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Differential dispersal propensities between individuals in male *Leucorrhinia intacta* (Odonata: Libellulidae)

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Abstract

I compared males of *Leucorrhinia intacta* collected at two permanent and two previously dried ponds to assess whether males colonizing formerly dried sites differed in morphology or level of mite parasitism from males at permanent sites. Males colonizing sites that had local extinctions in the previous year due to pond drying were more similar to each other in body size and levels of parasitism than to males at sites which had not dried. Males at the two permanent sites differed significantly from each other in body size and these differences appear to reflect different local conditions. Comparison of males at two adjacent sites, one permanent and one which previously dried, found that the males colonizing the previously dried site were larger, in better condition, and had lower rates and numbers of mite parasites than males at the permanent site. Results from this study suggest two non-exclusive hypotheses about dispersal and colonization in this species. First, dispersal is condition dependent in this species with size and body condition positively correlated and mite parasitism negatively correlated with dispersal. Second, some permanent sites produce more males with the characteristics associated with dispersal than other potential source populations and therefore may contribute greater numbers of individuals to the dispersal pool.

Introduction

Dispersal affects population dynamics and community composition in patchy habitats (Denno et al. 1991; Tilman 1994) and is the first step in determining community composition after disturbance events that cause local extinctions. Local extinctions resulting from drying events are common in aquatic systems. When ponds refill with water, new communities are formed by diapausing species and dispersers arriving from source populations that persisted (Williams 1987). Semi-permanent ponds, sites which hold water in many years but dry in others, provide a useful context to examine whether the individuals that disperse to these sites are a biased subset of the broader population pool. Although typically shallower than permanent sites, semi-permanent sites are often similar to permanent sites in other characteristics including area and the presence of emergent vegetation (McCauley 2005). Following the re-colonization of semi-permanent sites after drying provides insight into connections between local sites in the regional pool and the traits of individuals dispersing to new sites.

Dispersal is often a condition dependent process, affected by both internal states and environmental conditions experienced by individuals (Ims & Hjermann 2001). Identifying the characteristics associated with dispersers is critical for two reasons. First, it provides a foundation for a predictive framework to assess which species or populations are most likely to be dispersal limited based on individual characteristics. Second, it provides information on the relative level of inter-connection between populations created by patchy habitat structure. If colonists are derived from some sites in the landscape but not others, we would see a mixing of the populations linked through dispersal and increasing genetic isolation of those sites where recruitment is primarily or exclusively local (Hanski 1999). This pattern may be especially important in systems such as ponds where even very spatially close sites can differ widely in their local conditions and impose strong selection for local adaptation on these populations (Relyea 2002). Understanding how local populations are linked by dispersal is critical to conserving them effectively, particularly if direct management of dispersal linkages is planned (e.g. habitat corridors).

Odonates are a useful group for exploring the relationship between individual traits, dispersal, and colonization of new habitats. In species that over-winter as larvae and are not desiccation-tolerant, populations developing at ponds that have previously dried are the offspring of colonists from other sources. For odonates in these pond systems, dispersal principally occurs in the easily observed adult stage. Additionally, adult males that disperse to refilled ponds and establish territories can be identified by their behavior as colonists rather than transients. Although adults in this stage will continue to move away from water to feed and can still disperse in this period, the costs of territorial establishment and maintenance (Marden & Waage 1990; Plaistow & Siva-Jothy 1996) indicate that males engaged in territorial behavior are attempting to colonize these sites, not transients foraging at or passing through local sites.

To examine the individual characteristics associated with dispersal I conducted an observational study comparing adult males of *Leucorrhinia intacta* (Hagen), engaged in territorial behavior at sites which held water for the twelve months previous to males at sites which had dried in the previous twelve months. This species is a frequent colonist of previously dried ponds (McCauley 2005). However, *L. intacta* over-winters in the larval stage and can only complete development in habitats which hold water throughout the twelve month period of its development (Wissinger 1988). Therefore I compared males at sites where self-recruitment was expected to dominate (permanent sites) and sites in which a local extinction had occurred in the previous year so that all adults present were colonists (temporary sites). I tested whether the individuals from *L. intacta* colonizing refilled ponds were similar to males at permanent sites or if there were specific traits associated with individuals that disperse to and colonize these sites.

