Odonatologica 34(4): 397-405 *December 1, 2005*

POSSIBLE SETTLEMENT BENEFITS RELATED TO SITE FIDELITY FOR THE TERRITORIAL DRAGONFLY, *PERITHEMIS TENERA* (SAY) (ANISOPTERA: LIBELLULIDAE)

P.V. SWITZER
Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920, United States; – Phone 217-581-6951; – Fax 217-581-7141; – e-mail cfpvs@eiu.edu

Received January 8, 2005 / Reviewed and Accepted March 23, 2005

Site fidelity, the tendency to return to a previously occupied breeding location, is commonly observed in animals and yet often the benefit to such behavior is unclear. In this study, possible settlement benefits to site fidelity for *P. tenera* are examined. ♂♂ defend small mating territories on ponds and lakes to which they typically, but not always, return the following day. In an observational study, it was found that ♂♂ did not become territorial earlier in the day when site-faithful than when switching territories. However, ♂♂ switching territories were more likely to be seen examining oviposition sites (other than the site they ultimately defended) prior to becoming territorial than site-faithful ♂♂. In an experimental study, it was controlled for differences in territory and oviposition site structure, time of day, evictions and disturbance, and found that site-faithful ♂♂ spent significantly less time settling on a territory prior to defending that territory than ♂♂ settling at a site for the first time. Because ♂♂ examining sites are probably more at risk from predators, this study suggests that site-faithful ♂♂ may experience lowered settlement costs than males returning to their original territory.

INTRODUCTION

Many animal species exhibit breeding site fidelity, or the tendency to return to a previously occupied breeding location (GREENWOOD & HARVEY, 1982; SWITZER, 1993; CORBET, 1999). What individuals gain from being faithful to previous breeding sites is often unclear; in some taxa, however, an individual's site fidelity is related to its reproductive success. For example, studies on birds and dragonflies have found that individuals are site-faithful if they have experienced reproductive success at the site in the past, but unsuccessful individuals tend to switch territories (SWITZER, 1993, 1997a, 1997b). These switching individuals may be improving the quality of their territory by changing territories (e.g. BELETSKY & ORIANS, 1987).

Few studies in any taxon have examined differences in settlement behavior between individuals that are site-faithful versus those who are settling on a new territory (but see, e.g., EASON & HANNON, 1994; JAKOB et al., 2001). However, settlement is a crucial part of an individual's occupation of a territory and may involve high costs; thus, settlement is a likely place to look for the effects of site fidelity. When settling, an individual that switches territories has two general tasks, and both of these tasks may be more costly than if the individual had been site-faithful.

First, an individual moving to a new territory must find a suitable location. When searching for a new location, an individual may incur costs related to energy expenditure, predation risk, and missed foraging or mating opportunities (ISBELL et al., 1990; SWITZER, 1993; JAKOB et al., 2001). For example, JAKOB et al. (2001) found that the individuals of the colonial spider *Metepeira incrassata* incurred substantial lost feeding opportunities when they moved to a new web location relative to remaining on the same web. In addition, some studies have found that the earliest individuals to settle in a given period are site-faithful (e.g. FORSTMEIER, 2002); this difference in order of arrival may be partly explained by site-faithful individuals not having to search for a breeding location.

