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The costs of moving for a diurnally cryptic araneid spider

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Abstract. In orb web spiders that recycle webs and thus minimize the material costs of web relocation, the characteristics of their temporal movement patterns between web sites can be used to examine otherwise hidden costs. Previous studies have shown that one such cost is the extra risk from predation. An unusually long average residence time at web sites is one indicator of cost. In some cases the pattern of movements also appears to be indicative of high costs, similar to those experienced by spiders that do not recycle web proteins. Nocturnal *Poltys noblei* Smith 2006 (Araneidae) spiders are heavily reliant on good camouflage in their exposed daytime hiding positions. Thus the risk of moving to an unknown site where the spider may not match its background may impose a large cost on relocation. The temporal pattern and frequency of relocations of *P. noblei* in northern Sydney are compared to those reported for other orb web species. *Poltys noblei*, on average, is found to have a long residence period, and the pattern of movement of larger individuals in this species is found to be random. These data support the idea that moving is costly for this species. Finally, the seasonal timing of movements is examined for *P. noblei*. It is found that most spiders relocate in spring but it is unknown if this is to seek a better web site or for the spider to avoid predation.

Keywords: Web site tenacity, *Poltys*, seasonality, camouflage, material costs, predation

Spiders have often been used as model organisms when examining facets of predator-prey interactions and optimal foraging theory, both as predators (e.g., Olive 1982; Janetos 1982a) and as prey (e.g., Rypstra 1984; Wise & Chen 1999). Web building spiders have especially attracted the attention of researchers, in part because many are relatively easy to find and work with in the field and in the laboratory. Some rebuild all or part of their webs almost daily and so have the potential to react quickly to applied stimuli. A variety of models and ingenious measurement techniques have allowed researchers to estimate aspects of the cost of web construction with respect to the expenditure of silk and energy (e.g., Tanaka 1989; Nakata & Ushimaru 1999, 2004).

When a spider moves to a new web site there are potential costs from loss of hunting time, risks in entering an area of unknown quality with possible predators, as well as the costs in silk production and energy expenditure. For spiders that build materially expensive webs and do not recycle silk proteins, the high cost of silk and associated energy investment appears correlated to long web site residence times (Janetos 1982a; Tanaka 1989). In many orb web building species in the families Araneidae, Tetragnathidae, and Nephilidae ingestion of most of the web occurs before the spider moves away from a web site. The silk proteins, therefore, are largely recycled (Peakall 1971 in Janetos 1982a). This minimization of material costs has allowed researchers to focus on the other factors that affect orb web spiders' decisions to move, such as the effects of disturbance (e.g., Enders 1976) or prey abundance (McNett & Rypstra 1997). Two sources of information have most frequently been utilized: the temporal pattern of the movements and the frequency of relocation.

Temporal pattern of movements.—Janetos (1982a) showed that orb web building spiders with relatively low material costs of relocation may show non-random patterns of residence times at web sites, either tending to move on more quickly than expected, or staying much longer than expected. The implication of this finding is that these species are not constrained by costs and can move whenever it is most appropriate in terms of prey abundance or other factors. In contrast, some sheet-weaving spiders (Linyphiidae), which do not recycle their silk proteins, have a much greater energy cost when moving to a new site (Janetos 1982a). Accordingly, the relocation patterns of these sheet-weavers did not differ significantly from that expected due to random events (i.e., the cost of abandoned silk and energy is a strong deterrent to relocation unless necessitated by other factors). Based on this premise, a spider that recycles silk but has a random pattern of movement nonetheless may have a high cost of moving due to some other factor. An increased risk of predation during and after relocation was identified as this factor in the case of the orb web spider *Nephila clavipes* (Linnaeus 1767) (Vollrath & Houston 1986).

Frequency of relocation.—In work on orb web spiders, the frequency of relocation, or its inverse, the average length of residence at a site, has been used to demonstrate a response to factors such as changes in prey levels (Olive 1982; Vollrath 1985), web damage (Enders 1976), and intraspecific interactions (Smallwood 1993). These are among the many factors that together influence the suitability of a site for any particular spider at any given time (Riechert & Gillespie 1986). What may be most difficult to quantify are the negative influences, (i.e., those such as an increased risk of predation that could cause a spider to move less frequently than might otherwise be expected). These factors may be easiest to examine indirectly by comparing the habits of different species and their respective life histories, and considering the differences among them. As an example, Miyashita (2005) found that the likelihood of risk-taking in two *Nephila* Leach 1815 species appeared to correlate to their life histories—females of *N. pilipes* (Fabricius 1797) need to grow fast to reach the normally large adult body size, and this species is more likely to risk moving than the sympatric species *N. clavata* L. Koch 1878, which is smaller and may be able to afford periods of suboptimal growth.

