

**An Analysis of Colony Movement and The Effects of Movement on Fitness in the Western
Harvester Ant, *Pogonomyrmex Occidentalis***

A Senior Honors Thesis Presented to the Faculty of the
Department of Biology and Biochemistry
University of Houston

In Partial Fulfillment of the Requirements for
the Degree of Bachelor of Science

By
Maxximus Ramsaroop
August 2023

**An Analysis of Colony Movement and The Effects of Movement on Fitness in the Western
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ABSTRACT

Colony movement in ants (*Hymenoptera: Formicidae*), is well documented and several studies have explored the fitness costs and causes of colony movement in different species. Attempts to describe the purpose or patterns of colony movement have been made on many species within *Pogonomyrmex spp.* However, research into these aspects of colony movement has yet to be described in *P. occidentalis*, The Western Harvester ant. This thesis examines the fitness costs, potential causes, and behavioral syndrome associated with colony movement in *P. occidentalis*. I analyzed Dr. Cole & Dr. Wiernasz's data from 1993-2023 on colony movement, age, size, distances traveled, and survivorship for 6,066 colonies. Moved colonies were found to have a smaller colony size, shorter colony lifespan, and lower rates of survivorship when compared to unmoved colonies using t-tests and a Kaplan-Meier survivorship analysis. Moreover, moved colonies were compared against 1-year-old colonies, and were found to have a larger colony size. Colonies were also found to have a greater tendency to move later in age, and 16.6% of colonies had moved at least once. These results suggest that colonies that move incur fitness costs, as colony size and lifespan are proxies for fitness, and that colony movement is more costly for younger or smaller colonies. Furthermore, because *P. occidentalis* is notably long-lived, shows high nest fidelity, and their movements are associated with a loss in fitness, they likely exhibit an adventitious nest relocation syndrome. Through this thesis, we can better contextualize *P. occidentalis* in the greater scheme of animal architects and the decisions they make.

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INTRODUCTION

1.1 Ants & Animal Architects

Animal architects are a taxonomically widespread group, connected by their common ability to develop constructs, known as ‘animal architecture’. These constructs widely vary in complexity and function, but always serve to benefit the lives of their creators. Constructs can function as courtship displays, traps, shelters, food storage, or tools (Laidre, 2021). Architects like male bowerbirds (*Ptilonorhynchidae spp.*) create bowers from twigs and brightly colored objects to court females, increasing their likelihood of reproduction (Diamond, 1986). Orb-weaver spiders (*Araneidae spp.*) create webs from their own silk to capture prey, allowing them to gather food more efficiently (Pasquet et al., 2013). Female Polar bears create dens as a place to give birth to cubs and as shelters, increasing their cubs’ chances of survival (Messier et al., 1994). Animal architecture is a result of both the behavior and physiology of its creator, meaning that these builders often naturally have certain morphological traits and instincts (or otherwise learned traits) that allow them to create constructs. Thus, many animal architects have evolved specialized traits to create more effective architecture. Social insects, including the order *Hymenoptera* and *Isoptera*, have famously evolved several behavioral and morphological traits like castes, polyethism, and social coordination alongside nest construction (Laidre, 2021; Carroll & Janzen, 1973).

In particular, ants (*Formicidae spp.*) are social insects that utilize tactics like complex social hierarchies, eusociality, pheromonal cues, and physical or temporal castes, to build and defend some of the most intricate constructs in the animal kingdom (Carroll & Janzen, 1973).

Ant architecture takes the form of nests. These nests are multifunctional, providing shelter, food storage, brood storage, temperature regulation, and a place to socialize and communicate information (Laidre, 2021). Given the diversity of ants, different species can have vastly different nest forms and functions. Some ants, like Leaf-cutter ants (*Atta spp.*), create complex nests with several specialized rooms, spanning several hundred cubic feet. These leaf-cutters spend years creating and protecting a single colony (Della Lucia et al., 2013). Whereas ants like *T. sessile*, create smaller, inexpensive nests underneath logs or rocks that can be replaced several times per year (Smallwood & Culver, 1979). The difference between these nest types results from the different needs of their architects based on their niches. Leaf-cutter ants require larger permanent nests in order to grow and harvest fungi in their nests. Meanwhile, *T. sessile* is a generalist opportunistic nester that lives in an unstable environment with variable food sources, so they should be prepared to relocate quickly (Barbani, 2003). Although nests provide architects with several benefits, they inevitably cost the architect time, energy, and resources to build. These investment costs vary based on construct size, complexity, materials used, the architect's environment, the size of the architect, and many other variables. In addition to construction costs, maintaining and repairing nests cost architects time and effort, especially in events of catastrophic damage. As a result, cheaper nests are often favored when the benefits of nesting outweigh the costs of nesting. Nesting may be inefficient if ants live in an unstable environment, their food source within foraging ranges depletes often, materials are unsuitable for strong nests, and many other reasons.

Thus, ideally, ants and all animal architects should value their constructs greatly; why then do animals abandon their nests? Perhaps the nest has a temporary purpose like offspring care, courtship, or seasonal nesting, as seen frequently in many bird species (Diamond, 1986). The nest may be relatively cheap, weak, or easily replaceable, like those of *T. sessile* (Smallwood & Culver, 1979). Alternatively, nests may be abandoned due to disease, environmental disasters, high predation, low resource abundance, or other reasons (McGlynn 2012). These reasons are context-specific and closely related to the ecological role and biology of the organism. Whatever the case may be, these animals sometimes decide to move to new nests, which may provide new benefits or allow them to avoid the disadvantages of their initial nest.

1.2 Colony Movement

Colony movement (sometimes called colony relocation or nest relocation) is a phenomenon in which a colony of social insects, including their queen, vacate their nest, carrying with them their brood and food, and relocate to a new nest elsewhere. Colonies were originally considered sessile, but currently, colony movement to some degree is considered common in most social insects (McGlynn 2012). Colony movement can be an incredibly complex process. For example, *Apis mellifera* famously holds colony ballots in which individuals vote on where to relocate the nest, a process that can take several days (Seeley et al., 2006).

Although identified in many groups, colony movement has been extensively researched in ants (McGlynn 2012). McGlynn (2012) proposes several hypotheses for nest relocation, suggesting four behavioral syndromes in which ant colony movement can be described. Legionary nomadism describes ants that, while not ‘true’ army ants, relocate in a way that inconsistently simulates army ant movement. Legionary nomads move to secure a food source, then move again once the food source has been eliminated. Intrinsic nest relocation describes ants that, in some form, relocate as a part of their life history. Unstable nesting describes ants that build nests in unstable and ephemeral locations. These ants frequently move, and invest very little effort into building large nests. Adventitious nest relocation describes ants that invest heavily in large nests, show high nest fidelity, and move infrequently. Nest fidelity is defined as a colony’s loyalty to its current nest. Adventitious ants, including *P. barbatus*, *A. colombica*, and *A. cephalotes*, only move in response to major threats, and movement is not a part of their life history. It is well documented in these species that movement occurs in response to severe colony disturbances, predation, and disease (Rockwood, 1973; McGlynn 2012). Although this article does not describe *P. occidentalis* explicitly, many of the Western Harvester Ant’s closest taxonomic relatives are described. Most notably, *P. barbatus* is characterized by adventitious nest relocation, whereas *P. badius* and *P. californicus* are characterized by intrinsic nest relocation (McGlynn 2012). However, general colony movement can occur for a variety of reasons and is context specific. It is generally assumed that most ants relocate in response to disturbances, but upon closer inspection, this assumption is unclear as different species may encounter largely different environmental pressures (Smallwood & Culver, 1979). Parasitism, waste build-up,

competition, seasonality, nest deterioration, and colony growth have all been hypothesized to induce colony movement (McGlynn 2012). Among these hypotheses, it has been speculated that many species, including *T. sessile* and *P. badius*, have incurred fitness costs from movement (Tschinkel, 2014; Smallwood & Culver, 1979). In *T. sessile*, costs were attributed to large portions of time and energy spent on movement, increased vulnerability to predation, and passive accidental loss of workers, brood, and food (Smallwood & Culver, 1979). However, research has not been performed on *P. occidentalis* to support the idea that colony movement is fitness costly or to calculate the costs.

