

## Habitat fragmentation and parasitism of a forest damselfly

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### Abstract

We compared populations of a forest damselfly – *Calopteryx maculata* – in two kinds of landscapes. In fragmented landscapes, forested foraging patches were separated from streams (where oviposition and mating occur) by up to 500 m of pasture. In non-fragmented landscapes, there was continuous forest cover adjacent to streams. The prevalence and intensity of midgut infections of a gregarine parasite were significantly lower in the fragmented landscapes than in the non-fragmented landscapes. We have shown elsewhere that in the fragmented landscapes, damselflies move over greater areas to forage than in the non-fragmented landscapes. We postulate that these movements lower the rate of encounter between damselflies and oocysts, thus lowering the prevalence and intensity of infection. The differences suggest that actual habitat fragmentation events would alter the relationship between host and parasite, but that populations of both species would persist after fragmentation. Prevalence of parasitism is related to age but we found no residual effects of size on parasitism.

### Introduction

From the point-of-view of any given animal, we can define landscape structure by considering the types of resource patches in a landscape and their distribution – landscape composition and landscape configuration (Dunning *et al.* 1992) and the relative ability of an animal to move among the patches – landscape connectivity (Taylor *et al.* 1993). When a landscape is changed (through anthropogenic or natural disturbance for example) animals may have to cope with landscape structure different from that within which they evolved. Their persistence in that new landscape will reflect their ability to cope with the new landscape structure, through their ability to switch to new resources or to move between resource patches necessary for survival.

One change in landscape structure associated with anthropogenic activity is habitat fragmentation. Habitat fragmentation occurs when parts of a

continuously distributed habitat are replaced by new habitat that differs from the original in such basic environmental characteristics as microclimate or vertical structure (Lord and Norton 1989). An example is forest fragmentation – a landscape where parts of a continuous forest have been replaced by non-forest. Forest fragmentation can eliminate resources entirely (changing landscape composition) or rearrange resources into new configurations (*e.g.* Wegner and Merriam 1990). Fragmentation can also change the relative ability of an animal to move between resource patches (*i.e.* connectivity; Merriam 1984; Taylor *et al.* 1993). When animal populations persist in the face of change in landscape structure, it is because their existing behavioral mechanisms allow them to either continue to access vital resource needs such as feeding, mating and shelter within the altered landscapes or to switch to new resources. If they do persist, there will be consequences to the animals of altered behavioral regimes (for example, their interactions

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with predators and parasites). By comparing phenomena across different landscape structures we can gain insight into the effects of habitat fragmentation on animal behaviour and population dynamics.

Habitat fragmentation has been shown to alter the dynamics of insect populations and interactions with parasites, predators and parasitoids through a variety of mechanisms. For example, Kareiva (1987) showed that aphids in fragmented patches of goldenrods escaped predation from ladybird beetles long enough to produce more intense and frequent outbreaks than observed in non-fragmented patches. At a larger scale, Roland (1993) showed that in fragmented boreal forest, forest tent caterpillar (*Malacosoma disstria*) outbreaks lasted longer than in continuous forest landscapes. He suggests that a mechanism for the observed differences is that the interaction between forest-tent caterpillar and parasitoids is altered by forest fragmentation, possibly through differential effects of fragmentation on movement behaviours of hosts and parasites. Differences in infection rates of hosts by parasites will arise if the encounter rates between the host and the infective stage of the parasite change. For example, Zuk (1987a) suggests that sexual differences in gregarine infections in a species of cricket are due to lower mobility of the males. Male crickets stay near home burrows and will consequently re-infect themselves with oocysts (Zuk 1987a). Differences in intensity of parasite infection among individuals have also been shown to be associated with size and age (Forbes and Baker 1991) and mating success (Forbes 1991) in damselflies.

*Calopteryx maculata* (Odonata: Calopterygidae) live as larvae in streams, primarily through forest (Johnson 1962; Waage 1972). The adults mate and oviposit along the streams and forage in adjacent forest (Forsyth and Montgomerie 1987). We have also observed adults that mate and oviposit along streams flowing through pasture habitat. In these pasture landscapes, individuals forage at the edge of the stream and in patches of forest habitat up to 500 m from the edges of the streams. Damselflies tie the isolated resource patches (the stream and the forest) together by flying between them, and as a consequence, move over a larger area in pasture landscapes than in forest landscapes (Taylor and

Merriam 1995). The ecological neighbourhood (Addicott *et al.* 1987) of the damselfly is larger in the pasture landscape than in the forest landscape because the geographical extent of necessary resource patches is greater in the former (Taylor and Merriam 1995). In effect, the landscape structure differs, and the scale of movements differs between the two kinds of landscape. In our region *C. maculata* is heavily parasitised by a midgut gregarine and preliminary surveys suggested that the amount of parasitism differed with landscape structure.