Methods

This study was conducted between 16 June and 9 July 2003 at the E.S. George Reserve (ESGR), a research facility in Pinckney, Michigan, USA (42°28'N, 84°00'W). The site was administered by the Museum of Zoology at the University of Michigan. The ESGR encompassed 540 ha, of which 22% was covered by standing water that included a diverse set of water bodies from temporary pools to large permanent ponds with small-bodied fish, *Umbra limi*. Five of the 37 natural ponds surveyed on the site had *Leucorrhinia intacta* larvae in 2002 and held water throughout the 2002-2003 period (E. Werner unpubl.), making them potential source habitats for *L. intacta*. To compare resident and colonist populations, I collected males from two sites, a permanent site with a large larval population of *L. intacta* (Crane Pond) and its closest neighbor, a site which dried in late 2002 resulting in the local extinction of all over-wintering dragonfly larvae (Fishhook Pond). I also collected males at two other sites, one permanent (East Marsh) and one which dried in 2002 (West Marsh Dam). The second pair of sites was distant from the Crane-Fishhook pair and each other (Fig. 1), making extensive dispersal between these sites unlikely. Comparison of the characteristics of males collected at all four sites allowed me to test whether there was a general relationship between the characteristics measured here and the propensity to colonize new sites and how local conditions affected the development of these characteristics.

Adult males of *L. intacta* observed engaging in territorial behavior were collected. Sites were paired so that collections could be made within a two hour time frame to minimize differences in timing or weather conditions that might affect which males were flying at the ponds. The two sites which formed the central comparison of this study, Crane Pond and Fishhook Pond, were sampled on the same afternoons on three days (16 and 24 June, 9 July). East Marsh and West Marsh Dam were sampled on the same afternoons on two days (18 and 25 June). There was no third sampling date for these sites because of low numbers of individuals.

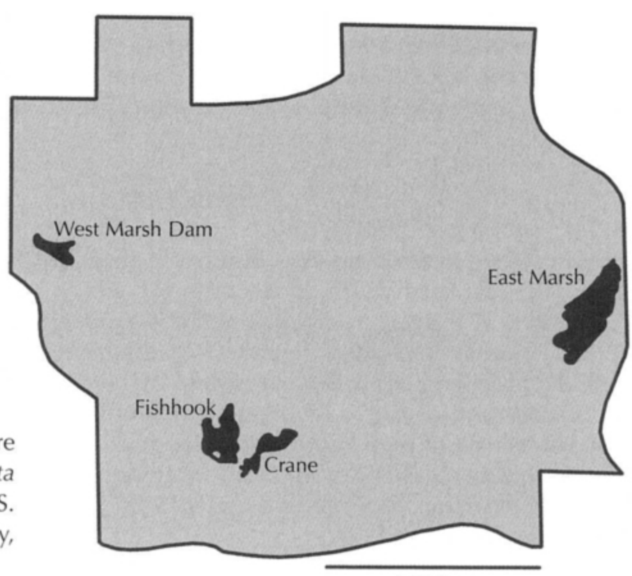

Figure 1: Map of sites where males of *Leucorrhinia intacta* were collected on the E.S. George Reserve, Pinckney, Michigan, USA.

Approximately 15 individuals were collected at each site during each collection date. Due to small population size at West Marsh Dam only six individuals could be collected on the second sampling date. All collecting was done on sunny days with low winds. Collections were made 13:00 - 15:00 or 14:00 - 16:00 h local time (US Eastern Daylight Savings Time). Solar noon was 11:37 h on 18 June and 11:41 h on 9 July.

