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Chapter 8

Territoriality in Aquatic Insects



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Abstract Research on territoriality has barely progressed beyond the descriptive stage in most aquatic insects, but some territorial species have been studied intensively and served as model organisms for testing certain aspects of evolutionary theory. After providing a brief introduction to territoriality in general, I review the taxonomic distribution and types of territoriality reported in aquatic insects, before delving into more theoretical topics. Larval feeding territories have been described in aquatic insects of several orders (Diptera, Ephemeroptera, Odonata, Plecoptera, Trichoptera), while adult feeding and mating territories have only been reported in Odonata (damselflies and dragonflies) and Hemiptera (water striders and ripple bugs). With mostly Odonata examples, I review the following subjects more critically: (1) determinants of territorial status and the outcome of territorial contests, (2) territorial signals and cues, (3) persistence of interspecific territoriality, and (4) agonistic character displacement. Important advances have been made in each of these areas using aquatic insects, but persistent methodological issues have also impeded progress. I offer some general advice for studying territoriality and conclude by identifying areas where more research is needed.

Keywords Territorial behavior · Contests · Character displacement · Agonistic interactions

For a large number of problems there will be some animal of choice or a few such animals on which it can be most conveniently studied—(Krogh 1929)

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8.1 Introduction

Territoriality is difficult to define in a completely satisfactory way. Simple definitions, such as “defense of space,” mean different things to different people, but attempts to define it more precisely often leave out phenomena that should be included (Kaufmann 1983). Of course, biology is messy and there are bound to be cases that are difficult to categorize, but there are also important distinctions to make between territoriality and related phenomena. I will attempt to clarify what does and does not qualify as territoriality while avoiding the pitfall of being overly narrow.

Territoriality is a form of social dominance in which the resident individual (or group) has priority of access to resources (e.g., food, mates, refuges) at a particular location. Dominant-subordinate interactions that are independent of location are not considered territoriality. Not all aggressive interactions are territorial, and not all territorial interactions involve aggression. Most territorial animals have some means of advertising their presence and warding off intruders without direct confrontation (e.g., song, scent marks, visual signals). In some species, territorial aggression is seldom observed, but site fidelity alone should not be equated to territoriality.

Territories range widely in size, function, and exclusivity. Some territorial animals defend multipurpose territories that supply all their daily needs and only occasionally venture outside their territory boundaries. In other species, territories are used only for specific purposes (e.g., mating, feeding, roosting) and cover a small portion of the home range. The distinction between territory and home range is that the territory is the portion of the home range, if any, which is defended against intrusion or resource utilization by some class of individuals. The excluded class typically includes conspecifics of the same age category and sex as the resident (e.g., sexually mature males), but can be broader or narrower. In some species, residents tolerate same-sex conspecifics if they behave in particular ways (e.g., Davies and Houston 1981; Alcock 1982).

Territoriality also varies temporally, such that residents are only active in defense at certain times of day or under particular weather conditions, and it is common for territory defense to be abandoned at very low or high resource levels or population densities (e.g., Gill and Wolf 1975; Wilson et al. 1978; Davies and Houston 1981; Wilcox and Ruckdeschel 1982). The difficulty of observing territorial interactions (in some taxa), combined with spatial, temporal, and situational variation in defense, helps account for conflicting reports about whether particular species are territorial. Territoriality can also vary geographically, however, such that some populations of a species are territorial while others are not (Brown 1964).

Much has been written about the functions, and fitness costs and benefits, of territoriality (Hinde 1956; Brown 1964; Baker 1983; Kaufmann 1983; Stamps 1994). Priority of access to resources is usually at the top of the list of potential benefits, followed by spacing and site fidelity benefits. Spacing benefits can be couched in group selection or individual selection terms. The idea that territoriality reduces population density and thereby decreases the likelihood that a species will exhaust

its resources is a group selection hypothesis. But there are several possible benefits of spacing at the individual level, such as avoidance of predators or parasites (Stamps 1994). Site fidelity benefits include being familiar with the location of resources and habitat features, such as efficient travel routes or refuges to escape from predators or inclement weather. While animals can be site faithful without being territorial, non-territorial animals might need to range over larger areas than territorial animals, because spacing reduces exploitative resource competition. Thus, the benefits of spacing, site fidelity, and priority of access to resources often come together as a package in territorial species.

Costs and benefits of territoriality are traditionally considered from the perspective of an undefeatable territory holder (Brown 1964; Gill and Wolf 1975; Adams 2001; Tanaka et al. 2011). This simplifies the problem to whether the benefit of having priority of access to resources in a space offsets the energetic and other costs of defending it. But in reality, territory holders are not undefeatable, and challenging intruders puts residents at risk of losing access to the space. A thorough consideration of the evolution of territoriality requires comparing the expected fitness payoff of territory defense to that of non-territorial tactics, such as scramble competition (i.e., nonaggressive resource exploitation). The payoffs are likely to be frequency dependent, meaning that the best tactic depends on what other individuals in the population are doing. This is not a trivial problem, theoretically or empirically (Grafen 1987; Kokko et al. 2006; Mesterton-Gibbons and Sherratt 2014; Sherratt and Mesterton-Gibbons 2015; Kemp 2018).

In many species, territorial behavior coexists with one or more non-territorial tactics. Much of the theoretical literature on this topic has focused on exploring scenarios in which territorial and non-territorial phenotypes represent different genotypes, and there are some well-documented examples of such genetic polymorphisms (reviewed in Taborsky and Brockmann 2010). However, in the vast majority of cases, the tactics are conditional; individuals develop into territorial or non-territorial morphs depending on their condition (e.g., body size, growth rate) at some critical stage or switch between tactics as their condition or social environment changes (Taborsky and Brockmann 2010). Usually, the territorial tactic has the highest fitness payoff for individuals with higher than average fighting ability (also known as resource holding power [RHP]) while the non-territorial tactic is the best available option for individuals with low RHP, but there are also known cases in which territoriality is the lower fitness tactic (Gross 1996).

