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The Role of Personality in Large Nut Dispersal by Sciurus carolinensis and its Implications for Seed Dispersal Across Human-Modified Landscapes

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THE ROLE OF PERSONALITY IN LARGE NUT DISPERSAL BY *SCIURUS CAROLINENSIS* AND ITS IMPLICATIONS FOR SEED DISPERSAL ACROSS HUMAN-MODIFIED LANDSCAPES

by

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ABSTRACT

Small mammals are well known seed dispersers, but their efficiency at seed dispersal is directly affected by their personality type. Anthropomorphic habitat change shifts the distribution of personalities within small mammal populations, thus altering the mechanisms by which seeds are dispersed across these areas. Little is known about how small mammals interact with sidewalks, roads, or parking lots during the seed dispersal process despite these areas' prevalence within human modified landscapes and the importance of understanding the ways in which seeds are transported across anthropomorphically altered regions. The goal of this study is to explore the role of personality in seed dispersal across sidewalks, streets, and parking lots by Eastern Gray Squirrels (*Sciurus carolinensis*), a common urban small mammal. Through a field study in Maine, this paper shows that anxious and active gray squirrels are more likely to disperse nuts across sidewalks, streets, and parking lots. These results represent a step towards a greater understanding of road ecology as it pertains to seed dispersal, but more work is needed to examine the direct effects anthropomorphic habitat change has on urban squirrel personality distributions as well as how these changes impact their role as seed dispersers.

DEDICATION

This paper is dedicated to the gray squirrel population of the Forest Preserve in Orono, Maine, and to all wildlife populations that have been subject to field research. Though ecological research brings us ever closer to understanding our world, these animals' lives are disrupted by our efforts to capture the essence of the natural world. The author acknowledges their sacrifice and expresses her gratitude through this dedication.

ACKNOWLEDGEMENTS

Firstly the author thanks her adviser, Dr. Alessio Mortelliti, for his invaluable guidance and coaching through every stage of this project. Special thanks go to Allison Brehm, Sara Boone, and Bryn Evans for their altruistic support of the field research and data analysis aspects of this study, and to Michael Clasby for his contribution towards the cache recovery process. Finally the author expresses warm gratitude to Eileen Cahoon, Jessica Beneski, Matthew Bonner, Emily Moore, Hayley Morgan, and Catherine Hoye and for their invaluable moral support not only during this project, but across the author's entire academic career and beyond. This work was made possible in part by the support of the Charlie Slavin Research Fund.

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INTRODUCTION

Many plants rely on animals to disperse their seeds (Howe & Smallwood 1982; Russo *et al.* 2006), and scatter-hoarding is considered the primary mechanism of animal-mediated seed dispersal (Bartlow *et al.* 2018). Scatter-hoarders cache food items singly and often considerable distances away from the parent tree, returning to the cache site hours to months later to consume the store (Bartlow *et al.* 2018; Koenig & Vander Wall 1990; Leaver *et al.* 2017). Some of these caches are inevitable unrecovered due to factors like predation, disease, or simply forgetting cache location, and these seeds may germinate to establish a new plant (Brehm *et al.* 2019; Goheen & Swihart 2003; Koenig & Vander Wall 1990). The scatter-hoarder's caching process is rife with decisions: is a particular seed of high enough quality to consider? If so, should it be eaten immediately or stored for future consumption? If it should be stored, where is the best site to cache it, in which risk of both cache pilferage and predation are minimized (Alpern *et al.* 2012; Delgado & Jacobs 2017; Leaver *et al.* 2017; Lichti *et al.* 2017)?

Scatter-hoarders residing in human modified areas encounter additional decisions involving crossing or avoiding intensely human modified areas such as sidewalks, streets, and parking lots (Hennessy *et al.* 2018; Fey & Selonen 2016). Research has shown that roads represent a significant barrier to many animals, including small mammals (Conrey *et al.* 2003; Goosem 2001; Hennessy *et al.* 2018; McGregor *et al.* 2008). Fey & Selonen (2016) found that though juvenile red squirrels (*Sciurus vulgaris*) readily crossed roads during their natal dispersal, adults were generally located father from roads and crossed roads in their home ranges less frequently than simulated walking paths. Thus, the very existence of roads alters the landscape around them by restricting regular movement within home ranges, or even preventing genetic exchange between populations (Brudin 2003; Conrey *et al.* 2003; Forman & Alexander 1998; Hennessy *et al.* 2018). Previous studies have examined squirrels' roles as seed dispersers, but no studies have explored how they interact with intensely human modified areas such as streets or parking lots during their caching process (Bartlow *et al.* 2018; Goheen & Swihart 2003; Lichti *et al.* 2017).