Collected individuals were placed in a cooler with ice packs in the field and then placed in a refrigerator overnight to sedate them for measurement. Sedated males were weighed and two aspects of male size, total length and head width, were measured with vernier calipers (accuracy: ± 0.01 mm). Additionally, the number of mites (Acari: Hydrachnellae: *Arrenurus* sp.) attached to each male was counted or estimated for males with extremely high mite loads where overlap by mites prevented exact counts. The presence of mite scars was also noted but the level of scarring was very low and not used in the analyses.

To assess whether the sampling period had an effect on adult size, total length and head width were compared for each sampling period within sites using a univariate analysis of variance. These traits were compared because they are fixed at emergence and insects commonly exhibit a decline in body size at emergence over the phenology of a season (Rowe & Ludwig 1991). Therefore a relationship between sampling period and these variables would suggest that all sampling periods were not comparable. Within each site, there was no significant effect of sample date on head width (all $p > 0.1$) or total length (all $p > 0.1$). Consequently, samples from all collecting intervals were pooled for each site.

A total of 146 adult males of *L. intacta* were collected from the four sites. Forty-nine were collected from Crane Pond and 46 from Fishhook Pond, while 30 were collected from East Marsh and 21 from West Marsh Dam. Six characteristics of males were compared to determine whether males at the four sites differed in any of these characteristics. Characteristics compared were total length, head width, mass, condition (mass/total length), and levels of parasitism measured by two parameters, parasitism rate (% of males carrying mites) and mite load (the number of mites per infested individual). I used Kruskall Wallis tests (SPSS 11.5) to determine whether site had a significant effect on any of these six measurements. Post-hoc tests for each analysis determined which sites differed significantly from each other at $\alpha = 0.05$.

RESULTS

Males collected at different sites differed in total length ($\chi^2 = 12.34$, d.f. = 3, $p = 0.006$; Fig. 2a), head width ($\chi^2 = 12.32$, d.f. = 3, $p = 0.006$; Fig. 2b), mass ($\chi^2 = 17.80$, d.f. = 3, $p < 0.001$; Fig. 2c), and condition ($\chi^2 = 16.39$, d.f. = 3, $p = 0.001$; Fig. 2d). Specific inter-site differences are summarized in Figure 2. Sites also differed in the proportion of males parasitized by mites ($\chi^2 = 49.11$, d.f. = 3, $p < 0.001$; Fig. 3a) and mite load ($\chi^2 = 11.29$, d.f. = 3, $p = 0.01$; Fig. 3b). Males at Crane Pond had a higher rate of parasitism than males at the other sites while infested males at the two permanent sites carried more mites than males at the temporary sites. Few males without mites had visible scarring from previously attached mites (< 10 of all individuals collected).

Discussion

Males of *Leucorrhinia intacta* collected at the two most closely connected sites, Crane (a potential source pond) and Fishhook (all individuals were colonists), differed in all characteristics measured. Males dispersing to Fishhook were larger, heavier, in better condition, and had lower levels of parasitism than males at the permanent site, Crane. Males at West Marsh Dam, a temporary site ca 1 km distant from Crane and Fishhook, were similar to the males at Fishhook, differing significantly in only head width. In contrast, males collected at the two permanent sites differed from each other in most measurements. Males at East Marsh were longer, had larger heads, were heavier, in better condition, and had a lower mite infestation rate than males at Crane, although infested males at the two sites did not differ in mite load.