8.2 Territoriality in Insects

In a forward-looking review, Baker (1983) asserted that every facet of territoriality in vertebrates is also exhibited by insects and that many questions about territoriality could probably be answered more easily with insects than with vertebrates. Baker (1983) did not explain the latter assertion, probably because it seemed self-evident, but at the risk of stating the obvious most insects are more abundant, shorter

lived, easier to catch, easier to manipulate experimentally, and also easier to get permission to study than most vertebrates. Some insects are also extremely easy to observe in the wild without disrupting their natural behavior. Thirty-five years later, the literature on territoriality is still vertebrate biased, but insects have featured prominently in testing certain aspects of theory relating to animal contests (Suhonen et al. 2008; Vieira and Peixoto 2013; Kemp 2018) and interspecific aggression (Grether et al. 2013; Tinghitella et al. 2018).

To the best of my knowledge, the only general review of territoriality in aquatic insects is that of Hart (1987). For most groups of aquatic insects, the relevant literature consists mainly of descriptions of the behavior of particular species. Research on the ecological and evolutionary causes and consequences of territorial behavior is rare in most groups of aquatic insects, the chief exceptions being adult damselflies and dragonflies (Zygoptera and Anisoptera: Odonata; Suhonen et al. 2008) and semiaquatic bugs (Heteroptera: Hemiptera; Arnqvist 1997).

In the first section below, I review what is known about territoriality in aquatic insect larvae before turning to what is known, with greater certainty, about territoriality in aquatic insects at the adult stage.

8.3 Territoriality in Aquatic Insect Larvae

Our knowledge of territoriality in aquatic insect larvae does not appear to have advanced much since Hart's (1987) review. Hart's (1987) Table 1 lists cases of larval feeding territories in damselflies and dragonflies (Odonata), caddisflies (Trichoptera), stoneflies (Plecoptera), mayflies (Ephemeroptera), moths (Lepidoptera) and black flies (Simuliidae; Diptera). According to Hart (1987) the only orders of aquatic insects in which larval feeding territories have not been reported are dobsonflies and alderflies (Megaloptera), spongeflies (Neuroptera), and beetles (Coleoptera). Hart (1987) concluded that feeding territories are seen primarily in species with small foraging areas and high resource renewal rates, and argued that this pattern matches theoretical predictions based on economic defendability (Brown 1964).

Hart (1987) was admittedly rather liberal in classifying species as territorial, and some of the evidence for larval feeding territories has since been disputed. Behavioral studies on aquatic insect larvae are often carried out in the laboratory under conditions of questionable relevance to the natural environment, and it is often unclear whether the aggressive interactions are site dependent (territorial) or site independent (non-territorial). Testing for site dependence requires tracking individuals, and this is rarely done in studies of aquatic insect larvae. In the absence of data on individuals, it is still possible to make reasonably robust inferences about whether aggression results in spacing, however.

Corkum (1978) observed aggression in one of the two species of larval mayflies that graze on periphyton (attached algae) under still-water conditions in the laboratory. She described larvae of the aggressive species (*Paraleptophlebia mollis*)

striking each other laterally with their abdomens or facing each other and touching each other with forelegs and antennae until one individual withdrew by a few millimeters. In some instances, one larva chased the other briefly. Based on these observations, Corkum (1978) suggested that aggression and drifting serve as alternative spacing mechanisms in mobile grazing mayflies. Williams (1987) also reported that aggressive interactions appeared to increase spacing among mobile grazing mayfly larvae under low-flow conditions in the laboratory.

Kohler (1992) drew a distinction between sessile grazers and mobile grazers, and questioned whether aggression among mobile grazers occurs under lotic (flowing water) conditions in the wild. Based on field and laboratory experiments, he concluded that spacing among mobile grazing mayflies (*Baetis tricaudatus*) and caddisflies (*Glossosoma nigrior*) in a stream in Michigan results from exploitative competition (i.e., periphyton depletion) alone, and that interference between mobile grazers and filter-feeding blackflies (*Simulium* spp.) and chironomids (*Rheotanytarsus* spp.) results from non-aggressive physical contact (as grazers move around, they bump into and displace filter feeders). By Kohler's (1992) account, only sessile grazers have been shown to exhibit territoriality under natural (i.e., lotic) conditions. For a particularly well-documented example of territoriality in sessile, grazing caddisflies, see Hart (1985).

Aggression appears to increase spacing among filter-feeding black fly larvae (Simuliidae: Diptera). Hart (1986) reported that *Simulium piperi* larvae were most aggressive toward upstream neighbors; filter-feeding rates increased after upstream neighbors were displaced; and aggression decreased when food availability was experimentally increased. Some filter-feeding caddisfly larvae have also been reported to be territorial. Matczak and Mackay (1990) varied food concentration and current velocity in the laboratory and found that the larvae were less aggressive and more closely spaced at higher food concentrations and flow rates. They suggested that spacing is maintained by a combination of aggression (bites and lunges) and signaling (stridulation). Some fights ended with one larva killing and partially consuming the other, but usually one larva was displaced (set adrift) (Matczak and Mackay 1990). Body-size differences and residency (possession of a retreat) both appeared to play a role in the outcome of interactions, and some larvae attempted to take over the retreats of other larvae.

