Site fidelity and the costs of movement among territories: an example from colonial web-building spiders

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Abstract: Species differ in whether they exhibit strong site fidelity or move readily among sites. To understand the adaptive significance of site fidelity it is necessary to measure the cost of relocating to new sites, but this is very difficult with most species because it entails following individuals during the entire course of their transition. We studied the colonial web-building spider *Metepeira incrassata* (Araneae: Araneidae), which defends individual orb webs within a large, shared frame web. Colonies are heterogeneous habitats, with more prey but also more predators at the periphery of the colony relative to the central core. We measured relocation costs in this species by breaking them into the following components, (*i*) searching costs, (*ii*) establishment costs, and (*iii*) lost-opportunities costs, or the potential benefits of alternative behaviors that an animal might engage in if it were not relocating. We observed spiders that were in the process of establishing their orb webs at the start of the foraging day and conducted experiments to examine the costs of relocation by transferring spiders between locations within the colony. Transferred spiders had more fights with conspecifics than non-transferred spiders did, and the number of fights was positively correlated with the distance moved. However, searching and establishment costs seem unimportant, as individuals moving within their territories were as active as individuals moving to new sites. Transferred spiders faced greater lost-opportunities costs in the form of time spent on prey-capture orbs, as they significantly delayed orb construction. Lost-opportunities costs seem to be the most important component of relocation costs in this species and are likely to be generally important among species. This study is one of the few to document movement costs through direct observation.

Résumé : Certaines espèces sont fidèles à un site, d'autres se déplacent d'un site à l'autre. Pour bien comprendre l'importance évolutive de la fidélité à un site, il faut mesurer les coûts reliés à la colonisation de nouveaux sites, ce qui s'avère une tâche très difficile chez la plupart des espèces, car il faut suivre des individus pendant toute la période de transition. Nous avons étudié des araignées orbitèles de l'espèce coloniale *Metepeira incrassata* (Araneae : Araneidae), qui défendent leur toile propre, contenue dans une toile plus vaste qu'elles se partagent. Les colonies sont des habitats hétérogènes qui contiennent plus de proies, mais aussi plus de prédateurs, en périphérie que dans la zone centrale. Nous avons évalué les coûts d'un déménagement chez cette espèce selon trois catégories, (*i*) la recherche d'un site, (*ii*) l'établissement et (*iii*) les occasions ratées ou les avantages potentiels d'autres comportements que pourrait adopter l'animal s'il ne déménageait pas. Nous avons observé des araignées occupées à construire leur toile circulaire au début d'une journée de recherche de nourriture et nous avons mis au point des expériences pour évaluer les coûts reliés au déménagement en déplaçant des araignées d'un site à l'autre au sein d'une colonie. Les araignées déplacées ont livré plus de combats les unes avec les autres que les araignées non déplacées et la fréquence des combats était en corrélation positive avec la distance du déplacement. Cependant, les coûts reliés à la recherche du site et à l'établissement semblent avoir eu peu d'importance puisque les araignées qui se déplaçaient dans leur territoire étaient aussi actives que celles qui ont gagné un nouveau site. Le araignées déplacées ont eu à faire face à des coûts plus élevés dûs à des occasions ratées, car elles passaient moins de temps à chasser sur leur toile parce qu'elles avaient pris un retard significatif à construire leur toile. Les coûts reliés aux occasions ratées semblent être la principale composante du coût du déplacement chez cette espèce et probablement aussi chez d'autres. Cette étude est l'une des premières à évaluer les coûts des déplacements par observation directe.

[Traduit par la Rédaction]

Introduction

Site fidelity is the propensity to return to a previously occupied location. Examples of site fidelity abound, and it occurs both in territorial species that defend particular areas and in nonterritorial animals that have undefended home ranges. For example, territorial male songbirds generally return to the same sites year after year (e.g., Greenwood and Harvey 1982), limpets return to the same resting sites after foraging excursions (Iwasaki 1995), and foraging dragon-

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flies return repeatedly to the same perches (Baird and May 1997). Site-faithful animals benefit because they reduce the risk that they will not find an appropriate new site. In addition, site-faithful animals may learn about the location of resources and escape routes (e.g., Stamps 1995) and incur reduced defense costs in interactions with familiar neighbors compared with strangers (Eason and Hannon 1994). However, even in species that show site fidelity, individuals sometimes change sites. The decision to be site-faithful or to switch sites is influenced by site quality, habitat stability, population pressure, knowledge of other sites, and predictability of the current site. Empirical support for each of these has been found (reviewed in Switzer 1993).

