14–15.5	15–20.5	14.6–16.3	19.8–24.1	16.15–18.07	20.15–23.77
Width at level of base of the oesophagus	–	–	200–240	290–310	170–235	220–306	185–225	245–298	285–355	300–360
Nerve ring	–	–	160–200	200–240	80–92	80–96	–	–	–	–
Oesophagus length	–	–	230–270	210–300	220–275	240–280	300–345	345–380	275–315	260–390
Gubernaculum	–	–	–	–	40–55	–	–	–	–	–
Spicules	360–400	–	440–490	–	400–500	–	510–555	–	350–400	–
Spicule length- Total body length ratio	38:1	–	32:1	–	33:1	–	29:1	–	46:1	–
Vulva to the posterior end	–	300–320	–	230–300	–	220–315	–	170–210	–	280–325
Tail	–	–	–	61–88	–	67–100	–	62–75	–	85–110
Eggs	–	40–50 × 70–80	–	–	–	–	–	34–44 × 58–68	–	–
Locality (Country)	–	–	France	–	France	–	Italy	–	Brazil	–

* All measures are in μm , except total body length is given in mm.