Based on laboratory experiments, Sjöström (1985) concluded that predatory larval stoneflies (Plecoptera) are territorial. The experiments involved placing two or three size-matched *Dinocras cephalotes* larvae together in aquaria and observing them compete over shelters. The evidence for territoriality is that the larvae responded aggressively to each other and the first larva introduced to an aquarium usually dominated newcomers. There are other reports of aggression between larval stoneflies, but whether the behaviors observed qualify as territoriality is not clear. In a laboratory experiment with unlimited food, Lieske and Zwick (2008) inferred that intraspecific interference competition influences the growth and development of the biofilm-consuming stonefly *Nemurella pictetii* and observed aggressive interactions between the larvae, but did not specifically document territorial behavior.

Larval odonates have a well-documented repertoire of agonistic behaviors. The larvae of some species have been described as territorial (Rowe 1980; Harvey and Corbet 1986; Corbet 1999), while others have been described as non-territorial (Baker 1981, 1983; Johnson 1991; Fincke 1996). In the clearest case of territoriality that I found in the literature, Rowe (1980) observed individually color-marked *Xanthocnemis zealandica* damselfly larvae in aquaria and reported that they used the same hunting perches for several days and repelled intruders with a combination of displays (abdomen swinging) and physical attacks (labium strikes). Most such encounters ended with the original occupant keeping the perch and the intruder retreating. Fincke (1996) questioned this and other reports of territoriality in larval odonates, mostly on the grounds that the experimental designs did not allow territorial behavior to be distinguished from non-territorial dominance interactions. Fincke (1996) studied *Megaloprepus caerulatus* damselfly larvae in containers and varied the availability of food and cover. She concluded that spacing within the containers resulted from a kind of size-dependent, site-independent dominance—not territoriality. The key evidence against territoriality is that individual larvae were not site faithful (most moved at least once per day within the containers) and size differences, not prior occupancy, determined the outcome of encounters (larger larvae dominated smaller larvae). Rowe (2006) accepted Fincke's (1996) argument against territoriality in *M. caerulatus* but argued that *X. zealandica* larvae are territorial. More research is needed to establish whether territoriality is common in larval odonates.

8.4 Taxonomic Distribution of Territoriality in Adult Aquatic Insects

Most aquatic insects are not territorial at the adult stage. Adult male mating territories appear to only have been documented in damselflies (Zygoptera: Odonata), dragonflies (Anisoptera: Odonata), and semiaquatic bugs (Heteroptera: Hemiptera). In other groups of aquatic insects, aggression between adults appears to be non-territorial. For example, male-male aggression has been reported in captive Mexican dobsonflies (*Corydalus bidenticulatus*; Megaloptera), but males only responded aggressively to each other in the immediate vicinity of females (Álvarez et al. 2017). If territoriality has been documented in other aquatic insects at the adult stage, I hope this review encourages the researchers to publish their findings.

8.5 Types of Territoriality Reported in Adult Aquatic Insects

- (a) Odonata (damselflies and dragonflies): The types of territories that have been reported in Odonata can be divided into feeding (hunting) territories and mating territories. While mating territories have only been documented convincingly in

males, both sexes can defend feeding territories (Corbet 1999). In species that hunt from perches, aggressive defense of preferred perches, which are typically higher than surrounding perches (Gorb 1994), is common, and females often dominate males in this context (Corbet 1999).

Mating territories are usually found at water bodies where females come to oviposit, but in some species males defend territories at other sexual rendezvous sites (e.g., forest gaps), and mating pairs travel in tandem (the male clasping the female) to the aquatic habitat where oviposition occurs (e.g., Conrad and Pritchard 1988). The length of time males spend on their territory varies widely, as does the degree of site fidelity exhibited across days. In some species, a male will spend a large proportion of his reproductive life defending the same territory, while in other species males establish new territories daily (reviewed in Corbet 1999).

Territorial odonates can be divided roughly into perchers and patrollers (also known as fliers). In perching species, males adopt a sit-and-wait strategy and rarely leave their perches except to evict male intruders or pursue females. In patrolling species, males regularly fly in a circuit around their territory, searching for females and intruding males. Many species exhibit both modes of territoriality, to varying extents (Corbet 1999). Species that spend most of their time patrolling generally have larger territories than species that spend most of their time perching (Corbet 1999), perhaps because males can only defend what they see. In typical perching species, territories are only a few square meters in area, while the territories of some patrolling species are over 100 square meters (Corbet 1999).

Territorial defense by patrolling is an energetically costly behavior that can limit the length of time males spend on their territories to a small portion of the day. In *Plathemis lydia* (Libellulidae), seven males in succession have been observed patrolling the same territory (portion of a pond perimeter) on a given day (Koenig 1990). Individual males tend to arrive around the same time and defend similar sites on subsequent days, resulting in a kind of temporal partitioning or “time sharing” arrangement (Koenig 1990). By contrast, in some perching species, such as *Hetaerina americana* (Calopterygidae), individual males can reliably be found on their territories throughout the day, except when guarding an ovipositing female (Johnson 1962; Weichsel 1987; Grether 1996b).

- (b) Heteroptera (water striders, ripple bugs): Feeding and male mating territories have also been documented in water striders and other semiaquatic bugs (Kaitala and Dingle 1993; Arnqvist 1997). The feeding territories consist of an area on the surface of a water body where the resident has priority of access to food (live or dead arthropods). Feeding territories are seen in both sexes, but females are generally larger and dominant over males and juveniles (nymphs). Experimental manipulations have shown that defense of feeding territories is dynamic and responsive to environmental and social conditions. For example, by manipulating food availability in the field and lab, Wilcox and Ruckdeschel (1982) showed that adult *Gerris remigis* of both sexes defend feeding territories when food availability is between two thresholds. Territoriality is abandoned

when food availability is above the upper threshold or below the lower threshold. By manipulating the age and sex composition of pools, Wilson et al. (1978) showed that both sexes and age classes of *Rhagovelia scabra* will attempt to defend territories on the inflow side of the pools, where food availability is highest, but females outcompete males for these positions; at high adult female densities, juveniles and males abandon feeding and cluster together.