Åbro (1974, 1976, 1987) investigated the biology of gregarines in several species of Zygoptera and showed that infection occurs when adults feed on small Diptera (primarily Chironomidae) that have oocysts attached to leg bristles (Åbro 1976). The ingested oocysts can produce several trophozoites that attach to a single cell in the midgut wall of the damselfly. They grow for up to 2 weeks then detach, at which point they are called gamonts (Åbro 1974; Zuk 1987a). In many species these gamonts associate in pairs (syzygy) and form a gametocyst that is passed out of the damselfly in the faeces. The development of zygotes, and oocyst formation, occur outside the host under suitable microclimatic conditions (Åbro 1974).

Here we ask whether the patterns of incidence and prevalence of a midgut protozoan parasite infecting a forest insect differ between a landscape of continuous forest (forest landscape) and a landscape of formerly continuous forest that has been fragmented by farming activities (pasture landscape). Demonstrating such correlations at large spatial scales suggests that interacting species are differentially responding to landscape structure in the two environments.

## Methods

**Study areas.** Surveys were conducted north of Ottawa, Canada (lat.: 45° 20'; long.: 75° 40') in a rolling landscape of pasture and forest. The area consists of granitic outcrops interdigitated with valleys. Valley bottoms are predominantly pasture actively grazed by cattle, and adjacent hillsides are covered in deciduous forest. Many small streams flow from lakes on the outcrops into the valleys; *C.*

*maculata* is abundant along many of these streams.

Damselflies were collected at three SITES<sup>1</sup>: Drury (UTM<sup>2</sup>: 18VF 288 490), Eardley (UTM: 18VF 150 465) and Masham (UTM: 18VF 182 601). Each SITE had both a forest and pasture LANDSCAPE. A LANDSCAPE comprised pasture and(or) forest habitats and a small flowing stream. The forest LANDSCAPE contained only forest habitat while the pasture landscape contained both forest and pasture habitats. Streams varied in width from 1 m to 2 m; I sampled along an approximately 250 m length of stream. At Drury and Eardley, the streams flowed first through forest, then pasture. At Masham one stream flowed through forest and joined a larger stream flowing through pasture. Both continued flowing throughout the duration of the study. Patches of Alder (*Alnus incana* (L.) Moench) bordered the streams in pasture. The nearby hillsides were forested (primarily deciduous) at distances of between 200 m and 500 m from the stream.

*Collections and dissections.* All collections were made between 1045 and 1200 EST using a standard insect net. Since individual damselflies can be parasitized several times by gregarines (Åbro 1976) parasite loads will vary with age. To reduce this variability we collected individuals at or immediately next to streams which tend to be sexually mature adults (Waage 1972; Forsyth and Montgomerie 1987). We also avoided collecting individuals that were teneral (*i.e.* recently emerged with smoky-grey wings and brown eyes) except to assess parasitism in young individuals.

We collected 5 individuals of each SEX from each pair of LANDSCAPES at a single SITE, on a single collecting day. Collections from the three sites were made on successive days within the MONTHS of June and July. The design is completely balanced: 2 SEXES × 3 SITES × 2 LANDSCAPES × 2 MONTHS (nested within SITE) for a total of 120 individuals. In additional surveys, 32 teneral and 35 non-teneral females were captured in the forest landscape over the duration of the flight season to assess changes in the prevalence of parasitism with age in *C. maculata*.

Development of ovarioles was used to age

females so we could assess how the prevalence of parasitism changed with age (Johnson 1973; Corbet 1980). We characterized ovarian development (OVARY) according to the following criteria: ovaries completely undeveloped with very little yolk visible in the terminal follicle (under a dissection scope at × 120) – category D; elongation of the terminal follicle so that yolk was visible – category C; complete development of the terminal follicle, but no hardening of the cuticular membrane – category B; and hardening of the cuticular membrane in developed ovaries – category A. OVARY was coded as an ordinal factor (young through old) for statistical analysis. Where individual ovarioles were in more than one category, we classified the individual by the condition of the majority of follicles.

