Factors affecting site fidelity in a territorial animal, *Perithemis tenera*

PAUL V. SWITZER

Animal Behavior Group, Section of Evolution and Ecology, University of California at Davis

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Abstract. This study investigated the factors affecting the site fidelity of the eastern amberwing dragonfly, *Perithemis tenera* (Odonata: Anisoptera), following the framework and testing the predictions of a theoretical model (Switzer 1993; *Evol. Ecol.*, 7, 533–555). Male amberwings defended territories around oviposition sites during the day and left the pond vicinity in the evening. Individuals were highly site-truthful between days: 32.5% of the time males returned to the same oviposition site, and 62.3% of the time males returned to within 3 m of their previous site. Mating success on the pond was temporally predictable and spatially variable. As the model predicted from these habitat characteristics, individuals were more likely to be site-faithful if they had obtained a mating at the site the day before, if their territory was of relatively high quality and when they were older. Males that voluntarily changed oviposition sites between days moved to higher-quality territories. In contrast to some other odonate and avian studies, territory evictions caused considerable site infidelity in amberwings both within and between days. Evictions caused most moves within a day, but the majority of moves between days were voluntary.

Many animals make multiple habitat choices during their lifetimes. Migrant birds, for example, must settle on a breeding site at least once a year (Howard 1920); male insects defending landmark territories must choose a site at least once a day (Alcock 1983). As might be expected, prior habitat choices often affect the habitats chosen later. In fact, individuals of many species return to their previous location, a phenomenon termed ‘site fidelity’.

Biologists have frequently focused their attention on site fidelity, both as an interesting phenomenon (reviewed in Greenwood & Harvey 1982; Alcock 1993; Switzer 1995) and due to its importance in other areas of biology, for example, mating systems (Wooton et al. 1986), sexual selection (Searcy 1979), orientation (Sinsch 1990), population biology (Villard et al. 1995) and conservation (Holmes & Sherry 1992). Many studies of site fidelity have concentrated on determining the factors that may influence whether an individual returns to its previous location or seeks out a new site (e.g. Newton & Marquiss 1982).

Despite all the attention, a number of key issues for site fidelity remain unresolved. For instance, age, territory quality and breeding success have all been suggested to affect site fidelity (e.g. Austin 1949; Newton & Marquiss 1982; Shields 1984). Because these factors may be correlated with each other, however, determining the importance of each can be difficult (Greenwood & Harvey 1982; Párt & Gustafsson 1989; Newton 1993). For species that have the potential to re-pair with a former mate, distinguishing mate fidelity from site fidelity can also be problematic (Greenwood & Harvey 1982; Newton 1993; Aebischer et al. 1995). Individuals may also differ in their tendency to move, a possibility that is seldom addressed (but see Picman 1981). Likewise, although habitat characteristics may play a role in site fidelity (McNicholl 1975; Burger 1982; Beletsky & Orians 1987; Shields et al. 1988), studies rarely use habitat characteristics to generate predictions. Although site fidelity has been observed in at least three phyla (Switzer 1993), most in-depth studies of site fidelity have been conducted on birds; the generality of our understanding of site fidelity is therefore unknown.

Theoretical Basis

Any investigation of site fidelity would benefit from being based on a strong theoretical
foundation. With this in mind, I developed a general model of site fidelity to identify when and how various habitat and individual characteristics would influence site fidelity (Switzer 1993). Characteristics considered in the model included spatial and temporal variation in territory quality, previous reproductive success, cost of changing territories and age. The results of the model outlined an approach for studying site fidelity and provided a series of qualitative predictions for how each factor should affect site fidelity. In particular, the model demonstrated the importance of categorizing spatial and temporal variation in territory quality for the study system. For example, individuals should change territories only in habitats that are spatially variable with respect to territory quality, where an individual has a chance to improve the quality of its location. If individuals are to benefit from paying attention to previous reproductive success, the success needs to be temporally predictable. Spatial and temporal variability have not been simultaneously considered in previous studies of site fidelity, however. The model, therefore, provides a general framework for investigating characteristics of site fidelity in all taxa. One first needs to categorize the habitat in terms of spatial and temporal variation; this categorization leads to a set of specific, testable predictions for individual behaviour.

Study Animal

One group of animals in which site fidelity is observed but seldom studied intensively is the odonates: the dragonflies and damselflies (Jacobs 1955; Koenig & Albano 1985; Alcock 1987; reviewed in Switzer 1995). The current study investigated site fidelity using the habitat selection behaviour of male eastern amberwings, Perithemis tenera (Libellulidae), a small, sexually dimorphic dragonfly species.