Male mating territories are most commonly seen in water strider species with “Type II” mating behavior (Arnqvist 1997). Typically, males anchor themselves to oviposition sites and attract females by sending out “calling” signals by rippling the water surface (Jablonski and Wilcox 1996). When females approach, males switch to “courtship” signals and the female inspects the oviposition site. The female is free to leave, but if she stays the pair copulates and the male usually guards the female from a short distance while she oviposits. Approaching males elicit aggressive “repel” signals and, if necessary, residents will fight physically to defend oviposition sites. By contrast, in species with “Type I” mating behavior, males usually exhibit non-territorial mate searching and attempt to mount and copulate with females without courtship. However, the correlation between territoriality and mating behavior is not perfect. In some territorial species, males attempt to mount females forcibly (Nummelin 1988) and in some non-territorial species males court females (Olosutean 2018). Alternative male mating tactics are found in some species, and males flexibly switch between tactics as conditions change (Arnqvist 1997).

8.6 Determinants of Territorial Status and the Outcome of Territorial Contests

A large body of research on territorial insects has been done in the service of testing animal contest theory (Suhonen et al. 2008; Vieira and Peixoto 2013; Kemp 2018). Much of this research can be characterized as attempting to identify the morphological and physiological determinants of RHP (Vieira and Peixoto 2013). This subject was recently reviewed for odonates by Suhonen et al. (2008), for insects in general by Kemp (2018), and for arthropods in general by Vieira and Peixoto (2013). One overall conclusion is that winners and losers of territorial contests usually differ from each other phenotypically, but the traits that correlate with winning are quite variable among species and cannot be predicted from the mode of fighting (Vieira and Peixoto 2013; Kemp 2018). In a meta-analysis of studies on the determinants of fight outcomes in arthropods, persistence-related traits, such as energy reserves, were not consistently better at predicting the outcome of contests than strength-related traits, such as body mass, or vice versa, regardless of whether the contests involve physical contact or instead appear to be pure endurance contests (Vieira and Peixoto 2013), which is a rather puzzling result.

Damselflies (Zygoptera) have featured prominently in this sector of the literature, but I am not convinced that we have truly learned much about how territorial contests are resolved in damselflies. I will illustrate the problem with a gem of the animal contest literature, a paper that has been cited over 300 times (Marden and Waage 1990). Taking advantage of Waage's (1988) discovery that neighboring *Calopteryx maculata* territory holders can be induced to engage in escalated fights by gradually merging their oviposition sites (clumps of bur weed, *Sparganium* spp.), Marden and Waage (1990) recorded the outcome of such fights, as well as some naturally occurring fights, and then recaptured the males, made mass and size measurements, and carried out whole-body lipid extractions. Winners usually had more remaining fat than losers but did not differ from losers in body size, wing loading, or flight muscle ratio. Since contestants mirrored each other in flight and presumably expended similar amounts of energy, winners must also have had more fat prior to fighting. Based on this, Marden and Waage (1990) inferred that "escalated damselfly territorial contests are energetic wars of attrition." Marden and Rollins (1994) subsequently replicated the study on another *C. maculata* population, with similar results. Most subsequent discussions have focused on questions such as whether male damselflies can assess each other's fat reserves and how they might do so (Marden and Rollins 1994; Mesterton-Gibbons et al. 1996; Payne 1998; Fitzstephens and Getty 2000). However, it is important to realize that while Marden et al. controlled the circumstances of staged fights, they had no control over attributes of the paired contestants. Contest outcomes might therefore have depended on factors correlated with fat reserves, instead of fat reserves per se. Young mature male *Calopteryx* usually contain more fat than older males and are also more likely to win escalated fights (Forsyth and Montgomerie 1987; Marden and Waage 1990; Marden and Rollins 1994; Plaistow and Siva-Jothy 1996). Do young males win because they have more fat, or do fat males win because they are younger? Out of 38 contests for which age estimates were available, 32 (84%) were won by the fatter male and 30 (79%) were either won by the younger male or there was no "discernable" age difference between the males (Marden and Rollins 1994). Taken at face value, these numbers suggest that fat is more important than age, but fat was measured much more precisely than age (Marden and Waage 1990; Marden and Rollins 1994). Furthermore, a male's chronological age, even if known precisely, might not correlate perfectly with age-related factors that affect endurance. In *Homo sapiens*, for example, young mature males can, on the average, outlast old males in endurance contests, but not all males senesce at the same rate (pers. obs.). Body fat reserves may well be one of the critical factors that determine the outcome of escalated contests in damselflies, but experiments disassociating fat content from other age-related factors would be required to test this rigorously.

Several other morphological and physiological variables have also been shown to correlate with territorial status and contest outcomes in damselflies (reviewed in Suhonen et al. 2008; Vieira and Peixoto 2013; Córdoba-Aguilar and González-Tokman 2014; Kemp 2018). The physiological correlates of territoriality have been particularly intensively studied in *Hetaerina* spp. damselflies (reviewed in Córdoba-Aguilar and González-Tokman 2014). Males classified as "territorial" and "non-

territorial” have been shown to differ in muscle mass, energy reserves, and immune response, and in all respects territorial males appear to be in better physiological condition than non-territorial males (reviewed in Córdoba-Aguilar and González-Tokman 2014). As in *Calopteryx*, a male’s ability to hold a territory first increases and then decreases with age postemergence (Guillermo-Ferreira and Del-Claro 2011; Fig. 8.1), but the relationship between physiological condition and age appears not to have been studied yet in *Hetaerina*.