Another factor that can influence site fidelity is the cost of relocation to new sites. An analytical model (Morris 1987) and a dynamic model (Switzer 1993) both predict that an increase in relocation costs will decrease the probability of an animal seeking an alternative site; the benefits of switching must increase to make up for these costs. The ideal species for the study of relocation costs would show a moderately high level of site fidelity, but also evidence of occasional relocation and variation in territory quality that might be sufficient to give individuals reason to relocate. It should be amenable to manipulation and continuous observation, and individuals should be numerous enough to accommodate robust experimental designs. Few study systems meet these criteria, so few empirical data exist on relocation (Switzer 1993). Two related problems, measuring the costs of natal dispersal and the costs of breeding dispersal, face similar methodological barriers, and empirical estimates of dispersal costs are also few (Johnson and Gaines 1990; Waser et al. 1994; Plissner and Gowaty 1996). Generally the costs of dispersal have been measured by assessing differences between classes of dispersers and non-dispersers (e.g., Ward et al. 1998 for aphids; Van Vuren and Armitage 1994 for marmots) rather than by following individuals. This and similar methodology have yielded valuable inferences about the costs of dispersal, but behavioral ecologists should take advantage of opportunities to verify these insights by observing organisms throughout the relocation period.

We studied an organism that is in many ways ideal for the study of relocation costs. Colonies of the orb-weaving spider *Metepeira incrassata* F.O. Pickard-Cambridge (Araneae: Araneidae) range in size from tens to thousands of individuals and are communal–territorial in organization. Spiders cooperatively construct a shared framework consisting of an irregular network of long silken lines strung in gaps in the vegetation. Within that framework, every morning each spider constructs its own orb web for prey capture. Orb webs are defended against other individuals. At the end of the foraging day, at dusk or when heavy rains begin, spiders take down their orb webs and ingest the silk. They are quiescent on the frame lines through the night (G.W. Uetz, unpublished observation; D. Kroeger, personal communication). At dawn, if it is not raining, spiders begin moving about in the communal framework, often laying down additional silk. Only at this time do they change position within the colony. After orbs are built, spiders do not willingly abandon them. These spiders occur in large numbers and can be observed continuously and marked and manipulated easily, and replicate colonies can be studied in a relatively short span of time. Both predation on the spiders (primarily by wasps) and prey capture can be directly observed and quantified (Rayor and Uetz 1990, 1993; Uetz and Hieber 1994; Rayor 1996).

Large *M. incrassata* colonies are heterogeneous habitats with respect to ecological costs and benefits, so territorial quality varies over short distances. In general, spiders at the periphery of the colony capture more prey, but face higher predation risk than do spiders in the central core of the colony, and the magnitude of these costs and benefits changes as spiders grow (Rayor and Uetz 1990, 1993). The optimal location for a particular spider to place its orb is affected by a number of variables, including the spider's size and its recent feeding success, and is likely to change over time (E.M. Jakob, A.H. Porter, and G.W. Uetz, in preparation). Colonies are generally size-structured, with larger spiders in the core and smaller spiders at the periphery. This structuring may reflect competition for web sites in the core (Rayor and Uetz 2000) as well as different priorities for spiders of different sizes: a dynamic model predicts that smaller spiders will be more driven by energetic needs, whereas large spiders will minimize predation risk (E.M. Jakob, A.H. Porter, and G.W. Uetz, in preparation).

Data from marked individuals show that *M. incrassata* do indeed change the positions of their orbs over time. In colonies approximately 8 m^3 in size, for example, spiders moved their orb webs an average of 40.5 cm (SE = 3.008 cm, range = 0–100 cm; N = 74) from one day to the next (E.M. Jakob, unpublished data). In another study, 8% of spiders that were not distributed by conspecifics moved to a new site in the morning prior to orb construction (Rayor and Uetz 2000). Movement rates were over 13% for those that were disturbed by conspecifics.

