2018. Journal of Arachnology 46:420–427

Survival, abundance, and movement of a synanthropic population of the brown recluse spider, *Loxosceles reclusa* (Araneae: Sicariidae)

Kenneth L. Cramer[1] and **Eric T. Hileman**[2]: [1]Dept. of Biology, Monmouth College, 700 E. Broadway, Monmouth, Illinois 61462, USA; E-mail: kenc@monmouthcollege.edu; [2]Biology Dept., Trent University, 2140 E. Bank Dr., Peterborough, ON K9J 7B8, CANADA

Abstract. We conducted a two-year mark-recapture study of a synanthropic population of the brown recluse spider *Loxosceles reclusa* Gertsch & Mulaik, 1940 in northwestern Illinois. We used joint live encounter and dead recovery models to estimate adult survival, recapture, and dead recovery probabilities. To estimate adult abundance, we used full-likelihood closed-population models. Monthly survival was constant between sexes (0.73, 95% CI = 0.66–0.78), but males were less likely to be recaptured and an additive effect of time revealed highest recapture probabilities in September. The probability of recovering a marked adult that died during the study was 0.13 (95% CI = 0.07–0.24). Average life expectancy for adults was 94 days, much lower than in prior laboratory studies. Causes of observed mortality were predation by conspecifics and cobweb spiders (*Parasteatoda tepidariorum* (C.L. Koch, 1841)) or undetermined. A likely source of mortality for this sit-and-wait predator is starvation. Model averaging of full likelihood closed-population models resulted in adult abundance estimates that were similar between males (28, 95% CI = 20–63) and females (28, 95% CI = 26–38). However, the total population of adults including those hidden in harborage (boxes, furniture, crevices etc.) was undoubtedly much higher. Based on count data, immature spiders were as abundant as adults early in the year, gradually increasing to a peak three times greater by mid-summer. Male spiders moved longer distances than females and were less likely to exhibit site fidelity. The average tenure of a female at a specific site was nearly 8 days.

Keywords: Joint live-dead models, mark-recapture, population structure, recapture probabilities, site fidelity

The brown recluse spider (*Loxosceles reclusa*, Gertsch & Mulaik 1940) is a well-known medically important spider of North America. As such, most prior research has focused on its venom, bite, potential treatments, and distribution (reviewed in Vetter 2015). Early studies of its general biology were conducted largely in the lab; little research has been conducted regarding aspects of its population biology, specifically survival (or longevity), abundance and movements, in more natural settings. Our study aims to fill this gap by following a marked synanthropic population of brown recluse spiders in a semi-natural setting, an urban garage.

Laboratory studies of brown recluse spiders' survival have focused on their apparently unusual longevity. Hite et al. (1966) first reported that female *L. reclusa* lived nearly 3 months longer than males, on average 628 days. Horner & Stewart (1967) housed female spiders individually, kept them at temperatures ranging from 24–36 °C and over-wintered them in a dirt floor of a garage where the low reached -4 °C. Thirty females survived at least four winters or a minimum of 1420 days under such conditions. Female spiders raised by Elzinga (1977) from egg to adult survived an average of nearly 800 days (over 2 years) with one surviving 1755 days or nearly five years. In all of these early studies, spiders were housed individually and fed at least twice a week or even daily. Using a different approach, Eskafi et al. (1977) brought field-captured brown recluse spiders into the lab and modeled the effects of several abiotic factors on weight loss and survival, finding that vapor pressure deficit, temperature, and food stress were the most important factors. Unfed adults lived on average only three months after being brought to the lab. The South American species, *Loxosceles intermedia* Mello-Leitão, 1934, has also been shown to be relatively long-lived in laboratory settings (Fischer & Vasconcellos-Neto 2005), and as in *L. reclusa*, females significantly outlived males.

Studies on *Loxosceles* population size are rarer still and typically consist of reports of minimum estimates based on capture rates in infested buildings, emphasizing the high numbers that may be encountered. Vetter & Barger (2002) reported on a home in eastern Kansas where occupants captured over 2,000 *L. reclusa* in a 6-month period. Researchers in Oklahoma were able to collect over 1,000 spiders from a single barn in three nights of collecting (Vetter 2015). Schenone et al. (1970) found an average of 163 *L. laeta* (Nicolet, 1849) per home in central Chile. Richman (1973) provided one of the few surveys of wild *Loxosceles*, counting *L. arizonica* Gertsch & Mulaik, 1940 by turning over downed saguaro cacti and other plant litter in a desert habitat. He observed that abundance declined in summer while the percent of spiderlings (< 3 mm) increased in winter. About 50% of the total spiders observed were immature.

Ferreira et al. (2005) reported on both abundance and movements of the cave-dwelling *L. similis* Moenkhaus, 1898, in Brazil. Using batch marking methods, they estimated population size using a modified Lincoln-Petersen index. Numbers fluctuated from 800 to over 1400 individuals in the main corridor of the cave which was 140 m long. Estimating individual movement, they found that some spiders moved 10–80 m in a single week. In contrast, Fischer (1996) reported much more limited movements, a mere 2 m/wk, in *L. intermedia*. The general consensus of arachnologists that *Loxosceles* are not great dispersers (Vetter 2015) is supported by studies revealing a largely sedentary behavior (Cramer 2015).

Here we present a demographic analysis of a population of brown recluse spiders inhabiting a large urban garage. Our study is the first to use individually marked adult brown recluse spiders to shed light on survival, abundance, and movements in a non-laboratory setting.