Second, once an individual settles in a particular location, it must learn the characteristics of that location. HINDE (1956) suggested that individuals that remain in the same location benefit from being familiar with foraging sites and predator refuges in that location. Hinde's argument, while originally proposed to help explain the benefits of territoriality, can be extended to include the benefits of breeding site fidelity (GREENWOOD & HARVEY, 1982). Thus, an individual who returns to a previous location may decrease the energy, predation risk, and lost opportunity costs associated with becoming familiar with neighbors, escape routes, predator refuges and foraging sites within its territory (SWITZER, 1993; STAMPS, 1995; TOBIAS, 1997; JAKOB et al., 2001). Although few studies have examined such consequences for site fidelity, evidence does suggest that familiarity benefits may exist for some species. For example, EASON & HANNON (1994) showed that willow ptarmigan (*Lagopus lagopus*) that initially settled next to familiar neighbors had considerably fewer aggressive interactions than those individuals settling next to unfamiliar neighbors. Because site fidelity is responsible for most of the neighbor familiarity, site-faithful individuals would experience less aggression than individuals who were settling on a new site. Also, TOBIAS (1997) found that the amount of time necessary to settle territory boundaries and begin foraging corresponded to the time delay for a newly settled European robin (*Erithacus rubecula*) becoming dominant on a new territory. Tobias' results suggest that in other species, factors lowering the settlement time, such as site fidelity, may increase an individual's ability to defend its territory.

In this study, I examine settlement behavior in the dragonfly *Perithemis tenera* to test three hypotheses: (1) site-faithful individuals will be less likely to search for other territories than individuals that are not site-faithful, (2) site-faithful individuals will settle on a territory earlier during a particular breeding period than individuals switching locations, and (3) site-faithful individuals will have shorter settlement durations when settling on a territory than individuals settling for the first time. I define "settlement duration" narrowly as the length of time between an individual's initial arrival on the territory that period and the onset of territory defense.

Male *P. tenera* defend small (approximately 3-5 m) breeding territories around oviposition sites (e.g. a floating stick or clump of vegetation) on slow-moving bodies of water (JACOBS, 1955). Although multiple oviposition sites may be present within a male's territory, he only defends, and courts females at, one oviposition site (JACOBS, 1955). Males are only present at the breeding site during the day (SWITZER, 2002a) and tend to occupy the same territory when returning to the pond the following day (JACOBS, 1955; SWITZER, 1997a, 1997b). This tendency to be site-faithful increases with territory quality, previous reproductive success on the territory, and the age of the male (SWITZER, 1997a, 1997b). Previous studies indicated that overall, the males arriving earliest on the pond tended to be site-faithful (SWITZER, 2002a). Thus, at the population level, site--fidelity seemed to be related to arrival time; however, whether individual males arrived earlier when they were site-faithful as compared to shifting territories was not determined.

Upon arrival at the breeding area, a male flies near potential oviposition sites and "examines" them by flying low and touching them with his legs (JACOBS, 1955; SWITZER, 1995). After locating a suitable oviposition site, the male begins to fly in slow, low circles of increasing size in the immediate area; these circular flights always include flying over the oviposition site. Finally, the male perches. A male may start chasing other males from the area (i.e. defending his territory) either during large circular flights (e.g. circles with a diameter approaching the average territory size) or following perching.

METHODS

This study was conducted on a small cattle pond in east-central Kansas, U.S.A. [see SWITZER (1995) for more information on the study site]. The perimeter of the pond was marked with surveyor's flags to facilitate recording locations. Males were captured and marked on their forewing with a permanent marker. Individuals marked in this manner could be identified without recapture using binoculars.

OBSERVATIONAL DATA – In 1992, data were obtained on the arrival times and locations of males as part of a larger study of territoriality and habitat selection (e.g. SWITZER, 1997a, 2002b). To record the locations of males, the pond was continuously scan sampled (at approximately 2 minute intervals); during these scans, I recorded the locations of any new males and any change in the location of existing males. I categorized a male as being site-faithful if he defended an oviposition site within 3 m of the previous day's oviposition site (SWITZER, 1997a). Three meters is the approximate, minimum territory diameter for *P. tenera* (JACOBS, 1955; SWITZER & EASON, 2000). From these data I could establish a male's arrival time (i.e. when he first began defending a territory) and whether a male was site-faithful between days. Note that a male may have arrived at the pond prior to being observed defending a territory; therefore, I also recorded the identity and location of males who were examining sites when possible.