Most models combine relocation costs into a single movement parameter, but Switzer (1993) suggested breaking costs into separate components. Here we suggest a slight modification of Switzer's scheme that includes searching, establishment, familiarity, and lost-opportunities costs. *Searching costs* comprise the increased energetic expenditure and predation risk of moving while trying to identify a new territorial site. *Establishment costs* comprise the energy expenditure and the risk of injury and predation involved in securing a site that has been located. *Lost-opportunities costs* are the expected energetic or fitness rewards that might have accrued had a territory been maintained during the relocation and reestablishment period. Switzer (1993) combined establishment and lost-opportunities costs into a single parameter. We distinguish them for two reasons: (1) because measuring lost opportunities requires knowledge of the abandoned site, whereas establishment costs do not, and (2) because lost-opportunities costs, unlike establishment costs, accumulate during the entire relocation process, and thus increase with the time necessary for relocation. Switzer also includes *familiarity costs* in his scheme, which comprise the energy expenditure and the exposure to injury and predation risk associated with becoming familiar with a newly established territory's refuges, foraging areas, neighbors, etc. Because *M. incrassata* essentially construct their own territories when they build a web, familiarity costs are restricted to fights with neighbors. We did not address familiarity costs in our study.

In examining the costs of relocating territories to new

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sites we had two main objectives. First, we wanted to identify which, if any, type of relocation cost is important for these spiders. Second, we were interested in the relationship between the distance moved between territories and the costs of relocation, which is important in understanding the decisions about territory placement made by these spiders. If relocation costs are incurred primarily through territorial establishment or lost opportunities rather than searching, then distance and cost would not necessarily be highly correlated.

Materials and methods

We conducted our study in Fortin de las Flores, Veracruz, Mexico (approximately 1000 m elevation), during the summer months of 1993. The study site was located in a coffee plantation typical of that region: multicrop tropical agriculture (coffee, bananas, citrus fruits, flowers) set amidst secondary tropical rain forest vegetation (see details in Benton and Uetz 1986; Uetz and Hodge 1990). We collected three spider colonies from nearby areas and established them in experimental open observation frames at the study site. Frames were constructed out of PVC plastic pipe, with exterior dimensions 2.8 × 2.8 × 2 m high. Within this frame, a network of rope created 1 × 1 m cubes, into which approximately 500 spiders were released. Spiders built scaffolding and spun webs within 2–3 days of release. This study was begun several weeks after colonies were established.

It was impossible to predict which individuals would choose to relocate and which would choose to remain in place on a given day, so to ensure that adequate numbers of relocating and site-faithful spiders were watched over our 2-month field season, manipulation was necessary. There were four treatment groups. Two of these were transfer groups: individuals were transferred from the periphery to the core or from the core to the periphery. Preliminary observations suggested that transferred spiders were likely to continue moving after release. We compared these transferred spiders with non-transferred spiders from the core and periphery. We first attempted to remove non-transferred spiders from the web and replace them in the same location (thus treating them exactly like the transferred spiders), but the disturbance generally caused spiders to begin moving through the colony. Instead, non-transferred spiders were not manipulated.

We began to observe spiders at dawn, prior to and during the initiation of orb-web construction. Focal observations were divided among the three colonies and among small, medium-sized, and large spiders. Large spiders were females (males do not construct orbs) and were not guarding egg sacs. Individuals were assigned to treatment groups by the roll of dice. We watched 8–10 spiders of each size class in each treatment group for a total of 115 spiders. Observations began when spiders first began moving about the frame web but before they began orb construction. Because larger spiders become active earlier in the day, while smaller spiders remain quiescent (Rayor and Uetz 1990, 1993, 2000; Jakob et al. 1998), a series of observations of different individuals on the same day could be undertaken. Spiders were not individually marked but were constantly observed. Non-transferred spiders rarely moved very far, so two could be watched simultaneously. On one occasion, two observed spiders interacted and one was selected by coin toss to remain in the dataset. On another occasion, a spider was lost from view and the sample was discarded. To maximize the number of different individuals that we watched, we ended focal observations after 30 min. Spiders were captured after observation and released elsewhere to ensure that they were not resampled. Samples were spread over 30 days.