Amberwings have several advantages for studying site fidelity. First, male amberwings are often faithful to their previous day’s oviposition site (Jacobs 1955), but switching of oviposition sites within a pond does occur, creating the potential to test for factors that influence site fidelity. Second, individuals are generally present on the pond for several days, permitting within-male comparisons in analyses to control for possible individual differences. Third, other than mating, male amberwings have no obvious bond with the females that they attract to their oviposition sites. Therefore, distinguishing between mate and site fidelity is not necessary. Fourth, when territorial males change locations, they do so within the same pond (Switzer 1995), so emigration and mortality are not confounding factors (Gavin & Bollinger 1988).

Jacobs (1955) and Switzer (1995) provided detailed descriptions of male amberwing behaviour. After arriving at a pond, males begin searching for a suitable oviposition site to defend. Oviposition sites consist of some type of vegetation or other substrate at the water’s surface (e.g. algae clumps, sticks). Searching for oviposition sites is costly for male amberwings; males examining sites are especially vulnerable to predators, and males who have not settled at a specific site are consistently rejected by females for mating (Jacobs 1955; Switzer 1995). Once a male locates a suitable site, he defends the site and the surrounding area from other males and attempts to bring females to the site to mate. The male flies out to a passing female, leads her back to his oviposition site, and ‘shows’ her the site by hovering low next to the site. The female may then mate with the male. In the evening, males fly away from the pond and roost in surrounding pastures and fields. In the current study, males rarely roosted near the pond (i.e. within 20 m), flying at least 50–100 m away before settling (Switzer 1995). No individuals were observed staying overnight within 10 m of the pond’s edge. Because males reoccupied the pond daily, my timescale for site fidelity was from day to day (sensu Alcock 1989).

This study applied the model’s framework to amberwing behaviour, testing the model’s predictions while examining the factors that influence site fidelity in male amberwings. The study pond habitat was first determined to be spatially variable and temporally predictable. Based on this categorization, I then tested whether a male’s previous reproductive success affected his site fidelity and whether individuals were more site-faithful when on relatively high-quality territories, when they were older, and when the cost of changing territories was relatively high.

METHODS

The study was conducted during June, July and August 1992 on a small cattle pond located in
east-central Kansas, U.S.A., approximately 12 km west of the city of Burlington. The pond has a circumference of 152 m; I marked the perimeter at 1-m intervals with surveyor’s flags to aid in recording dragonfly and oviposition site locations (Switzer 1995). I captured males and individually marked them with an alphanumeric code on their right forewing using a permanent black marker.

I took continuous-scan observations using binoculars while amberwings were on the pond, noting the time of all observations to the nearest minute. I recorded male perch and oviposition site locations to the nearest 0.5 m (both along the shore: ‘X-coordinate’ and 90’ out from shore: ‘Y-coordinate’). I also noted all male–male interactions (‘fights’; not including brief pursuits) and male–female interactions (‘courtship’; e.g. showing the oviposition site), using six categories for the fight behaviour and four categories of courtship (Switzer 1995). For fights, I recorded all changes in the category of the fight (i.e. when the fight behaviours changed from one type to another), including the outcome. For courtships, which were briefer than fights, I recorded only the outcome (e.g. mated). If more than one event occurred simultaneously (e.g. an attempted mating during a fight), the same time was recorded for the events, but they were recorded in the order observed.

Because the time scale I used for amberwing site fidelity was from day to day, I defined the distance moved as the shortest shoreline distance (X-coordinate) between the last oviposition site a male defended on day \( t \) and the first oviposition site the male defended on day \( t+1 \). For distances of less than 1 m along the shoreline, I used the straight-line distance between successive oviposition sites (i.e. I included the Y-coordinate). The resulting data for each male included a series of distances moved from day to day. Distance data was not included in the analyses if a male did not hold a territory on 2 consecutive days or if I could not determine a male’s exact oviposition site.

Two measures were used to define site fidelity. First, fidelity was measured as the distance between successive oviposition sites (defined above): the smaller the distance moved, the more site-faithful the male was. Second, fidelity was measured as return to the same territory. Although specific measurements of territory boundaries were not taken, I used a standard territory size unit of 3 m of shoreline distance, which represents an estimate of the minimum average territory size for male amberwings (Jacobs 1955; personal observation). Males not returning to within 3 m of their previous oviposition site were assumed to have changed territories, and those returning to within 3 m were assumed not to have changed territories.