Web site residency times are given as examples in Table 1. Most are for orb web spiders that recycle their silk; other web

Table 1.—Examples of "natural" (i.e., undisturbed) average lengths of web site residencies (days or nights) recorded for various orb web spider guilds or species (Ar = Araneidae, N = Nephilidae, Te = Tetragnathidae) and exemplars from the Agelenidae (Ag), Linyphiidae (L) and Theridiidae (Th). Entries based primarily on adult female spiders are in bold. Entries are ordered from shortest to longest mean residence time. Figures are calculated or extrapolated from a variety of formats given in the original cited studies. Explanatory notes: † Original figures are for web site tenacity (probability or percentage of spiders remaining per day, Enders 1973). Mean residence = 1 / 1 – prob. (wst). In Enders 1975, 1976 there are often two sets of figures, one set referring to individual spiders on certain nights, the second to gross pooled observations. Here only the latter kinds of figures are used, as these are generally in accord with the methodologies of other authors. # Mix of adults and juveniles. * Original figures are for mean days per residence. ^ Original figures are for turn-over (probability or percentage of spiders leaving per day). Mean residence = 1 / prob. (turn over). ** No calculation made in original paper: extrapolated from figures in text and based on few actual spider movements.

Species (Family) or guild	Mean length of residency (days or nights)	Reference	Notes
Orbweavers (Ar, Te, Uloboridae)	2.2 to 2.4*	Janetos 1982a	1978 and 1979; juvenile and sub- adult
Argiope aurantia Lucas 1833 (Ar)	2.6 to 4.5†	Enders 1975	June dates, 5th instar (from text)
***Argiope aurantia* (Ar)**	**3.4 to 7.7†**	**Enders 1976**	**control regimes (two field experiments)#**
***Tetragnatha elongata* (Te)**	**3.8***	**Smallwood 1993**	**low density of spiders, prey-poor habitat**
***Cyclosa argenteoalba* (Ar)**	**4.3^ to 5.6^**	**Nakata & Ushimaru 2004 & 1999, respectively**	**controls from separate field experiments**
Sheetweb weavers (L)	4.8 to 5.0*	Janetos 1982a	1978 and 1979; sub-adult and adult
Argiope aurantia (Ar)	5.3 to 14.3†	Enders 1975	August dates, probably subadult females, 8th to 9th instars
***Micrathena gracilis* (Walckenaer 1805) (Ar)**	**6.7* to 8***	**Hodge 1987b & a, respectively**	**control figures from each experiment; informal longest residency estimate of "weeks"**
***Argiope trifasciata* (Forskål 1775) (Ar)**	**8.7***	**McNett & Rypstra 1997**	**control replicates**
Nephila clavipes (N)	16*	Vollrath 1985	spiderlings in prey-poor habitat (enclosures)
Cyclosa octotuberculata (Ar)	16.9^	Nakata & Ushimaru 2004	juveniles (probably subadult)
Latrodectus revivensis (Th)	17.9*	Lubin et al. 1993	juveniles; probably affected by marking procedure
***Tetragnatha elongata* (Te)**	**17.9*^**	**Gillespie & Caraco 1987**	**low density of spiders, prey-poor habitat**
***Cyclosa octotuberculata* (Ar)**	**26.3^**	**Nakata & Ushimaru 2004**	
***Latrodectus revivensis* (Th)**	**44.1***	**Lubin et al. 1993**	**probably affected by marking procedure**
Nephila clavipes (N)	58.8**	Vollrath 1985	spiderlings in prey-rich habitat (enclosures). Longest recorded periods ≥ 42 days
***Agelena limbata* Thorell 1897 (Ag)**	**143 to infinity^**	**Tanaka 1989**	**adult spiders did not relocate**

builders are included for comparison. Even among the orb web builders a wide range of variation can be seen between those at the top of the table, which move most frequently, and those at the bottom with the longest residency times. In this paper, I examine the frequency and pattern of the web site movements of the araneid spider *Poltys noblei* Smith 2006 in bushland near Sydney, Australia. I compare the results with those of other species in Table 1 and discuss the risks of predation and the role of camouflage in prolonging web site residence times. Unlike many other spiders, *P. noblei* may over-winter at almost any size (Smith 2006b). The data gathered for the web site tenacity study is useful for examining the seasonality of movements of these spiders through the year.