Data for analyses of site examination and arrival time required some manipulation to control for possible confounding variables. First, I examined the relationship between site-fidelity and the likelihood of a male being seen examining sites other than his eventual territory. For this comparison, I first did an overall test pooling across males, and then did a pairwise comparison of occurrences within males using McNemar's test (ZAR, 1999). Because some males had multiple moves that could qualify, for the within-male comparison I used the first move of each type (i.e. site-faithful or switching territories) for each male to avoid pseudoreplication.

Second, because time of arrival will be affected by weather conditions (SWITZER, 2002a), I standardized arrival time by calculating it relative to when the first male settled on the pond. For instance, if the first male arrived at 1000 hr, and the male of interest arrived at 1030 hr, then the arrival time for that male would be 30 min (SWITZER, 2002b). Also, to control for possible, confounding effects from being evicted from a previous territory (SWITZER, 1997a), I only included data for males that had not been evicted from their previous day's territory. Consistent differences existed in the arrival times among individual males (SWITZER, 2002b); that is, some males consistently arrived earlier than other males. To take these differences among males into account, analyses of arrival time used pair-wise comparisons within an individual male, comparing his average time of arrival when he was site-faithful versus when he changed locations. In total, 12 males met these criteria for the pair-wise comparison.

SETTLEMENT DURATION EXPERIMENT – In order to examine the settlement duration on a particular territory, I conducted a more controlled experiment during July and August, 1994 in which I focused in detail on a particular area of the pond. During the study period, individuals were continually marked and the study area was continually observed. I therefore knew which males had experience at oviposition sites in the study area throughout the duration of the study.

Clearly, the type of oviposition substrate could have an effect on how long an individual took to settle at a location. Consequently, to standardize oviposition sites as much as possible, I removed natural oviposition substrate in the study area and replaced them with constructed sticks for use as oviposition sites (see SWITZER, 1997b for a more detailed description of these oviposition sticks). Both male and female *P. tenera* readily used the provided sticks as suitable oviposition sites and these sticks were used for all observations. I also placed sticks for perches near each oviposition site.

To obtain the settlement duration for a male, focal observations were done on the study area. Arriving males were timed with a digital stopwatch as they arrived and examined specific oviposition sites. To define the onset of territorial defense, I did not wait until the focal male actually defended his site, because this behavior would have been necessarily dependent on the arrival of intruding males. Instead, I defined "settlement duration" as the time between when a male first started examining an oviposition site until he stopped examining the site and either perched or began flying in large circles. Typically, a resident will pursue intruders if he has reached the stage of flying in large circles or perching on his territory (personal observation).

The design of this study also controlled for two additional confounding variables. First, if a male or a female interrupted a settling male, his time was not included in the analysis. Second, to control for any possible time-of-day effects on settlement time, only males settling within the first three hours of *P. tenera* occupation on the pond that day were recorded. This time period included the major settlement period for the day (SWITZER, 2002b).

I defined "naïve" individuals as those individuals who did not have any previous experience at that particular oviposition site. Thus, although naïve individuals may have been territorial at other locations, they had no experience at the site in question. In contrast, "site-faithful" individuals had defended that particular oviposition site the previous day.

Non-parametric statistics take tied-values into account when appropriate. All means are reported ± S.E.

RESULTS

SITE EXAMINATION AND THE TIME OF TERRITORY SETTLEMENT

Following their arrival at the pond, males that were not site-faithful were significantly more likely than site-faithful males to be observed examining sites other than the one in which they eventually settled. When settlement data were pooled for all days for all males, males were seen examining before 23/59 (39%) switching days versus 3/72 (4%) of site-faithful days ($\chi^2 = 24.7$, df = 1, P < 0.0001). The pattern also held when a within-male comparison was made for those males that were both site-faithful and not site-faithful (on different days) (Fig. 1; McNemar's test; binomial P = 0.01). For the onset of territorial behavior, however, no significant pattern existed. Seven out of the 12 individuals (58%) who met the criteria for the pairwise comparison settled earlier when site-faithful than when they were settling on new territories (median overall difference = 10.8 minutes sooner when site faithful; Wilcoxon signed rank test, n = 12, T = 34, P = 0.69).