In many odonates, territorial evictions are common (e.g. Tsubaki & Ono 1986) and evictions have the potential to obscure any underlying influences on site fidelity. To search for possible eviction effects, I classified moves into three categories according to the probable cause of the movement: ‘eviction moves’, ‘voluntary moves’ and ‘ambiguous moves’. Eviction moves consisted of situations when the male was evicted from the last territory he held on day \( t \) or before he established a territory on day \( t+1 \). Evictions were assumed to have occurred if the territory resident did not return to the territory following a fight and the intruding male became the new territory resident. If a resident male changed locations, but no eviction was observed, the move was assumed to be voluntary. In some cases, a fight was not observed, but a different male held a territory within 3 m of the focal male’s previous oviposition site before the focal male established a territory elsewhere. In these situations, the cause of these moves was categorized as ambiguous.

After eviction and ambiguous moves were taken into account, I investigated other possible influences on site fidelity. To arrive at predictions concerning these other factors, it was necessary to categorize the pond in terms of spatial and temporal variability in reproductive success (Switzer 1993). To facilitate this categorization, I divided the pond into arbitrary territories, or ‘sections’ (sensu Searcy 1979), again using 3 m as my estimate of territory size. Because the pond has a 152-m circumference, and hence is not evenly divisible by three, one of the sections was 2 m long. This length difference did not affect the results, however.

Categorizing the pond’s spatial variability in reproductive success required a measure of territory ‘quality’. For the purposes of this study, I determined the relative quality of the 3-m sections by ranking the sections on the basis of their mating rate. The mating rate for a given section was defined as the number of matings that occurred per minute that any male occupied a site.

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Switzer: Site fidelity

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on that section. I also ran analyses using mating rate defined as ‘matings per occupied day’ instead of ‘matings per occupied minute’, and achieved equivalent results. For some analyses, it was necessary to calculate a separate set of rankings for each male, so a male’s behaviour could be examined relative to territory quality in an unbiased manner (i.e. examined relative to rankings independent of his contributions). These independent rankings were determined by eliminating the contributions of that male to both the minutes occupied and matings achieved for a section.

With mating rates calculated for all the sections, it was possible to classify the sections into three types (A, B and C) based on occupation and mating success. Type A sections were occupied at some point by males, and males had matings while resident on these sections. Type B sections were also occupied by males, but males never had any matings on these sections. Type C sections were never occupied. I then used these three categories to test for consistent spatial variation in mating success on the pond.

To categorize the pond with respect to temporal variability in reproductive success, I computed the transition probability for mating success on the pond in the following manner. If at least one mating occurred on a 3-m section during a day, the day was defined as ‘good’ for that section; if the section was occupied but no matings occurred, then the day was ‘bad’. Possible transitions occurred when the section was occupied 2 days in a row and the section went from good to good, good to bad, bad to good or bad to bad. To control for individual male effects, I used only consecutive days where a different male occupied the section each day, and each individual contributed only one data point to the analysis. The transition probability was computed by totalling the transitions of different types and calculating the percentage of the total number of transitions that were ‘consistent’ (i.e. either good to good or bad to bad). A transition probability of 0.5 would demonstrate ‘unpredictability’. That is, half of the time the section stayed the same between days, and half of the time it switched (i.e. a mating today may or may not mean a mating tomorrow). Values closer to 1.0 imply ‘consistency’ or ‘predictability’ (i.e. a mating today means a mating tomorrow is likely).

I studied the effect of the density of males on evictions and site fidelity by first defining density.

![Figure 1. Survivorship of male amberwings (N=57). The figure includes only those individuals seen after marking.](image-url)

The maximum number of males present on the pond was determined for each day during the study period. A ‘high density’ day occurred when the maximum number of males present exceeded the mean ($\bar{X}=13.7$ males). On ‘low density’ days, the maximum number of males was less than the mean.

In many analyses, only one observation was used for a male to eliminate potential individual male biases. For such analyses, I chose the first observation (temporally) that met the necessary qualifications for the analysis. This procedure did not mean, however, that these data consisted of only the observations for when males were on the pond for the first time; the first observation that qualified was often not the first observation recorded for the male (e.g. due to eviction moves).

Significance values for non-parametric tests were from Daniel (1990). For most analyses, theoretical predictions were in a specified direction; I therefore used one-tailed tests unless otherwise noted. I report means as $\bar{X} \pm$ se.