METHODS

Spiders of the genus *Poltys* C.L. Koch 1842 are nocturnal orb web builders that remove their web around dawn and rebuild it each evening. *Poltys noblei* and other southern species inhabit bushland areas where trees and bushes commonly have patches of dead twigs. During the hours of daylight, when not in a web, the spiders rest camouflaged by shape and color on a bare, dead twig, often in an exposed position (Fig. 1a). *Poltys* males are small and can mature in just a few weeks if emerging during the summer months, but females have a longer lifespan, which in *P. noblei* probably lasts from one to two, or even more, years. Spiderlings are similar in abdominal morphology but a wide range of abdominal shapes and coloration develops as individuals grow towards maturity (Fig. 1 a–d; Smith 2006a, b). This intraspecific variation is likely to be important for the effective camouflage of spiders in the field.

Short-term observations of residence time.—Three periods of overnight transects were undertaken, an 8-night pilot study during autumn 2000, then 10-night periods in spring 2002 and autumn 2003. The sites were all located in the northern Sydney area, two in the Ku-ring-gai Chase National Park (Myall Track [33°40′18″S, 151°08′06″E], and Resolute Picnic Area on West Head [33°34′50″S, 151°17′05″E]) and one on the Waitara Creek Fire trail ([33°42′51″S, 151°05′23″E] the site detailed under "Long-term observations" below). Each transect route was surveyed several times through the night from dusk to daylight and the positions and activities of *Poltys* specimens were recorded on each pass. Web details and damage were also recorded as additional information. Following individuals at regular intervals from sunset to sunrise minimized the possibility that spiders were swapping sites without my knowledge since spiders are usually sedentary during the day. *Poltys noblei* is the only species in the genus recorded from this area (Smith 2006a). Specimens from these sites or close by, examined during the revision of Australian *Poltys* referenced above, are deposited in the Australian Museum.

Figure 1.—Female *Poltys noblei*. a, in a typical position on an exposed dead twig hanging over a track in the Ku-ring-gai Chase National Park near Sydney (right lateral view). b–d. typical specimens showing some of the variation in shape and color pattern, b and c show mainly dorsal abdomen (apex downwards), d is laterodorsal but with most of flank lost in shadow. Photo 1b by Ramon Mascord.

Long-term observations of residence time.—The long-term study was run along 400 m of the Waitara Creek fire trail, a remnant of urban bushland connected to the Berowra Valley Regional Park, between Hornsby and Normanhurst in the northern fringes of Sydney. This site was surveyed at approximately 7–10 day intervals from April 2002 to April 2004 (112 transects at an average of 8.49 day intervals) and then observations were continued on just a few selected spiders until the last had disappeared in late November 2004. Transects were started at least one hour after dark, later if possible to ensure that most specimens had already made webs, and generally on nights with suitable weather conditions for locating spiders. The details of each *Poltys* seen along the route were recorded. The temperature was noted at the beginning of each survey, at the turn-around point, and again on return to the start. Because of public access to the area and not wishing to draw the attention of potential bird predators to the locations of spiders, web locations were not marked and I avoided seeking out the specimens during the day (although a few were easily visible, which allowed further confirmation that the same specimen was using the site throughout the putative period of residence). Instead, web locations were described or sketched in relation to vegetation features. No attempt was made to mark specimens for a number of reasons (see below), but abdominal shape was noted. The approximate size of each specimen was estimated by eye, without the aid of templates; hence the size ranges used in the analysis are approximate. Slight changes in web site within the same bush or tree (up to about 20–30 cm for a small spider or 50–100 cm for a larger specimen) were noted but were not considered moves unless there were other reasons to suspect that the specimen in the new site was not the original, or that the specimen was now using a different resting position.

Although the long term transects were initiated after only the pilot study of the short term surveys was completed, the further 10-day short term studies confirmed that these observations were valid. Overall, the short-term observations were found to indicate that (i) many spiders use the same, or a closely adjacent, web site night after night; and (ii) the likelihood of a similarly sized and shaped spider moving into a vacated web site soon after departure of the first was small unless there was a high local population density. Therefore, it was indicated that in general it was possible to monitor individual spiders without marking them, even though this introduced a small amount of uncertainty into the results. Marking spiders was decided to be unsuitable for this study because of the increased likelihood of relocation of disturbed specimens (and the likelihood of repeated disturbance when trying to get close enough with a bright light to confirm specimen identity), as well as potential disruption of camouflage and the likelihood of injury to small specimens.