The answer to this question likely varies from individual to individual, and could be considered a product of personality. Personality is a trait, with components like anxiety or boldness; it is defined as the behavioral differences across individuals and is consistent over time and across situations (Boon *et al.* 2007; Boon *et al.* 2008; Brehm *et al.* 2019; Dingemanse *et al.* 2010). Research has not only shown that personality is partially heritable, but that it differs extensively between individuals (Boon *et al.* 2007; Boon *et al*. 2008; Dingemanse *et al.* 2010; Sih *et al.* 2019). With such extreme variation between individual animals it is not surprising that personality type has related fitness consequences; the effects of personality are far-reaching and have been shown to interact with many if not all aspects of an individual's life (Boon *et al.* 2007; Boon *et al*. 2008). Brehm *et al.* (2019) found that repeatable behavioral traits in scatter-hoarding small mammals predicted the ways in which they interacted with seeds including preferred seed type, dispersal distance, and final cache location. This study indicates that small mammal personality plays a critical role in shaping the structure of the environment since the personality-correlated decisions made during the caching process determine which seeds get cached where, and these seeds may successfully germinate (Brehm *et al.* 2019; Goheen & Swihart 2003; Koenig & Vander Wall 1990).

With this in mind it is especially important to consider how intensely human modified areas impact scatter-hoarders' caching decisions, but no studies have examined this. Like other caching decisions it is likely that encounters with intensely human modified areas are dictated largely by personality (Brehm *et al.* 2019; Sih *et al.* 2019), but are also influenced by the environment. Previous studies have shown that corridors and narrow extensions allow for greater animal exchange between as well as facilitate seed dispersal across otherwise isolated patches of habitat (Levey *et al.* 2008; Tewksbury *et al.* 2002). Dispersal distance is generally shorter in heterogeneous landscapes than in homogenous landscapes (Levey *et al.* 2008), and habitat fragmentation combined with its subsequent defaunation upsets the delicate balance between seed density and disperser density (Ding *et al.* 2018). Considered together these findings could indicate that landscapes completely divided by intensely human modified areas are heavily impacted by these alterations, and thus understanding the interaction between small-mammal mediated seed dispersal and intensely human modified areas is crucial. The Eastern Grey Squirrel *Sciurus carolinensis* (henceforth referred to as the gray squirrel) is an ideal model for studying this phenomenon because they are ubiquitous in developed areas along the eastern portion of North America (Cassola 2016; Leaver *et al.* 2017; Manski *et al.* 1981; Steele *et al.* 2008) and their scatter-hoarding patterns are highly studied (Bartlow *et al.* 2018; Hopewell *et al.* 2008; Steele *et al.* 2008). They are known to cross intensely human modified areas within their territories, with documented crossing of interstate highways with bridges or culverts and roads (Hennessy 2018; Oxley *et al.* 1974). However it is unknown if gray squirrels will carry a nut across an intensely human modified area and cache it on the other side.

The goal of this study is to examine the intersection between gray squirrel personality and their decisions to cache across an intensely human modified area, if they do at all. A specific focus is placed on if individuals with certain personality traits are more or less likely to distribute a seed across an intensely human modified area. Since patterns of human modified areas impact how animals disperse seeds (Ding *et al.* 2018; Levey *et al.* 2008; Tewksbury *et al.* 2002) and the ecology of the surrounding landscape is significantly influenced by the presence of such areas (Bartlow *et al.* 2018; Boone & Mortelliti 2019; Brehm *et al.* 2019), understanding these interactions is a topic of major ecological importance. As different personality traits influence which species of seeds are cached as well as cache location, if certain personality types are more inclined to approach and cross an intensely human modified area the presence of such areas may be favoring certain plant species (Mortelliti 2019; Brehm *et al.* 2019).

Since personality is a major determinate in cache location and contents, it is important to understand how individuals of different personality types interact with intensely human modified areas (Mortelliti 2019; Brehm *et al.* 2019). If seed dispersal across intensely human modified areas varies with personality type, the resulting consequences will have direct and long-reaching implications for the structure of the ecosystem (Bartlow *et al.* 2018; Brehm *et al.* 2019; Goheen & Swihart 2003; Koenig & Vander Walls 1990).