I am not aware of any published studies in which morphological or physiological variables have been manipulated experimentally to evaluate their influence on the outcome of territorial contests in aquatic insects. Manipulative experiments have

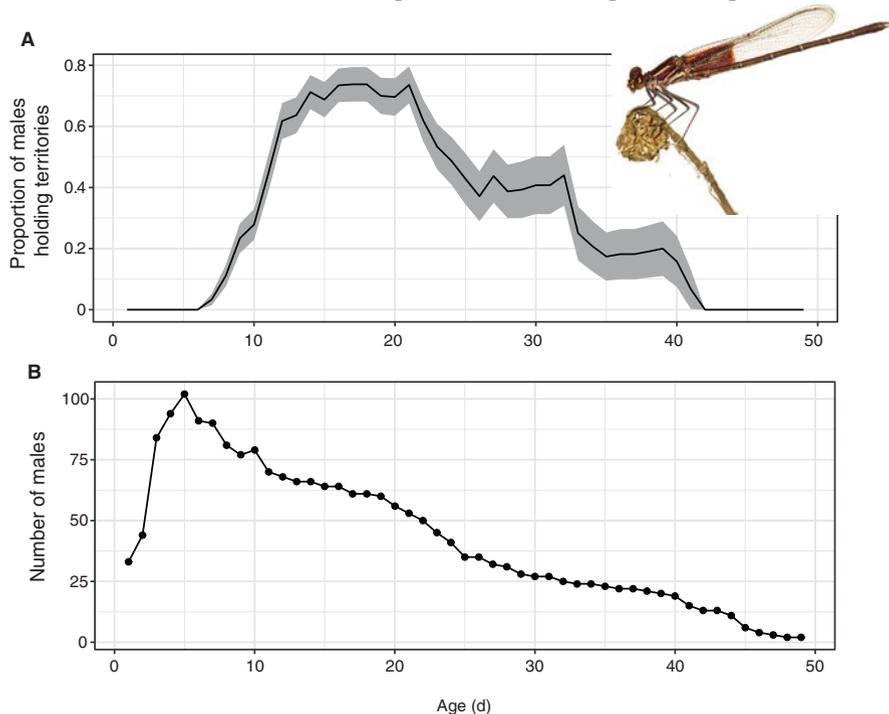


Fig. 8.1 The rise and fall in territorial fighting ability in the damselfly *Hetaerina americana*. **(a)** Variation in the probability of territory ownership with age (0 is the day of adult emergence). The shaded area shows the standard error of the proportions. Most males first acquired territories between 10 and 15 days of age. Territory-holding ability declined sharply after age 21, but some males managed to acquire a second or third territory, which probably accounts for the stepped shape of the declining function. **(b)** Sample sizes on which the proportions and standard errors in **(a)** are based. These data were collected from August 14 to October 22, 1991, on a cohort of $N = 140$ males on a stream in Northern California (for further details, see Grether 1996b, a). Age was either known precisely to 1 day or estimated using a multiple regression equation based on the known-age males and phenotypic traits that change with age (Grether 1996a). Sample sizes increase between ages 1 and 5 due to variation in the age at which males were marked and included in the study. Males that were sighted outside the study area, or were missing for one or more days after age 9 until their final disappearance or documented death, were excluded from the cohort. Inset photo of a male *H. americana* courtesy of Neil Losin

been carried out on other territorial insects to test for effects of specific traits on contest outcomes. For example, Kemp et al. (2006) reared butterflies (*Pararge aegeria*) under different thermal and photoperiod treatments to increase variation in morphological traits related to flight performance and staged contests between individuals with different flight morphologies. Interestingly, the only significant predictor of contest outcome was age (Kemp et al. 2006).

8.7 Territorial Signals and Cues

In the animal signaling literature, a cue is a trait that has an effect on the behavior of receivers and a signal is a trait that evolved to have a particular effect on the behavior of receivers (Laidre and Johnstone 2013). Cues and signals affect the behavior of other individuals because they convey information about the signaler, or to be more specific because they reduce uncertainty about the signaler's attributes or future actions (Maynard Smith and Harper 1995). In many if not most cases, signals are likely to have evolved from cues. For example, the disturbance of the water surface caused by a water strider's legs might have originally served merely as a cue that a conspecific is nearby, but over time become modified by selection to serve different functions, such as calling females, courting females, and repelling males (Arnqvist 1997). In this case, we can recognize that there are three distinct signals each with a different function. In other cases, the same trait might serve as a signal in multiple behavioral contexts. For example, color patches on the wings of *Hetaerina* damselflies are used for sex recognition (i.e., distinguishing between the sexes; Grether et al. 2015), male mate recognition (i.e., distinguishing between conspecific and heterospecific females; Drury et al. 2015), competitor recognition within species (i.e., distinguishing between immature and mature males; Grether et al. 2015), and competitor recognition between species (i.e., distinguishing between conspecific and heterospecific males; Anderson and Grether 2010a), and might also serve as indicators of territorial fighting ability (Grether 1996b; Contreras-Garduño et al. 2006; Contreras-Garduño et al. 2007; Guillermo-Ferreira and Del-Claro 2011; Álvarez et al. 2013; González-Santoyo et al. 2014; but see Raihani et al. 2008; González-Santoyo et al. 2010). It is not surprising that one trait (or the homologous trait in males and females) can serve multiple functions, but this is different from showing that it evolved in multiple contexts. For example, did pink wing spots evolve in immature male *Hetaerina* to reduce aggression from mature males, or is pink just a necessary transition in the development of red wing spots? The burden of proof for showing that a trait is a signal is considerably higher than that for showing that it is a cue.