**RESULTS**

**Reproductive Life span and Site Fidelity**

I defined a male’s ‘reproductive life span’ to be the time between the first day he was observed at the pond and the last day he was known to be alive. Using this definition, males had a mean
reproductive life span of 6.5 ± 0.67 days (N=57, range: 1–23 days; Fig. 1). Males were not necessarily present at the pond on every day of their reproductive life span; hence, the mean number of days a male was on the pond was slightly lower (5.6 ± 0.59 days; N=57, range=1–19 days).

To determine the overall level of site fidelity in male amberwings, I constructed a frequency distribution of all the distances moved by males (Fig. 2). Male amberwings are highly site-faithful from day to day; 32.5% (62/191) of the time males returned to the exact oviposition site, and 62.3% (119/191) of all moves were back to the same territory (<3 m from the previous site).

Categorizing the Pond Habitat

Predicting how a given factor (e.g. reproductive success or territory quality) should influence site fidelity requires a qualitative categorization of the habitat with respect to temporal and spatial variation quality (Switzer 1993). To categorize the temporal variation in reproductive success for the pond, I computed the transition probabilities for the 3-m sections. When all the sections were pooled, 11 of 16 transitions were either good to good or bad to bad, yielding a transition probability of 0.69. The probability of getting this value if the true transition probability is 0.50 approaches significance (Binomial test: \( P=0.067 \)). If 0.69 is the actual value of the transition probability, however, the low sample size would prevent detection of statistical significance at \( P=0.05 \). Because a qualitative categorization is needed, I pooled all transitions for all males and all sections to increase sample size. This procedure confirmed that the transition probability was greater than 0.50 (197/360 transitions were consistent (0.55), Binomial test: \( P=0.008 \)). Although this transition probability is statistically greater than 0.50, the small difference may not be biologically significant. For this reason, I categorized mating success on the pond as predictable but note where this categorization affects the predictions.

To categorize the habitat in terms of spatial variation in territory quality, I used the section ranks of relative mating rate, and divided the 51 sections into the three section types (Fig. 3). The results indicate that there are three ways to consider spatial variation in mating rate for the pond. First, the male amberwings never occupied the type C sections; they apparently found those sections unsuitable, at least compared with types A and B.

Second, type A and type B sections may differ from each other in terms of mating success. Owing to the contribution of individual males, a pooled diagram like Fig. 3 may be misleading. Therefore, to see whether there were consistent differences between sections of these two types, I used the section rankings based on mating rate that were independent of an individual’s contribution. I first calculated the average number of matings an individual had on type A sections and the average number of matings an individual had on type B sections. A pair-wise comparison of these two averages was then made for each male. In other words, I compared each individual’s average mating success on section types A and B, with the section type based on how other males did on those sections. Individual males had a higher average number of matings on type A sections than on type B sections (Wilcoxon matched-pairs test: \( T=1.5, N=9, P<0.005 \)), indicating that consistent variation in mating rate existed between section types A and B.

Third, there may be consistent variation in mating success between the A sections. To test for this, I divided type A sections in half based on
their relative mating rate, calculated an average number of matings on each half for each male, and performed a within-male pair-wise comparison like that used for the type A versus B analysis above. For this analysis, however, I used males who only held territories on type A sections. I detected no significant difference in the average number of matings on the upper half of the type A rankings versus the lower half within each individual (Wilcoxon matched-pairs test: $T=59.5$, $N=15$, $P=0.50$). Consequently, no consistent, detectable differences occurred between group A sections.

In summary, two of the three ways of considering spatial variation indicated that consistent, inter-territory variation in mating success existed on the pond. The pond, therefore, can be categorized as being spatially variable.

**Model Predictions**

Taken together, these results suggest that the study pond may be categorized as temporally predictable and spatially variable with respect to mating success. Given this categorization, the model makes the following predictions (Switzer 1993): (1) previous reproductive success should affect a male amberwing’s subsequent site choice; males should be less site-faithful (i.e. move a greater distance) following an unsuccessful mating day than a successful mating day; (2) males should be more site-faithful on relatively high quality (i.e. high average mating rate) sections; (3) males that do move should move to higher quality sections; (4) site fidelity should increase as the males become older; (5) less site fidelity should be observed when the cost of changing territories is high. If the pond were not temporally predictable (i.e. the difference between 0.50 and the observed transition probability is not biologically significant), only the first prediction would change: previous mating success should not affect a male’s site fidelity.

**Intra-male Consistency and Evictions**

Before testing the model’s predictions, I needed to consider two factors potentially affecting site fidelity that were not considered in Switzer (1993):
consistency in movement behaviour of individual males and territorial evictions. If these two factors, either singly or together, were responsible for all of the observed patterns of site fidelity, I would not need to look further to explain site fidelity in male amberwings.