METHODS

Study Site And Subject Trapping

This study was conducted in the Forest Preserve in Orono (approximately 44.53517N, -68.39538W) and on the University of Maine Campus, east-central Maine, USA. A mark-recapture technique was employed across approximately 0.5 hectare of forest and in discrete patches on campus from the end of August 2019 through the beginning of November 2019. 54 Tomahawk traps were set 0.5m-2m inside the western and southern tree line of the Forest Preserve spaced 2m apart from the end of August through early November. From late October to early November, 11 traps were removed from the forest area and situated on the University of Maine Campus at planned camera trap locations (approximately 44.89687N, -68.66812W; 44.89624N, -68.66915W; -44.89510N, -68.66842W; and 44.89578N, -68.66715W.) Trap locations were established by a combination of frequently used foraging areas determined from telemetry collar data (Figure 1c and Figure 1c) and observations of popular squirrel foraging spots. Traps were opened 2-3 hours following sunrise and closed 1-2 hours before sunset, and were baited with peanut butter and sunflower seeds. Traps were covered with either a translucent plastic sheet and rubber bands or an opaque corrugated plastic cover lined with camouflage duct tape. For a brief period of time, campus traps were covered with cardboard. Forest traps were checked twice a day and campus traps were checked every 1-2 hours. Trapping occurred 4-5 days each week. See Figure 1a for a detailed map of trap locations. All work on this project was completed under the auspices of the University of Maine's IACUC, approval number A2015_11_02.