METHODS

We marked 99 brown recluse spiders with unique tags in a large (20 × 10 m) urban garage in Monmouth, IL (USA) during 22 marking periods between June and September 2014. We created individual paper tags approximately 1.5 mm^2 with a unique two-digit or two-letter code in size three font on card stock. To avoid blurring of the code, we applied clear artist's spray fixative before cutting and trimming the tags to size. We then captured adult spiders, anesthetized them using carbon dioxide and affixed the tags to the cephalothorax with SuperGlue^{TM}. We used the blunt tip of a paper clip to apply a small drop of glue to the cephalothorax and, using fine forceps, immediately lowered a tag onto the glue. Behavioral and survival effects of carbon dioxide anesthesia have been reported in arthropods (Nicolas & Sillans 1989) and we cannot completely exclude this as having an impact on our study. However, our spiders were fully immobilized for approximately one minute after which they recovered rapidly and were released. Sixty-five percent of marked spiders were recaptured at a subsequent date and showed no apparent ill effects. One marked female successfully overwintered and produced an egg sac that hatched 74 offspring.

We surveyed spiders under red light over two active seasons (mid-May to mid-October) from 2014–2015 by searching the garage for approximately 1 hour between 22:00 and 24:00. Following a prescribed path roughly along the inner perimeter of the garage (but also investigating near undisturbed areas such as stored vehicles and other items), we searched every 2–4 days for marked and unmarked spiders, using a handheld magnifier when necessary to read marks. Thus, in this study a "recapture" indicates a spider that was seen again but not physically captured and released. In all, we sampled 100 times over the two-year study. Additionally, we divided the garage into a grid of 0.5 m^2 sections and recorded the location of each marked spider when encountered.

Population modeling.—We used mark–recapture models within program Mark version 8.2 to estimate population parameters (White & Burnham 1999) and to model survival and abundance. For model selection, we used an information-theoretic approach and Akaike's information criterion adjusted for small sample size (AICc; Akaike 1973; Burnham & Anderson 2002). We used model averaging and unconditional standard errors to account for model selection uncertainty if the top ranked model received $< 90\%$ of the model weight (Anderson 2008).

Survival.—To estimate adult survival, we used joint live encounter and dead recovery models (Burnham 1993; Williams et al. 2002). These models use conditional likelihood to estimate survival (S), recapture (p), dead recovery (r), and fidelity (F) probabilities. Emigration is assumed to be a random process (Burnham 1993). Briefly, live animal encounters are recorded at each sampling occasion followed by an interval where recovered dead animals are recorded (Williams et al. 2002). This sampling design results in construction of a paired live/dead encounter history where animals are recorded as encountered alive (1) or unobserved (0) during the live sampling occasion and as dead (1) or unobserved (0) during the interval following the live sampling occasion. Excluding immatures and spiderlings, which were too sparse to model, resulted in a truncated encounter history of 80 paired live encounter and dead recovery events. We adjusted intervals lengths to correct for uneven sampling and estimate monthly (30-day) adult survival. Because all live encounters (with two exceptions, see results for details) and dead recoveries occurred within the sampling area, we fixed the fidelity parameter to 1 in all models (Cooch & White 2017).

Our global model of survival (S) included sex as a factor and season as an additive effect. We modeled season as a dummy variable to evaluate if monthly survival during the active season (6 June–7 Oct 2014 and 13 May–27 Sept 2015) differed from monthly survival during quasi-winter, defined here by the sampling occasions that bracketed winter (7 Oct 2014–13 May 2015). The recapture parameter (p) included a sex by time interaction. The dead recovery parameter was treated as time invariant but with differing probabilities based on sex. We assessed the fit of the global model by estimating an overdispersion factor ($\hat{C}$, Fletcher 2012). If overdispersion was detected (i.e., $\hat{C} > 1.00$), we assumed it was due to parameter heterogeneity and corrected for it using quasi-likelihood and $QAIC_{c,}$ (Wedderburn 1974; Burnham & Anderson 2002). We include 13 nested iterations of the global model for a total of 14 candidate models (Table 1). We estimated adult life expectancy (e_x) assuming constant survival using life table analysis and the following life expectancy equation: $e_x = \frac{T_x}{l_x}$, where (T_x) is the number of monthly intervals survived beyond the first month as an adult, and (l_x) is the fraction of adults alive at beginning of the first month interval (Case 2000).

Abundance.—To approximate the assumption of demographic closure (i.e., no births, deaths, immigration or emigration) so that closed-population models could be used to estimate abundance, we identified and excluded immature captures. In addition, we restricted analysis to adults captured in 2014 during a period of ≤ 19 days for each sex to maximize the number of captures yet reasonably assume no mortality during the sampling period.

We estimated sex-specific adult abundance using full likelihood closed-population finite mixtures models (Norris & Pollock 1995; Pledger 2000). These models estimate four fundamental parameters: probability of first capture (p), probability of recapture (c), number of animals never captured (f), and a finite mixture (π). The number of animals never captured (f) forms part of the likelihood and is required to derive estimates of abundance but is not explicitly modeled. The remaining three parameters are modeled and fitted to the data (Chao & Huggins 2005). We considered two finite mixtures to account for latent heterogeneity in capture and recapture probabilities and fixed mixtures to one for models that did not include latent heterogeneity effects so that the eight models of Otis et al. (1978) could be compared using the same likelihood-framework (Pledger 2000; Cooch & White 2017). These models range in complexity from a null model that treated capture and recapture probabilities as constant, to the most parameterized model that included time (t), behavior (b, a response induced by initial capture and marking), and latent heterogeneity effects (2 mixtures) to explain capture and recapture probabilities (Otis et al. 1978; Chao & Huggins 2005). Including sex effects among the parameters described above resulted in 16 candidate models. We used R version

Table 1.—Fourteen joint live encounter and dead recover candidate models used to estimate adult monthly survival. Model parameters include survival (S), recapture (p), and dead recovery (r) probabilities. Sex is a factor with two levels. Time is considered alone or as an additive (+) or an interaction (*) effect with sex. Season (a constrained time model) is a factor with two levels: active season and quasi-winter. The notation (.) indicates the parameter is treated as constant.