Data analysis.—For the short-term transects, the average web site residence time for each transect site was calculated (in nights). Mean residence = total spider observation nights/total departures. For the long-term study, all calculations were performed using the average sample period as the unit of residence time (1 sample period = 8.49 nights). The sample mean and standard deviation were calculated for all spiders with unambiguous records. This excluded specimens for which the moving-in date was unknown (i.e., they were already present on the first transect night), or those for which there was likely to have been interference from conspecific spiders.

Two size classes were recognized, based on the field estimates. The "Small" class contained spiderlings, juvenile males (which cease making webs and become mobile when they mature), and juvenile females of a similar size. Therefore, small spiders in this context are those up to instar two or three (post emergence). This size-class cut-off point may be important as the abdomens of females are beginning to differentiate in shape at this size (Smith 2006b) and camouflage may begin to play a more important role. The "Large" class, therefore, comprised only juvenile and adult females. Some spiders grew from one class into the next while resident at a single web site. The class used here is the size at arrival.

The distribution of residence times of Small spiders was compared against those of the Large class using the χ^2 test on contingency tables and pooling most columns with expected values < 5 (note: it is not necessary to remove all expected values less than 5, Parker 1979). All subsequent tests used the two size classes separately.

For each size class the recorded pattern of residence times was compared with a random hypothesis, following the methods of Janetos (1982a) and Hodge (1987a, b). This method is based on the expectation that compounded random events such as web damage or disturbance by a predator should result in spider movement events that can be explained by a Poisson process (Janetos 1982a). A negative exponential series was generated (using the "expondist" function in Microsoft Excel), which models the expected distribution of spider movement events over time according to this random hypothesis. This distribution of class frequencies was then compared with that collated from the recorded data.

Seasonality of spider relocations.—In order to compare differences in spider relocation as a function of season, the same size classes were used as for the calculation of residence periods except that the Large spider size class was split into Medium and Large. Thus, Large in this context only contains adult and subadult females; these were split off because all adults die by winter and will therefore leave a web site. Data were extracted for each residency from the long-term observations at Waitara Creek—the season a spider moved into a position and its size, the seasons during which it was resident at a position, and the season and size at which it moved on (Smith 2006b). If a spider had grown between size-classes during its period of residence, the original data were examined to separate the seasons in which the two different size classes were present. For each kind of move, in or out, and for each size class of spider, the total number of moves per season was calculated as a proportion of the numbers of spiders in that class recorded during the season.

RESULTS

Short-term observations of residence time.—The residence period through each short-term transect period is 24.9 nights, averaged over all three sites. Per site the averages are: Myall, 26.3 nights; Waitara Creek, 23.5 nights; West Head, 23.9 nights. The presence of individual spiders through the recording period at each site is depicted in Fig. 2. All spiders were used for the calculations, which therefore include movements due to conspecific interference.

Long-term observations of residence time.—The mean residence time for all spiders is 4.80 recording periods (40.75 days), SD = 5.57, n = 218. The longest recorded residence is 31 recording periods (approximately 263 days) (Fig. 3a). When Small and Large residence times are compared, the distribution of residence times is found to be significantly different between the two size classes ($P = 0.012$). The mean residence times are 3.77 sampling periods, (32 days), for Small spiders (SD = 4.51, n = 138), and 6.59 sampling periods (56 days), for Large spiders (SD = 6.69, n = 80). Most aggregated spiders were omitted in calculating these figures; hence movements due to conspecific interference are minimal.

The distribution of residence times of Small spiders is significantly different from the random hypothesis ($0.05 > P > 0.025$) (Fig. 3b). This is not the case for the Large spiders; the distribution of residency times for these is not significantly different from random ($0.5 > P > 0.1$) (Fig. 3c). For the complete data set see Smith 2006b.

Seasonality of spider relocations.—Summer and autumn are shown to be the peak seasons for beginning a period of residence (Table 2a); spring and summer are the peak seasons for leaving (Table 2b). Winter is a period of relatively low mobility, at least for spiders arriving into a new web site.