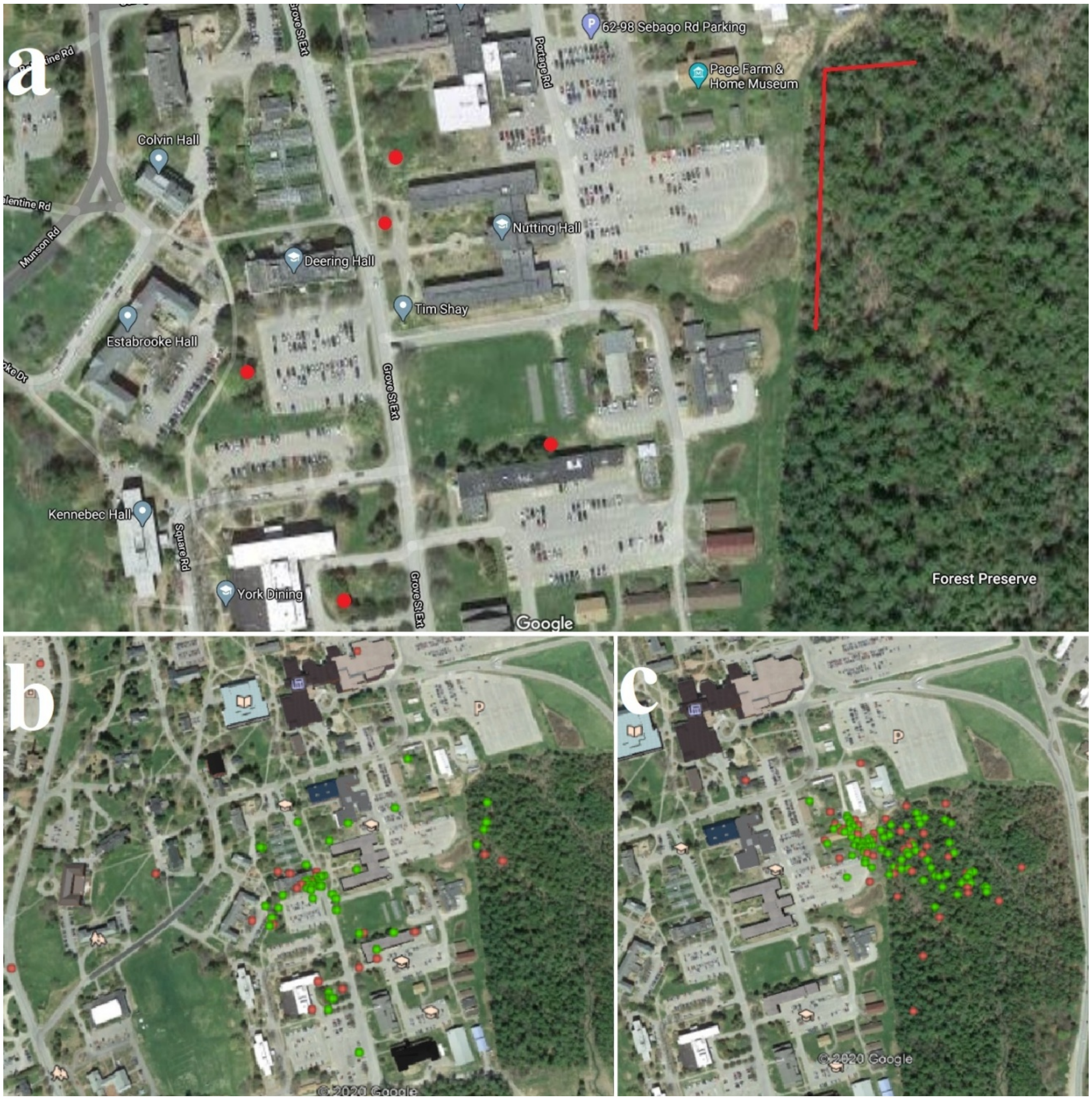

Figure 1 Trap locations and GPS collar data. Tomahawk trap were baited with peanut butter and sunflower seeds and partially to fully covered with opaque plastic sheets, corrugated plastic, or cardboard. Traps were active approximately 2-3 after sunrise and closed 1-2 hours before sunset for 4-5 days a week. (a) Locations of traps are depicted by red lines and dots (Google Maps). Traps were positioned every 2m on red lines. Each dot represents 2-4 traps. (b) & (c) GPS marks from two collared squirrels (Google Earth). Green dots represent certain points while red dots represent uncertain points. Marks were taken once an hour from sunrise to sunset for 9 days. These visuals were used to determine high traffic foraging sites for camera trap deployment.

Behavioral Tests

An Open Field Test was used to measure personality in terms of activity and exploration of a novel environment (Perals *et al.* 2017; Walsh & Cummins 1976; see Figure 2 for a depiction of apparatus), and all individuals were processed before any additional handling occurred. Seven key parameters were tracked using the behavioral tracking software ANY-maze© (version 5.1; Stoelting CO, USA): mean distance from center (m), time mobile (s), distance covered (m), grooming (s), rearing (s), jumping, and hanging (s). See Appendix F for operational definitions of behaviors and Appendix D for full behavioral test results. Open Field Tests were conducted in the Forest Preserve, and individuals were released at the site of measure (approximately 44.89758N, -68.66497W.)

Following behavioral analysis individuals were sexed, weighed with a one kilogram hang scale, and marked with ear tags adorned with either pipe cleaners for males or heavy gauge, colored wire for females. Each individual received a unique color combination of ear tags. Females were classed as not reproductive, pregnant, or lactating while males were classed as either not reproductive or reproductive. Reproductive state was determined by physical appearance of abdomen and nipples for females, and by presence or absence of scrotal condition for males. Individuals who were stressed, injured, or had been ear tagged in the past but lost the tags through tearing were not processed.

At the beginning of the study session, three individuals were fitted with GPS/telemetry collars (LotekLitetrack 10) set to capture a mark every hour from sunrise to sunset. Following the behavioral test and data collection described above, individuals were anesthetized with isoflurane and fitted with collars. After collar attachment, individuals were placed in a trap and left alone for a 10-15 minute period to regain motor and cognitive function. Two collars were recovered, but the third was lost before the individual was recaptured. See Figure 1b and 1c for depictions of GPS marks, which were considered as the home ranges for these individuals.