Model	QAIC$_c$	ΔQAIC$_c$	w_i	K	-2log($\mathcal{L}$)
S (.) p (sex + time) r (.)	-10993.030	0.000	0.947	79	1597.153
S (season) p (time) r (.)	-10986.944	6.086	0.045	79	1603.681
S (.) p (time) r (sex)	-10982.704	10.326	0.005	79	1608.229
S (sex) p (time) r (.)	-10981.277	11.753	0.003	79	1609.759
S (season) p (sex + time) r (.)	-4836.807	6156.223	0.000	80	1590.956
S (sex) p (sex + time) r (.)	-4831.180	6161.850	0.000	80	1596.991
S (sex + season) p (sex + time) r (sex)	-1762.323	9230.707	0.000	82	1583.966
S (sex + season) p (sex * time) r (sex)	1092.243	12085.273	0.000	157	1508.414
S (season) p (sex) r (.)	1563.751	12556.781	0.000	5	1665.758
S (.) p (sex) r (sex)	1567.812	12560.842	0.000	4	1672.561
S (.) p (sex) r (.)	1567.833	12560.863	0.000	5	1670.137
S (sex) p (sex) r (.)	1570.074	12563.104	0.000	5	1672.541
S (.) p (.) r (.)	1586.178	12579.208	0.000	3	1694.644
S (.) p (time) r (.)	1657.525	12650.555	0.000	78	1610.620

Models are ranked in ascending QAIC$_c$ order. ΔQAIC$_c$ is the QAIC$_c$ difference between model *i* and the top-ranked model. w_i is the adjusted model weight, *K* is the number of parameters, and -2log($\mathcal{L}$) is a measure of the relative fit for a given model.

3.4.0 (R Core Team 2017) and the ggplot2 package (Wickham 2009) to graphically depict recapture probabilities.

Population structure.—We surveyed marked and unmarked spiders, stratifying individuals as adult males, adult females, immatures ($\geq$ 3 mm body length) and spiderlings ($<$ 3 mm), and tallied count data for each grouping. We restricted our analysis of population structure to the 2015 sampling season (13 May–27 Oct) because temporal sampling across age classes was sporadic in 2014. To aid visual representation of seasonal changes in population structure, we pooled sexes for adults and used a stacked bar graph created in IBM SPSS Statistics 21 (SPSS Inc., Chicago, IL, USA).

Movement and site fidelity.—To estimate movement frequency and distance, we recorded the interval (days) between sightings and estimated the minimum linear distance traveled between point locations on those dates. We also estimated site fidelity to a given location using an *a priori* definition of "resident" spider as one moving less than 1 m between observations and encountered at least twice after its initial marking but with no more than one week between encounters. The rationale for the latter restriction was to adequately approximate the assumption that a spider had not left the site for a significant period of time and later returned. These data were analyzed on Minitab (Minitab Inc., State College, PA, USA) using nonparametric tests (Spearman's correlation, Mann-Whitney). For frequentist statistics, we *a priori* set $\alpha = 0.05$.

RESULTS

We encountered 99 spiders (79 adults and 20 immature individuals) 385 times and recovered 11 adult dead spiders (7 males, 4, females) between 6 June–7 Oct 2014 and 13 May–27 Sept 2015. Sixty-five percent were seen on at least one subsequent occasion and we observed one tagged female that successfully overwintered and produced and guarded an egg sac that hatched 74 spiderlings the spring following her first capture. One dead, recovered adult male likely died due to complications from a forceps injury. This individual was treated as a known removal (-1) in the joint live encounter and dead recovery analysis, along with two other adult marked males discovered well outside the survey area, one of which may have been inadvertently transported when an item was removed from the garage.

Survival.—We detected slight evidence of overdispersion ($\hat{C} = 1.07$) for the global model so we used QAIC$_c$ for model selection and inflated our variance estimates accordingly using the overdispersion factor ($\hat{C}$). The top-ranked model garnered 0.947 of the model weight (w_i, Table 1). The majority of the remaining trivial support ($w_i = 0.045$) went to a model where survival varied based on season, recapture probabilities varied by time, and dead recoveries were treated as constant. Thus, model averaging was unnecessary. The strongly supported top-

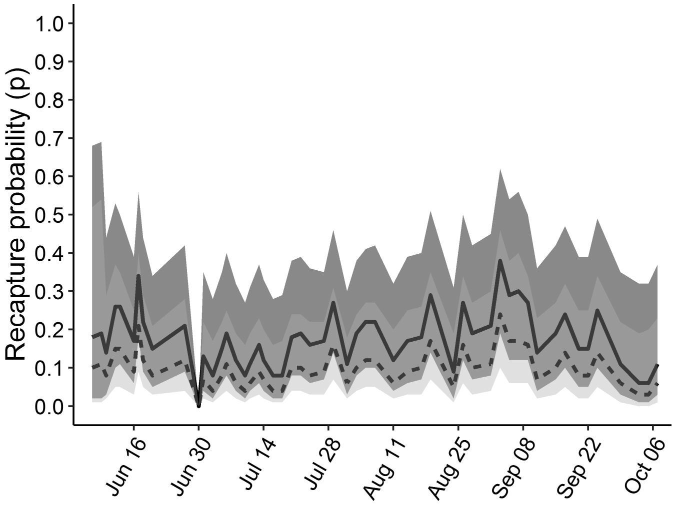

Figure 1.—Day of year (2014) plotted against sex specific adult recapture probabilities resulting from the joint live encounter dead recovery analysis. Solid black lines represent female point estimates and 95% CI (dark gray). Dashed black lines represent male point estimates and 95% CI (light gray).