We took data relevant to the costs of searching, establishment, and lost opportunities, but we did not attempt to measure the costs of orb-site familiarity in these spiders. In particular, we noted the time spiders spent moving through the colony, the estimated path length a spider moved along the lines of the frame web prior to initiating construction, the net distance an animal moved in the colony from the start of the observation period to its end (the shortest distance between its starting and ending points), the total number of fights the focal spider had, and the time spent constructing or sitting on an orb. Fights included instances when the focal spider responded to another spider in any of the ways described by Hodge and Uetz (1995): freezing in response to another spider's movement, retreat from another spider, plucking the web, approaching another spider, shaking the web, bouncing, and chasing or contacting the opponent. One fight may include a number of these behaviors. Fights were considered to have ended when neither spider was oriented towards the other for at least 2 min. Focal spiders sometimes interacted with the same individual several times during the observation period.

Each of the five behaviors listed above was tested as the dependent variable in a complete three-factor analysis of variance (ANOVA) with all interaction terms. Factors included the colony in which the trial took place (one of three), treatment (core, periphery, transferred from core to periphery, or transferred from periphery to core), and spider size (small, medium, or large). We also examined the relationships between time spent moving, path length, net distance moved, and number of fights. Because we do not know the cause and effect relationship between these variables (more mobile spiders may encounter more individuals and have more fights, or spiders that have more fights may be forced to move more), we used correlation rather than regression analyses.

Results

Searching costs

We consider three possible sources of searching costs for *M. incrassata*: moving a longer distance on frame lines prior to initiating orb construction (which might correlate with energy expenditure), the possibility of more fights during movement, and any increased risk of predation during moving.

Transferred spiders (both core-to-periphery and periphery-to-core classes) moved longer net distances than did non-transferred spiders ($F_{[3,67]} = 22.051$, $p < 0.0001$; Fig. 1A). This was the desired effect of transfer, as we were attempting to induce manipulated spiders to search for new sites. There was a significant interaction between treatment and colony ($F_{[6,67]} = 2.608$, $p < 0.03$) because spiders transferred from periphery to core moved exceptionally long net distances in one colony.

However, when we compared the path lengths of spiders along the frame lines we found no significant differences across the four treatment groups (periphery: 271 ± 40 cm; core: 223 ± 40 cm; core to periphery: 339 ± 47 cm; periphery to core: 227 ± 49 cm; $F_{[3,77]} = 1.621$, $p > 0.19$). Thus, there were no searching costs attributable to the energy spent in physically moving. Spider size did significantly affect path length: medium-sized spiders had the longest paths, followed by small, then large spiders (medium-sized spiders: 346 ± 45 cm; small spiders: 261 ± 32 cm; large spiders: 189 ± 34 cm; $F_{[2,77]} = 5.036$, $p < 0.01$), but only medium-sized and large spiders differed significantly in Scheffé's post-hoc tests ($p < 0.01$). No other terms were significant.

Treatment significantly affected the number of fights that spiders had ($F_{[3,77]} = 12.810$, $p < 0.0001$; Fig. 1B). Spiders in the core-to-periphery transfer group had the most fights,