One obvious but often overlooked explanation for a pooled distribution of moves (Fig. 2) is that consistent differences exist between males with respect to their movement behaviour (but see Pieman 1981). Although I was unable to test for continuous variation between males in the tendency to move, I could analyse whether some individuals always returned to the same location, while other males always moved. To examine this possibility, I considered individuals for which I had more than one site fidelity measure (i.e. over more than 2 nights), and looked at the number of individuals that never changed territories (moved less than 3 m; 7/51: 13.7%), always changed territories (4/51: 7.8%), or had both changing and within-territory moves (40/51: 78.4%). A significantly higher proportion of males did show individual variation in how far they moved from day to day (i.e. both changed territories and moved within a territory) (N=51, Binomial test: z=4.06, P<0.0001). Therefore, consistent differences in movement behaviour were not solely responsible for the distribution in Fig. 2; variation for move distance existed within individual males.

To see whether territory evictions played a role in male movement, I looked at the proportion of eviction, voluntary and ambiguous moves. Of all between-day moves resulting in a change of territory (>3 m) 31% (22/71) followed an eviction; 42% (30/71) of all changes of territory were voluntary and 27% (19/71) of territory changes were classified as ambiguous. These ambiguous moves were not considered in the rest of the analysis. Because being evicted from a territory the previous day does not necessarily preclude returning to that territory the next day, I tested the hypothesis that evictions cause more males to change territories than expected. The number of changes in territory following an eviction was compared with the number following a non-eviction, using the first move of known cause for each male. A higher proportion of males than expected changed territories following an eviction (8/11 changed after an eviction, 12/40 changed after a non-eviction; \( \chi^2 = 6.61, P = 0.01 \)). Therefore, territory evictions caused significant site infidelity.

Within a day, evictions caused the majority of all changes of territory. Using one territory change per male, evictions were responsible for 72% (33/46) of territory changes within a day (the remainder being voluntary), which is in contrast to the 42% of changes caused by evictions between days. This shift in the proportion of evictions is significant (\( \chi^2 = 8.59, P = 0.003 \)). Therefore, males seemed to be more likely to make voluntary shifts when returning to the pond the next day than they did within a day.

The density of males on the pond might be expected to influence the number of evictions between days, with more evictions occurring on high density days. However, the density of males on the pond did not appear to affect the number of evictions, when either all moves were pooled (high density, 18/94 males were evicted; low density, 15/51 males were evicted; \( \chi^2 = 1.98, P = 0.16 \)), or each individual contributed only one move (high density, 6/32 individuals were evicted; low density, 0/14 individuals were evicted; \( \chi^2 = 3.01, P = 0.082 \)).

Although evictions significantly affected individual site fidelity, they were not responsible for all territory changes between days (i.e. 12/20 or 60% of territory changes in the sample above were voluntary). This result suggests that factors other than evictions may influence the site fidelity of male amberwings. The remainder of the results examined these other factors by testing the five model predictions listed above.

**Testing the Predictions**

To test whether previous mating success affected site fidelity, I used a within-male, pairwise comparison of a male’s voluntary moves between days. For each male, I separated days in which he had at least one mating and days in which he had no matings. I then averaged the distances moved from the previous day’s oviposition site following successful and unsuccessful mating days and compared the averages within each male. Individual males moved significantly further following days without a mating than following successful days (4.0 ± 5.1 m further; Wilcoxon matched-pairs test: \( T = 61.5, N = 21, P = 0.031 \)). This difference remained significant when I used the same set of males, but ignored male identity and compared the distances moved after successful (4.7 ± 2.3 m) and unsuccessful
Therefore, a male's mating success the previous day appeared to affect his site fidelity.

Individuals were predicted to be more site-faithful on high-quality territories. I used the section ranks based on mating rate to look at whether a male was more likely to be site-faithful (move less than 3 m) following an unsuccessful day if he was on a high ranking section. Owing to small sample sizes, I was unable to use the A, B and C section categories used above. Instead, I divided the A and B section ranks (i.e. those that had been occupied) in half and defined ‘low-ranking sections’ as sections falling in the lower half of the rankings, and ‘high-ranking sections’ as sections falling in the upper half of the rankings. I used one observation for each individual; for a move to qualify, it had to be (1) voluntary, (2) following a day without a mating and (3) from a section on which he had no territorial experience before that day. Males were more likely to move if the section was of low rank (6/9 or 67% moved greater than 3 m) than if the section was of high rank (5/21 or 24% moved) \((\chi^2=4.98, P=0.026)\). Therefore, males were more site-faithful on high-ranking sites.

