



Biology of Gregarine Parasites

C. Vijaya*

Research Scholar, Singhanian University, Rajasthan

V.B. Chinked**

M.S.I Degree College, Gulbarga-585102, Karnataka

Gregarine parasites are among the most ubiquitous and diverse groups of protozoan parasites (phylum Apicomplexa) (Smith and Clopton 2003). They infect a variety of invertebrates, particularly annelids and insects (Manwell 1961). Among insect hosts, orthopterans and odonates are the most heavily infected (Corbet 1999), and additional insect hosts include roaches (Blattodea), mosquitoes (Diptera), and beetles (Coleoptera). However, only a small percentage of invertebrates have been surveyed for these apicomplexan parasites (Roberts and Janovy 2005). Clopton (2006) estimates over 1 million gregarine species worldwide making them among the most diverse group of organisms infecting a broad range of hosts.

Gregarine systematics and taxonomy is complex, young, and rapidly developing. Clopton (2002) recognizes 1,656 species within 244 genera of gregarines in the order Eugregarinorida infecting more than 3,124 host species. However, many species of the North American gregarine fauna are undescribed (Clopton *et al.*, 1993).

Phylum Apicomplexa contains parasitic organisms without cilia/flagella (except for some gamete stages). Three classes are recognized by Roberts and Janovy (2005): 1) Perkinsasida, 2) Acnoidasida, and 3) Conoidasida. The gregarines of interest for this research are in the class Conoidasida and the order Eugregarinorida. Most parasitize their host's hemocoel, reproductive system, or intestinal tract (as in Odonata) (Manwell 1961).

Morphology

Morphology of gregarines varies greatly. They range in size from a few mm to 16 mm (Manwell 1961) and can be so large that 19th century zoologists placed them with the worms. A gregarine body is composed of ectoplasm and endoplasm. Endoplasm contains the organelles and is crowded with reserve food in the form of paraglycogen and fat globules (Manwell 1961). Two major body plans for gregarines are 1) acephaline and 2) cephaline. Acephaline gregarines have a simple body plan without well defined body regions, but may have an anterior anchoring device called a mucron. Cephaline gregarines are more complex and the most frequently

encountered. They have three body regions: 1) rostrum (anterior), 2) protomerite, and 3) deutomerite (posterior). An epimerite, the anchoring device for cephalines, is on the rostrum. This region may be reduced or lost when the gregarine detaches to become a gamont (free-roaming within the intestinal lumen) (Manwell 1961). The protomerite and deutomerite typically are divided by a septum. Some deutomerites appear to be segmented (“polycystid”) while others appear unsegmented (“monocystid”).

Life Cycle

The life cycle of eugregarinorid gregarines studied involves a single invertebrate host (Omoto et al 2004). Eugregarinorids have no merogony (asexual form of reproduction in which multiple mitoses and subsequent cytokineses produce many daughter cells) but undergo multiple fissions within a cyst (gametocyst) during gametogenesis (Roberts and Janovy 2005). During gametogenesis, two gamonts of opposite mating types coalesce to form a stable mating pair called a syzygys (Zuk 1987). Some gregarine species fuse in an anterior to posterior fashion whereas others fuse side to side (Roberts and Janovy 2005). In anterior-posterior fusion, the anterior cell is the “primate” and the posterior cell is the “satellite.” Once fused, a cyst forms around the two gamonts to form the gametocyst. This cyst passes out with the host’s feces (Zuk 1987) and the nucleus in each gamont divides repeatedly by binary fission to produce many nuclei that line the periphery of the membrane of each gamont. The nuclei give rise to many gametes inside each gamont. Once the gametes are mature, the membrane separating the two gamonts disintegrates and fertilization produces zygotes. The zygotes secrete a protective membrane around themselves to become oocysts (spores) (Roberts and Janovy 2005). Hundred of oocysts form within each gametocyst and each nucleus within each oocyst undergoes multiple divisions to produce eight sickle-shaped sporozoites within each oocyst. The oocysts are liberated from the mature gametocyst either through spore-releasing ducts or the rupturing of the gametocyst.

When the oocyst is ingested by an odonate host, it ruptures and releases the sporozoites. The sporozoites then attach to the host gut epithelium and become trophozoites that feed on gut contents grow, detach from the epithelium, and join others of the opposite mating type to form a gametocyst for reproduction (Cordoba-Aguilar et al 2003).

Role of the Environment :

Despite the many reports of gregarine infections in invertebrate populations, little is known about the environmental conditions/parameters that influence gregarine parasitism. Marden and Cobb (2004) reported prevalence variation for *Libellula pulchella* (Anisoptera: Libellulidae) in two habitats where gregarine prevalence and intensity were higher in one habitat compared to the other. Unfortunately, research on variation in gregarine prevalence and intensity among different habitats is lacking. Overall, while interactions between host species and their

parasites have been well studied, the role of the environment in mediating the outcome of the interaction is still generally unknown (Belden 2006).

Fitness Costs :

Some authors (Canning 1956) have regarded gregarines as harmless commensals. However, recent studies indicate detrimental effects of some gregarine infections. Åbro (1971, 1974) first reported that gregarines negatively impact their odonate hosts. Gregarine trophozoites may form a barrier between the epithelium and the food in the lumen and interfere with digestion and absorption (Åbro 1971). Harmful alterations to the epithelium may be due to gregarine metabolites/toxins, or the intense parasite infections may cause lesions in the midgut wall during parasite movement. Åbro (1971) observed masses of discarded epithelial cells in damselfly guts with heavy infection. Specimens of *Coenagrion hastulatum*, *Enallagma* spp., and *Pyrrhosoma* spp. (Zygoptera: Coenagrionidae) had eroded areas in the midgut with only the muscle layers remaining. Such specimens were reportedly easy to recognize in the field because they were poor fliers and their abdominal pigmentation was reduced. Reports of massive infections are not exclusive to damselfly adults, however. Damselfly naiads of *Ishnura heterosticta* (Zygoptera: Coenagrionidae) may also harbor many gregarine trophozoites.