Showing that a trait is a territorial cue (if not also a signal) requires showing that it affects the behavior of other individuals in a territorial context, and the most direct way to do that is to manipulate the trait experimentally. For example, after finding that male *Mnesarete pudica* (Zygoptera, Calopterygidae) with larger red wing spots are more likely to win territorial contests, Guillermo-Ferreira et al. (2015b) pre-

sented territory holders with male intruders with and without experimentally augmented red wing spots. They found that territory holders with relatively large wing spots responded more aggressively to experimental males than to control males, whereas territory holders with relatively small wing spots did not differ in their responses to the two treatment groups. Why males with larger red spots have an advantage in territorial fights remains to be determined, but this study leaves little doubt that the red spots are involved somehow. Numerous studies have provided correlational or experimental evidence that coloration affects the outcome of territorial contests in Odonata (Grether 1996b; Tsubaki et al. 1997; Hooper et al. 1999; Plaistow and Tsubaki 2000; Tynkkynen et al. 2004, 2005, 2006; Cordoba-Aguilar et al. 2007; Contreras-Garduno et al. 2008; Guillermo-Ferreira and Del-Claro 2011; Guillermo-Ferreira et al. 2014, 2015a, b; Iyengar et al. 2014; Vilela et al. 2017; Pestana et al. 2018).

There are several possible ways that territorial signals could evolve (Box 8.1). A systematic review of the evidence for, and against, the various models in aquatic insects (or more generally) would be valuable, but is beyond the scope of this chapter. However, there is good evidence that the wing coloration of male odonates directly affects their ability to hold territories (see previous paragraph), is costly for survival (Grether and Grey 1996; Grether 1997), and correlates positively with various measures of phenotypic condition (reviewed in Suhonen et al. 2008; Vieira and Peixoto 2013; Córdoba-Aguilar and González-Tokman 2014; Kemp 2018), which seems most consistent with the handicap model (Box 8.1).

Box 8.1: Classic Models for the Evolution of Territory Signals

Priority model: Territorial signals evolve from cues about the territory owner's presence and increase in conspicuousness to a level that balances the benefits of being detected by conspecifics with the costs of producing the trait and being conspicuous to predators and prey. Territory owners and receivers benefit from avoiding unnecessary interactions, but all the signal conveys to receivers is that the owner is present on the territory (Hansen and Rohwer 1986; Butcher and Rohwer 1989).

Handicap model: Traits with no effect on fighting ability evolve to become honest indicators of fighting ability because larger values of the trait are more costly and the cost of a given value of the trait is lower for individuals with higher fighting ability (Zahavi 1977; Grafen 1990).

Uncorrelated asymmetry model: The size of the trait signals aggressiveness, not fighting ability. For this type of signal to be evolutionarily stable, aggressive individuals must incur a cost independent of any particular contest, the value of the contested resource must be low relative to the costs of fighting, and individuals with deceptively large values of the trait must be punished when they encounter aggressive conspecifics (Maynard Smith and Harper 1988; Johnstone and Norris 1993).

(continued)

Box 8.1: (continued)

Arbitrary identity badge model: Territory signals evolve from cues that initially gave good fighters an advantage by making them more recognizable, but then spread through the population by mimicry; however, once such a trait is fixed in the population, it is no longer useful as a signal of fighting ability (Rohwer and Røskoft 1989).

8.8 Interspecific Territoriality

Territorial aggression between species is quite common in Odonata. In some cases, aggressive responses to other species can be explained as recognition errors (Grether 2011). For example, territorial male *Perithemis tenera* (Libellulidae) chase horseflies and butterflies that are similar in size, color, and flight height to the dragonflies (Schultz and Switzer 2001). Schultz and Switzer (2001) considered multiple alternative hypotheses and concluded that the mistaken identity hypothesis (also known as the misdirected intraspecific aggression hypothesis; Murray 1981) is the most plausible explanation. While male *P. tenera* do not seem to benefit from chasing horseflies and butterflies, the encounters are infrequent, and the costs of failing to respond to conspecific intruders might prevent improvements in discrimination ability from evolving. Similar explanations for the persistence of interspecific aggression have been offered for *Leucorrhinia* spp. dragonflies (Singer 1989, 1990) and *Calopteryx* spp. damselflies (Tynkkyne et al. 2004, 2005, 2006).

A different explanation has been proposed for interspecific territoriality in *Hetaerina* spp. damselflies. Drury et al. (2015) found that levels of territorial aggression between sympatric species in this genus are positively correlated with levels of reproductive interference (i.e., interspecific mating attempts; Fig. 8.2). Pre-clasping courtship is absent in *Hetaerina*, and males initiate mating by clasping females in flight. Females invariably reject heterospecific males, but in the time that takes the female can be transported outside the territory where she was clasped. Thus, from the standpoint of a territory holder, tolerating males of another species could be disadvantageous if they fail to discriminate between females of the two species. Evolutionary simulations based on the damselfly system showed that when males of two species compete locally for females, interspecific territoriality can evolve and be maintained indefinitely (Drury et al. 2015).

8.9 Agonistic Character Displacement

When costly territorial aggression occurs frequently between species, and there are no countervailing benefits, selection should cause the species to diverge in ways that reduce the frequency and costs of the interaction, an evolutionary process known as agonistic character displacement (ACD; Grether et al. 2009, 2013, 2017). Territorial damselflies have provided some of the best evidence for ACD.