1.3 The Western Harvester Ant

The Western Harvester Ant (*P. occidentalis*) is one of the most populous and ecologically important ant species in the deserts of the western United States, Canada, and Mexico. *P. occidentalis* occupies North American deserts and grasslands, creating large conical pebbles and dirt mounds, acting as a core primary consumer and generalist seed harvester (Rogers, 1972; Cole & Wiernasz, 2002). *P. occidentalis* is notably long-lived, and have been estimated to live up to 42 years, with an average lifespan of roughly 15 years (Keeler, 2022). Young colonies first develop small mounds with one queen and several female workers. As the nest grows in size, colonies rapidly populate the nest to a mean size of 3,880 ants but have the potential to grow beyond 10,000 individuals (Wiernasz & Cole, 1995; Lavigne, 1969). As colonies age and their populations expand, they must expand their nest size, thus size and age are positively related (Fig. 1).

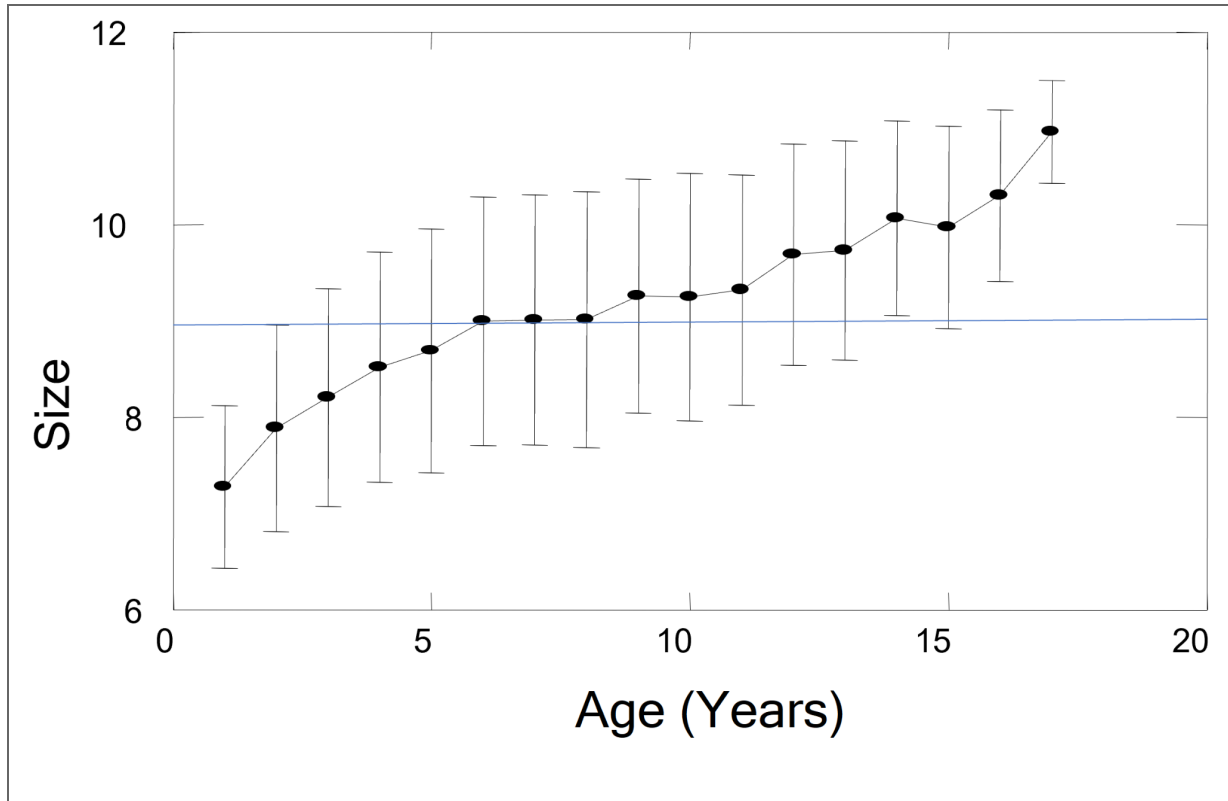


Fig. 1 Scatterplot of Size & Age. Size (Y-axis) in size units and Age (X-axis) in years are demonstrated to have a statistically significant positive relationship. Size units were calculated by using the formula $\ln(\text{length} * \text{width} * (\text{height} + 1\text{cm}))$. The bars above and below the data point represent the standard deviation. This graph was generated by Dr. Cole & Dr. Wiernasz from records of size and age from 1996-Present (Unpublished).

In this study, the nest size was log-transformed to provide a linear scale from 0 to 20 (Wiernasz & Cole, 1995). Sexual maturity generally occurs when a colony passes the 9.5 size category threshold, and colonies that maintain this size or greater have a much greater likelihood of reproducing consistently (Cole & Wiernasz, 2000; Fig. 2).

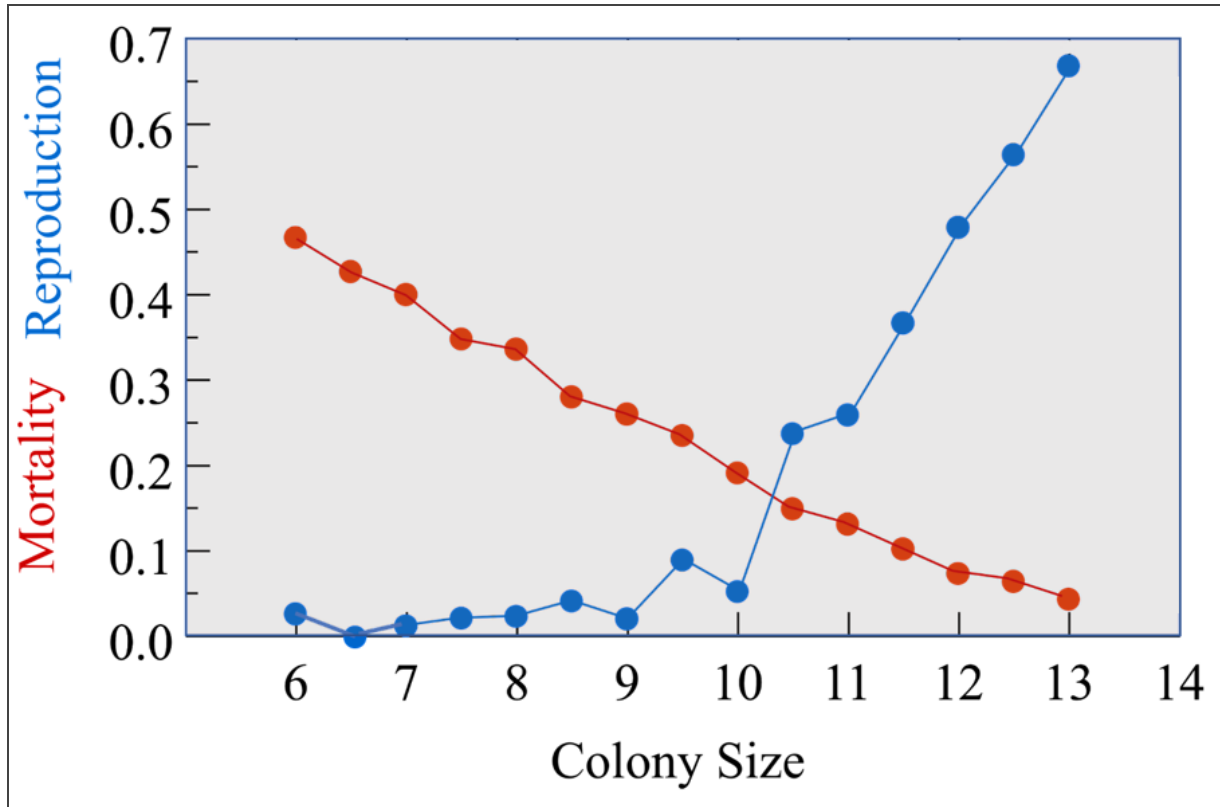


Fig. 2 Correlation between Mortality & Reproduction over Colony Size. The proportion of colonies that reproduce (Blue line) increases as colony size increases. The proportion of colonies that die (Red line) decreases as colony size increases. The Y-axis represents a proportion out of 1.0. This supplemental graph was generated using data from Dr. Cole and Dr. Wiernasz's record of mortality & reproduction (Unpublished). Reproduction (Blue line) was calculated from 4,819 colonies. Mortality (Red line) was calculated from 27,986 colonies. Data were recorded from 1996-present.