DISCUSSION

The average residence time of 24.9 nights for *P. noblei* (spiders of all instars) in the short-term observations is just slightly shorter than the residence time of adult females of *Cyclosa octotuberculata* Karsch 1879 (26.3 days, Nakata & Ushimaru 2004). The residence time of a wide variety of spiders is shown in Table 1 in order of increasing length, and both of these species fit in towards the bottom of the table, i.e. they have long average residence periods. The figures for *Poltys* were calculated in a similar way to the majority of the

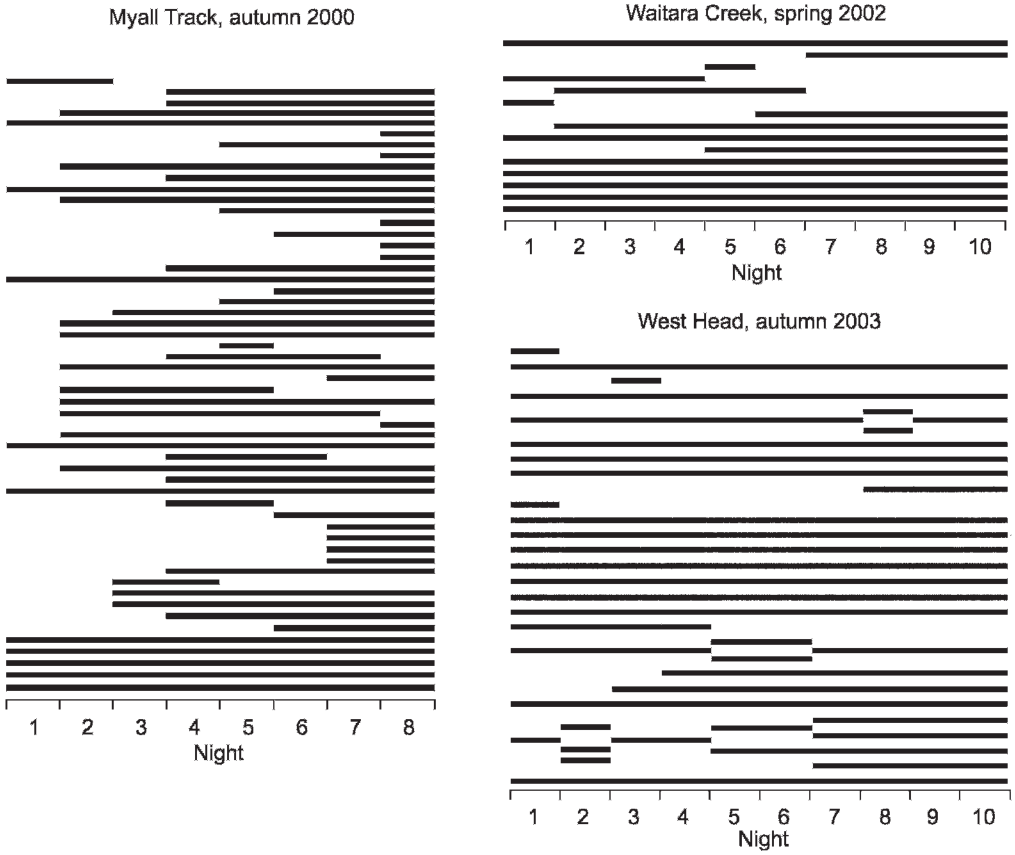

Figure 2.—Spider presence at Myall, Waitara Creek and West Head short-term transects. The length of each bar represents the presence of a particular spider through one or more nights. Spiders ordered as positioned along transect route, nearest axis at start.

species shown here, from the rate of departure of spiders from web sites over several consecutive nights of observation. The major difference between the short-term results for *Poltys* and most of the other studies included here is the wide range of instars represented in the current studies and the inclusion of some spiders known to have experienced interactions with conspecifics. The overall figure from the long-term transects (all ages) is rather longer at 40.75 nights and is only second to the residence times of *N. clavipes* spiderlings among the silk recycling species in these examples. These *Nephila* were protected from predators in enclosures and provided with abundant prey, however, which is hardly a natural situation, and there are similar caveats for the long-term transect results for *Poltys*, discussed below. *Nephila clavipes* and *P. noblei* (Large spiders), have been shown to have an essentially random pattern of relocation from web sites (Vollrath & Houston 1986; Smith this paper); the pattern of relocation of the other orb web species at the bottom of the table has not been tested. These characteristics of long residence period and random relocation pattern suggest some hidden high cost of moving may be present for each species in comparison to the presumed freely moving spiders at the top of Table 1.