Table 2.—Sixteen full likelihood closed-population candidate models used to estimate adult abundance. Models vary in their treatment of sex, time (M_t), behavior (M_b), and heterogeneity (M_h) to explain capture and recapture probabilities. Interactions among parameters are denoted by (*).

Model	AIC$_c$	ΔAIC$_c$	w_i	K	$-2\log(\mathcal{L})$
Sex*M_0	203.729	0.000	0.717	4	194.704
Sex*M_b	206.331	2.602	0.195	6	192.061
M_0	210.240	6.510	0.028	3	203.640
M_b	210.424	6.695	0.025	4	201.399
M_{bh2}	211.563	7.834	0.014	6	197.292
M_{h2}	211.708	7.979	0.013	5	200.129
Sex*M_{h2}	213.161	9.432	0.006	8	193.047
Sex*M_{bh2}	216.451	12.722	0.001	10	189.784
M_t	227.268	23.539	0.000	11	197.018
M_{tb}	230.554	26.825	0.000	12	196.490
M_{th2}	231.425	27.696	0.000	13	193.292
M_{tbh2}	234.701	30.972	0.000	14	192.218
Sex*M_t	253.484	49.755	0.000	20	176.962
Sex*M_{tb}	268.155	64.426	0.000	22	175.964
Sex*M_{th2}	285.951	82.222	0.000	24	174.793
Sex*M_{tbh2}	307.523	103.794	0.000	26	172.935

Models are ranked in ascending QAIC$_c$ order. ΔQAIC$_c$ is the QAIC$_c$ difference between model *i* and the top-ranked model. w_i is the adjusted model weight, *K* is the number of parameters, and $-2\log(\mathcal{L})$ is a measure of the relative fit for a given model.

ranked model treated monthly survival as constant between sexes but allowed recapture probabilities to vary by sex (males were less likely to be recaptured) with an additive effect of time (Fig. 1, only recapture probabilities from 2014 shown). Mean 30-day adult survival probability was 0.73 (95% CI = 0.66–0.78). Average life expectancy for adults was 94 days.

The probability of recovering a marked adult if it died during the course of the study was constant between sexes (0.13, 95% CI = 0.07–0.24). Recapture probabilities were on average highest in September followed by June, August, July and October (Fig. 1). From 2014–2015, recapture probabilities ranged from 0.00–0.56 for males and 0.00–0.72 for females, but female recapture probabilities (0.23) were higher than those of males (0.13) on average.

Abundance.—Of the 16 full likelihood closed-population models considered, only the top-ranked model that treated captures and recaptures as equal but differing by sex received notable support (w_i = 0.717, Table 2). The next most supported model (w_i = 0.195) was an embellishment of the model above but included a behavioral effect which treated captures and recaptures as unequal. However, this effect was considered uninformative as it did not decrease the -2log likelihood enough (≥4 units) to overcome the AIC$_c$ penalty term for having two more parameters than the top-ranked model. The remaining models received little ($w_i \leq 0.028$) to no support. Model averaging of full likelihood closed-population models resulted in abundance estimates of 56 adults with a 1:1 sex ratio for 2014 (Table 3). The density of adults in this 200 m^2 garage was approximately 0.28 spiders/m^2 although spiders were not evenly dispersed but clustered near walls and other potential refugia such as permanently stored vehicles and furniture.

Table 3.—Model averaged estimates of adult abundance from candidate models in Table 2. M_{t+1} = number of unique individuals encountered; $\hat{N}$ = abundance estimate.

Group	M_{t+1}	$\hat{N}$	SE	Lognormal 95 % CI
Males	18	28	8.9	20 – 63
Females	26	28	2.4	26 – 38
Combined	44	56	9.5	47 – 91

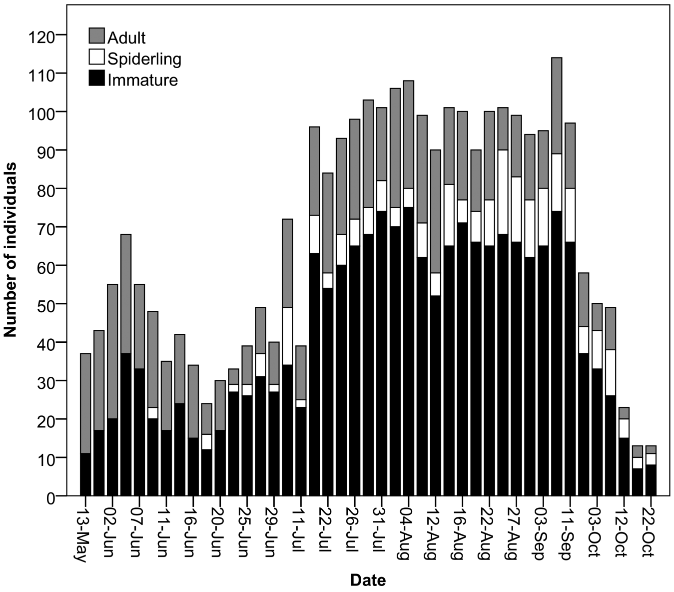

Figure 2.—Stacked bar graph representing the total number of unique adults (gray), immatures (black), and spiderlings (white) observed on a given date in 2015.