In both sexes, we counted numbers of gregarine trophozoites and gamonts (hereafter called gamonts) and gametocysts. We differentiated two size categories of gamonts and gametocysts – small and large – believing that they might represent different species. Both were readily visible by the naked eye but some small trophozoites were only visible under the dissection microscope at × 120. There was a corresponding dichotomy in sizes of gametocysts. Within each size category there was variation in size, but we did not directly measure this. Individuals could usually be confidently called large or small. When in doubt, we assigned individuals to the large form. Sizes of gametocysts were less variable, and could always be confidently placed in either category. When counts exceeded 75, we estimated the count to the nearest 25 or 50 parasites.

We measured the femur length of each damselfly to test for additional effects of host size on gregarine prevalence and abundance.

*Statistical methods.* Generalized linear models (glms; McCullagh and Nelder 1989) were fitted using S-plus (Chambers and Hastie 1989). Distributions of deviance residuals versus fitted values, and fitted versus actual values were examined to determine adequacy of fit. Tests of the significance of terms against appropriate null distributions were conducted after final model selection. We did not set maximum type-I error rates *a priori*, but rather present actual probabilities of type-I errors and assess the significance based on biological meaning and degree of effect. Principal component

<sup>1</sup>Throughout the text factor names included in statistical models are in a SMALL CAPS font.

<sup>2</sup>UTM – Universal Transverse Mercator grid system.

analyses were fit using SYSTAT (Wilkinson 1990).

*Prevalence and intensity of gregarine parasitism.* Trophozoite counts among individuals within factors were non-normal with heterogeneous variances. We therefore fit two kinds of GLMs. The first assessed the effects of the independent variables SITE, SEX, MONTH (nested in SITE) and LANDSCAPE on the presence/absence of small and large gamonts (*i.e.* the prevalence of parasitism), the second assessed the effects of the same independent variables on non-zero counts of gamonts (*i.e.* the intensity of parasitism). The first model was fit with binomial errors and a log link function (a logistic regression model) and the second was fit with gamma errors and a log link. The gamma model was appropriate because the error variance increased with approximately the square of the mean (McCullagh and Nelder 1989).

We then fit binomial models to the presence/absence of large and small gametocysts. In addition to the four independent variables above, we also included in the models the deviance residuals from the corresponding models (binomial) that we had fit to the counts of gamonts. Since gametocysts are formed from gamonts, hosts with gamonts are expected to have gametocysts; these relationships are expected to exist within the gregarine size categories, but not necessarily between them. In effect, this is an independent test of the meaning of the two size classes we recognized. The residuals are fit rather than actual counts so effects of the independent variables on the response are included in the model only once.

## Results

*Gamonts.* The relationship between the prevalence of gamonts and the independent variables was similar for both large and small forms (Table 1). *C. maculata* was marginally significantly more likely to be parasitized by either form in forest than in pasture (Table 1; LANDSCAPE effect-large  $p(\chi^2) = 0.039$ , small  $p(\chi^2) = 0.071$ ) although this effect was confounded by an interaction with MONTH nested within SITE for small gamonts (Fig. 1). Prevalence of gregarines in infected individuals differed significantly by MONTH nested in SITE for both forms. Large gamonts were significantly more prevalent in

June (85% vs. 60% –  $p(\chi^2) = 0.0003$ ) and small ones were marginally more prevalent in July (77% vs. 67% –  $p(\chi^2) = 0.071$ ).

Models assessing the effects of the independent variables on the intensity of parasitism were similar for large and small gamonts. In each case, intensity of parasitism differed by SITE, LANDSCAPE and MONTH within SITE (Table 2) with the effect of LANDSCAPE confounded by an interaction with MONTH within SITE (Fig. 2). If parasitized, *C. maculata* in forest had more parasites than *C. maculata* in pasture, but the differences between forest and pasture varied between months. Large gamonts were found in greater numbers in June than in July, whereas small gamonts were found in greater numbers in July.

*Prevalence of gametocysts.* Presence of large gametocysts was dependent upon SITE and the residuals from the model predicting presence of large-form gamonts. The latter effect indicates a consistent relationship between large-form gamonts and the corresponding gametocysts (Table 3). Presence of small-form gametocysts depended upon SITE, LANDSCAPE and MONTH nested in SITE, and was marginally dependent upon residuals from both large and small-form trophozoite models (Table 3). The latter effect indicates a consistent relationship between small-form gamonts and small-form gametocysts. Both forms of gametocysts were more prevalent in forest than in pasture landscapes and Eardley had a markedly higher prevalence of both forms than either Drury or Masham.