The risk of predation, or expenditure of energy associated with avoiding such a fate, has previously been suggested to be this hidden cost for the diurnal species with long residence periods. For *Nephila* there is a direct risk after relocating due to the lack of protection usually afforded by an extensive barrier web (labyrinth) at an established site (Vollrath 1985). In the case of *C. octotuberculata*, the spider hides among debris and egg sacs that are incorporated in a line across its web. The line of debris is taken by the spider when it relocates and although this protects the spider after arrival at a new site, carrying such a burden takes more energy and time (Nakata & Ushimaru 2004). In the same study *Cyclosa argenteoalba* Bösenberg & Strand 1906 was compared with *C. octotuberculata*. This species does not use debris for camouflage in the web and correspondingly was found to have a much shorter average residence time (Table 1). Even in certain spiders that do not recycle web proteins, predation during relocation has been found to be a major cost that favors long residence periods. Only 60% of desert widow spiders, *Latrodectus revivensis* Shulov 1948, survived relocation, far outweighing the material cost due to loss of silk (Lubin et al. 1993).

Like the desert widow spider mentioned above, the remaining orb web species with long residence times, *P. noblei* and *Tetragnatha elongata* Walckenaer 1842, are primarily nocturnal. Nocturnally active spiders largely avoid the dangers of being exposed in a web by day, but still require a strategy to avoid predation during this time while the majority of predators are active. Some, like *L. revivensis*, hide in a retreat that may offer a physical barrier against some predators as well as concealing the spider; other taxa, such as these *Poltys* and *Tetragnatha* Latreille 1804 species, rely on camouflage. This camouflage is manifested both in coloration and shape. *Tetragnatha* are elongate and usually lie on vegetation with legs extended linearly, blending in with the