Population structure.—Summed over 13 May–27 Oct 2015, we had 241 observations of adult males, 563 observations of adult females, 1,828 observations of immatures, and 286 observations of spiderlings. Because of their small size, spiderlings may be underrepresented in our counts. For a given day, the number of observations was equal to the number of unique individuals observed (Fig. 2). The first detection of spiderlings occurred on 9 June (Fig. 2), less than one month after spiders became active. An approximate three-fold increase in immatures observed began 10 July and persisted through 11 September.

Movement and site fidelity.—As noted above, females were recaptured more often than males. Distance moved (m) between recaptures was positively correlated with interval (days) between captures (Spearman $\rho = 0.57$, $P < 0.001$). Males moved five times farther on average than females (Fig. 3), with a median ($\tilde{X}$) of 0.6 m/day versus 0.12 m/day for females (Mann-Whitney test; $P < 0.001$; 95% $\tilde{X}_F - \tilde{X}_M = -0.37$ [CI $\pm$ – 0.17]). Two males traveled to an adjacent building; one that traveled 20 m was excluded from this analysis because there was a remote chance it may have been transported accidentally when the homeowners moved some items from the garage to the house. Excluding the second male (that moved 28 m) discovered in the adjacent house did not significantly change the results or estimates (Mann-Whitney test; $P < 0.001$; $\tilde{X}_F - \tilde{X}_M = -0.33$ [CI +/- –0.14]). No females were observed to leave the garage; the maximum distance traveled by a female was 20.5 m.

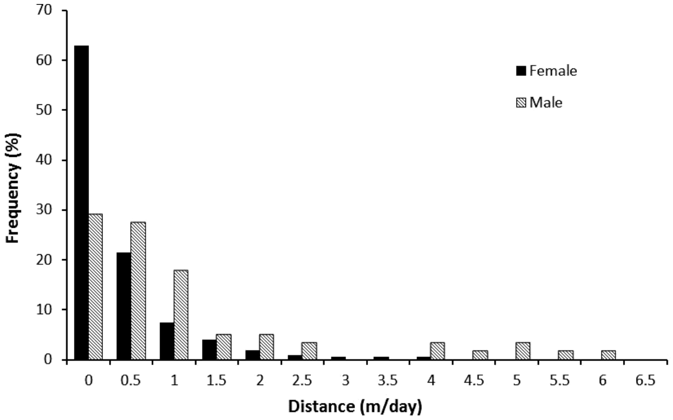

Figure 3.—Frequency distribution of mean distance moved per day by male (n = 61) and female spiders (n = 228). Two outliers, one female at 10.5 m/day and one male at 12 m/day are not shown.

Mean distance moved per day can be misleading given that spiders would often stay in the same area for a few days and then move a long distance in a short period of time. For this reason, we established a definition of a resident spider in order to analyze the site fidelity of those resident spiders. We found 34 instances (77%) in which females could be defined as resident, but only four males (19%) that met our definition ($X^2 = 19.8$, $P < 0.001$). The mean tenure for resident females was 7.7 days (SE = 1.01) with an extreme of 38 days (Fig. 4). A female observed guarding an egg sac for 28 days was excluded from this analysis. While the sample is too small to statistically compare mean differences between the sexes, males (n = 4) stayed on average 4.3 days (SE 1.65) at a site.

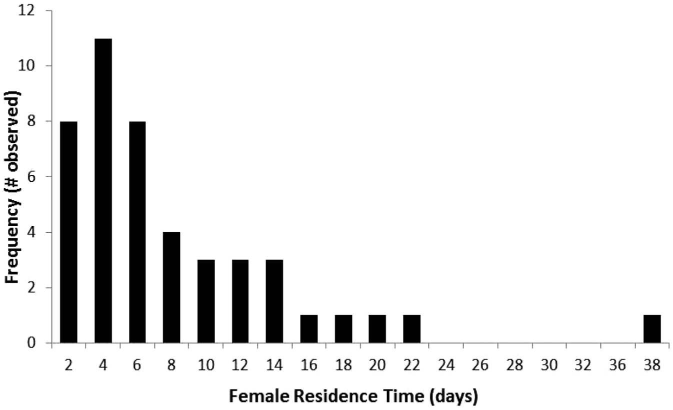

Figure 4.—Frequency distribution of the number of days a resident female spider (n = 45) remained in the same 1 m^2 area. Spiders were considered resident if they were encountered at least twice after marking within 1 m or less of their previous location (with no interval between encounters greater than one week). Males are not shown because only 4 males met the definition of resident.

DISCUSSION

Observed longevity in *Loxosceles* from laboratory studies (Hite et al. 1966; Horner & Stewart 1967; Elzinga 1977; Eskafi et al. 1977) is dramatically higher (up to four years) than our estimate of life expectancy for adults (94 days or 1.3 years from hatching) in a free-ranging synanthropic population. Other mark-recapture studies demonstrate the wide variability among spider species in survival and recapture rates. Framenau & Elgar (2005) marked a population of wolf spiders using bee tags and found a very high rate of survival from 75-85% over 6 months. Male survival was lower in the spring cohort likely because of risks associated with searching for mates. In contrast, survival in our population was 73% per month (not six months) and we found no difference in male and female survival rates. Framenau & Elgar (2005) also report substantially higher recapture probabilities (0.3–0.7) than ours (Fig. 1). Interestingly, they report lower recapture rates for females than males, the opposite of our results. In another study of a smaller species of wolf spider, *Pardosa agrestis* (Westring, 1862), Kiss & Samu (2000) reported recapture rates comparable to ours (0.19 to 0.5) in alfalfa fields.