*Relationship between size and parasitism.* To test whether the prevalence or intensity of parasitism was related to size of the damselflies we obtained the residuals from the four models relating prevalence and counts of gamonts to SEX, SITE, LANDSCAPE and MONTH within SITE, and also from four identical models using femur length as the response variable. The residual variation in femur length represents the size of the hosts after taking into account variation due to the independent variables. We then tested if prevalence or counts of gamonts were dependent upon size using a model-II regression (PCA with two factors). Two of the four models had slopes significantly different from zero (one +ve, one -ve;  $p < 0.05$ ; full tables not shown) but none explained more than 7% of the overall variance. There is no substantial variation remaining in parasite load that can be attributed to

Table 1. Analysis of deviance table. The response variables are the prevalence of large- and small-form gregarine parasitism in *Calopteryx maculata*. The model is a logistic model (i.e. a generalized linear model with binomial errors).

Effect	df	Deviance			
		Large	$p(\chi^2)$	Small	$p(\chi^2)$
Null	119	141.16		143.06	
SITE	2	1.81	0.404	14.65	0.001
SEX	1	0.38	0.536	0.74	0.388
MONTH {IN} SITE	3	18.76	<0.001	7.02	0.071
SITE $\times$ SEX	2	2.10	0.350	2.60	0.273
SEX $\times$ (MONTH {IN} SITE)	3	2.11	0.550	2.34	0.506
LANDSCAPE	1	4.26	0.039	3.26	0.071
LANDSCAPE $\times$ (MONTH {IN} SITE)	5	9.44	0.093	14.37	0.013
LANDSCAPE $\times$ SEX	1	0.29	0.588	0.17	0.678
Residual	101	102.00		97.91	

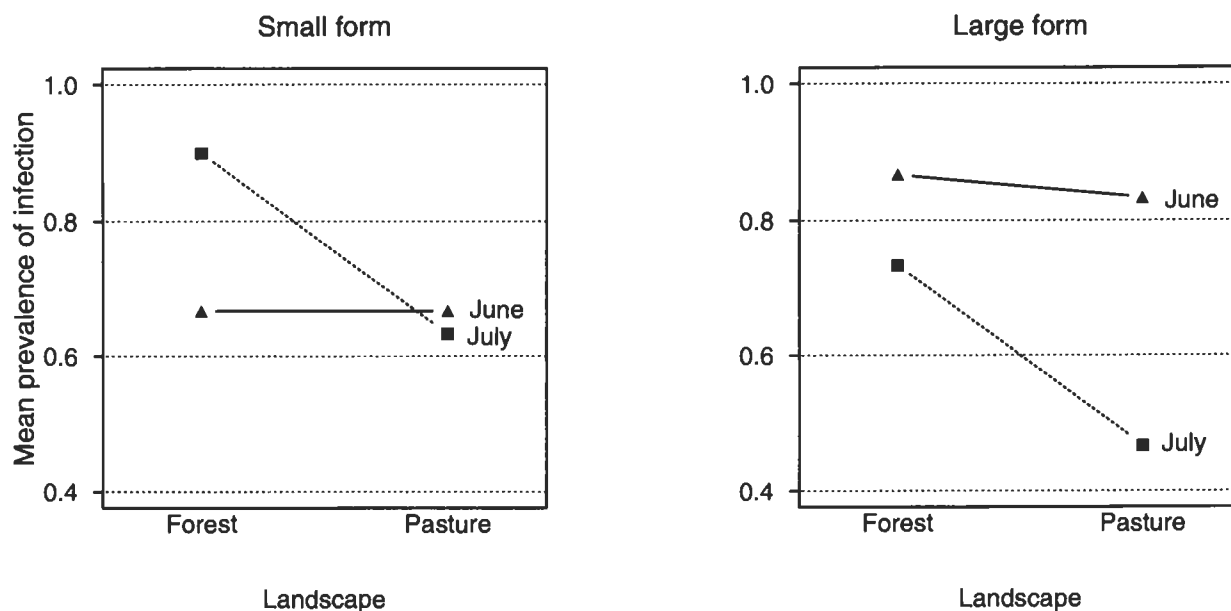


Fig. 1. The mean prevalence of small- and large-form gregarines in *Calopteryx maculata* is shown for the combinations of the factors LANDSCAPE and MONTH.

the size of the individuals after taking into account variation due to landscape type.