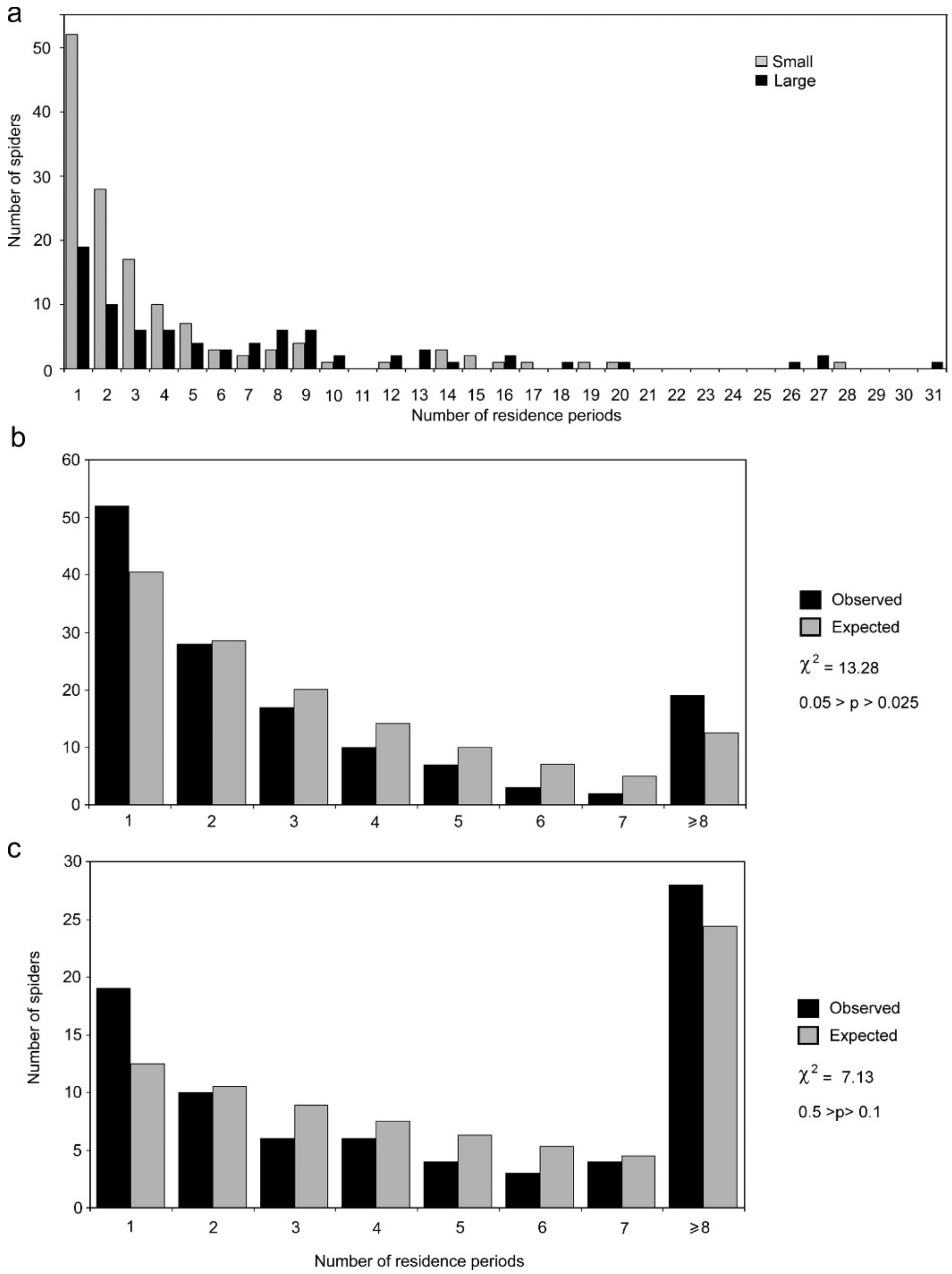

Figure 3.—The frequency of occurrence of spider residency periods: a. Small compared to Large spiders; b. histogram of residency periods of Small spiders (tail values pooled) compared to a random hypothesis; c. ditto for Large spiders. Calculations in both 3b and 3c use 6 degrees of freedom because two parameters of the expected series are derived from observed values (details in Smith 2006b).

twig or leaf, while *Poltys* sit on the side or end of a twig with legs tucked in, appearing like a broken twig end or a dead leaf bud. Voluntary relocation would take place during the night, so one cost is loss of foraging time. But for these spiders the main danger in moving from a known "safe" web site may be the risk of not matching the substrate at a new, unknown, site and thereby becoming easily visible to a predator.

Movement strategies of spiders in different age classes are provided by the long-term results of the present study (Figs. 3a–c) and the seasonal analysis (Tables 2a, b). For *P. noblei*, the non-random pattern of residence of Small spiders compared to the apparently random pattern of Large spiders suggests that the risk associated with relocation increases as spiders become larger and thus more reliant on effective camouflage. Such changes in foraging patterns with age due to changing costs were predicted by Janetos (1982b). This changing relationship between efficient foraging for growth and the need for camouflage can also be seen in the seasonal shift in moves in and out of web sites. For *P. noblei* a general strategy is to move in spring and summer when rapid growth is

Table 2.—The percentages of spiders which move on a seasonal basis, classified by spider size. A. Spiders beginning residency (moving in); B. Spiders ending residency (moving out). The number of spiders in size classes differs due to specimens which grow from one size class to another during their period of residence. Large = adult plus subadult females; Medium = all other juvenile females; Small = juvenile males and females too small to sex (up to about 3 molts).

A.

Moving IN % (n_{move})

Spider size class	Winter	Spring	Summer	Autumn
Large	100 (3)	83 (10)	69 (9)	100 (1)
Medium	30 (6)	63 (17)	87 (13)	81 (21)
Small	45 (9)	62 (13)	100 (85)	67 (31)
All spiders	42 (18)	67 (40)	95 (107)	73 (53)

B.

Moving OUT % (n_{move})

Spider size class	Winter	Spring	Summer	Autumn
Large	50 (1)	86 (12)	93 (14)	100 (2)
Medium	68 (13)	88 (22)	77 (10)	54 (15)
Small	56 (10)	100 (20)	85 (68)	78 (31)
All spiders	62 (24)	92 (54)	85 (92)	69 (48)

occurring, but by autumn many spiders are settling into sites where they will remain until spring (Tables 2a & 2b). Spring is a time of high mobility in all size classes. In fact, 100% of Small spiders end their residence during spring, even though only 60% begin a residence during this period. The 40% discrepancy in numbers will be largely due to the maturation of males. Other size classes also show a high percentage of spiders moving out of established web sites (i.e., ending a period of residency) in spring. This may be to seek a prey-rich web site after a long period of low prey availability over winter. Indeed the model of Leclerc (1991) based on observations of the linyphiid *Tenuiphantes flavipes* (Blackwall 1854) predicted differential optimal strategies with regard to staying or moving dependent upon the spiders' body fat reserves. So many spring movements could also indicate that staying too long carries risks that balance the dangers of moving. Predators may learn to associate a build up of silk lines with the likely presence of spider prey. For instance, it is often unclear what cue initiates the cryptic prey flushing behavior reported in *Sceliphron laetum* (F. Smith) (Coville 1987), a technique observed in the capture of *Poltys* spiders by this wasp (R. Raven pers. comm.).