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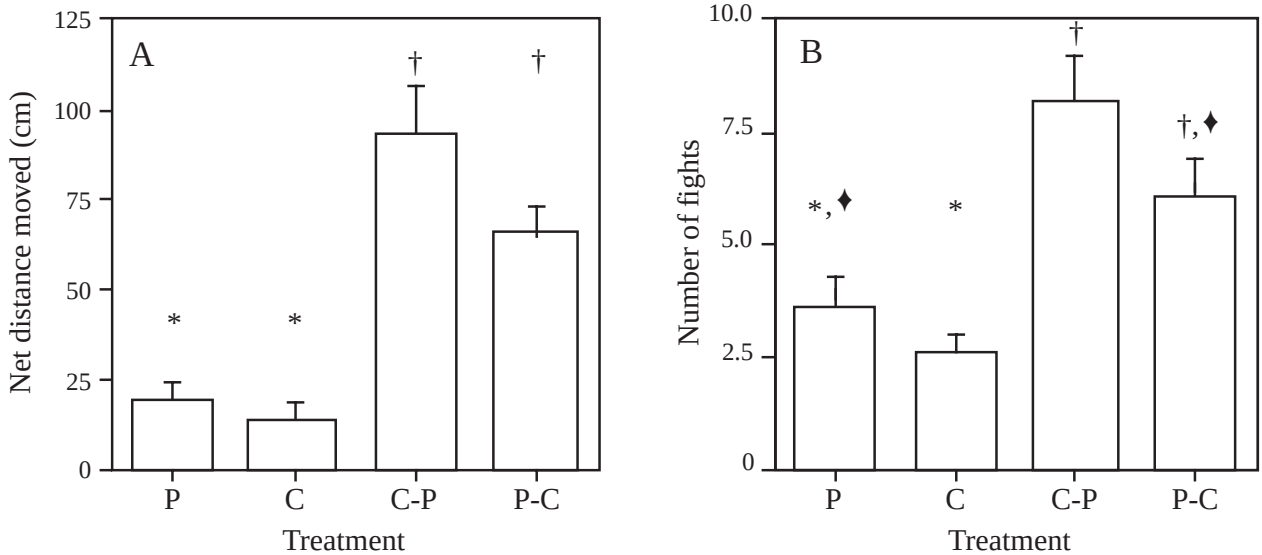
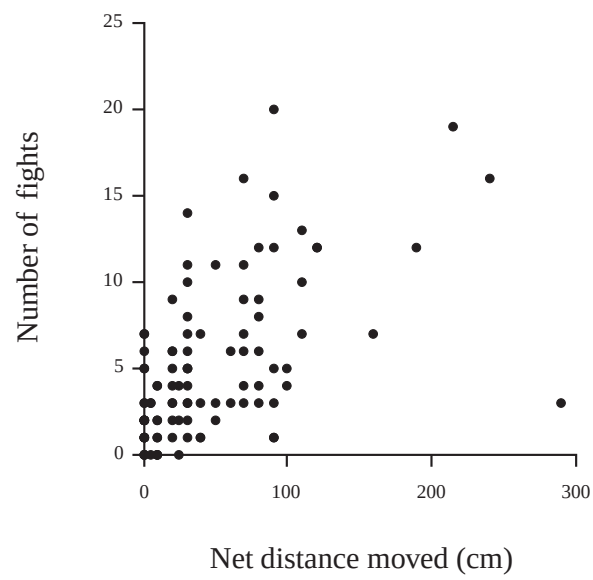
Fig. 1. (A) Total net distances moved (mean and standard error) by spiders in four treatment groups, on the periphery (P), in the core (C), transferred from the core to the periphery (C-P), and transferred from the periphery to the core (P-C), from the start to the end of a 30-min observation period. (B) Numbers of aggressive fights (mean and standard error) of spiders in the four treatment groups during a 30-min observation period. Bars with the same symbol are statistically indistinguishable (Scheffé's post-hoc tests following ANOVA).



followed by the periphery-to-core transfer group, periphery group, and core group. No other main effects or statistical interaction terms were significant. For the pooled dataset, net distance moved was highly positively correlated with number of fights (r = 0.555, p < 0.0001; Fig. 2).

We saw no predation attempts on any spider during this experiment.

Fig. 2. Correlation between net distance moved from the start to the end of a 30-min observation period and the number of fights focal spiders had.



Establishment costs

Each day, all *M. incrassata* must establish a new territory by building an orb web, regardless of whether or not they move. However, spiders might be able to take over an orb rather than investing in construction. We saw seven web takeovers in the 57.5 h of observation, but these were not significantly biased towards any treatment group: five were transferred spiders (three periphery-to-core and two core-to-periphery) and two were resident periphery spiders. Four intruders were small and three were large. In six of the seven cases the orb was lost by a small spider. One medium-sized spider lost its orb to a large focal spider.