*Presence of gregarines in teneralis.* Finally, we compared parasitism of teneral and non-teneral females to determine when damselflies became parasitized. Female ovarian states provide good physiological age-estimates that are correlated with chronological age (Johnson 1973; Corbet 1980) so we elected to examine only females. To reduce variation due to landscape type, we collected only from the forest landscape away from the stream.

We fit a logistic regression model (a glm with binomial errors and a log-link) with parasitism as the binary response variable and MONTH and OVARIOLAR STATE as possible explanatory variables.

The model contained a significant effect of both MONTH ( $p(\chi^2) = 0.002$ ) and OVARIOLAR STATE ( $p(\chi^2) = 0.031$ ) but no interaction. 4/32 females with undeveloped ovaries (stage D) were parasitized versus 20/35 females with developed ovaries (stage A). All (4/4) very newly emerged individuals (eyes pale brown, wings and body not hardened) lacked

Table 2. Analysis of deviance table. The response variables are the counts of large- and small-form gregarine gamonts in infected *Calopteryx maculata* (i.e. the intensity of infection). The model is a generalized linear model with errors from a gamma distribution.

Effect	df	Deviance			
		Large	$p(\chi^2)$	Small	$p(\chi^2)$
Null	85,86	209.35		192.59	
SITE	2	27.95	< 0.001	79.51	< 0.001
SEX	1	2.17	0.229	2.27	0.117
MONTH {IN} SITE	3	31.93	< 0.001	14.40	0.002
SITE $\times$ SEX	2	0.83	0.755	1.13	0.538
SEX $\times$ (MONTH {IN} SITE)	3	2.45	0.647	4.21	0.208
LANDSCAPE	1	31.18	< 0.001	14.81	< 0.001
LANDSCAPE $\times$ (MONTH {IN} SITE)	5	36.47	< 0.001	15.12	0.010
LANDSCAPE $\times$ SEX	1	3.55	0.073	0.01	0.905
Residual	67,68	72.85		61.13	

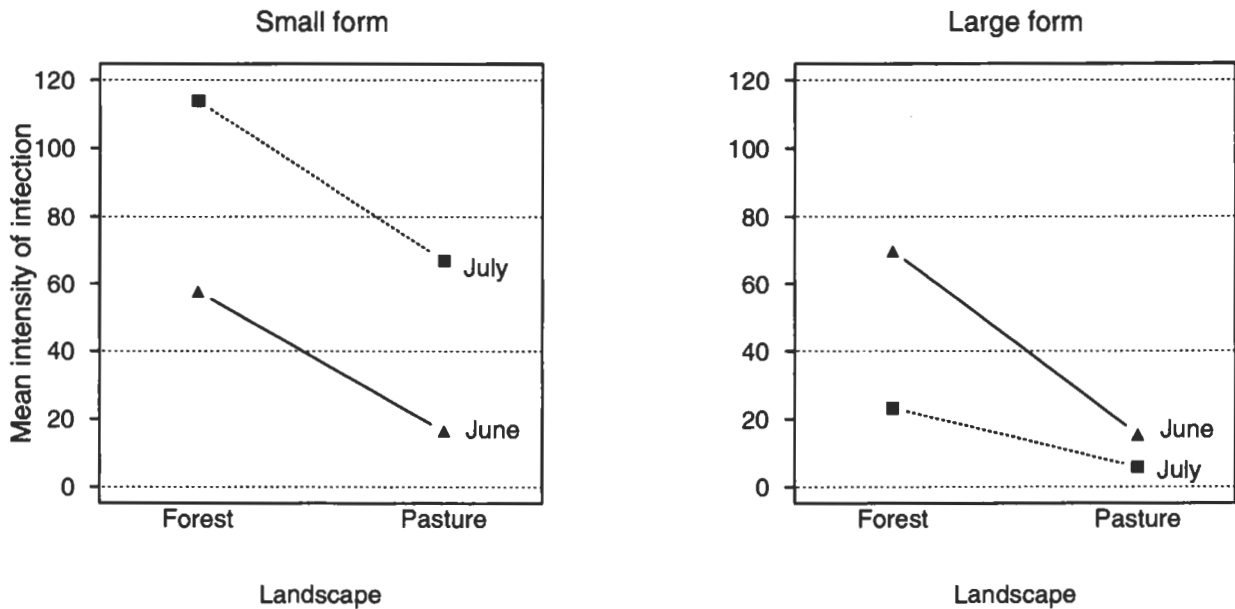


Fig. 2. The mean intensity of small- and large-form gregarine parasitism in infected *Calopteryx maculata* is shown for the combinations of the factors LANDSCAPE and MONTH.