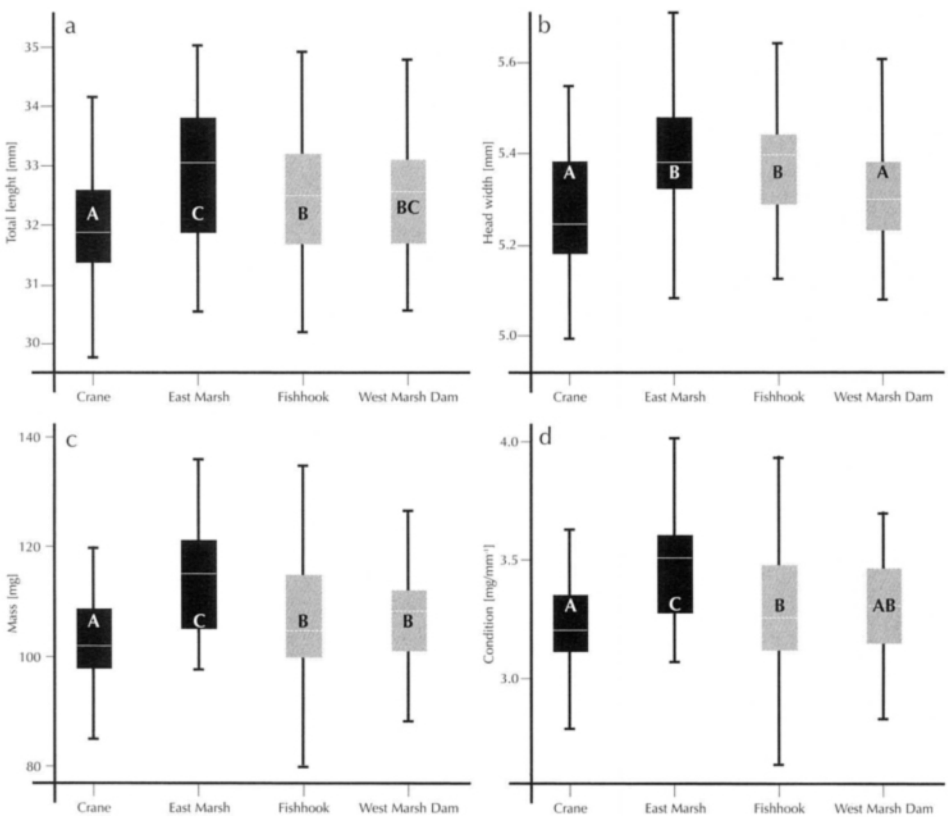

Figure 2: Characteristics of adult males of *Leucorrhinia intacta* collected at four ponds, two permanent sites (black bars) and two temporary sites (grey bars) — (a) total length; (b) head width; (c) mass; (d) condition. Boxes encompass 50% of the data from the 25th to the 75th percentile, the horizontal line indicates the sample median, and bars encompass 90% of data from the 10th to 90th percentiles. Bars labeled with the same letters do not differ significantly while bars labeled with different letters were significantly different ($p \leq 0.05$).

A comparison of males at Crane and Fishhook strongly suggests conditional dispersal in this species. At the closest point these sites were separated by ca 10 m. Crane supported the largest population of *L. intacta* larvae on the ESGR. Therefore based on both distance and population size, Crane should have been the strongest source of males at Fishhook. A comparison of males at these two sites suggests that size and condition are positively correlated with dispersal propensity while parasitism level is negatively associated with dispersal. The effect of mass and condition may be underestimated because mass measurements were not corrected for parasitism levels and the numbers of infested individuals. Also, the number of mites that infested individuals carried was greater in the males collected at Crane, suggesting that in these males mass was overestimated relative to measurements on males from Fishhook. Making the assumption that males at Fishhook were drawn primarily from the population at Crane pond, it appears that males with higher expected fitness (Sokolovska et al. 2000) were preferentially establishing territories at and attempting to colonize previously dried habitats.

Males colonizing the two temporary sites did not differ in most characteristics measured. West Marsh Dam is approximately equidistant (ca 1 km) from three potential sources of *L. intacta*, of which Crane Pond had the largest population. The similarity between colonist males at Fishhook and West Marsh Dam may reflect common origins or a shared propensity for dispersal associated with the characteristics they have in common. If males at West Marsh Dam include dispersers from Crane Pond this pattern would support the hypothesis that larger, better condition males with fewer parasites disperse more often than other males in the population. However, without knowing the actual origin of these males, this remains a hypothesis. Nonetheless, the high degree of similarity between males colonizing the two previously dried ponds which are spatially distant from each other suggests that the pool of males dispersing from their natal sites and therefore available to colonize previously dried sites are a non-random subset of the regional population.