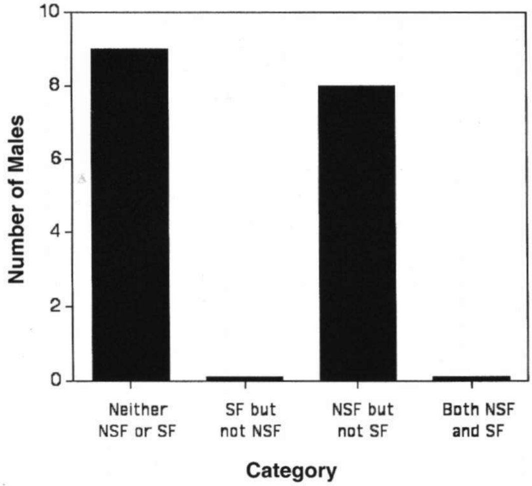

Fig. 1. Within-male comparison of whether a *P. tenera* male was observed examining sites other than his eventual territory only when he was site-faithful (SF), only when not site-faithful (NSF), when both SF and NSF or was not ever observed examining sites prior to settlement. Only the 17 males that had at least one day in which they were site-faithful and one day in which they were not site-faithful were included in the analysis. For those males that had more than one day that was SF or NSF the first observation (chronologically) was used in each category.

SETTLEMENT DURATION

Although all settlement durations were relatively brief, once they arrived at a site, site-faithful males took significantly less time when settling on their territories than did naïve males. When each individual contributed

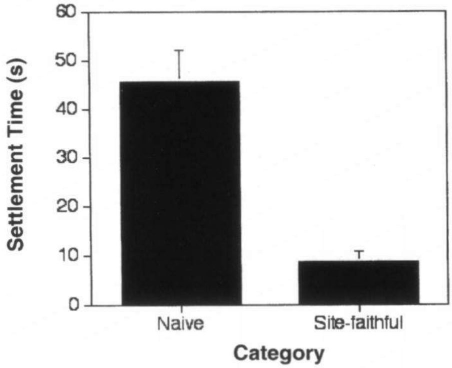

Fig. 2. Average settlement time (± SE) for naïve (N = 11; median 45 s) and site-faithful (N = 11; median 7 s) male *P. tenera*.

only one observation to the analysis, naïve males spent almost five times longer settling than site-faithful males (Fig. 2; Mann-Whitney U, T=1, P < 0.001).

The pattern of decreased settlement time for site-faithful males holds when looking within individuals. A comparison of naïve versus site-faithful settlement times revealed that the same individual spent more time settling when he was new to a site than when he returned to a familiar site (median difference = 28 s; N = 7; Wilcoxon Matched-Pairs; T = 0; P < 0.018). Age could be a possible confounding variable with these results, because naïve settlements might be before site-faithful settlements in most cases. However, for 2 of the 7 males used in the within-male comparison, the site-faithful observation came prior to the naïve observation; thus they were older for the naïve observation. For both of these males, the naïve settlement time was longer than the site-faithful time. In addition, the specific oviposition site did not seem to affect the pattern between different site-faithful and naïve individuals (e.g., site 128, site-faithful males, N = 4, 8.0 ± 3.9 sec.; naïve males, N = 7, 57.9 ± 8.5 sec.; Mann-Whitney U, T = 0, P < 0.005). Finally, the settlement comparison may be further limited to the four males for which I have both day 1 (naïve) and day 2 (site-faithful) settlement times at the same oviposition site. All four males took less time settling when site-faithful, although this sample is too small for statistical comparison.