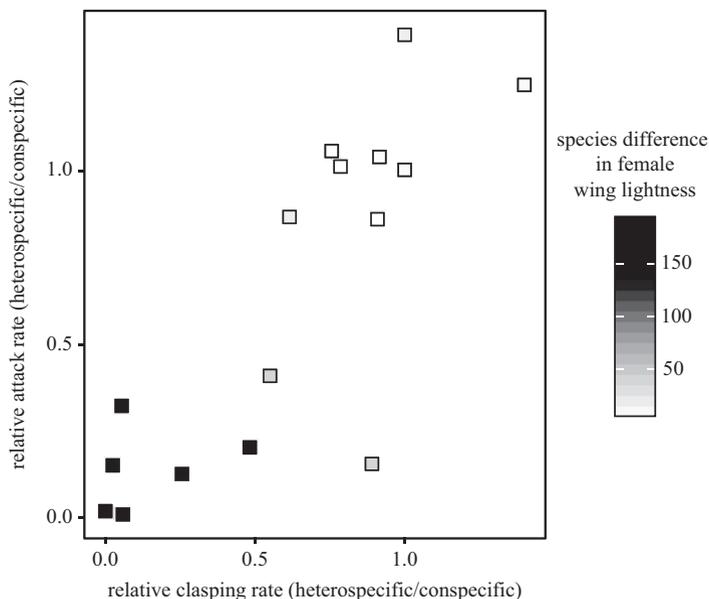


Fig. 8.2 Correlation between reproductive interference and interspecific aggression in *Hetaerina* damselflies. Relative attack rate, a measure of interspecific aggression, was obtained by presenting live, tethered males to territory holders and dividing the number of attacks elicited by heterospecific male intruders by the number of attacks elicited by conspecific male intruders. Relative clasping rate, a measure of reproductive interference, was obtained by presenting live, tethered females to territory holders and dividing the proportion of females that elicited sexual responses in trials with heterospecific males by the proportion of tethered females that elicited sexual responses in trials with conspecific males. Grayscale: Species differences in female wing lightness, as measured by reflectance spectrometry. Each point represents a population at a sympatric site. From Drury et al. (2015) (authors are allowed to reuse their own figures without permission from the publisher)

ACD has been reported in two pairs of *Calopteryx* species, one in Europe and the other in North America (Tynkkynen et al. 2004; Iyengar et al. 2014). Males of one species in each pair have fully black wings (*C. virgo* and *C. maculata*) and males of the other species have partially black wings (*C. splendens* and *C. aequabilis*). In both cases, the species with partially black wings shows a geographic pattern of character displacement in male wing coloration (Waage 1979; Tynkkynen et al. 2004; Mullen and Andres 2007; Honkavaara et al. 2011; but see Hassall 2014; Suhonen et al. 2018). Simulated territory intrusion experiments revealed that males of the species with fully black wings respond more aggressively to heterospecific males with larger amounts of black wing pigmentation (Tynkkynen et al. 2004; Iyengar et al. 2014). As further evidence that geographic wing color shifts in the European species pair were caused by ACD, Tynkkynen et al. (2005) found that survival selection on *C. splendens* wing spots switched from positive to negative as the relative abundance of *C. virgo* increased. Experiments in which *C. virgo* was removed provided further evidence that interspecific aggression is responsible for

the character displacement pattern in *C. splendens* (Tynkkynen et al. 2005, 2006). Nevertheless, reproductive character displacement (RCD) is a viable alternative hypothesis for the same geographic patterns because female mate recognition is also based on male wing coloration (Honkavaara et al. 2011; Kuitunen et al. 2011), and evolutionary simulations suggest that RCD would dominate ACD in this situation (Okamoto and Grether 2013).

Two pairs of *Hetaerina* species show geographic patterns indicative of divergent ACD in both wing coloration and competitor recognition (Anderson and Grether 2010a, b). The alternative hypothesis that these patterns were caused by RCD was rejected based on evidence that female mate recognition is not based on male wing coloration (Grether 1996b; Drury and Grether 2014). The key evidence was obtained in a field experiment in which male wing coloration in one species, *H. americana*, was manipulated to resemble that of a sympatric congener, *H. titia*. Compared to controls, male *H. americana* with *H. titia* wing coloration were involved in more interspecific fights and had reduced territory tenure and survival, but experienced no reduction in any component of mating success potentially under female control (Drury and Grether 2014).

Another potential case of ACD has been reported in *Mnais* damselflies (Fig. 8.3). In allopatry, *M. costalis* and *M. pruinosa* both exhibit a male color polymorphism

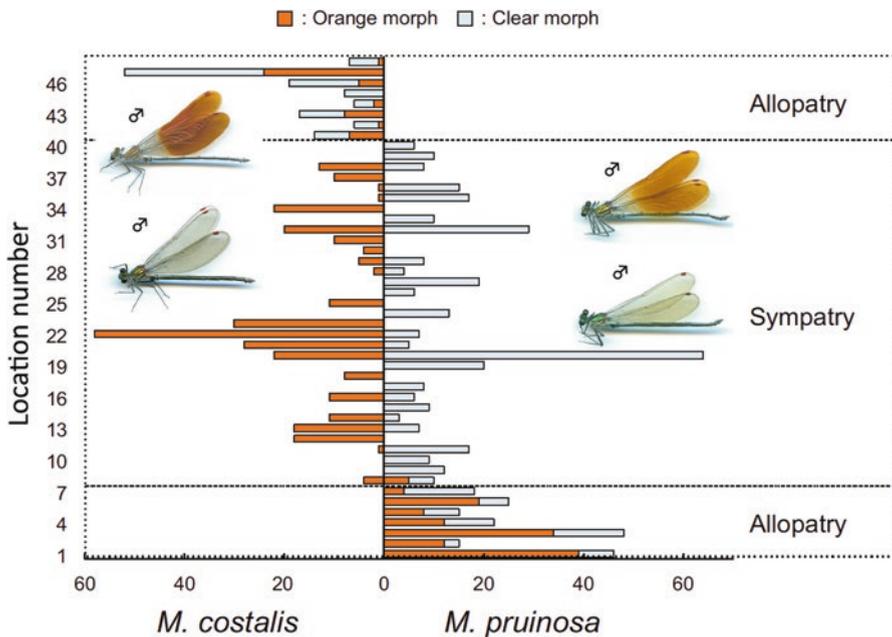


Fig. 8.3 Character displacement pattern in wing color morph ratios of *Mnais* damselflies in Japan. Bars show the number of males of the clear and orange morphs collected at each sampling location. Inset photos show orange and clear male morphs of the two species. From Tsubaki and Okuyama 2016, with permission from Springer Nature