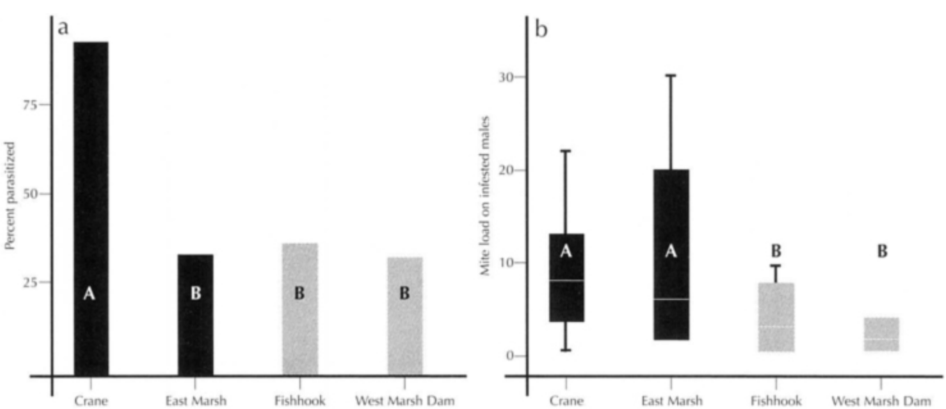

Figure 3: Mite parasitism on adult males of *Leucorrhinia intacta* collected at two permanent sites (grey bars) and two temporary sites (black bars) — (a) percentage of males parasitized at each site; (b) number of mites on infested individuals. Boxes encompass 50% of the data from the 25th to the 75th percentile, the horizontal line indicates the sample median, and bars encompass 90% of data from the 10th to 90th percentiles. Bars labeled with the same letters do not differ significantly while bars labeled with different letters were significantly different ($p \leq 0.05$).

The timing of territory establishment was not determined in this study but may have important consequences for understanding the mechanisms that affect male dispersal behavior. Males may reach previously dried sites during the period after emergence when they typically move away from their natal sites (Corbet 1999: 387-388). Although all individuals move away from their environments after emergence, males in better condition may move further and be more likely to establish territories at more isolated sites. This study does not find strong evidence to support this hypothesis as the sole mechanism producing the observed differences. It may be a plausible explanation of the differences between males at Crane Pond and those at West Marsh Dam, a more isolated site, but is unlikely to explain the differences between males at Fishhook and Crane given their proximity. It is possible that males with varying levels of condition have equivalent encounter rates with new ponds, including those which had previously dried but differ in their choices of where to establish territories.

Differences observed between males at permanent and previously dried sites may also reflect a 'bet-hedging' strategy (Philippi & Seger 1989) with males spreading their reproductive risk across temporally variable sites. Larger, better condition males may be more likely to move between ponds and attempt at least some of their breeding at previously dried sites. These sites are likely to be high risk, high reward sites with higher risks of local extinction from drying but potentially high gains because of lower competition and the elimination of some predators through earlier drying. Resolving the timing of territory establishment by males would provide insight into the forces underlying the movement of males between alternative habitat types. Additionally, examining the abundance of females as well as their traits (including body size and age) at previously dried sites would give greater insight of the actual colonization of these ponds by larvae of *L. intacta* and the forces that may select for movement to these sites or between a range of habitat types. The relationship between body size, condition, and dispersal observed in this study appears to be common in odonates. Body size, or morphological traits that positively correlate with size, and condition have been found to be positively related to dispersal rates in a number of inter- and intra-specific studies of odonates (Anholt 1990; Michiels & Dhondt 1991; Conrad et al. 2002; Angelibert & Giani 2003) although not all (Thompson 1991). Results have been less consistent for the relationship between parasite load and dispersal. Although parasite load was negatively related to flight distance in one coenagrionid, *Nehalennia speciosa* (Charpentier) (Reinhardt 1996), other studies in odonates suggest that the energetic demands of higher mite loads appear to decrease time spent at the pond and may increase dispersal as result of incidental displacement due to foraging (Forbes 1991; Conrad et al. 2002). In this study, males colonizing new sites were less likely to be infested by mites than males at their most probable source pond. Additionally, infested males at previously dried sites had fewer mites than infested males at the permanent sites. Although larger males may also have greater energetic demands that result in higher foraging rates and incidental dispersal, the combination of traits associated with colonists – larger size, better condition, and lower levels of mite parasitism – suggest that dispersal to and colonization of previously dried sites is a conditional strategy adopted by high quality males.