The model predicted that individuals making voluntary moves between days would move to higher-quality sections. To test this hypothesis, I used the first voluntary change in territory (move >3 m) for a male, assumed that a male had an equal chance of moving to a higher or lower-ranking section and compared the ranks of his sections before and after the move. Individual males moved from lower-ranking to higher-ranking sections with voluntary changes in territory \((8/9\) males increased section rank; Wilcoxon matched-pairs test: \(T=3, N=9, P<0.01\)). As a comparison, one can look at this same set of individuals and compare their section ranks after being evicted. These males did not significantly change section ranks after being evicted \((4/9\) males increased rank; Wilcoxon matched-pairs test: \(T=15.5, N=9,\) two-tailed \(P=0.46\)). This result suggests that males making voluntary moves did tend to move to sites of relatively higher quality.

To test the hypothesis that site fidelity increases with age, I compared the distance moved on the first and last day move for individual males that had at least three moves \((5.7 \pm 0.69\) moves). By using first and last moves, I analysed site fidelity by relative age, not absolute age. Individuals moved further on first moves than last moves \((9.8 \pm 6.7\) m further; Wilcoxon matched-pairs test: \(T=23.5, N=15, P=0.019\)).

One possible explanation for this age effect is that older males were more likely to have matings than younger males and were therefore more likely to be site-faithful. However, previous success does not appear to be responsible for the age effect; if anything, males tend to have more matings when younger \((5/15\) had more matings before their first move than before their last move; 1/15 individuals had more matings before their last move than before their first move; Wilcoxon matched-pairs test: \(T=5.5, N=6,\) two-tailed \(P=0.38\)). Another potential explanation for the age effect is that males may be more likely to get evicted from their territory at certain ages (e.g. their first move). To control for this possibility, I used the subset of males whose first and last moves included only voluntary moves. Individuals were still significantly more site-faithful when older \((\text{Wilcoxon matched-pairs test: } T=2, N=8, P=0.012)\). The increase in site fidelity with age is also not simply a result of males holding higher quality territories when older. Males were not on higher-ranking sections before their last move than before their first move, when either males with all move types are included \((6/15\) increased ranks; Wilcoxon matched-pairs test: \(T=46.5, N=14,\) two-tailed \(P=0.74\)) or when males with only voluntary first and last moves are considered \((2/8\) increased ranks; Wilcoxon matched-pairs test: \(T=11, N=7,\) two-tailed \(P=0.69\)). Although separating age and seasonal effects can be problematic, there appeared to be no relationship between date and the mean distance moved by males \((N=30;\) Spearman \(r_s=-0.013;\) two-tailed \(P=0.94\)), so the effect was not simply due to the time of year. Therefore, even when considering the relatively small sample sizes of the tests, the trends for matings and territory quality were in the wrong direction, and evictions and time of year do not explain the pattern. Thus, site fidelity did increase with age.

The model predicted that males would be more site-faithful when the cost of changing territories was relatively high. The cost of changing territories can be difficult to estimate, however. In general, one might expect the cost of moving to be positively related to the number of males per available sites \((\text{Greenwood 1980; Weatherhead &}\)
Boak 1986; Bensch & Hasselquist 1991; Switzer 1993; Beletsky & Orians 1994). As the number of males increases, it becomes more likely that suitable sites will be occupied; males will then have to either search longer for an available site (costly in terms of predation, missed matings, and interactions with territory residents) or evict a male at an occupied site. Therefore, one would expect males returning to the pond on high-density days to be more site-faithful (i.e. move a shorter distance) than males on low-density days.

To test this hypothesis, I compared the distances of voluntary, between-day moves on high-density and low-density days, using a single move for each individual. On average, males tended to move further on low-density days (11.9 ± 5.4 m) than on high-density days (7.9 ± 3.6 m), but the trend only approached significance (Mann–Whitney U-test: \( z = 1.55, N = 38, P = 0.061 \)). Given the borderline nature of this result, only weak evidence supports the hypothesis that site fidelity should increase with the number of males on the pond, and therefore increasing movement cost.

**DISCUSSION**

The results present a picture of how social, experiential and habitat factors may influence site fidelity. In amberwings, other males influence an individual’s habitat selection by causing him to switch locations through evictions, and increasing the number of males on the pond may make him more likely to stay in the same location if he can. The quality of the location affects an individual’s habitat selection; males are more likely to return to high-quality territories, and when they move voluntarily, they move to better locations. An individual’s previous experience also influences his habitat selection; previously successful males are more likely to be site-faithful. Finally, as males get older, their site fidelity increases.