After the first monsoonal rains (or a particularly heavy rain) males and virgin queens begin reproductive flights to high-elevation hills in the early summer (Cole & Wiernasz, 2000). There, new queens mate with several males and then fly to a new site to burrow and develop a nest (Mull & Christ, 1993; Cole & Wiernasz, 1999; Cole & Wiernasz 2002). Furthermore, a majority, but not all, of colony relocations have been observed by Dr. Cole & Dr. Wiernasz shortly after the first monsoonal rains (Cole & Wiernasz Personal Communication). Additionally, if monsoons occur later than expected, their moves may not have been identified in transit by Dr.

Cole & Dr. Wiernasz but are detected in the following year. Colony mortality is inferred to start exceptionally high and decrease rapidly as colony size increases (Fig. 2). For reference, size 6 colonies have a 48% mortality rate, whereas size 13 colonies have a mortality rate of roughly 5% (Fig. 2). This pattern results in young colonies often dying within one year of their initial development, while the few colonies that establish themselves, become prolific and can live well for several decades (Keeler, 2022). Additionally, foragers travel between 14.48 and 22.88 meters on average and are often active during the cooler times of the day (Cole et al., 2010; Fewell, 1988). Much of the colony's actual size is below ground. *P. occidentalis* colonies create a single nest that can reach well over 30 centimeters tall and several meters deep (Wiernasz & Cole, 1995). These colonies often take many years to grow to full size, and potentially a decade to become sexually mature (Cole & Wiernasz, 2000; Fig. 2). Furthermore, it has been documented that long-lived ant species that invest in relatively large nests are more vulnerable to environmental changes and stress (Ord, 2023). With this in mind, *P. occidentalis* colony movement should occur rarely and be expensive, since colonies should value their nests.

Yet, as I will show, roughly 17% of identified colonies relocate, and apart from identification and speculated association with rainfall, no research has been performed to understand the purpose, causes, effects, or fitness costs of these movements in *P. occidentalis* (Anderson & Mull, 1992). Answering these questions about movement would thereby allow us to better characterize the sorts of challenges that other animal architects may experience when building and moving their respective structures. In turn, this information can be utilized to protect ecosystem engineers and keystone species (many of which are animal architects), that

provide valuable ecosystem services (Laidre, 2021). Additionally, this research can be used to characterize *P. occidentalis* and other ant species by their behavioral syndromes. This thesis aims to quantify the fitness costs associated with colony movement, identify potential mechanisms that result in fitness costs, and discuss the significance of these findings in a greater scope. I hypothesize that *P. occidentalis* experience fitness costs as a result of colony movement and that colonies display the adventitious nest relocation syndrome. I quantify fitness costs using proxies such as colony size, survival time, and survivorship, as these are strongly related to a colony's fitness (Tschinkel, 2014; Cole & Wiernasz, 2000). Furthermore, I aim to identify potential causes of colony movement, and the effects movement may have on colonies that have moved. By investigating this hypothesis, we can better understand the mechanisms that control colony movement and structural investments in *P. occidentalis*, social insects, and other animal architects. Here, I will describe data on the range of distances colonies travel, the distribution of moved colony sizes, and the survivorship of moved colonies against colonies of similar size groups to support this prediction. Additionally, I have included figures generated by Dr. Wiernasz & Dr. Cole to support the relationships between mortality and reproduction, size and age, the probability of movement and age, and the effects of movement on the size/age relationship. (Fig. 1; Fig. 2).

METHODS & MATERIALS

2.1 Data Acquisition

Field data is gathered annually from a study site roughly 16 kilometers north of Fruita, Colorado by Dr. Cole & Dr. Wiernasz. The habitat type of the site is Adobe Badlands, which is characterized by hills, shale-derived clay, sparse vegetation, and a dry climate (Wiernasz & Cole, 1995). The study site covers 29 hectares and is a native habitat of *P. occidentalis* (Fig. 3).

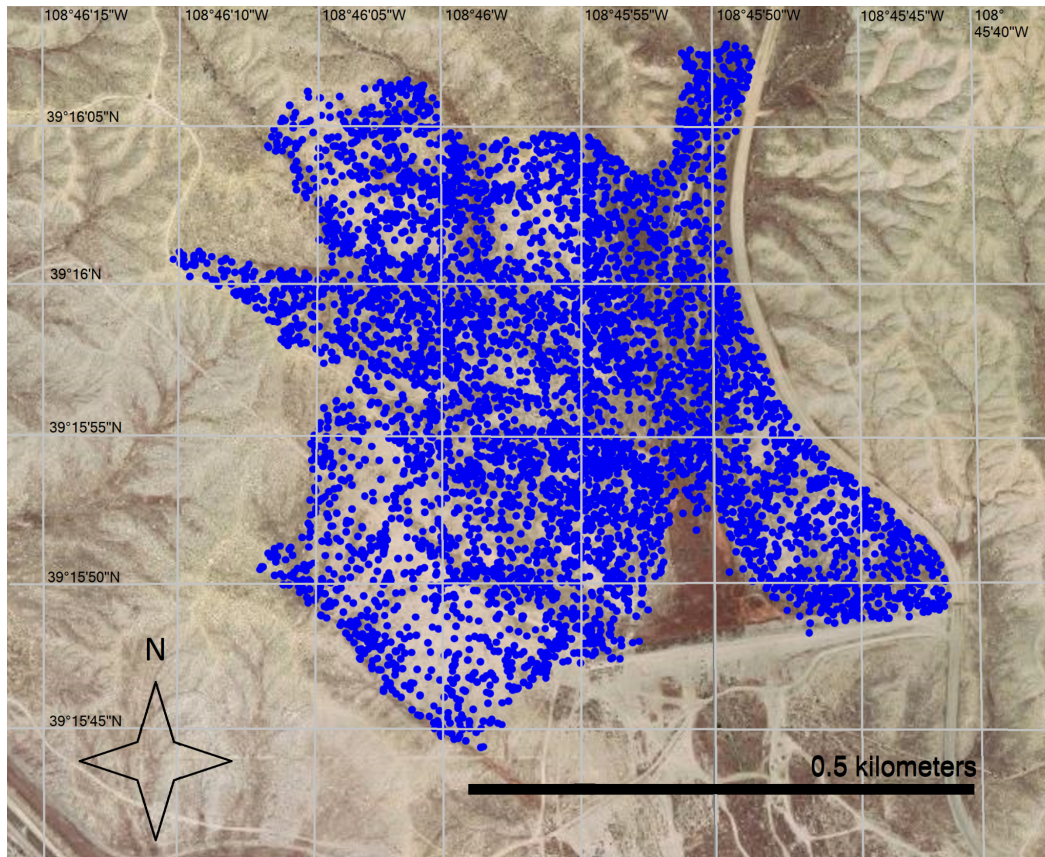


Fig. 3 Study Site Map. Aerial view of the geographic map of the *P. occidentalis* study site 10km NW of Fruita, Colorado. Each blue dot represents an individual colony. All blue dots represent all of the individual colonies that have appeared, 6,066 colonies (Circa 2020). The black bar (bottom right of image) represents $\frac{1}{2}$ of a kilometer.

Colony size, movement distance, and age were all collected via observation and manual measurements. Dr. Cole & Dr. Wiernasz divided the study site into 136 quarter-hectare plots and censused the plots by walking 1m transects. Some plots are partial and could contain up to 50 1m transects per plot. They measured the physical size, relative position, and additional notes on unique features of the colonies. Data was collected from 1993 to the present, each summer from mid-May to June. Dr. Wiernasz & Dr. Cole determined colony age by observation of colony founding, then yearly observations of colony presence until the colony relocates to a new nest or dies. Dr. Cole & Dr. Wiernasz determined colony movement by a set of characteristics unique to recently moved colonies. Recently moved colonies are characterized by fresh, newly excavated, friable, lightly colored, and loosely distributed dirt around the colony. Dr. Wiernasz & Dr. Cole determined colony death by observation of a disheveled nest cone, unmaintained dirt on nest cones, weeds growing in and throughout the nest cone, and an absence of ants. Colonies must appear dead for two consecutive years before they were counted as dead. Each colony was designated an identification number. The first two numbers in the name designate the year discovered with 1992 as 00, increasing by one yearly. The latter three numbers designate the physical location of the colony, relative to other colonies. If a colony relocated to a new nest, it was given a new designation for the year it moved.