Males at the two permanent sites, Crane Pond and East Marsh, differed in all the characteristics measured with the exception of mite load on infested individuals. Males at East Marsh were larger, in better condition, and had lower rates of mite parasitism than males at Crane. These differences suggest that local conditions can strongly influence the development of the characteristics examined here. These two sites are both permanent, have populations of larval *L. intacta* in most years, and share a common top predator – *Umbra limi*. There is, however, one striking difference in the conditions they experienced during development: conspecific density. In the summer prior to this study, during the larval period of these males, Crane Pond had greater than 10x the larval density of *L. intacta* than East Marsh (19.1 larvae m^{-1} in Crane and 1.8 larvae m^{-1} in East Marsh; E. Werner unpubl.). Nutritional constraints can result in smaller size at emergence in odonates (Rolff et al. 2004; De Block & Stoks 2005) and larval densities in anisopterans have been negatively associated with body size in final instar larvae under some conditions (Van Buskirk 1993). Therefore, if the adult males captured at Crane are principally developing in Crane, their smaller size may be the result of high levels of competition during the larval period relative to that experienced by males at East Marsh. If developmental conditions of larvae affect the expression of characteristics associated with dispersal propensity, variation in site conditions and habitat quality may affect the inter-connectedness of local populations. Local differences in the development of characteristics associated with male colonists in *L. intacta* suggest that some habitats may be contributing a larger fraction of individuals to the disperser pool than others. Given the prevalence of conditional dispersal strategies in animals (Ims & Hjermann 2001; Weisser 2001) the influence of developmental habitat on the probability of dispersal between habitats deserves more attention. Understanding the feedbacks between local processes affecting individual development and regional processes affecting the probability of individuals arriving at local sites will greatly enhance our understanding of the contributions of local and regional factors to community composition.

Conclusions

This study presents preliminary results that suggest that dispersal in males of *Leucorrhinia intacta* is conditional and that the traits associated with dispersal are influenced by conditions experienced in the developmental habitat. The combination of similarities in the characteristics of males at previously dried sites and dissimilarities in these characteristics in males at permanent sites suggest two non-exclusive hypotheses. First, that males dispersing to and establishing territories at temporary sites have higher potential fitness than males that are resident at permanent sites. If males collected at previously dried sites are breeding at multiple sites, dispersal may represent a 'bet-hedging' strategy, spreading reproductive investment across habitats with varying levels of risk and potential fitness rewards. Second, the effect of local conditions on the development of characteristics associated with dispersal may result in some populations contributing a larger fraction of individuals to the pool of dispersers available to colonize new sites. Identifying mechanisms responsible for dispersal and the traits associated with dispersal provides critical information for conservation decision making. Understanding the mechanisms underlying dispersal may allow us to assess whether all sources contribute equally to the pool of dispersers and to more effectively prioritize what sites should be protected as nodes in habitat linkages. Additionally, determining why individuals disperse and which individuals are most likely to disperse improves our ability to assess the probable success of different arrangements of habitat connections.

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