**The Importance of Spatial and Temporal Variability**

A unique aspect of this study was categorizing the spatial and temporal variability in mating success and using that categorization to generate the predictions (Switzer 1993). Studies have demonstrated the importance of spatial variability, either by relating the spatial variation to site fidelity generally, showing that individuals tended to switch to higher-quality territories or both (Newton & Marquiss 1982; Lanyon & Thompson 1986; Tsubaki & Ono 1986; Beletsky & Orians 1987; Bensch & Hasselquist 1991). To my knowledge, Beletsky & Orians (1987) provided the only other empirical study that explicitly considered temporal variation in relation to site fidelity; male red-winged blackbirds, *Agelaius phoeniceus*, apparently responded to previous reproductive success in a habitat where success was temporally predictable. Before the current study, though, an a priori linking of both spatial and temporal variation in territory quality was seldom, if ever, attempted in studies of site fidelity.

In a study of mate fidelity, however, Desrochers & Magrath (1993) considered both types of variability in their study of divorce in European blackbirds, *Turdus merula*. They found that breeding success was temporally predictable and spatially variable, and individuals were more likely to change mates if they had been on a low-quality territory. Thus, spatial and temporal variation in reproductive success are important for both site and mate fidelity. Future studies of these phenomena should take these environmental characteristics into account when making predictions.

In the current study, mating success was determined to be temporally predictable and to affect site fidelity. The temporal predictability, while present, was not extremely strong. For individuals to benefit from knowledge of previous reproductive success, however, a 1.0 probability of mating on the same territory on successive days may be both unlikely and unnecessary. A less than perfect correlation in mating success between days may be influenced by changes in the weather, female density and arrival and male density. Also, if male quality plays any role in mating success, changes in the territory’s resident could affect the mating outcome on a given territory. On the other hand, any consistency in outcome would potentially give an individual with experience more information about site quality than he had previously. Switzer (1993) showed that for these middle ranges of consistency, other factors (e.g. relative differences in quality among territories and the cost of changing territories) may be more important in determining optimal habitat selection decisions than they are at more extreme values of consistency.
Mating Success and Territory Quality

The current study suggested that previous mating success influenced amberwing site fidelity, a result reported in numerous avian studies (reviewed in Greenwood & Harvey 1982; Switzer 1982). An alternative explanation, however, is that the correlation between mating success and site fidelity is merely a by-product of individuals responding to cues of territory quality other than direct reproductive experience. That is, males are more site-faithful on high-quality territories and, because they are on a high-quality territory, are more successful in obtaining matings. The opposite is true of males on low-quality territories. Switzer (in press) isolated mating success from territory quality, however, and found a direct relationship between mating success and site fidelity.

Demonstrating that male amberwings respond to spatial variation in territory quality begs the question of how individuals can determine this quality. Male amberwings may be able to recognize a high-quality territory either directly, indirectly or both. First, males may be able to directly assess habitat quality by recognizing some intrinsic character(s) that correlates with relatively high-quality sites (Orians & Wittenberger 1991), such as a certain type of oviposition substrate or the absence of predators. This study suggests that, in addition to intrinsic habitat cues, males may also be using their own mating experience to determine territory quality. Second, males may be able to determine territory quality indirectly by either observing females mating or relying on the occupancy of the site by other males as a cue (Stamps 1987). Although I have no data on female amberwing site fidelity for this population, Jacobs (1955) found that individual females tended to return to the same oviposition sites. This fact, combined with the tendency of males to be more site-faithful following a day with a mating, creates a situation in which individuals may profit by using the residence of other males as an indirect cue for territory quality. A territory resident may also indicate an oviposition site that is relatively safe from predators. Finally, and perhaps most likely, individuals may use both indirect and direct cues as information on territory quality. Whether direct or indirect cues take precedence in habitat selection may depend on factors such as his experience and the time available for settling on a territory.

Territorial Evictions and Site Fidelity

Alcock (1993) presented a conceptual framework for how factors similar to those considered in this study should affect the site fidelity of territorial male insects. Superficially, some of his predictions appear to differ from those of the current study. For example, he predicted that site fidelity should be lower when the competition for sites is high, but the current study predicted that site fidelity should increase with site competition. Most of Alcock’s (1993) predictions, however, concern factors that would increase the likelihood of males being evicted from their territories; his framework did not distinguish voluntary and involuntary moves. His prediction focused on the idea that more males would be evicted when the competition for sites is high, leading to low site fidelity (Alcock 1993). The current study separated analyses concerning territorial evictions from analyses considering other factors.