Lost-opportunities costs

In this species, lost opportunities are represented by the foraging time that spiders would have gained had they not moved. The magnitude of lost opportunities depends on the time spent in relocation and the rewards expected at the abandoned site. Spiders that were transferred from core to periphery spent significantly more time moving on the frame web than spiders in the other treatment groups ($F_{[3,77]}$ = 5.809, p = 0.0012; Fig. 3A). Smaller spiders spent more time moving than larger spiders (small spiders: 722 ± 52 s; medium-sized spiders: 584 ± 71 s; large spiders: 428 ± 77 s; $F_{[2,77]}$ = 5.649, p = 0.0051). The main effect of source colony on time spent moving was not significant. The interaction between colony and size class was significant ($F_{[4,77]}$ = 2.553, p < 0.05) as was the three-way interaction among treatment, colony, and size class ($F_{[12,77]}$ = 2.257, p < 0.02). These significant interactions resulted from one colony where time spent moving was the same for all size classes.

Time that was not spent in moving could be spent in preparing an orb for prey capture or waiting for prey in the center of an orb. We examined the total time that spiders spent either constructing an orb or sitting at its hub (either during construction or on the hub of an orb that they took over). We found significant effects of treatment ($F_{[3,77]}$ = 3.44, p < 0.03; Fig. 3B). Significant effects were found in the interaction between treatment and size class ($F_{[6,77]}$ = 2.505, p < 0.03) and between colony and size class ($F_{[4,77]}$ = 2.609, p <

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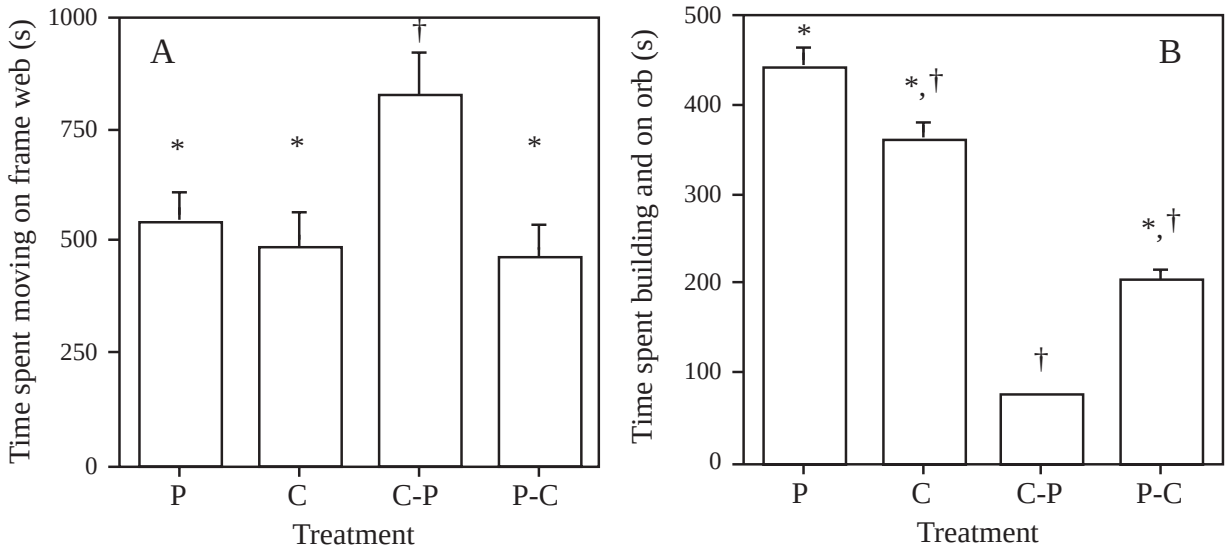
Fig. 3. (A) Time (mean and standard error) spent moving on the frame web by spiders in four treatment groups, on the periphery (P), in the core (C), transferred from the core to the periphery (C-P), and transferred from the periphery to the core (P-C). (B) Time (mean and standard error) spent building an orb or sitting at an orb hub by spiders in the four treatment groups. Bars with the same symbols are statistically indistinguishable (Scheffé's post-hoc tests following ANOVA).