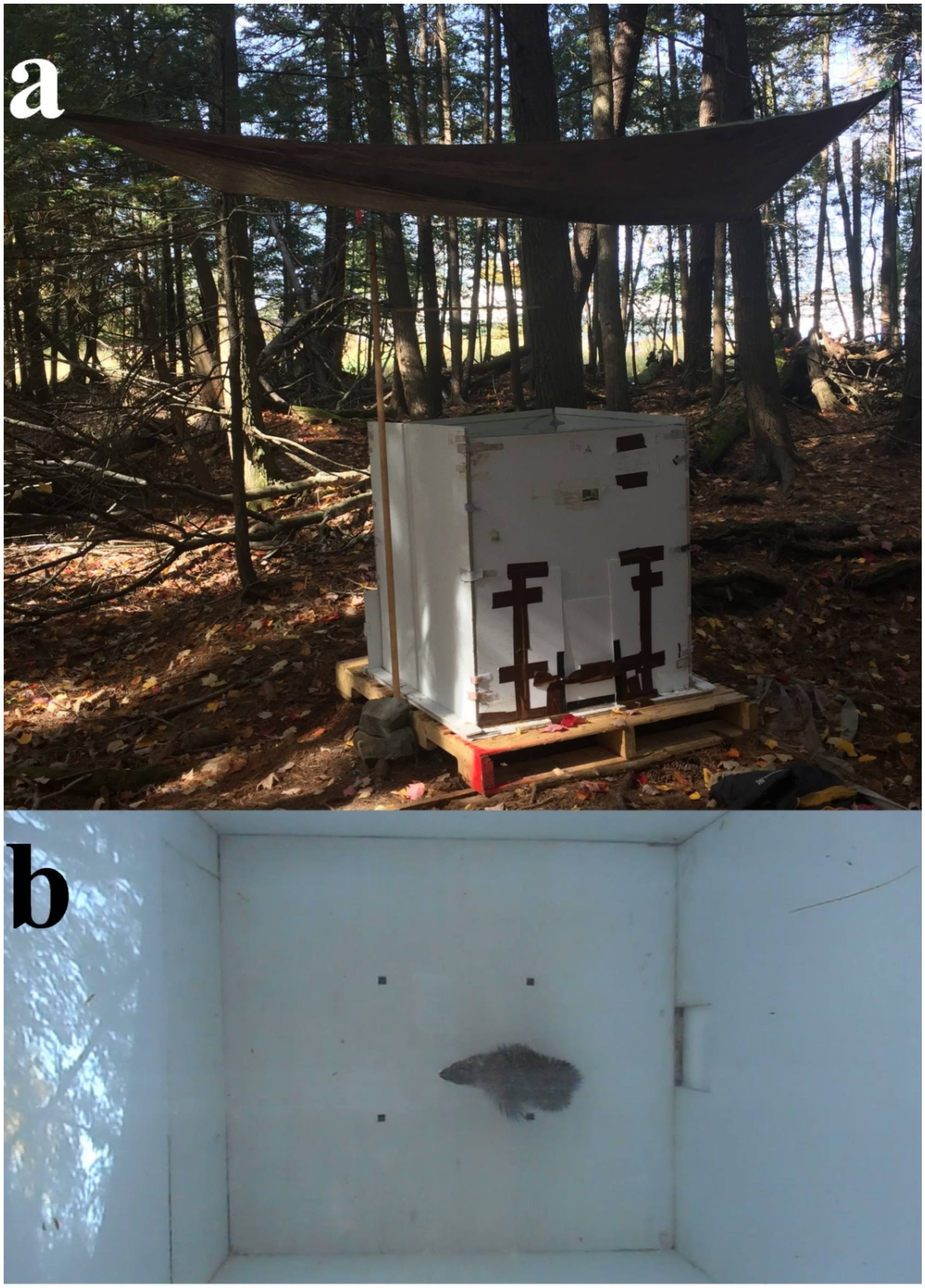

Figure 2 Open Field Test apparatus. (a) Apparatus was constructed from white corrugated plastic sheeting and secured using Velcro and duct tape. A wooden pallet was arranged underneath the box to ensure an even surface, and a tarp was suspended in the overhead branches to obscure view of the canopy. Clear Plexiglass was used for the apparatus lid. A simple camera stand was constructed from wood scraps, to which a small digital camera was attached using Velcro command strips, and secured by burying approximately 6 inches in the ground. The stand was reinforced with large rocks to prevent swaying in high wind. (b) Interior of apparatus. Debris such as leaves or bugs were removed from the apparatus before testing. Apparatus floor was cleaned with 70% Isopropyl alcohol before and between tests.

Seed Dispersal Experiment

To capture the caching process of gray squirrels, four dispersal sites were chosen across the southern side of the University of Maine Campus; see Figure 3 for exact site locations and GPS coordinates. Nuts were offered across six days: 09 November 2019-11 November 2019, and 23 November 2019-25 November 2019. Two Bushnell camera traps (Bushnell HD Early View) were situated at each site, one in a top-down orientation and one positioned laterally to view the entire site. Camera traps were set to record one minute videos with a one second interval between movement events. Two species of nuts were deployed under the camera traps: acorns of the Scarlet Oak (*Quercus coccinea*) and nuts of the American Hazelnut (*Corylus americana*.) Nuts were flagged by poking a hole through the shell and flesh (for acorns) or by drilling through the shell and flesh (for hazelnuts). Wire was looped through the hole and secured by twisting around itself, and a flag made of reflective tape was attached and secured with hot glue. Each nut received a unique code of either A (for hazelnuts) or B (for acorns) followed by a number (Fig 4).