All map and notebook data on putative moves were converted into Excel spreadsheets to be statistically analyzed. To perform analyses on data from these tentatively designated movements, first I had to evaluate the credibility of each observed movement. Movements were scored on a numerical credibility scale of 1 to 6, highest credibility to the lowest credibility

respectively. Only movements scored 1 or 2 were used for this study. Secondly, credible movements were connected to an origin colony and/or subsequent destination colony. Colonies were sorted into either 'Initial Colony' or 'Subsequent Colony' categories to indicate whether they were moved from or moved to, respectively. A score of 1 or 2 was assigned if initial and subsequent movements occurred within a 30-meter range of each other, and were within 3 size units of each other. The relative locations of colonies, colony death rates, colony survival rates, the number of living colonies per year, and the total number of moved colonies were gathered from Dr. Cole & Dr. Wiernasz's data set. Systat 13.1, a statistical analysis software, was then used to analyze credible movements and the parameters surrounding said movements (Systat Software Inc. 2009).

Colonies are distinguished by size, age, movement status, and position relative to other colonies. To calculate colony size, Dr. Wiernasz & Dr. Cole used the formula $\ln(\text{length} * \text{width} * (\text{height} + 1\text{cm}))$; the data were log-transformed to provide a normal distribution (Wiernasz & Cole, 1995). Mean survival time post-movement is defined as the number of years a colony survives after relocation. Mean survival time was calculated for colonies using data on colony death and colony movement or after other events/ages in a colony's life.

2.2 Data Analysis

Data analysis on colonies, movements, positions, and other relevant parameters was performed using Systat 13.1 (Systat Software Inc. 2009). These movements were stratified by year, and all movements with unknown origins or unknown destinations were designated with a

“?” and were eliminated from data on the distance and size of colony movement. Data on colonies with unknown origins or destinations were used in all other data sets because of their confirmed movement status via observation. Statistics on the size and 1-year-old status of colonies that moved were calculated based on data supplied by Dr. Wiernasz and Dr. Cole.

The mean colony size of all unmoved colonies over 30 years was compared against the mean size of colonies one-year post-movement using a two-tailed t-test. Since colonies change in size as they age, unmoved colony sizes were averaged over their entire lifespan. 24,582 measurements of unmoved colony sizes were measured against 651 moved colonies. Any colonies that had ever moved were considered moved colonies, and their sizes were recorded one-year post-movement. Both origin and destination colonies were separated from the unmoved colony data set. The two-tailed t-test was used to identify whether, on average, the size of moved colonies differed from that of unmoved colonies. This test was used because the moved colonies were a separate population of colonies from unmoved colonies. The standard deviation, range, and frequency distribution, in both, moved and unmoved colonies were additionally generated.

1-year-old colonies were tested against moved colonies at one-year post-movement. This comparison was made to determine whether, given a similar time frame, the sizes of 1-year-old colonies and the sizes of newly moved colonies differed. If the sizes of 1-year-old colonies and moved colonies were similar, then it would suggest that nest construction and transportation take a large flat amount of time and energy from colonies despite the difference in age and number of workers. Thus, it could be inferred that colony construction could play a very large role in colony movement. The average, range, standard deviation, and frequency distribution of the size of

1-year-old colonies were calculated. The average size of moved colonies was tested against the average size of newly relocated colonies using a two-tailed t-test since 1-year-old colony sizes are of a separate population from moved colonies. 1,385 1-year-old colonies were tested against 1,067 moved colonies.

Ideally, t-tests for moved colonies against unmoved colonies or moved colonies against 1-year-old colonies would have been controlled for the year of occurrence. The growth rate and success of colonies are dependent on the availability of resources, natural disasters, and weather in that year. However, having no data or means to determine the availability of resources or other parameters that may control colony growth, I chose to pool data from all 30 years to measure against movements from all 30 years.

To demonstrate that moved colonies exhibit less growth and a weakened size-age relationship compared to unmoved colonies, I compared the size of colonies in successive years. I produced a scatterplot comparing colonies of moved and unmoved status using the initial sizes and subsequent sizes of unmoved colonies from [1998 to 1999, 2000 to 2001, 2005 to 2006, 2007 to 2008], and the sizes of all moved colonies in their first year post-movement (Fig. 9). Data from these specific yearly subsets were chosen arbitrarily, to show the variation between years. The initial size for unmoved colonies is defined as the size of said colony in the labeled year. The subsequent size is defined as the size of the same colony in the subsequent year. The initial size for moved colonies is the colony's size in the year before movement occurred, and subsequent size is the size in the subsequent year. 95% confidence interval ellipses are used in

Fig. 9 to represent the general distribution of moved and unmoved colonies as red ellipses and black ellipses respectively along the scatterplot.

Moved colonies are provided a new designation in the year they move, additional N values are created for each movement with a known origin and destination. This dilutes the proportion of colonies that are moving. Thus, to determine the proportion of colonies that have moved, the equation $M/(N-D)$, in which M represents the number of colonies that moved, regardless of whether their origin or destination was known. N represents the total number of colonies. D represents the number of moved colonies with known origin and destination nests. This equation removes the additional N values created by movements with known origins and destinations.

Coordinates were mapped by Dr. Cole & Dr. Wiernasz using a Leica total station and used to calculate distances (m) between original nests and nests of relocated colonies through Systat 13.1 (Systat Software, Inc. 2009). The average, range, and standard deviation of distances between all colonies of known origin and destination were generated (n=704). A frequency distribution was generated to represent the distribution of distances colonies moved (Fig. 4).

Because of the relationship between colony size and mortality, size has a major influence on the survival time and survivorship of the colony (Fig. 2). Thus, I controlled for colony size in my calculations of mean survival time and survivorship. While it would have been ideal to control measurements of survival time and survivorship for age, years measured, and any environmental conditions, there were insufficient data to control for these variables at the same time. Additionally, the central focus is to understand the relationship between size and mortality

broadly, and how movement affects size, thus mortality (Fig. 1). The mean size of colonies that move is 8.493 size units ($sd=1.668$), which matches the size of 6-year-old colonies roughly. Thus, for mean survival time and the Kaplan-Meier survival analysis, I compared moved colonies against colonies that did not move and were more than 6 years old. Colonies that did not move and reached 6 years of age are abbreviated as ‘controls’. I used age-matched colonies as a proxy to control for size so that the survival time of colonies that did not move was not skewed by the large variability in survival time for colonies of varying sizes. Mean survival time and mean survival time post-movement are variables that average the time in years that colonies with a certain value are expected to live. Mean survival time post-movement was calculated by averaging the year of colony movement subtracted from the year of colony death. The mean survival time for control colonies was calculated by taking the average of their age subtracted from their age at death. Colonies that survived to the end of the study’s time frame were not included in calculations on mean survival time. The mean survival time was calculated for all control colonies. Standard deviations, 95% confidence intervals, and two-tailed t-tests were performed between these two groups to test the statistical significance of the difference between them.

To determine the difference between survivorship in moved and control colonies, I developed a life table analysis to determine the survivorship of control and moved colonies over 23 years. Survivorship curves represent the likelihood that organisms will survive to the current time interval. Colonies that survived to the end of the study were right-censored (designated 0 in the survival analysis), and colonies that died during the study (uncensored) were given a censor

status of 1. 221 colonies that moved survived to the end of the study and were right-censored. Therefore, it is impossible to determine how long they have lived, only that they have lived to the end of the study. The Kaplan-Meier (K-M) survival analysis was used to measure the survival statistics for both control and moved colonies. If a colony survived beyond 23 years, in 2020, it was censored from the data. 1,067 moved colonies and 607 unmoved age 6 colonies were used to generate the Kaplan-Meier analysis. Additionally, 95% confidence intervals were generated to provide a fair estimate of survivorship for any given year.

RESULTS

3.1 Size Distributions & Proportions of Moved Colonies

Data from 6,066 colonies, 1,067 instances of colony movement, and 24 years of observation of *P. occidentalis* in the study site were used to create the following analyses and graphs. Each year an average of 1,074 colonies were alive, ranging from 1,275 to 867 colonies per year. Of the 1,067 instances of colony movement, 197 were of colonies that had already moved at least once before. On average, roughly 2 to 3% relocated each year, with a standard deviation of ± 59 colonies per year and a range of 15 to 309 colonies. The total proportion of ants that moved represents 16.6% of the 6,066 identified colonies.

Colonies of known origin and destination ($n=704$), were tested for the distance moved. The distances that all moved colonies traveled averaged 5.85 meters away from the origin, with a standard deviation of ± 3.7 meters and a range of 1 to 25.98 meters (Fig. 4).