Territory evictions constitute one of the primary causes of site infidelity for male amberwings, a result also found for the dragonfly Namophya pygmaea (Tsubaki & Ono 1986). On the surface, a relationship between evictions and site infidelity may appear obvious; however, territory evictions do not necessarily lead to changing territories in other dragonfly species. Male Libellula (Plathemis) lydia (Campanella & Wolf 1974) and Paltothemis lineatipes (Alcock 1987) ‘temporally partition’ their territories. In these species, a series of territory evictions throughout the day creates a sequence of different territorial males on the same territory. Individuals are also commonly site-faithful, often occupying the same territory in a similar sequence the next day. The effect of territory evictions on site fidelity, therefore, seems to differ at least between species of dragonflies.

Evictions may or may not be important in site fidelity in avian systems. Many species of birds are generally considered to have a ‘prior residency advantage’, where the resident male is able to both hold the territory during the entire breeding season and evict any newcomer at the beginning of the next season (Nolan 1978; Lawn 1982; Lanyon & Thompson 1986; Jakobsson 1988). In these species, evictions may not have been implicated as influencing site fidelity either because they are infrequent or rarely observed. Other avian studies have mentioned the potential for intra-specific competition to affect site fidelity (Newton
& Marquiss 1982; Dow & Fredga 1983; Pärt & Gustafsson 1989; Bensch & Hasselquist 1991; Newton 1993), but few studies have shown that evictions were responsible for a significant proportion of site infidelity. Site fidelity of female goldeneyes, Bucephala clangula, however, does appear to be affected by evictions (Dow & Fredga 1983). Also, in their study of mate fidelity, Ens et al. (1993) concluded that evictions either directly or indirectly contributed to a substantial number of divorces and territory changes in oystercatchers, Haematopus ostralegus. This apparent disparity between avian and dragonfly species may simply be due to a difference in emphasis and perceived importance in studies of site fidelity in the two groups. In any case, future studies in all taxa would profit by including an analysis of how evictions affect site fidelity.

Age

Site fidelity increases with age in male amberwings. This result appears to be inconsistent with dragonfly studies that have shown less territoriality and more movement as the males age (e.g. Forsyth & Montgomerie 1987). The current study considered only moves between days when the male was territorial, however, eliminating any potential age groups of males that were not competitive enough to hold a territory. Many avian studies have also shown that older individuals are more site-faithful (reviewed in Switzer 1993). Except for a few studies (e.g. Newton & Marquiss 1982; Pärt & Gustafsson 1989; Newton 1993), however, separating the effect of age from those of the many potential confounding variables in these bird species has proven difficult. In this study, previous mating success, mate fidelity, territory quality, and seasonal effects could not explain the increase in site fidelity with age. Therefore, age itself appears to be the most likely candidate for the change in male amberwing behaviour.

In the model, the predicted increase in site fidelity with age was due to a decrease in the opportunity to make up the fitness cost of changing territories (Switzer 1993). An individual incurred the same cost each time it changed territories. As the male came closer to the end of its life span, it had fewer chances to make up this cost by obtaining the increase in reproductive success on the new territory. Whether this shrinking opportunity is responsible for the change in amberwing behaviour is unclear, because at least one other consistent explanation exists. The increase in site fidelity might be due to information accumulated by the individual over time on a specific region of the pond. This information base may decrease some of the uncertainty involved in future oviposition site choices, and therefore increase the benefit to the individual for remaining site-faithful as it becomes older (Beletsky & Orians 1987; Pärt & Gustafsson 1989).

The results of this study suggest that amberwing site fidelity is comparable to the site fidelity of other taxonomic groups. This is an interesting conclusion, because the time scales of site fidelity may differ widely between taxa (e.g. years for birds versus days for dragonflies). Relative time may actually be what is important to the individual, however. Due to the relatively short reproductive life span for male amberwings, the time a male spends off the pond represents a significant proportion of his reproductive time, as does the time spent on wintering grounds for a migratory bird. Future studies on other taxa, investigating both the generality of these site fidelity predictions and the importance of time scale on site fidelity, would significantly increase our understanding of this interesting phenomenon.

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REFERENCES


Ornithol. Monogr., 26.

Ornithol. Monogr., 26.

Ornithol. Monogr., 26.