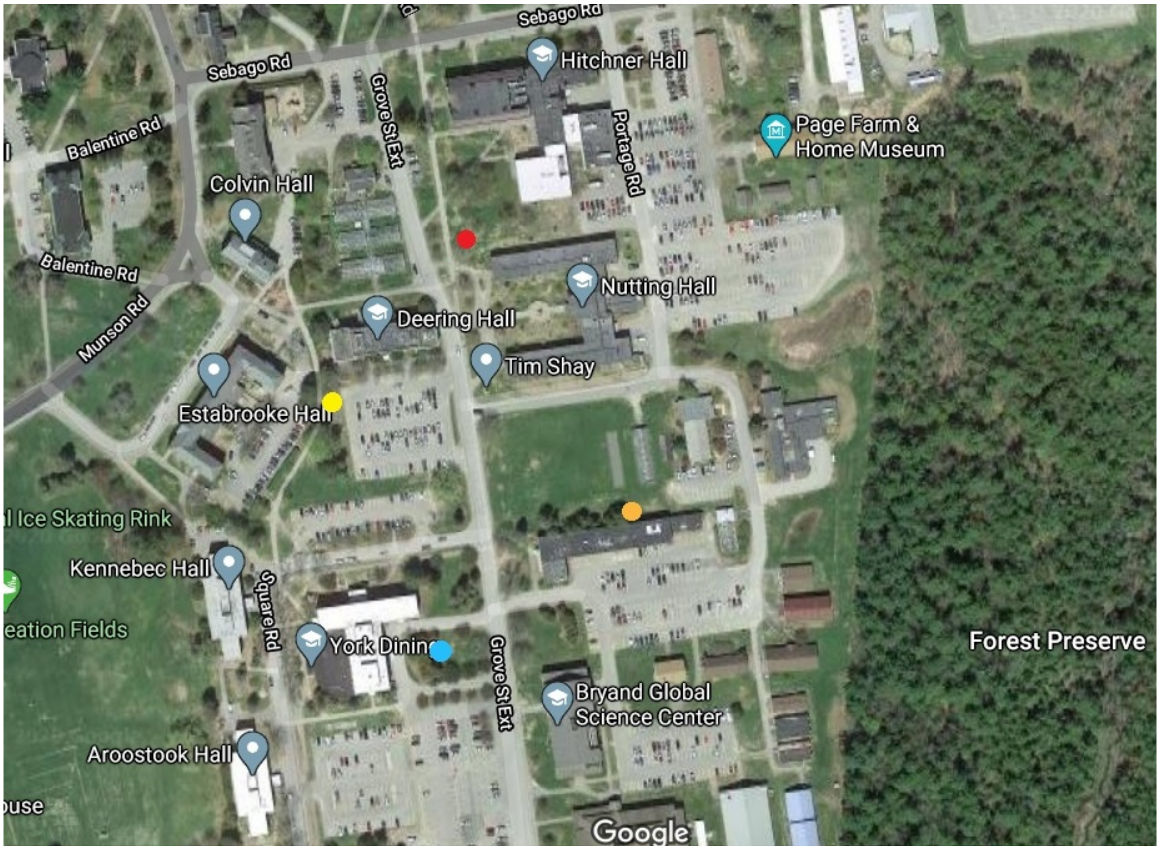

Figure 3 Camera trap and seed dispersal locations. Locations were determined via points of frequent use from GPS tracking of two gray squirrels (Figure 1b & 1c) and observations of local gray squirrel population land use. Two Bushnell camera traps were deployed at each location: one viewing the site laterally and one in a top-down orientation to view nuts (See Figure 4). GPS coordinates are as follows: 44.89687N, -68.66812W; 44.89624N, -68.66915W; 44.89578N, -68.66715W; 44.89510N, -68.66842W.

Figure 4 Flagged nuts as viewed through a camera trap. Two species of large nuts were used in this study: acorns of the Scarlet Oak (*Quercus coccinea*) and nuts of the American Hazelnut (*Corylus americana.*) Nuts were flagged by poking a hole through the shell and flesh (for acorns) or by drilling through the shell and flesh (for hazelnuts). Wire was looped through the hole and secured by twisting around itself, and a flag made of reflective tape was attached and secured with hot glue. Each nut received a unique code of either A (for hazelnuts) or B (for acorns) followed by a number. Nuts were arranged on the bare ground with codes visible to the camera.

Video Analysis and Cache Recovery

Videos were processed by pairing measured individuals with the nuts they dispersed: a squirrel who dispersed a nut was labeled as a “disperser.” Individuals were identified via their unique ear tag colors and, in one case that a distinctive individual lost both ear tags, unique morphological characters (pelage color and shape of ear tears from losing tags.) Three other individuals who visited camera traps had been measured and lost both ear tags, but were not identifiable due to their overall common appearance (gray, average sized, and no distinct markings.) Nuts were identified via their unique flag code.

Following selection and dispersal of nuts by squirrels, nut location was determined through manual search techniques. Searching occurred from 09 November

2019- 27 November 2019, until weather conditions (snow and ice) obscured nut flags. A brief thaw the following month made it possible for an additional search period to be held from 11 December 2019-13 December 2019. After darkness a grid was walked through the study area and flagged nuts were located using a headlamp (Black Diamond Cosmo 225 Headlamp). The GPS location of nuts were taken and they were classed as cached, eaten, or rejected (see Table 1 for operational definitions.) Eaten and rejected nuts were collected, but cached nuts were left in place. Since gray squirrels are known to monitor and move their caches up to five times, and the third cache location is significantly farther away from the parent tree than the first or second cache location (Bartlow *et al.* 2018), it was determined that leaving the cached nuts in the ground was more conducive to capturing the full caching process than removing them. Subsequently, every cache location was recorded during every searching event regardless of if the cache location had been recorded before in order to track the cache's movement. See Appendix E for a full list of cache location details.