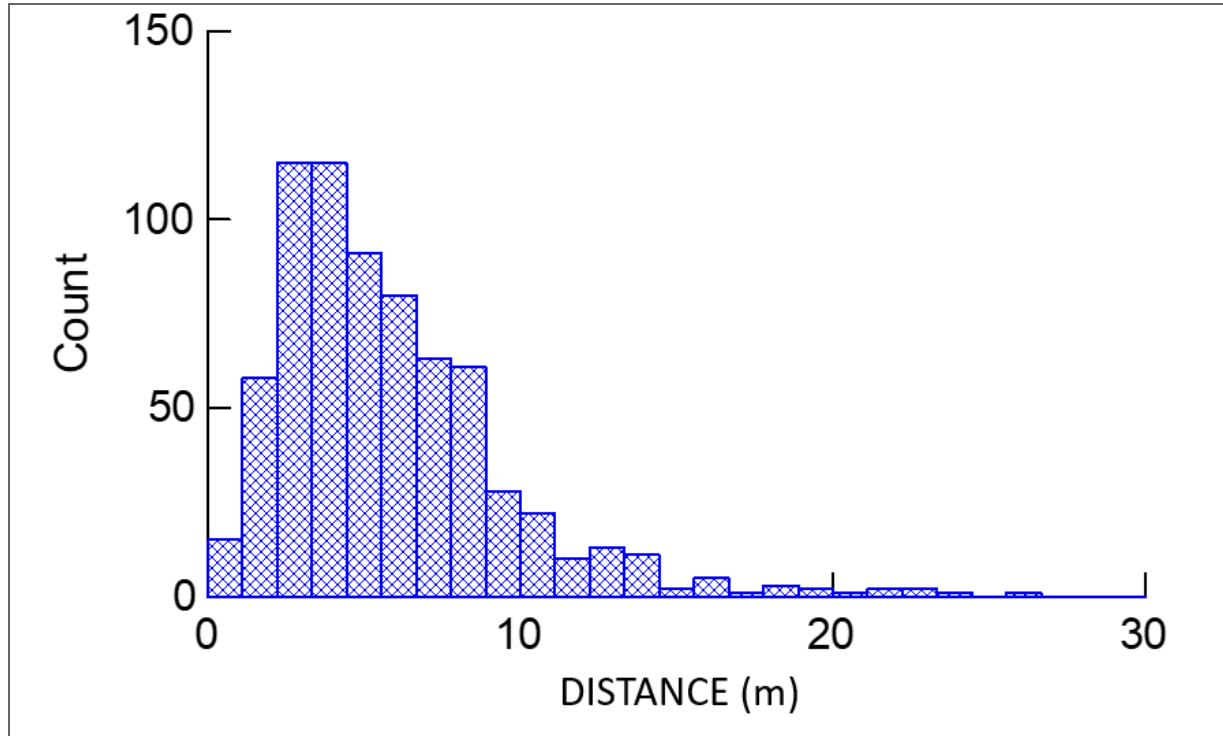


Fig. 4 Frequency Distribution of Distances Moved. Frequency distribution of the known distances moved between origin and destination colonies. Count (Y-axis) measures the number of colonies within each bar. Distance (X-axis) measures the distances in meters for each colony. Data were recorded from 704 instances of movement from 1996-present.

The proportion of colonies that moved as a function of age averaged between 1.3% and 4.0% at each age. The mean proportion of colonies that moved as a function of age was 2.6%, with a standard deviation of $\pm 1.4\%$. A regression analysis was developed for Fig. 5, resulting in a regression coefficient of $+0.00084$ ($t=2.78240$; $p=0.01468$). The regression proves that an increase in the proportion of movements is significantly and positively correlated with time.

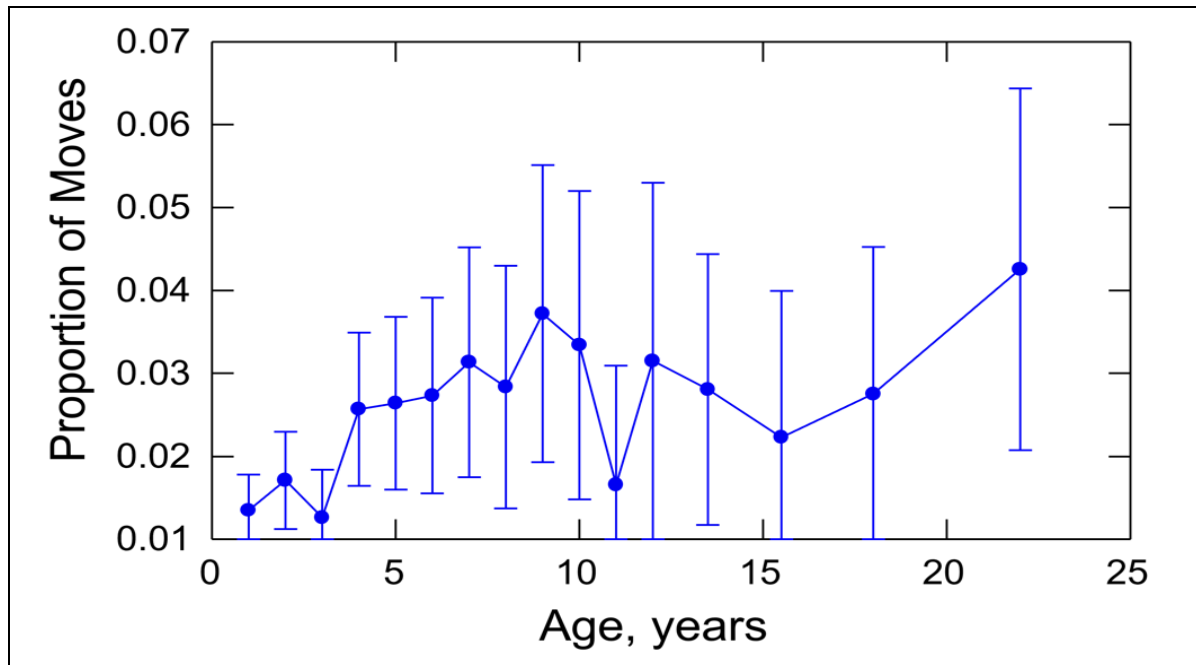


Fig. 5 Proportion of Movements Line Graph. Line graph describing the relationship between the proportion of colonies that move at each age group. The proportion of moves (Y-axis) measures the proportion of colonies that moved out of total colonies for any given age. Age (X-axis) measures the age at which colonies moved. The graph was developed using 244 movement data points and 12,568 total colonies.

The size distribution of moved colonies is shown in (Fig. 6) (n=651). The mean size of colonies post-movement was 8.493 size units (sd=1.668, range=2-13) (Fig. 5).

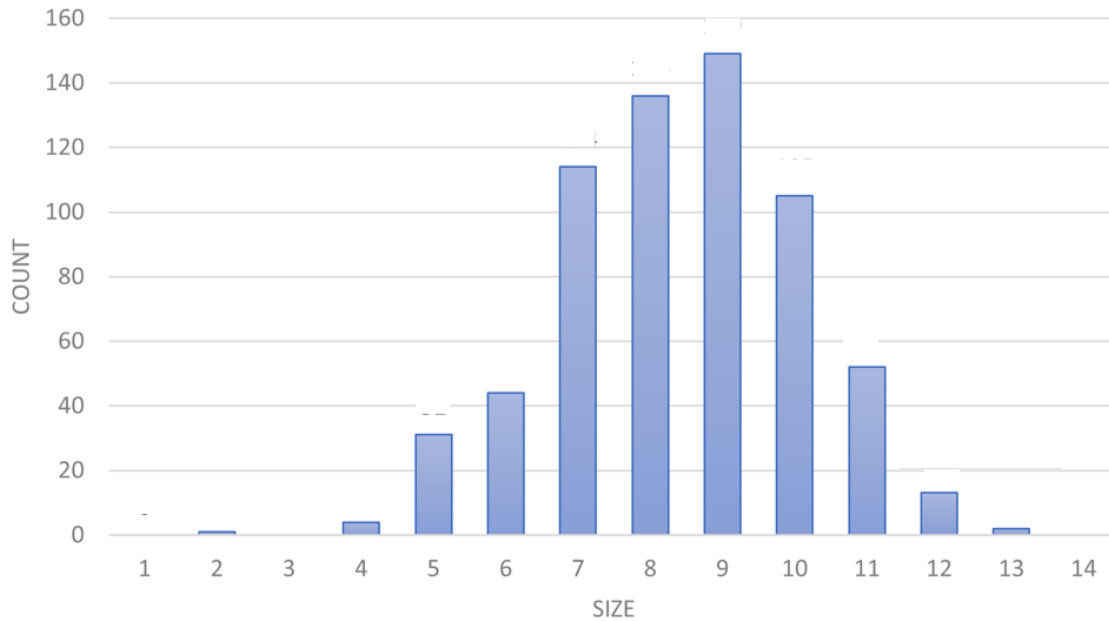


Fig. 6 Size Distribution of Moved Colony Sizes. The above frequency distribution represents 651 moved colonies of known size, origin, and destination between 1996-present. Count (Y-axis) is a measurement of the number of colonies. Size (X-axis) measures the size of colonies on a scale of 1-14.