Survival rates in *Loxosceles reclusa* could be influenced by predation mortality from other spiders, including conspecifics. Of the 11 instances of mortality we observed, two (one male, one female) were caught in webs of *Parasteatoda tepidariorum* (C.L. Koch, 1841). Sandidge (2004) also noted predation by this common house spider on brown recluse spiders, observing a weak negative correlation between the presence of *P. tepidariorum* and *Loxosceles* in synanthropic populations. Cannibalism is widespread in spiders (Wise 2006) and not uncommon in *Loxosceles*. Cramer (2015) observed that spiders comprised 25% of prey captured by *L. reclusa*, and 40% of those were conspecifics, thus comprising 10% of their diet. In the current study, 3 of the 7 males recovered dead were cannibalized by females. Together, these observations suggest that cannibalism is potentially a significant source of mortality in *L. reclusa*.

Despite their low metabolism (Carrel & Heathcote 1976) and longevity in the lab, starvation is probably a significant cause of mortality in *L. reclusa* in natural populations. Six of the eleven marked spiders that we found dead in this study had no evidence of other causes of death. Eskafi et al. (1977) found that temperature and vapor pressure deficit were significant factors in brown recluse spider survival, but that spiders which had fed before beginning the experiment endured significantly longer. Brown recluse spiders have very low rates of water loss and rely on metabolic water when water stressed, but lack of food ultimately caused death within 55 to 94 days. In contrast, spiders that began the experiment "engorged" increased their survival to 151 to 222 days. Our calculated life expectancy of 94 days is in the upper range of spiders who have not fed, lending credence to the argument that starvation is a biologically important source of mortality. Although Sandidge (2003) considered scavenging to be a significant source of nutrition for brown recluse spiders that enabled them to persist in urban settings and avoid starvation, its importance has been contested in subsequent studies (Cramer 2008, 2015; Vetter 2011). Observations by Cramer (2015) demonstrated that *L. reclusa* is a sit-and-wait predator that does not actively search for prey and therefore is unlikely to scavenge even when freshly dead prey items are placed within a meter of their webs.

Accurate estimates of *Loxosceles* abundance or density that include some estimates of error are lacking. Most are simply reports of enormous numbers (usually *L. reclusa*) captured in short periods of time in various structures (e.g., Schenone et al. 1970; Vetter & Barger 2002). Thus, our abundance estimate of 56 adults (05% CI 47–91) or 0.28 adult spiders/m^2 are not comparable to these studies. Including immature spiders elevates our density estimate to one spider/m^2 or 200 spiders in the entire structure. However, our estimate is likely low because many areas of the garage could not be inspected due to, e.g., abundant harborage in the floor, walls, and stored materials, as well as the rafters and ceiling. Our estimate is limited to spiders principally on the floor or visible without disturbing materials stored in the garage.

Other mark-recapture studies show that site fidelity varies among species of arachnids. Samu et al. (1996) created artificial web sites for linyphiids inhabiting wheat fields in order to examine site fidelity. Spiders frequently moved webs, averaging only 1.7 days per site with a maximum tenure of 8 days. Such shifts were caused equally by competition from conspecifics, destruction of a web, or simple abandonment. In contrast, the wolf spider *Pardosa agrestis* adopted a "sit-and-move" foraging strategy (Samu et al. 2003). Ninety percent of the time, the spiders sat inactive (for periods of 2.5 min on average). These periods of inactivity were interrupted by brief periods of movement to change location. Both sexes moved on average < 4 m/day. Similar to our results, movement distance was highly skewed toward shorter distances, though some individuals moved up to 20 m/d. Arguably, brown recluse spiders also adopt a sit-and-move strategy, but with much longer intervals between significant movements, on the order of days rather than minutes. In another study of wolf spiders, Ahrens & Kraus (2006) found that no more than half of the individuals of the riparian spiders (*Pirata* spp.) they studied moved to an adjacent one meter section per day; many never moved even one meter.

Other researchers have reported significant sex differences in movement and site fidelity as we report here for brown recluse spiders. Dodson et al. (2015) studied site fidelity and movements in another sit-and-wait (or sit-and-move) predator, *Misumenoides formosipes* (Walckenaer, 1837). Using a variety of methodologies, they found that males moved six to ten times farther than females. Females also remained at a site more than twice as long as males. This is consistent with many studies of male and female behavioral differences in arachnids where males are more mobile, presumably in a search for mates, which potentially exposes them to greater risks of mortality. For instance, Kasumovic et al. (2006) showed that mate searching in *Nephila plumipes* (Latreille, 1804) exposed males to high mortality risk (a survival rate of 36% over the 25-day course of their mark-recapture study). Even this tiny male orb weaver would travel about an average of 10 m in 3.5 days. Hebets (2002) also demonstrated sex differences in site fidelity in amblypygids. While there was no difference in frequency or distance of movement, females were much more likely to be sedentary. Framenau (2005) recorded greater activity of male than female wolf spiders, but only during two months when males were searching for more sedentary females. As in our study, males were less often recaptured than females, most often being encountered only once after marking. Framenau (2005) suggested that selection for longer leg length (sex dimorphism) in males was driven by mate searching behavior. *Loxosceles reclusa* is also a sexually dimorphic species in regard to relative leg length. Measurements of *L. reclusa* taken by Gertsch & Ennik (1983) show that all male legs are longer than females, especially the first two pair, by 19 and 33%, respectively. Nonetheless, while male brown recluse spiders in our study moved more frequently and farther than females, we did not detect any difference in overall survival between the sexes.