linked to territorial behavior: males with orange wings are territorial while males with clear wings usually pursue a non-territorial sneaking tactic but can switch to territorial behavior if orange males are absent (reviewed in Tsubaki and Okuyama 2016). In sympatry, however, *M. costalis* exhibits only the orange morph and *M. pruinosa* usually exhibits only the clear morph (Fig. 8.3). Apparently, the selection trade-off that maintains the color polymorphisms in allopatry (Tsubaki et al. 1997; Plaistow and Tsubaki 2000; Tsubaki 2003) is disrupted in sympatry (Tsubaki and Okuyama 2016). Whether the character displacement pattern has resulted from aggressive or reproductive interference between the species, both kinds of interference, or some other unknown factor, remain to be determined (Tsubaki and Okuyama 2016; Tsubaki and Samejima 2016).

8.10 General Advice for Studying Territorial Behavior

Studying territorial behavior does not usually require highly specialized techniques or instruments, but it does require attention to certain details that are often overlooked, or disregarded, in studies of aquatic insects. I do not wish to criticize specific papers, but counterexamples to each of the common-sense suggestions below are easy to find in the literature. This complicates making comparisons between species, and even between studies of the same species by different researchers. While different methods might be warranted in studies with different goals, the vast majority of studies of territoriality would benefit from the following practices.

First and foremost, it is essential to have a robust method for distinguishing between individuals. Assuming that animals perching, skating, or flying in the same area at different times are the same individual is totally invalid, as demonstrated, for example, by Koenig's (1990) discovery that seven or more dragonflies can occupy the same territory in succession, on a single day. With rare exceptions, reliably distinguishing between individuals requires marking them with unique codes. It is important to choose a marking technique that allows individuals to be identified without recapturing them or otherwise affecting their behavior, and also to verify that the marks themselves do not affect territorial behavior, mating success or survival (Anderson et al. 2011; Álvarez-Covelli et al. 2015).

Second, it is important to have clearly defined, empirically based criteria for classifying individuals as territory holders and non-territory holders. Ideally, this would involve multiple observations of territory defense, but at a minimum should include establishing that an individual is site faithful on an appropriate timescale (which varies by species). Verifying territory defense does not necessarily require waiting for naturally occurring encounters; it is often possible to test for aggressive responses by simulating territory intrusion (e.g., by presenting conspecifics, models, or other stimuli that evoke territorial responses). It is also important to recognize that being a territory holder is a temporary state, not a characteristic of the individual. In some species, all individuals of a particular age and sex class are territorial

in the sense that they would occupy and defend space if they had the opportunity and ability to do so.

Third, while it might be convenient to assume that individuals that have disappeared from the study area have died, this is a very tenuous assumption for flying insects, unless the study area encompasses the dispersal range of the species. Equating disappearance to death is particularly problematic in studies correlating territorial behavior and associated phenotypic traits with components of fitness, such as survival and mating success (i.e., selection studies), because individuals that fail to secure a territory in the study area might succeed elsewhere. Survival analysis is a statistical method that allows “censored” observations to be included without bias, and is often a good choice for analyzing these kinds of data.

Finally, as is always the case in science, it is important not to confuse a statistical correlation between two variables with evidence that one variable has a causal influence on the other. In a true experiment, the researcher has control over one or more independent variables. Just because a manipulation of some sort has been carried out does not necessarily mean that the hypothesis of interest has been subjected to an experimental test. This issue has surfaced repeatedly in studies attempting to identify the determinants of territorial status or the outcome of territorial contests. Unless the predictor variable has been manipulated experimentally, it might be confounded with other variables that also affect territorial contests (Grether 1996a; Suhonen et al. 2008).

Overcoming the methodological issues described above is relatively easy with damselflies and water striders, and some species of dragonflies are highly tractable too. In addition to being easy to catch and mark individually, these insects habituate to humans and consequently can be observed directly at very close range. If more behavioral ecologists followed Krogh’s (1929) principle, I think territorial aquatic insects would be even more popular for ecological and evolutionary studies than they already are.

8.11 Future Directions

Most behavioral ecologists would probably rank territoriality among the best understood and least controversial subjects in their field. But it is rather easy to identify important questions about territoriality that have received very little rigorous scientific attention. Why are some species territorial while others are not? Why do some species defend multipurpose territories while others only defend mating or feeding territories? What effects does territoriality have on dispersal and population connectivity? Does territoriality regulate population size? What role does territoriality play in speciation? Under what circumstances is interspecific territoriality adaptive? How do territorial interactions between species affect their coexistence and evolution? How does interspecific territoriality affect the structure of ecological communities? Does territoriality affect whether introduced species become invasive? Should territoriality be taken into account when projecting effects of climate change

on species ranges? None of these questions is specific to aquatic insects, but as Baker (1983) suggested they could probably be answered more easily with insects than vertebrates.

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