The size distribution of 1-year-old colonies is shown in (Fig. 7) ($n=1673$). 1-year-old colonies had an average size of 7.026 size units ($sd=1.221$). The resulting p value from the two-tailed t -test between moved and 1-year-old colonies was ($p<0.0001$, $t=21.05$, $df=2185$). The mean difference between 1-year-olds and moved colonies was 1.36 size units, 1-year-old colonies being 1.36 size units smaller than moved colonies (Fig. 7).

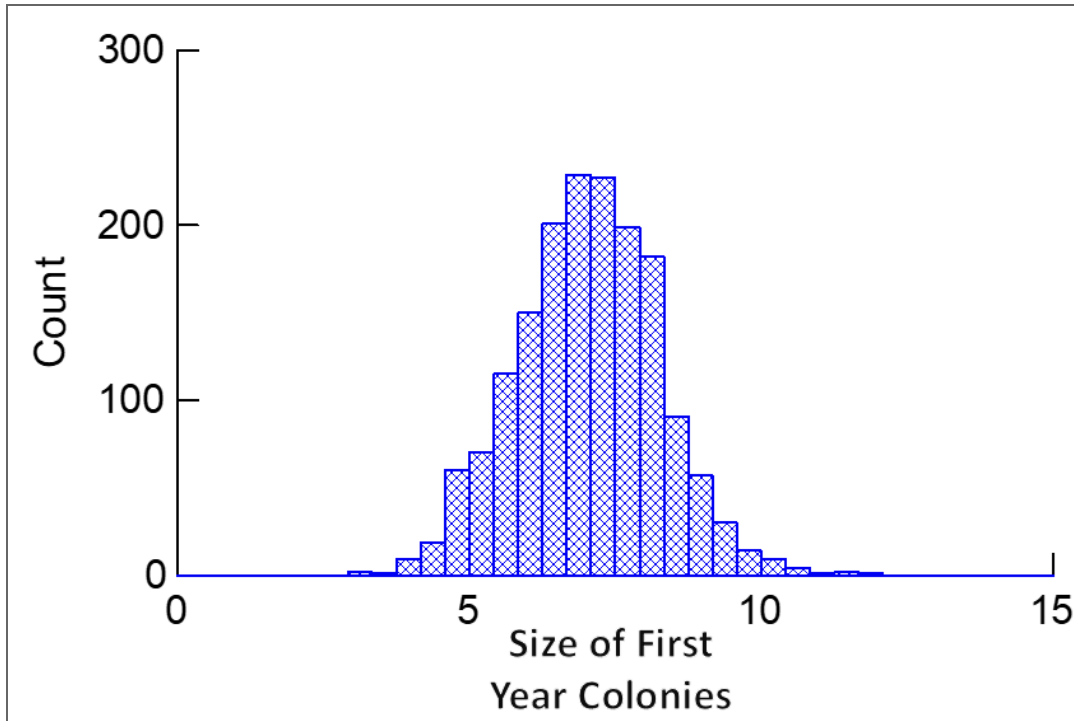


Fig. 7 Size Distribution of 1-Year-Old Colony Size. The frequency distribution of 1-year-old colony sizes. Count (Y-axis) is a measurement of the number of colonies. The size of 1-year-old colonies (X-axis) measures the size of colonies on a scale of 0-15. Distribution was generated from (n=1385) 1-year-old colonies of known size between 1996-present.

The size distribution of unmoved colony sizes is shown in (Fig. 8) (n=24,582). The average size of unmoved colonies was 9.649 size units (sd=1.968).

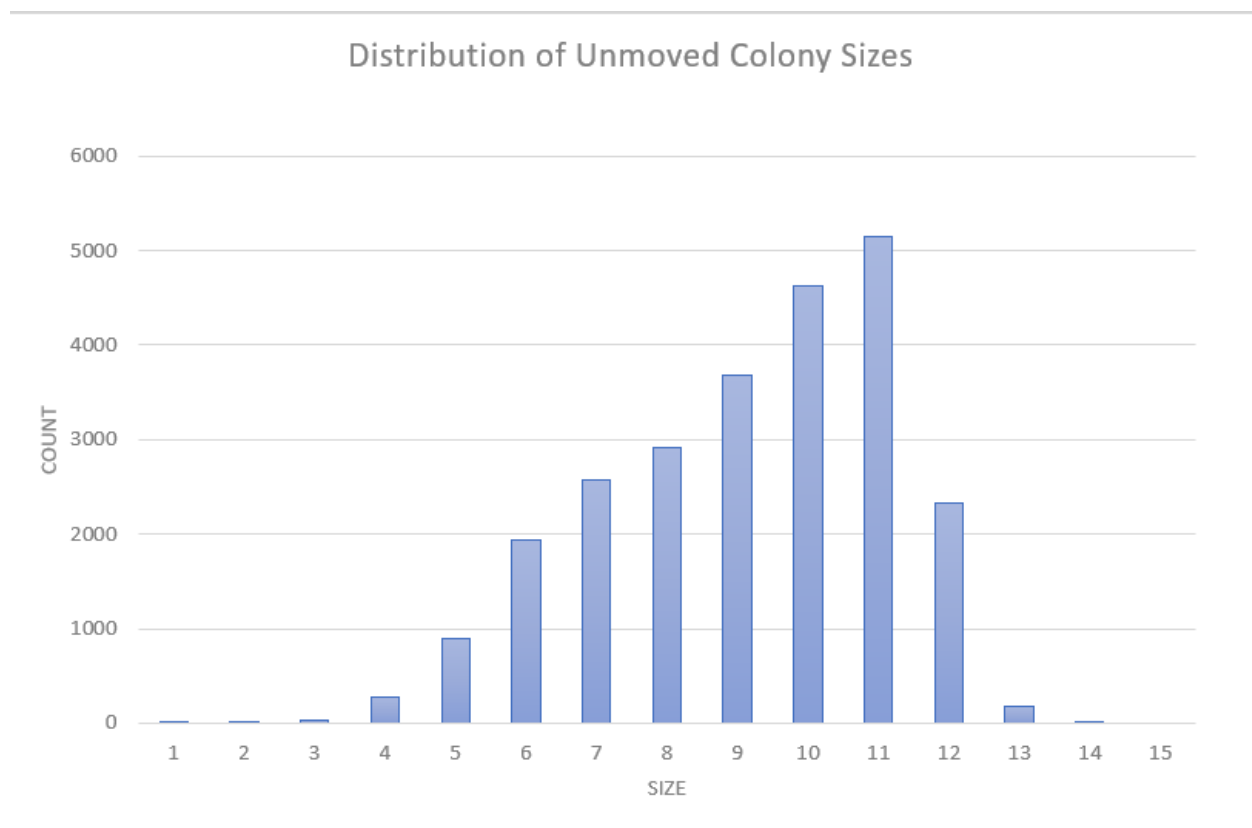


Fig. 8 Size Distribution of Unmoved Total Colony Sizes) The frequency distribution of all unmoved total colony sizes, at any age (n=24,582). Count (Y-axis) measures the number of colonies. Size (X-axis) measures the range of colony sizes.

The average of unmoved colonies was tested using a two-tailed t-test against the average of moved colonies. The resulting $p < 0.0001$, $t = 14.521$, $df = 25231$. The mean difference between the size of colonies that did not move and colonies that moved was -1.156 size units, meaning colonies that did not move were 1.156 size units larger than colonies that did move.

3.2 Mean Survival Time, Growth, & Survivorship

The post-movement mean survival time averaged 5.79 years with 95% confidence intervals of [5.39 to 6.19] years, while the average survival of control colonies was 6.77 with 95% confidence intervals of [6.15 to 7.39] years (Fig. 10). The p value resulting from a two-tailed t-test between post-movement mean survival time and control mean survival time was $p < 0.001$, $t = 39.25$, $df = 1673$. The mean difference between moved colonies and control colonies is 0.98 years. Additionally, both control and moved colonies had survival time ranges of [1 to 24].