The long-term figures for *Poltys* residence times are overestimates to some extent. In particular, many spiders may have been missed because they both arrived and left a web site between samples and this factor would make the long term average residence period more comparable with the figure from the short-term studies. Another factor that accounts for some of the difference between long-term and short-term average residence periods is the omission of spiders that were in aggregations from the former. Nevertheless, many of the studies listed in Table 1 also excluded moves caused by conspecific interactions, so this does not affect the within-table comparison. Finally, the life history of *P. noblei*, which often extends over more than one season, leads to the inclusion of winter records in the long term averages. Winter is a season of low general mobility and was not sampled in any other study listed in Table 1. Therefore, it can be seen that a realistic figure for the average residence period for *P. noblei* that is comparable to other studies lies somewhere between the short-term and long-term results reported here. Nevertheless, the long-term results provide information on maximum stays, the distribution of residence times, and some information on differences between spiders of different ages. In fact the single longest recorded stay of *P. noblei*, of approximately 263 days, seems remarkable for a silk recycling species. Unfortunately this cannot be compared to other species both due to the "snapshot" nature of most studies and due to the differing life-histories. All other species examined are essentially univoltine and this time period would have covered the entire life-cycle from emergence; for this *P. noblei*, however, this period accounted for approximately two-thirds of its growth, the record covering it from the small end of Medium, through to adult, probably around five instars.

An attraction for web sites with conspecific silk has been demonstrated in at least one orb web species (Schuck-Paim & Alonso 2001) which might indicate the further possibility of overestimation of the period of web site tenacity of *Poltys* if web site take-overs occurred frequently. This error is most likely to occur among records for smaller specimens that were not individually distinctive and so I excluded aggregated spiders from the long term data if I became unsure about which spider was which at any time through the study. If present to a significant degree this error would be indicated by longer web site residencies for Small spiders than those of Large spiders, which were more recognizable as individuals. Instead the Small specimens show the most frequent movements, which is in agreement with the findings of other studies shown in Table 1. The lengths of some residence periods were further corroborated by observations of distinctive individuals that were using easily visible day-time hiding positions. Nevertheless, the spatial distribution of specimens in some cases, especially spiderlings, and reuse of sites, did suggest that *P. noblei* may be attracted by conspecifics, and/or that web sites were limiting. In the habitats where I found *Poltys* commonly, as in the areas where these studies were carried out, there were many more apparently suitable web sites than spiders. However the significance of spider spatial distribution was not tested here because of the complications of habitat heterogeneity, wind currents, and the structural suitability of different plant species for the webs and hiding places for spiders of different sizes.

The paucity of studies on nocturnal orb web spiders to some extent reflects the inconvenience of working odd hours, but nocturnal spiders may also make less ideal models than diurnal species due to differences in behavior. Diurnal species normally construct the new web within the frame of the previous one (e.g., Hodge 1987a). Thus, with no disturbance, the web will be in exactly the same place and repeated occupancy can be assumed to be a direct measure of the suitability of the web site for the spider. In contrast, nocturnal spiders such as *Poltys*, may spend up to 17 hours each day without a web, leaving in place only the bridging line, which is easily broken, and access lines between and along twigs. Except in an extremely simple structural situation, or in calm weather, the position of the web is therefore unlikely to be exactly replicated from night to night. In the observations reported here, I discounted small changes in web sites, as did, for example, Enders (1975) in the studies listed in Table 1 and possibly others who did not report on the precise details. However, in a habitat where supports are widely separated, even the relocation of a single support line may significantly change the web position and so could be considered as relocation (e.g., Nakata & Ushimaru 2004). Such heterogeneity in recording protocol and in spider behavior makes detailed comparisons between studies difficult. Nevertheless trends do emerge from this range of data and, in particular, the new data on *Poltys* add support to the findings of previous authors who suggested the connection between long residencies, random patterns of movement, and a high cost of relocation due to predation risks. Among the species with long web site residence times the precise *modus operandi* of the threat differs between the two diurnal species, *N. clavipes* and *C. octotuberculata*, but the requirement for effective camouflage may well be the key factor for both of the nocturnally active, diurnally cryptic species, *T. elongata* and *P. noblei*. Despite presenting interesting challenges, nocturnal and/or cryptic spiders provide useful insights into otherwise hidden facets of predator prey interactions.

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