Movement and site fidelity may be linked to mortality risk from starvation which is a widespread in spiders (Wise 2006). Variation in site tenure in brown recluse spiders may reflect a "win/stay – lose/shift" strategy as seen in pholcids that was related to food availability and presence of conspecific competitors (Jakob 2004). She noted that spiders would leave the web when food-deprived and would be more likely to do so if a larger conspecific were sharing the web. Similarly, Miyashita (2005) reported that giving supplemental food to *Nephila* increased residence time. Crab spiders, *Mecaphesa* (as *Misumenops*) *asperatus* (Hentz, 1847) prefer patches of goldenrod with a greater number of inflorescences and spiders in higher quality patches remain there longer (Robakiewicz & Daigle 2004). In contrast, Vetter & Rust (2008) found no link between degree of starvation and tendency to shift refugia in a laboratory study of *L. reclusa*. On average, spiders shifted refugia every two to three days, about twice as often as we observed. Gillespie & Caraco (1987) reported a somewhat counterintuitive strategy in long-jawed spiders. Low prey availability led to increased residence time whereas in areas of high prey availability spiders were more likely to relocate. Although we did not directly estimate prey availability, this hypothesis suggests another avenue to investigate to explain the sedentary, sit-and-wait foraging strategy of brown recluse spiders.

In this paper, we examined survival, abundance and movement of *L. reclusa* as well as differences in these variables between the sexes. We report an average life expectancy of 94 days for adult spiders, far less than reported for spiders reared in the laboratory, some of which have lived for more than four years. Thus, turnover in synanthropic populations of brown recluse spiders is much higher than what can be inferred from prior laboratory studies. The abundance of adult spiders we report in this setting is consistent with prior anecdotal reports but perhaps underestimated due to an inability to detect all individuals by thoroughly searching the entire structure. Females were far more sedentary than males, often remaining in the same area for more than a week. Males moved much more frequently than females, traveled greater distances and were less likely to be recaptured. Nonetheless, despite this marked difference in movements, we detected no difference in survival between males and females.

ACKNOWLEDGMENTS

We wish to thank Ian and Sarah Moschenross for allowing access to their garage at all hours of day and night, and for resisting all attempts to control, eliminate or otherwise interfere with the natural behavior of the spiders. The Monmouth College Department of Biology provided material support. We thank Tim Tibbetts and anonymous reviewers whose voluntary efforts provided helpful feedback that greatly improved this manuscript. We also thank Collin Jaeger for providing R code to modify a previous version of Fig. 1.

LITERATURE CITED

Ahrens, L. & J.M. Kraus. 2006. Wolf spider (Araneae: Lycosidae) movement along a pond edge. Journal of Arachnology 34:532–539.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pp. 267–281. *In* Proceedings of the Second International Symposium on Information Theory. (B.N. Petrov, F. Csaki, eds). Akademiai Kiado, Budapest.

Anderson, D.R. 2008. Model Based Inference in the Life Sciences: a Primer on Evidence. Springer-Verlag, New York NY.

Burnham, K.P. 1993. A theory for combined analysis of ring recovery and recapture data. Pp. 199–213. *In* Marked Individuals in the Study of Bird Population (J.D. Lebreton, P.M. North, eds.). Birkhauser, Basel.

Burnham, K.P. & D.R. Anderson. 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. Spring-Verlag, New York NY.

Carrel, J.E. & R.D. Heathcote. 1976. Heart rate in spiders: influence of body size and foraging energetics. Science 193(4248):148–150.

Case, T.J. 2000. An Illustrated Guide to Theoretical Ecology. Oxford University Press, New York NY.

Chao, A. & R.M. Huggins. 2005. Modern closed-population capture-recapture models. Pp. 58–87 *in* Handbook of Capture-recapture Analysis (S.C. Armstrup, T.L. McDonald, B.F.J. Manly eds.). Princeton University Press, Princeton NJ.

Cooch, E.G. & G.C. White. 2017. Program MARK—a gentle introduction (17th edition). Online at http://www.phidot.org/software/mark/docs/book/. Accessed 25 June 2017.

Cramer, K.L. 2008. Are brown recluse spiders (*Loxosceles reclusa*) scavengers? The influence of predator satiation, prey size and prey quality. Journal of Arachnology 36:140–144.

Cramer, K.L. 2015. Activity patterns of a synanthropic population of the brown recluse spider, *Loxosceles reclusa* (Araneae: Sicariidae) with observations on feeding and mating. Journal of Arachnology 43:67–71.

Dodson, G.N., A.G. Anderson & L.M. Stellwag. 2015. Movement, sex ratio, and population density in a dwarf male spider species, *Misumenoides formosipes* (Araneae: Thomisidae). Journal of Arachnology 43:388–393.

Elzinga, R.J. 1977. Observations on the longevity of the brown recluse spider, *Loxosceles reclusa* Gertsch & Mulaik. Journal of the Kansas Entomological Society 50:187–188.

Eskafi, F.M., J.L. Frazier, R.R. Hocking & B.R. Norment. 1977. Influence of environmental factors on longevity of the brown recluse spider. Journal of Medical Entomology 14:221–228.

Ferreira, R.L., X. Prous, S.F. Machado & R.P. Martins. 2005. Population dynamics of *Loxosceles similis* (Moenkhaus, 1898) in a Brazilian dry cave: a new method for evaluation of population size. Revista Brasileira de Zoociencias Juiz de Fora 7:129–141.

Fischer, M.L. 1996. Biologia e ecologia de *Loxosceles intermedia* Mello-Leitão (Araneae, Sicariidae), no Município de Curitiba, PR. Dissertação de mestrado em ciencias biológicas – zoología, Universidade Federal do Paraná.

Fischer, M.L. & J. Vasconcellos-Neto. 2005. Development and life tables of *Loxosceles intermedia* Mello-Leitão 1934 (Araneae, Sicariidae). Journal of Arachnology 33:758–766.