DISCUSSION

Previous research found that the earliest *P. tenera* males to settle on territories were more likely to be site-faithful than the last arriving males (SWITZER, 2002a). However, the current study found that an individual male did not tend to settle earlier on the days that he was site faithful as compared to those days in which he switched territories. This indicates that although at the population level the earliest males to settle might be site-faithful, no overall relationship exists between site fidelity and time of settlement. Consequently, if early settlement yields any benefits in *P. tenera*, such benefits are not being accrued by site-faithful individuals more than by individuals switching locations.

At a particular site, however, the results indicate a substantial difference between naïve and site-faithful males in the time it takes from arrival to becoming territorial. The study design eliminated the possibility that this difference could be explained by oviposition substrate or location. In addition, neither the specific time of day nor disturbance from other *P. tenera* could be responsible for increased time for naïve individuals. Age could be a potential confounding variable, because age affects site-fidelity in *P. tenera* and other species (SWITZER, 1997a; KEMP, 2001). However, the two males for which site-faithful settlement preceded naïve settlement both had longer settlement times when naïve. Therefore, overall the data suggest that site-faithful males do need a shorter amount of time than males new to a site. If settlement time is positively related to settlement cost, perhaps because of increased predation risk, missed mating opportunities, or establishment of prior residency advantage, then these results would indicate that site-faithful males would experience a lowered settlement cost relative to naïve males.

Of these possible costs, predation risk is more likely than missed mating opportunities or prior residency advantage. Males examining sites may be more likely to be eaten by predators than territorial males that are not engaged in mating or fighting (JACOBS, 1955; SWITZER, 1995). Indeed, anecdotally it seems easier for humans to capture males that are examining sites than to capture territorial males. Although females are likely to desert a male who has not established a territory (SWITZER, 1997b), males tend to establish territories prior to female arrival (JACOBS, 1955; SWITZER, 2002b), which makes missed mating opportunities unlikely. Furthermore, prior residency advantage is typically only associated with nonescalated interactions between the resident and intruder in which the intruder is examining the oviposition site; when actual contests for oviposition sites occur, no residency advantage exists (SWITZER, 2004).

Though the results indicated a clear difference between the settlement durations of site-faithful and naïve males, the overall settlement times were quite brief, which begs the question of whether these time differences are biologically significant or just statistically significant. However, focusing on just this brief difference in time is likely to misrepresent the actual settlement cost difference for two reasons. First, my experimental sites were structurally very simple; they consisted of a single, short oviposition stick floating in the water with a few small, thin sticks projecting from the water for possible use as perches. By design, all other floating and emergent vegetation had been removed. The behavior exhibited by a settling male – circles of increasing size which include the oviposition site – seems consistent with the hypothesis that a male's settlement behavior allows him to learn the location of his oviposition site so that he can take a female directly to his site without wandering; a female will desert a male if he does not take her directly to his site (SWITZER, 1997b). If this hypothesis were correct, then more structurally complex habitats would likely provide a more challenging task for spatial learning. Consequently, a more natural oviposition site and territory may lead to longer settlement times for males and perhaps larger differences between site-faithful and naïve males.

Second, males shifting sites were more likely to be seen examining other sites than site-faithful males. As stated above, examination of sites is costly behavior; not only does it take time, but it potentially exposes males to predators (JACOBS, 1955; SWITZER, 1995). Thus, males returning to a previous day's territory may be substantially lowering their predation risk.

Interestingly, on average males initiated territories at the same time when shifting territories as when site-faithful, and yet males were more likely to examine sites prior to settling when they shifted territories. This result leads to the interesting possibility that males that shifted sites might have been arriving earlier at the pond to compensate for their need to find a new, suitable territory. Indeed, males that shifted sites were rarely seen at their previous territory, while site-faithful males arrived at their previous territory immediately. This pattern indicates that any "decision" to switch sites likely occurs prior to arrival at the pond; therefore, the opportunity for arriving earlier to compensate for changing territories is at least logistically plausible. At this point, however, this idea remains speculation and awaits future study.