gamonts. One newly emerged individual (eyes almost completely dark, but with fresh wings) had a single small gamont in its midgut. Some infection may be occurring in larvae, but significant infection must be occurring in the adults to produce such a strong effect of MONTH on the presence or absence of gamonts.

## Discussion

*Landscape structure and the damselfly-gregarine host-parasite relationship.* *Calopteryx maculata* is often considered a forest damselfly (Johnson 1962; Waage 1972; Forsyth and Montgomerie 1987) primarily because mating and oviposition generally occur along streams through forests. In half of the populations we studied, mating and oviposition

Table 3. Analysis of deviance table. The response variable is the prevalence of large- and small-form gametocysts in *Calopteryx maculata*. The model is a logistic model (i.e. a generalized linear model with binomial errors).

Effect	df	Deviance			
		Large	p( $\chi^2$ )	Small	p( $\chi^2$ )
Null	119	108.14		125.44	
SITE	2	25.05	< 0.001	22.77	< 0.001
SEX	1	2.65	0.103	0.24	0.621
MONTH {IN} SITE	3	3.24	0.356	18.84	< 0.001
SITE $\times$ SEX	2	3.03	0.220	0.23	0.890
SEX $\times$ (MONTH {IN} SITE)	3	1.95	0.583	0.16	0.983
LANDSCAPE	1	1.37	0.242	7.70	< 0.001
RESIDUALS – PREVALENCE SMALL PARASITE MODEL (TABLE 1)	1	0.52	0.471	3.58	0.059
RESIDUALS – PREVALENCE LARGE PARASITE MODEL (TABLE 1)	1	11.73	< 0.001	5.02	0.025
Residual	105	58.60		66.89	

occur along streams through pasture landscapes, where resource patch configuration is different than it is in forest landscapes. In the pasture landscapes, some of the foraging component of their behaviour occurs away from the streams (Taylor and Merriam 1995). Damselflies link isolated resource patches in the pasture landscapes by flying between them. Correlated with these large-scale differences in structure between the landscapes (and the associated differences in feeding behaviours) is the result that damselflies in pasture landscapes are less likely to be parasitized, and have fewer parasites, than those in forest landscapes.

The result means that encounter rate between host and parasite must differ in the two landscapes; we argue here that these differences in encounter rate can be related to differences in landscape structure. Landscape structure could directly influence population dynamics of the gregarine if some habitats were more or less suitable for its development. It could indirectly influence encounter rates through influences on movement of the host or vectors. Other work on host-parasite/parasitoid systems has directly or indirectly implicated changes in movement behaviours of host or parasite when rates of parasitism or predation differs with landscape structure. For example, Kareiva (1987) showed that in fragmented patches of goldenrod, beetle predators could not find aphids fast enough, and so aphid populations escaped into outbreaks. Kruess and Tschardtke (1994) showed that isolation of habitat patches reduced the size of the para-

site community as well as rates of parasitism. Roland and Taylor (1995) showed that a dipteran parasite of forest tent caterpillar (*Malacosoma disstria*) did not parasitize cocoons isolated by > 200 m and that this was reflected in reduced rates of parasitism in fragmented landscapes at larger spatial scales. In each of these cases the interaction between movement behaviours of host and parasite and landscape structure has implications for the population dynamics of the species at larger spatial scales (e.g. Roland 1993, Ives *et al.* 1993). We have no data to assess whether landscape structure is influencing the damselfly-gregarine system directly through effects on gregarine development, or indirectly through influences on the movement of the host or vector. However, we have shown elsewhere that movement behaviours of the host damselfly do differ between the two landscapes (Taylor and Merriam 1995) and suggest that this would be a productive avenue of further research.

*Gregarine biology.* Our observations of gregarine infection in *C. maculata* conform to those of Åbro (1974, 1976). We observed free and attached gamonts in the midgut (and occasionally in the foregut in massive infections) and gametocysts in the posterior midgut and hindgut. No gamonts were observed in very recently emerged adults, and there was a strong positive association between age of females and the prevalence of parasitism. Adults must be acquiring the parasites while feeding; possibly by ingesting oocysts on the legs of small Diptera as outlined by Åbro (1976).