Fletcher, D.J. 2012. Estimating overdispersion when fitting a generalized linear model to sparse data. Biometrika 99:230–237.

Framenau, V.W. 2005. Gender specific differences in activity and home range reflect morphological dimorphism in wolf spiders (Araneae, Lycosidae). Journal of Arachnology 33:334–346.

Framenau, V.W. & M.A. Elgar. 2005. Cohort dependent life-history traits in a wolf spider (Araneae: Lycosidae) with a bimodal life cycle. Journal of Zoology 265:179–188.

Gertsch, W.J. & F. Ennik. 1983. The spider genus *Loxosceles* in North America, Central America, and the West Indies (Araneae, Loxoscelidae). Bulletin of the American Museum of Natural History 175:264–360.

Gillespie, R.G. & T. Caraco. 1987. Risk-sensitive foraging strategies of two spider populations. Ecology 68:887–899.

Hebets, E.A. 2002. Relating the unique sensory system of amblypygids to the ecology and behavior of *Phrynus parvulus* from Costa Rica (Arachnida, Amblypygi). Canadian Journal of Zoology 80:286–295.

Hite, J.M., W.J. Gladney, J.L. Lancaster, Jr. & W.H. Whitcomb. 1966. Biology of the brown recluse spider. Arkansas Experimental Station Bulletin 711:3–26.

Horner, N.V. & K.W. Stewart. 1967. Life history of the brown spider, *Loxosceles reclusa* Gertsch and Mulaik. Texas Journal of Sciences 19:333–347.

Jakob, E.M. 2004. Individual decisions and group dynamics: why pholcid spiders join and leave groups. Animal Behaviour 68:9–20.

Kasumovic, M.M., M.J. Bruce, M.E. Herberstein & M.C.B. Andrade. 2006. Risky mate search and mate preference in the golden orb-web spider (*Nephila plumipes*). Behavioral Ecology 18:189–195.

Kiss, B. & F. Samu. 2000. Evaluation of population densities of the common wolf spider *Pardosa agrestis* (Araneae: Lycosidae) in Hungarian alfalfa fields using mark-recapture. European Journal of Entomology 97:191–195.

Miyashita, T. 2005. Contrasting patch residence strategy in two species of sit-and-wait foragers under the same environment: a constraint by life history? Ethology 111:159–167.

Nicolas, G. & D. Sillans. 1989. Immediate and latent effects of carbon dioxide on insects. Annual Review of Entomology 34:97–116.

Norris, J.L., III & K.H. Pollock. 1995. A capture-recapture model with heterogeneity and behavioural response. Environmental and Ecological Statistics 2:305–313.

Otis, D.L., K.P. Burnham, G.C. White & D.R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:3–135.

Pledger, S. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. Biometrics 56:434–442.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Online at http://www.R-project.org/.

Richman, D.B. 1973. Field studies on the biology of *Loxosceles arizonica* Gertsch and Mulaik (Araneae: Scytodidae). Journal of the Arizona Academy of Science 8:124–126.

Robakiewicz, P. & W. Daigle. 2004. Patch quality and foraging time in the crab spider *Misumenops asperatus* Hentz (Araneae: Thomisidae). Northeastern Naturalist 11:23–32.

Samu, F., K.D. Sunderland, C.J. Topping & J.S. Fenlon. 1996. A spider population in flux: selection and abandonment of artificial web-sites and the importance of intraspecific interactions in *Lepthyphantes tenuis* (Araneae: Linyphiidae) in wheat. Oecologia 106:228–239.

Samu, F., A. Sziranyi & B. Kiss. 2003. Foraging in agricultural fields: local 'sit-and-move' strategy scales up to risk-averse habitat use in a wolf spider. Animal Behaviour 66:939–947.

Sandidge, J. 2003. Scavenging by brown recluse spiders. Nature 426(6962):30.

Sandidge, J. 2004. Predation by cosmopolitan spiders upon the medically significant pest species *Loxosceles reclusa* (Araneae: Sicariidae): limited possibilities for biological control. Journal of Economic Entomology 97:230–234.

Schenone, H., A. Rojas, H. Reyes, F. Villarroel & G. Suarez. 1970. Prevalence of *Loxosceles laeta* in houses in central Chile. American Journal of Tropical Medicine and Hygiene 19:564–567.

Vetter, R.S. 2011. Scavenging by spiders (Araneae) and its relationship to pest management of the brown recluse spider. Journal of Economic Entomology 104:986–989.

Vetter, R.S. 2015. The Brown Recluse Spider. Cornell University Press, Ithaca NY.

Vetter, R.S. & D.K. Barger. 2002. An infestation of 2,055 brown recluse spiders (Araneae: Sicariidae) and no envenomations in a Kansas home: implications for bite diagnoses in non-endemic areas. Journal of Medical Entomology 39:948–951.

Vetter, R.S. & M.K. Rust. 2008. Refugia preferences by the spiders *Loxosceles reclusa* and *Loxosceles laeta* (Araneae: Sicariidae). Journal of Medical Entomology 45:36–41.

Wedderburn, R.W.M. 1974. Quasi-likelihood functions, generalized linear models, and the Gauss–Newton method. Biometrika 61:439–447.

White, G.C. & K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Wickham, H. 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York NY.

Williams, B.K., J.D. Nichols & M.J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press, Cambridge MA.

Wise, D.H. 2006. Cannibalism, food limitations, intraspecific competition, and the regulation of spider populations. Annual Review of Entomology 51:441–465.

Manuscript received 5 September 2017, revised 18 April 2018.