0.05), and in the three-way interaction among treatment, colony, and size class ($F_{[12,77]} = 2.041$, $p < 0.04$). Small spiders responded differently to treatments than did medium-sized and large spiders, spending more time on orbs in the periphery-to-core treatment and less time in the periphery treatment. In addition, medium-sized spiders in one colony spent more time on orbs than did those in the other colonies. Although we did not watch all spiders until they initiated orb-building, we noted that several transferred spiders had not begun building an orb web even 90 min later.

We found a significant negative relationship between net distance moved and time spent building webs during the 30-min observation period, although the correlation coefficient was low ($r = -0.263$, $p < 0.01$). This shows that relocating spiders needed more time to initiate construction at their new sites. The low correlation may be due to the fact that most spiders had not begun building by the end of the focal observation period: 52% of spiders that did not move initiated orb construction, while only 21% of spiders that moved even a short distance initiated orb construction.

Discussion

We found several costs of movement among territories in *M. incrassata*, but not all were important. A spider's decision to shift territories is likely to be influenced by searching and lost-opportunities costs, especially the latter. We argue that establishment and familiarity costs are not likely to be important for *M. incrassata*. It is likely that the relative costs of these relocation categories, and therefore the source and strength of selection on territory relocation, vary greatly across species. However, few studies are available that kept track of individuals during the relocation process and were thereby able to consider these cost breakdowns in detail.

Searching costs

Of the three searching costs we examined, we found no evidence for an effect of the physical exertion of moving, as individuals that stayed in the same area moved as far in the frame web as individuals moving to new sites. The non-transferred spiders simply restricted their movements to the immediate area around their building site, whereas the transferred spiders moved greater net distances. We did find evidence of a second cost. Transferred spiders had more fights than non-transferred individuals (Fig. 1B), and the number of fights correlated well with the net distances that focal spiders moved after being transferred (Fig. 2). Fights are not particularly dangerous for these spiders: only a handful of injuries and deaths have been seen in hundreds of person-hours of observation (G.W. Uetz, personal observation; D. Kroeger, personal communication). Nevertheless, vigorous movement associated with conspecific interactions may lead to increased energy expenditure, which has been estimated to be at least 40% greater than resting metabolism for orb weavers the size of *M. incrassata* (Anderson 1970; Tanaka 1989; Uetz and Hieber 1997; but see Riechert 1988). But these spiders have very low resting metabolism and even with twice the number of fights, it is difficult to argue that the increased energetic expenditures would make up a significant proportion of the total relocation cost or of a daily energy budget.

We found no evidence of another expected searching cost, an increased probability of predation while moving. The danger of moving among territories has been widely studied, probably more than any of the other elements of movement costs we describe here, especially in natal and breeding dispersers. However, most of these studies rely on assumptions about movement patterns to distinguish between mortality and dispersal off the study area (Koenig et al. 1996). Although dispersal seems inherently dangerous (Van Vuren and Armitage 1994), estimates of mortality risk during dispersal range from extremely high (59% for dispersers vs.

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26% for nondispersers in breeding dispersal in red-cockaded woodpeckers, *Picoides borealis*; Daniels and Walters 2000) to negligible or zero (natal dispersal in marmots, Van Vuren and Armitage 1994; snowshoe hares, Gillis and Krebs 2000). These mortality costs are usually presumed to be due largely to predation. In spiders, the cost of searching has been found to be important in solitary species that shift their web sites by walking through dangerous territory. Vollrath (1985) found that even starved *Nephila clavipes* (Araneae) were reluctant to shift web sites, and attributed this to an increased risk of mortality during travel. Similarly, Lubin et al. (1993) found that the probability of the desert spider *Latrodectus revivensis* (Theridiidae) surviving a 2-day interval dropped from 98% for spiders at their web sites to 59% for those that moved. In contrast, *M. incrassata* are probably not at a meaningfully greater risk of predation while moving to new sites within the colony. Only 5.5% of all predator attacks occur before 10:00, when webs are being set up and the activity level is at its highest, because the most common predators (wasps) are not active until later in the day (Rayor and Uetz 2000).