In Fig. 9, I show the relationship between initial size and subsequent size in moved and unmoved colonies.

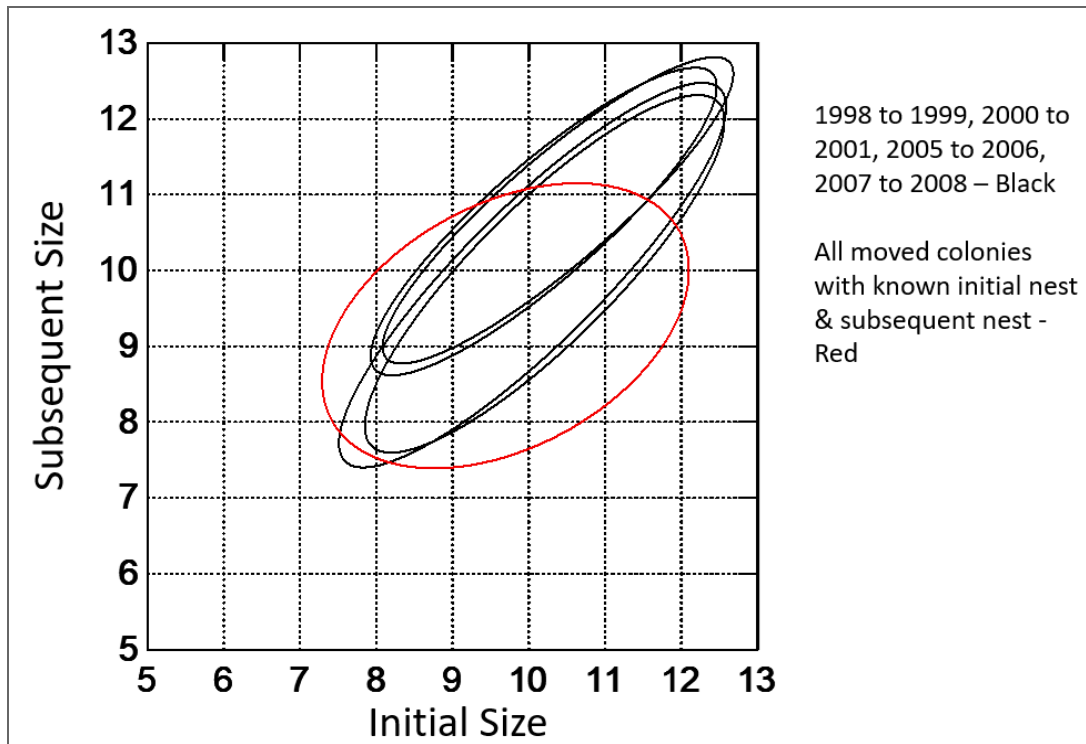


Fig. 9 Scatterplot of Unmoved & Moved colony sizes. Unmoved and moved colonies distributed onto a scatterplot. Size (X-axis) measures the size of the initial colony from 5 to 13. Size (Y-axis) measures subsequent colony size from 5 to 13. Black ellipses represent the 95% confidence interval area of unmoved colonies from the years 1998, 1999, 2000, 2001, 2005, 2006, 2007, and 2008. Red data points represent the 95% confidence interval area around moved colonies between 1996-present, with a known origin, destination, age, and size. 244 unmoved data points and 651 moved data points were used to generate the graph.

Confidence interval ellipses between moved and unmoved colonies show differences in size, shape, and slope. The relationship between initial and subsequent size in unmoved colonies creates a stricter, thinner ellipse with a strong positive slope. The relationship between initial and subsequent size in moved colonies creates a wider, larger ellipse with a positive slope. Additionally, the moved ellipse is centered at a lower subsequent size (Y-axis) than confidence ellipses for colonies that did not move.

Using a Kaplan-Meier survival analysis I analyzed the differences between survivorship in moved and control colonies (Fig. 10).

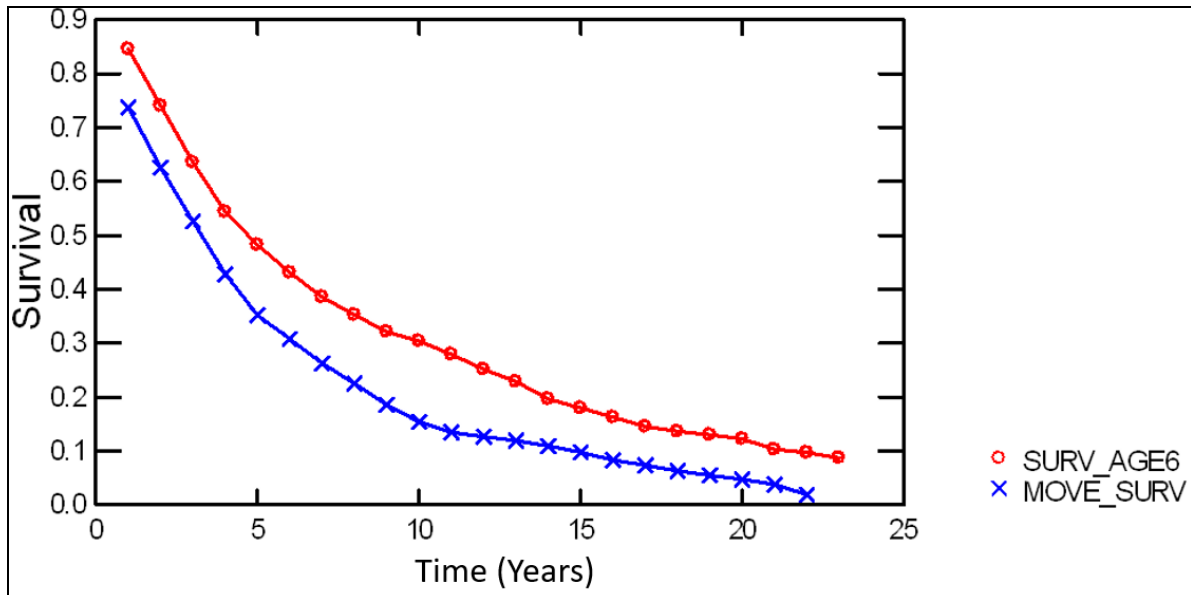


Fig. 10 Kaplan-Meier Survival Analysis. Life table analysis graph presenting the survivorship of moved colonies (Blue line) and colonies starting at 6 years of age (Red line). Survival (Y-axis) measures the proportion of colonies that survived out of 1.0. Time (X-axis) measures the time in years post movement or 6 years of age that a colony exists. This analysis was developed with 1,067 moved colonies and 608 total colonies at 6 years of age.

Moved colonies and control colonies (colonies starting at 6 years of age) differed in their survivorship and first year mortality. Control colonies started at 6 years of age so that we could control for the initial size when comparing them to moved colonies. Mortality is defined as the slope between two points on the survivorship curve, or the loss in population in any given year. 95% confidence intervals for the survivorship of moved and control colonies were generated for each year in the analysis. Survivorship at time= 0 for both control and moved colonies is 1.0 (Fig. 10). However, at time=1 the survivorship of moved colonies was 0.737, and the

survivorship of control colonies was 0.855, showing that moved colonies suffered a greater loss in survivorship than control colonies (Fig. 9). This difference between survivorship between time=0 and time=1 can be interpreted as a heightened mortality rate among moved colonies compared to control colonies. Control colonies have a mortality rate of 0.145, and moved colonies have a mortality rate of 0.263 between time=0 and time=1. Additionally, between time=[5 to 15], the mortality rate of control colonies begins to decrease compared to the mortality of moved colonies, creating a steeper divergence in survivorship. The mean difference between control colony survivorship and moved colony survivorship averaged between [0.079 to 0.132].

DISCUSSION

4.1 Distance & Proportion of Movements

The occurrence of colony movement yearly, and with some seasonality suggests that colony movement is a significant and common aspect of a colony's life.

Although relatively common, movement only occurs in 16.6% of colonies suggesting that it may not be a part of *P. occidentalis*'s life history. Since life history can be defined as all of the phases of life an individual must go through in order to fully develop, then a majority, if not all, of individuals should go through this phase at a certain part of their lives. However, movement does not occur in a majority, much less all colonies, nor does it seem to occur at a particular age, given its large range. Thus, it is unlikely that movement is an aspect of *P. occidentalis*'s life history. In Fig. 5, the proportion of movements at each age is shown. The linear regression analysis of Fig.