Gregarine infections were common in both landscapes, and all sites and months (60–85% prevalence). They were higher than those observed in populations of field crickets (Zuk 1987a). The two forms had different temporal abundances – large forms were more frequent in June, and small forms were more frequent in July. This, coupled with the unambiguous relationship between large gamonts and large gametocysts suggests that the two forms may be different species.

The effects of varying levels of gregarine parasitism on host behaviour and physiology are poorly known. Åbro (1987) investigated some of these effects and demonstrated increased longevity in lightly versus heavily parasitized individuals. Zuk (1987b) showed no significant effects of gregarines on longevity or fecundity when hosts were fed *ad libitum*, but did show small differences in longevity in adults with suboptimal diets. Siegel *et al.* (1992) showed a correlation between gregarine infection and increased mortality in the mosquito *Aedes triseriatus*. We have no evidence to suggest that these gregarines are either harmful or beneficial to *C. maculata*. However, intensity of parasitism in some individuals was so great that the entire midgut was occluded. These individuals might be subject to increased mortality from other sources as Zuk (1987b) suggests. For instance, at high levels of infection there could be a reduction in the ability of individuals to derive nourishment from food.

Recent studies have suggested links between parasitism, size and mating success or mating strategy (*e.g.* Forbes 1991). Siegel *et al.* (1992) showed a relationship between gregarine infection of larval *A. triseriatus* and wing-length but these effects were not consistent across locations, sexes or years. The prevalence and intensity of parasitism in our populations differed consistently between forest and pasture landscapes but after taking seasonal and landscape effects into account, we found only weak and ambiguous correlations between parasite loads and body size. As Siegel *et al.* (1992) point out, caution is necessary: any experiments designed to examine effects of parasitism on mating strategy, reproductive success or correlations between size and parasite load must take into account the possible influences of landscape structure and habitat.

Forsyth and Montgomerie (1987) found a dichotomy in the behaviour of male *C. maculata*

after ca. 14 days of post-teneral life. About 1/2 of the marked males they followed switched from a territorial mating strategy to a strategy where males sneak copulations of females being guarded by territorial males. If the population they studied is also infected with gregarines an interesting alternate hypothesis for the switch in male behaviours they observed can be proposed. An increase in gregarine parasitism may lower the ability of *C. maculata* to extract energy from food. Small energy costs would in turn decrease a male's ability to defend territories (Marden and Waage 1990). We predict that males exhibiting territorial behaviour will have lower counts of gregarine parasites than males of the same age exhibiting sneaking behaviour.

### Summary

We have shown that the damselfly-gregarine host-parasite relationship (as measured by the prevalence and intensity of infection) differs between two kinds of landscapes – continuous forest landscapes and landscapes fragmented into forest and pasture habitats. The host-parasite relationship differs in a consistent way with the fragmentation or the landscape – as a result of some combination of change in the behaviour of the parasite, the host, or the vector of the parasite. The key result is that the effects of forest fragmentation are not necessarily obvious. Heterogeneity at a large scale (forest fragmentation) can alter the population dynamics of other animals (such as the gregarines) that are responding to the landscape at finer scales (for a discussion see Kotliar and Wiens 1990). The nature of the interaction between the host and parasite is altered by habitat fragmentation which could have effects on damselfly population dynamics at larger spatial scales (*e.g.* Roland 1993; Ives *et al.* 1993).