Table 1 Outcome of the interaction between a squirrel and a nut. Following nut deployment and after the onset of darkness, a grid was walked through the study area and flagged nuts were located using a headlamp. The GPS location of nuts were taken and they were classed as cached, eaten, or rejected. Eaten and rejected nuts were collected, but cached nuts were unrecovered. Since gray squirrels are known to monitor and move their caches up to five times, and the third cache location is significantly farther away from the parent tree than the first or second cache location, it was determined that leaving the cached nuts in the ground was more conducive to capturing the full caching process than removing them.

Outcome	Definition
Eaten	The nut is at least half eaten, including fully consumed with only a flag recovered.
Rejected	The nut is less than half consumed, was chewed but not consumed, or was removed from the camera trap location but neither cached nor eaten.
Cached	The nut was clearly cached in an at least partially obscured location (in the ground, under leaf litter, tucked behind a bench leg, etc.)

Statistical Analysis

Analysis was completed using R packages *lme4* and *AICcmodavg* to fit linear mixed effect models to the data (Bates *et al.* 2015). Variables from behavioral tests such time spent grooming and total distance covered were used as independent variables in addition to physiological features like sex and weight (see Appendix A for a full list of independent variables). Though reproductive state was noted, only one individual in reproductive state visited camera traps and so the variable was not analyzed. Many dispersers were recaptured multiple times over the course of the experiment, but personality was determined from the first testing session since Brehm *et al.* (2019) established the consistency of small mammal personality traits. Additionally, Mazzamuto *et al.* (2019) found that squirrels showed lower activity rates in second and third Open Field Test trials, indicating a habituation to the apparatus that affects test results.

Individual ID was used as the random effect to account for the lack of dependence between observations from the same individual. The dependent variables explored in these analyses were first cache distance, final cache distance, and likelihood of crossing an intensely human modified area. AIC ranking was used to rank multiple hypotheses, and only models within 2 ΔAICc were considered for inference (see Appendix B for AIC rankings).

RESULTS

Two key behavioral traits in gray squirrels are associated with seed dispersal across intensely human modified areas: grooming and activity. Grooming was positively related to dispersal distance for the first caching event (Figure 5). This result indicates that time spent grooming during an Open Field Test predicts dispersal distance for the first caching event, with more time spent grooming leading to a larger distance to cache. Similarly grooming was also positively related to dispersal distance for the final caching event (Figure 6), indicating that more time spent grooming predicts a farther final cache distance. Time mobile was positively related to likelihood of dispersal across an intensely human modified area (Figure 7). This finding suggests as activity increases, likelihood of movement across intensely human modified areas also increases.