ACKNOWLEDGEMENTS

I would like to thank A.B. SWITZER, C. SCHIF and D. SCHIF for hospitality and access to the study pond, A.M. SWITZER and J. SWITZER for assistance collecting data, and P. EASON, I. SWITZER and L. SWITZER for comments on an earlier version of this manuscript.

REFERENCES

BELETSKY, L.D. & G.H. ORIANS, 1987. Territoriality among red-winged blackbirds. I. Site fidelity and movement patterns. *Behav. Ecol. Sociobiol.* 20: 21-34.

CORBET, P.S., 1999. *Dragonflies: behaviour and ecology of Odonata*, Harley Books, Martins.

EASON, P. & S.J. HANNON, 1994. New birds on the block: new neighbors increase defensive costs for territorial male willow ptarmigan. *Behav. Ecol. Sociobiol.* 34: 419-426.

FORSTMEIER, W., 2002. Benefits of early arrival at breeding grounds vary between males. *J. Anim. Ecol.* 71: 1-9.

GREENWOOD, P.J. & P.H. HARVEY, 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* 13: 1-21.

HINDE, R.A., 1956. The biological significance of the territories of birds. *Ibis* 98: 340-369.

ISBELL, L., D.L. CHENEY & R.M.SEYFARTH, 1990. Costs and benefits of home range shifts among vervet monkeys (Cercopithecus aethiops) in Amboseli National Park, Kenya. *Behav. Ecol. Sociobiol.* 27: 351-358.

JACOBS, M.E., 1955. Studies on territorialism and sexual selection in dragonflies. *Ecology* 36: 566--586.

JAKOB, E.M., A.H. PORTER & G.W. UETZ, 2001. Site fidelity and the costs of movement among territories: An example from colonial web-building spiders. *Can. J. Zool.* 79: 2094-2100.

KEMP, D.J., 2001. Age-related site fidelity in the territorial butterfly Hypolimnas bolina (L.) (Lepidoptera: Nymphalidae). *Aust. J. Ent.* 40: 65-68.

STAMPS, J.A., 1995. Motor learning and the value of familiar space. *Am. Nat.* 146: 41-58.
SWITZER, P.V., 1995. *Influences on the site fidelity of territorial animals: theoretical and empirical studies*. Ph.D. diss. Univ. California, Davis.
SWITZER, P.V., 1997a. Past reproductive success affects future habitat selection. *Behav. Ecol. Sociobiol.* 40: 307-312.
SWITZER, P.V., 1997b. Factors influencing the site fidelity of a territorial animal, Perithemis tenera. *Anim. Behav.* 43: 865-877.
SWITZER, P.V., 2002a. Territory quality, habitat selection, and competition in the amberwing dragonfly, Perithemis tenera (Odonata: Libellulidae): population patterns as a consequence of individual behavior. *J. Kans. ent. Soc.* 75: 145-157.
SWITZER, P.V., 2002b. Individual variation in the duration of territory occupation by males of the dragonfly Perithemis tenera Say (Odonata: Libellulidae). *Ann. ent. Soc. Am.* 95: 628-636.
SWITZER, P.V., 2004. Fighting behavior and prior residency advantage in the territorial dragonfly, Perithemis tenera. *Ethol. Ecol. Evol.* 16: 71-89.
SWITZER, P.V. & P.K. EASON, 2000. Proximate constraints on intruder detection in the dragonfly Perithemis tenera (Odonata: Libellulidae): effects of angle of approach and background. *Ann. ent. Soc. Am.* 93: 333-339.
TOBIAS, J., 1997. Asymmetric territorial contests in the European robin: the role of settlement costs. *Anim. Behav.* 54: 9-21.
ZAR, J.H., 1999. *Biostatistical analysis*, [4th edn] Prentice-Hall, Upper Saddle River, N.J.