Åbro (1974) reported that the frequency of infected adult damselflies increased as the flight season progressed in western Norway. Such infections and tissue damage may strongly impact survivorship and fitness and speculated that infection may impair survival during rapid environmental changes or long-lasting weather conditions (dry/wet/cool/hot) that limit available food and also found gregarine intensity to be less in dragonflies compared to the damselflies, but the parasites' impact on behavior, fitness, and survivorship may be as severe. for example, suggests that a single trophozoite likely impacts a host the same as does 100 trophozoites if a toxin is being released by the parasite.

As mentioned by Åbro (1971, 1974), food availability may be critical to the overall impact of infection. Since gregarine parasites appear to inhibit a host's absorption of nutrients (or may feed on the food in the lumen), low food availability probably amplifies the parasites' detrimental effects. Tsubaki and Hooper (2004) found a negative correlation between host survivorship and gregarine abundance under a low feeding regime but no relationship under high feeding regimes. Parasite burden, therefore, may have little effect on host survival and fitness when food availability is abundant. If this is true, gregarine parasitism may hasten declines in host populations during the fall when prey items become more scarce.

Odonate competition for resources, territories, and mates involves ornaments, coloration patterns/intensity, chemical signals, etc. (Marden and Cobb 2004). Such external traits signal the overall condition of the individual to potential mates or competitors (Hooper *et al* 2006). In addition, performance-based activities (vocalizations, mating dances, fighting, etc.) also clearly communicate an individual's condition. All of these traits are more or less energy-dependent. Competition for mates and resources demands high energy expenditure (Marden and Cobb

2004). Such traits depend on the physiological health of the organism and can reveal a compromised physiological condition.

In many species where males compete for resources (e.g., quality oviposition sites for odonates) to attract mates, dominant males monopolize quality resources and consequently have a mating advantage (Qvarnström and Forsgren 1998). Among the several signals odonates are thought to use to communicate their condition/health to a potential competitor or mate are wing/body coloration and flight ability. Gregarine-infected hosts may exhibit reduced wing/body pigmentation (Åbro 1971) poor flight ability/sustainability (Schilder and Marden 2006), and failures during territorial battles.

Gregarines likely suppress host pigment deposition since pigment development is constrained by nutrient absorption (Cordoba-Aguilar *et al* 2003). Åbro (1971) found that the damselfly, *Pyrrosoma nymphula*, with dull colors and reduced flight abilities at the end of the season harbored hundreds of gregarines in their midgut. Some specimens with severely faded pigmentation had intestinal walls perforated and partly dissolved. Cordoba-Aguilar *et al* (2003) reported sexual behavior modifications common to individuals with reduced pigmentation. In the damselfly, *Calopteryx haemorrhoidalis*, large gregarine infection rates occur in both males and females. Individuals with large gregarine intensities, regardless of gender, exhibit modified mate selection and pre/post copulatory behaviors. Several studies of calopterygid species (Cordoba-Aguilar *et al* 2003) have shown that males with more intense wing pigmentation survive and defend territories for longer periods of time, and are preferred by females. Highly infected females tend to accept a mate more rapidly than do uninfected females. Infected males also mate with infected females more frequently than with uninfected females. In both cases, decreased damselfly wing pigmentation apparently indicates a high parasite burden. Cordoba-Aguilar *et al* (2003) suggest that an uninfected male's intense pigmentation may signal his condition to other males and indicate his ability to resist parasites to females. Additionally, female wing pigmentation may signal her reproductive value and can affect the amount of time she is guarded from intruder males during post-copulatory ovipositing (Cordoba-Aguilar *et al* 2003). The bolder the pigmentation, for example, the more protection she gets.

Several studies Marden and Cobb (2004), Schilder and Marden (2006) have also shown effects of gregarine infection on muscle power output and fat content/distribution in odonates. Marden and Cobb (2004) reported decreased fat content in infected individuals whereas Schilder and Marden (2006) reported that infected specimens of *Libellula pulchella* (Anisoptera: Libellulidae) have an impaired lipid catabolism in their muscles. This impaired catabolism results in an accumulation of lipids in flight muscles and a sole-dependency on carbohydrate-catabolism for flight. In uninfected odonates, a mixture of carbohydrates and lipid substrates provide energy for flight (Schilder and Marden 2006). Such parasite-induced metabolic shifts may impact sustained flight necessary for territorial defense and mating success because lipid catabolism is needed for flight after the first few minutes (Marden and Cobb 2006).

When dragonfly females mate with territory-holders, they consistently mate with physiologically and immunologically superior males (Marden and Cobb 2004) and likely gain genetic benefits (more viable offspring). Marden and Cobb (2004) found that males successfully defending territories and the females ovipositing in them had a reduced gregarine burden (mean intensity = 11 trophozoites host⁻¹). In addition, so called “submissive satellite males” were never observed to defend a territory and exhibited elevated gregarine burdens (mean intensity = 30 trophozoites host⁻¹). Gregarine parasites have been shown to alter the physiology and behavior of their odonate hosts and, consequently may play a significant role in determining the overall fitness of the hosts.

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