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## References

- Åbro, A. 1974. The gregarine infection in different species of Odonata from the same habitat. *Zool. Scripta* 3: 111–120.
- Åbro, A. 1976. The mode of gregarine infection in Zygoptera (Odonata). *Zool. Scripta* 5: 265–275.
- Åbro, A. 1987. Gregarine infection of Zygoptera in diverse habitats. *Odonatologica* 16: 119–128.
- Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. and Soluk, D.A. 1987. Ecological neighbourhoods: scaling environmental patterns. *Oikos* 49: 340–346.
- Anholt, B.R. 1992. Sex and habitat differences in feeding by an adult damselfly. *Oikos* 65: 428–432.
- Chambers, J.M. and Hastie, T. 1989. *Statistical models in S*. Wadsworth & Brooks, Pacific Grove, CA, USA.
- Corbet, P.S. 1980. Biology of Odonata. *Ann. Rev. Ent.* 25: 189–217.
- Dunning, J.B., Danielson, B.J. and Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65: 169–175.
- Forbes, M.A. 1991. Ectoparasites and mating success of male *Enallagma ebrium* damselflies (Odonata: Coenagrionidae). *Oikos* 60: 336–342.
- Forbes, M.A. and Baker, R.L. 1991. Condition and fecundity of the damselfly, *Enallagma ebrium* (Hagen): the importance of ectoparasites. *Oecologia* 86: 335–341.
- Forsyth, A. and Montgomerie, R.D. 1987. Alternative reproductive tactics in the territorial damselfly *Calopteryx maculata*: sneaking by older males. *Behav. Ecol. and Sociobiol.* 21: 73–81.
- Ives, A.R., Kareiva, P. and Perry, R. 1993. Response of a predator to variation in prey density at three hierarchical scales: Lady beetles feeding on aphids. *Ecology* 74: 1929–1938.
- Johnson, C. 1962. Breeding behaviour and oviposition in *Calopteryx maculatum* (Beauvois) (Odonata: Calopterygidae). *Am. Mid. Nat.* 68: 242–247.
- Johnson, C. 1973. Ovarian development and age recognition in the damselfly, *Argia moesta* (Hagen 1961) (Zygoptera: Coenagrionidae). *Odonatologica* 2: 69–81.
- Kareiva, P. 1987. Habitat fragmentation and the stability of predatory-prey interactions. *Nature* 326: 388–390.
- Kotliar, N.B. and Wiens, J. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59: 253–260.
- Kruess, A. and Tscharntke, T. 1994. Habitat fragmentation, species loss, and biological control. *Science* 264: 1581–1584.
- Lord, J.M. and Norton, D.A. 1990. Scale and the spatial concept of fragmentation. *Cons. Bio.* 4: 197–202.
- Marden, J.H. and Waage, J.K. 1990. Escalated damselfly territorial contests are energetic wars of attrition. *Anim. Behav.* 39: 954–959.
- McCullagh, P. and Nelder, J.A. 1989. *Generalized Linear Models*. Chapman & Hall, London.
- Merriam, H.G. 1984. Connectivity: a fundamental ecological characteristic of landscape pattern. *In Proceedings of the First International Seminar on Methodology in Landscape Ecological Research and Planning – Theme 1*. pp. 5–15. Edited by J. Brandt and P. Agger. International Association for Landscape Ecology, Roskilde University, Roskilde.
- Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* 93: 25–30.
- Roland, J. and Taylor, P.D. 1995. Herbivore-natural enemy interactions in fragmented and continuous forests. *In Population Dynamics: New Approaches and Synthesis*. pp. 195–208. Edited by N. Cappuccino and P.W. Price. Academic Press.
- Siegel, J.P., Novak, R.J. and Maddox, J.V. 1992. Effects of *Ascogregarina barretti* (Eugregarinida: Lecudinidae) infection on *Aedes triseriatus* (Diptera: Culicidae) in Illinois. *J. Med. Ent.* 29: 968–973.
- Taylor, P.D., Fahrig, L., Henein, K. and Merriam, G. 1993. Connectivity is a fundamental element of landscape structure. *Oikos* 68: 571–573.
- Taylor, P.D. and Merriam, G. 1995. Wing morphology of a forest damselfly is related to landscape structure. *Oikos* 73: 43–48.
- Waage, J.K. 1972. Longevity and mobility of adult *Calopteryx maculata* (Beauvois, 1805) (Zygoptera: Calopterygidae). *Odonatologica* 1: 155–162.
- Wegner, J.F. and Merriam, G. 1990. Use of spatial elements in a farmlands mosaic by a woodland rodent. *Biol. Conserv.* 54: 263–276.
- Wilkinson, L. 1990. *SYSTAT: the system for statistics*. Evanston, IL, USA.
- Zuk, M. 1987a. Seasonal and individual variation in gregarine parasite levels in the field crickets *Gryllus veletis* and *G. pennsylvanicus*. *Ecol. Ent.* 12: 341–348.
- Zuk, M. 1987b. The effects of gregarine parasites on longevity, weight loss, fecundity and developmental time in the field crickets *Gryllus veletis* and *G. pennsylvanicus*. *Ecol. Ent.* 12: 349–354.