Establishment costs

Because *M. incrassata* must invest in a new orb each day regardless of whether or not they shift territories, all spiders pay establishment costs. They can circumvent these establishment costs by usurping an orb owner, but this strategy was no more likely to be used by transferred spiders than non-transferred spiders. One potential establishment cost that we could not measure was whether spiders that moved were constrained by conspecifics from establishing their orbs in optimal locations or orientations, thereby incurring a reduction in future prey intake. Leborgne and Pasquet (1987) found that settlement of orb weavers within a site occupied by conspecifics also influenced their web size, with late arrivals being constrained to build smaller webs in suboptimal locations. Fights may have even subtler influences on settlement patterns in *M. incrassata*, perhaps contributing to the delayed web construction seen in smaller size classes (Rayor and Uetz 2000), although additional factors are also likely to influence time of construction (Jakob et al. 1998).

Establishment costs have been measured separately from search costs in some species. Small et al. (1993) found that there was no difference in mortality between these two phases of movement in radio-tagged ruffed grouse, *Bonasa umbellus*. In comparison, we expect that establishment costs will be much higher in species that invest in more permanent modifications to their environment, like cavity-excavating species (e.g., woodpeckers, bark beetles), burrowers (e.g., desert isopods, Baker 1998; many rodents), and dam builders (beavers).

Lost-opportunities costs

Spiders that invested time in relocation lost time foraging on their orb webs. Significantly fewer transferred spiders than non-transferred spiders began an orb web during the observation period. In the season when this experiment took place, heavy rains shortened the foraging day to an average of approximately 5 h, so spiders were likely to be particularly energetically stressed. Thus, a half-hour delay in orb construction meant 10% less time spent foraging. Time spent foraging is crucial to the success of these spiders. Foraging success has important life-history consequences for spiders (Jakob and Dingle 1990) and in *M. incrassata*, a dynamic model (E.M. Jakob, A.H. Porter, and G.W. Uetz, in preparation) suggests that small and medium-sized spiders are driven primarily by their need to maximize food intake. For *M. incrassata*, the costs of lost opportunities are therefore likely to be a major component of the total cost of relocation.

Lost-opportunities costs are likely to be an important part of relocation costs in many other species as well. Lost-opportunities costs accrue for every potential territory that is rejected (Baker 1998), so they are probably important in all movement decisions, even in natal dispersal, where there is no initially abandoned territory.

Familiarity costs

Familiarity costs are especially relevant to animals that need to explore their territory to find resources, escape routes, and resting sites (e.g., Isbell et al. 1990). These territory attributes are not relevant for colonial web-building spiders. Nevertheless, two other familiarity costs that we did not measure may be relevant to *M. incrassata*. First, there is evidence that these spiders become familiar with neighbors and establish dominance hierarchies during web set-up (Uetz and Hodge 1990). This would tend to reduce the costs of fights and the time taken to construct the web. We suggest that this familiarity would be more important for increasing foraging time and daily prey intake than for reducing the minor energetic costs and injury risks of interacting. Secondly, other web-building spiders have been shown to assess the prey availability at their sites and shift sites accordingly (e.g., Enders 1975; Gillespie and Caraco 1987). Web sites within a *M. incrassata* colony vary in prey availability but prey are encountered stochastically (Uetz 1989), so a residency period may allow spiders to more accurately assess prey levels. *Metepeira incrassata* also assess predation risk and will move in response to perceived increases (E.M. Jakob and G.W. Uetz, in preparation). Repeated observations of marked individuals interacting during orb-web construction would provide a measure of the benefits of increased familiarity.

Existing models of site fidelity show an important explanatory role for the costs of movement (Morris 1987; Switzer 1993). This case study provides an example of a species in which the cost of movement can be precisely broken down into separate, measurable components. This formulation helps in structuring data collection in site-fidelity studies because these components are often not measurable with the confines of a single experiment. We found that the cost of lost foraging opportunities is the major cost component affecting site fidelity in *M. incrassata*. It will be interesting to see if this pattern is upheld in other species.

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