5 produces a positive regression coefficient (+0.00084) and P-value <0.05, meaning the proportion of colonies that move increases with age significantly. This suggests the hypothesis that movements are more likely to occur once a colony is older and likely larger because the fitness costs of movement are greater at a younger age. However, older colonies have had more time to accumulate damage like potential diseases or general nest damage. Furthermore, since older colonies take up more space, they are more likely to compete with other colonies. These possibilities, however, assume that colonies move in response to competition or disease.

4.2 Fitness Costs

The aforementioned results describe colony size, survival time, and survivorship decreasing in moved colonies. The post-movement mean survival time is roughly 1 year shorter than the survival time of control colonies, as described in the Kaplan-Meier survivorship curve. Additionally, colony movement seems to weaken the expected growth rate and size-age relationship (Fig. 9). Coupled with the results of (Fig. 9), it is clear that moved colonies experience a fitness cost in size and survival time. Moved colonies are roughly 1.1 size units smaller than colonies that did not move. Furthermore, colonies that moved had a survival time roughly 1 year shorter than their unmoved counterparts of similar size. Moved colonies are 1.36 size units larger than 1-year-old colonies (Fig. 6 & Fig. 7). This is unsurprising as 1-year-old colonies are started by a single queen, while moved colonies often have hundreds of workers. But, this shows that moving colonies is easier than starting a colony de novo, and this success is likely due to the large population of supporting workers that moved colonies carry with them.

Size and survival time are strong proxies for fitness because colonies can only reproduce once they grow beyond a size threshold (Tschinkel, 2014; Cole & Wiernasz, 2000). Thus a size reduction can either result in a loss in reproductive ability or an increased necessary time spent before reproduction can occur. Additionally, survival time is important because colonies can consistently reproduce once they have achieved a particular size threshold, though they do not reproduce every year. Each year spent beyond the size threshold increases the colony's likelihood of producing viable offspring. Therefore, a loss in survival time inevitably reduces colonies' ability to reproduce or live long enough to reproduce. This is notable because ant colony movements are inconsistent; some species can experience devastating costs while some reap remarkable rewards from relocating nests. These expenses can all be considered fitness costs, as they hinder a colony's ability to reach maturity and produce viable offspring. Furthermore, because of *P. occidentalis*'s mortality-reproductivity relationship, the fitness impact of decreased survivorship and survival time may vary dependent on what age or size the colony moves at (Fig. 2). The Western Harvester ant gains longevity and reproductive ability as they increase in size and age. This is thought to occur because colonies that survive to large enough sizes can avoid many of the causes of mortality. Considering the results of testing 1-year-old colonies against moved colonies, it appears that it is more expensive to start a colony de novo than to relocate. This is unsurprising as 1-year-old colonies have fewer individuals in their colonies than established colonies. However, if having more workers makes nest building more efficient, then it would be ideal for colonies to move at points when they have a larger worker population. Since colonies improve in reproductive success and survivorship the longer they live or the larger they

are, movement may be more costly to younger colonies than older colonies. This could explain why colonies appear to tend toward movement at later ages rather than earlier ages (Fig. 5). Alternatively, one possibility is that the movement of large colonies may be more readily detected, given their size. Large colonies would then appear to have a greater proportion of movements, but, it would be a bias from observation.

The discovery of colony movement's fitness costs has several implications. If a colony is making the decision to move, which is costly, it may likely be moving to avoid some occurrence or thing that is or will likely decrease fitness even further. Given what is understood of *P. barbatus* and other relatives of *P. occidentalis* that utilize adventitious nest relocation, movement in *P. occidentalis* may be caused by nest damage, weather, or predation (McGlynn 2012). It may be the case that the colony is moving towards something that will increase its fitness, but were this the case, colonies that moved and survived well beyond the year of movement should return to survivorship levels of unmoved colonies. It has been observed that a majority of movements occurred shortly after a heavy summer rain, at roughly the same time colonies would begin mating (Cole & Wiernasz Personal Communication; Anderson & Mull, 1992). In *P. barbatus*, movements are also documented to occur most frequently shortly after heavy rain, and at roughly the same time that colonies begin mating (Gordon, 1992). It was suggested that *P. barbatus* may require wet soil for nest construction, thus the same could be said about *P. occidentalis* (Gordon, 1992). Wet soil may be easier for ants to manipulate, giving them the opportunity to relocate colonies when conditions are most energy efficient for them. Alternatively, colonies could move in response to heavy rainfall or flooding, as suggested by Anderson & Mull (1992). However,

not all colony movements have occurred after rainfall, and often, rainfall is not dramatic enough to flood large *P. occidentalis* nests (Cole & Wiernasz Personal Communication). While these ideas make logical sense, research into the real-world factors that cause colony movement, like disease and environmental duress is necessary to provide a mechanism for this hypothesis.

Another relevant implication is that fitness costs must come from somewhere. These costs may come from the energetic expenses of mining and building a new colony, which takes up time and energy from workers. Long-lived ant species show increased vulnerability to environmental change and stress, providing some evidence to suggest environmental stress or catastrophes may be worse for *P. occidentalis*, and cause relocation (Ord, 2023). Increased risk of predation or desiccation from long-term transportation of broods and food above ground may also create fitness costs. Additionally, movement seems to carry inherent costs, since colonies have been observed to passively lose workers, brood, and food during transportation (Cole & Wiernasz, Personal Communication). However, the most likely answer may be any combination of these solutions or others, and more in-depth research on colony construction and movement observation must be done. Ideally, experiments subjecting colonies to artificial heat, rainfall, or physical damage could be performed to identify putative influencers of colony movement. Monitoring transportation of queens, brood, and food, and rates of energy expenditure during movement could help understand the passive and energetic costs of movement as well.

Adventitious nest relocation syndrome, which is utilized by *P. occidentalis*'s close relative *P. barbatus*, is characterized by high nest fidelity (McGlynn 2012). *P. barbatus* share a similar lifestyle and niche with *P. occidentalis* by creating large, long-lived nests, and living in a

similar habitat. Furthermore, *P. barbatus* movements appear to occur at similar timeframes to the movements of *P. occidentalis*. Species that utilize this behavioral syndrome can relocate, although relocation is relatively uncommon and not incorporated into their life histories. Species with this behavioral syndrome establish long-term nests and are assumed to only move when absolutely necessary, such as in life-threatening situations. *P. occidentalis* demonstrates these attributes as we have gathered that relocation does not occur in the majority of colonies, and does not seem to be a part of their life history. If relocation were an aspect of the species' life history, then we should expect that movement occurs in a majority of colonies and is associated with a certain age, size, or seasonality. However, movements are variable, occurring through a wide range of ages and sizes, covering almost all of the age and size groups of an unmoved colony. Additionally, it is established that colonies establish large, long-term nests, and we have speculated that colonies move in response to some fitness-costly stimulus. For these reasons, adventitious nest relocation is likely the behavioral syndrome found in *P. occidentalis*.

These ideas on movement, fitness costs, and behavioral syndromes help us contextualize *P. occidentalis* in the greater scheme of animal architects. Although the behavioral syndromes described in McGlynn (2012), were designed for ants and other social insects, one can imagine that these syndromes could be used to characterize other animal architects that relocate. We can infer that other architects with high construct investment may frequently experience fitness costs associated with architecture abandonment, or that environmental duress may cause them to abandon their constructs, further impacting their fitness.

CONCLUSION

The aims of this thesis were to evaluate the fitness costs of colony movement and describe the potential causes and behavioral syndrome associated with colony movement in *P. occidentalis*. It was determined that colonies that have undergone movement experience fitness costs in the form of decreased colony size, decreased survival time, and decreased survivorship, in comparison to colonies that have not undergone movement. However, when measured one-year post-movement, moved colonies were not as small as 1-year-old colonies. Additionally, it was determined that the distance between origin and destination colonies are highly variable, and roughly 16.6% of all colonies had moved at least once. Through analysis of previous scientific literature, it was found that *P. occidentalis* display long lifespans, large nests, and high nest fidelity. These traits can be used to characterize *P. occidentalis* as an adventitious nest relocater within McGlynn (2012)'s framework of the four nest relocation syndromes. Several potential causes of colony movement are described based on literature describing other closely related species, other adventitious nest relocators, and an analysis of the results in this study. Potential causes of colony movement include, but are not limited to, heavy rainfall and nest damage. By answering these questions regarding colony movement, this thesis creates a foundation that could lead to a more nuanced and comprehensive understanding of colony movement and animal architects on a greater scale.

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