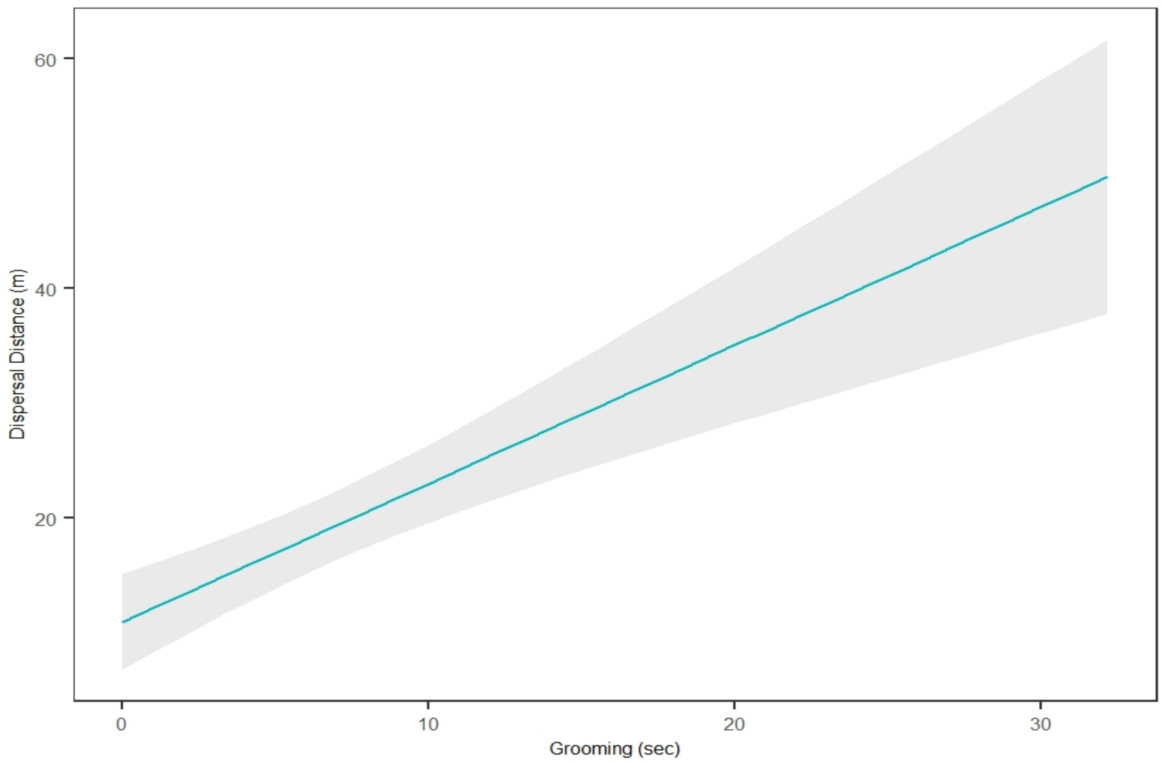

Figure 5 Effects of personality on dispersal distance at first caching event; y= 1.204x+ 10.985. Dispersal distance increases with time spent grooming, a measure of anxiety. Results were obtained from linear mixed models. Confidence intervals are shown at 95%.

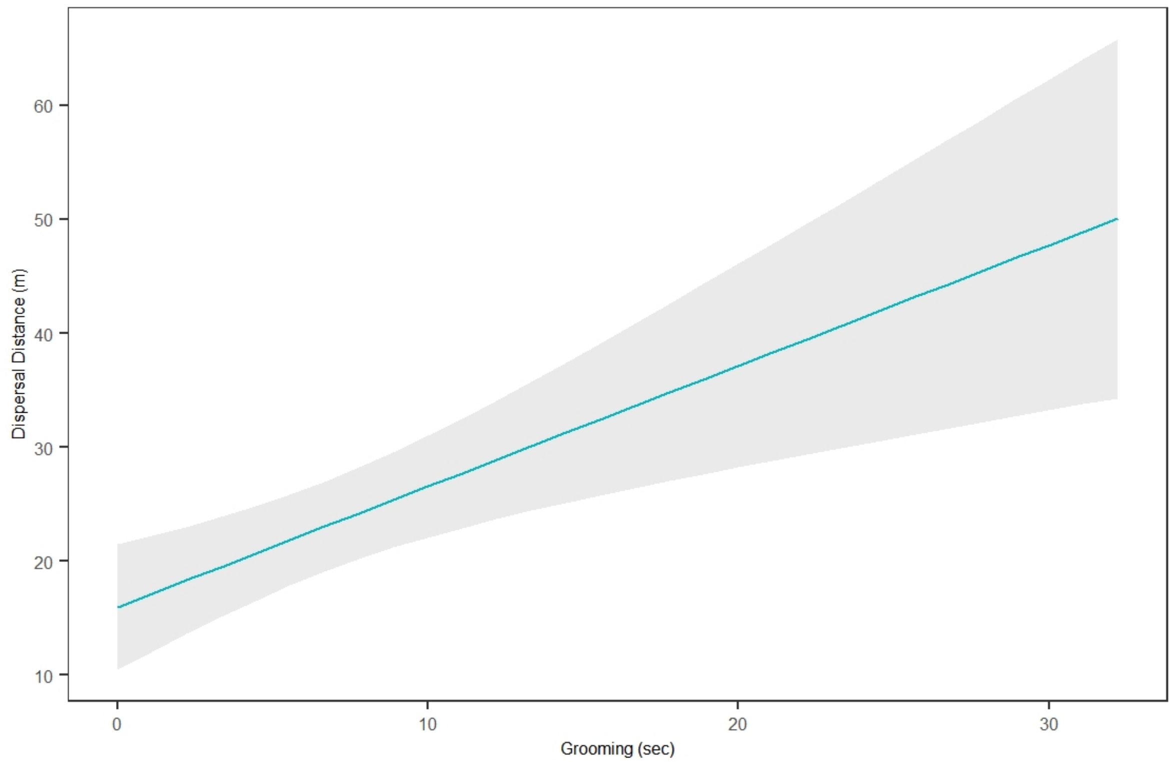

Figure 6 Effects of personality on dispersal distance at final caching event; y= 1.059x+ 15.965. Dispersal distance increases with time spent grooming, a measure of anxiety. Results were obtained from linear mixed models. Confidence intervals are shown at 95%.

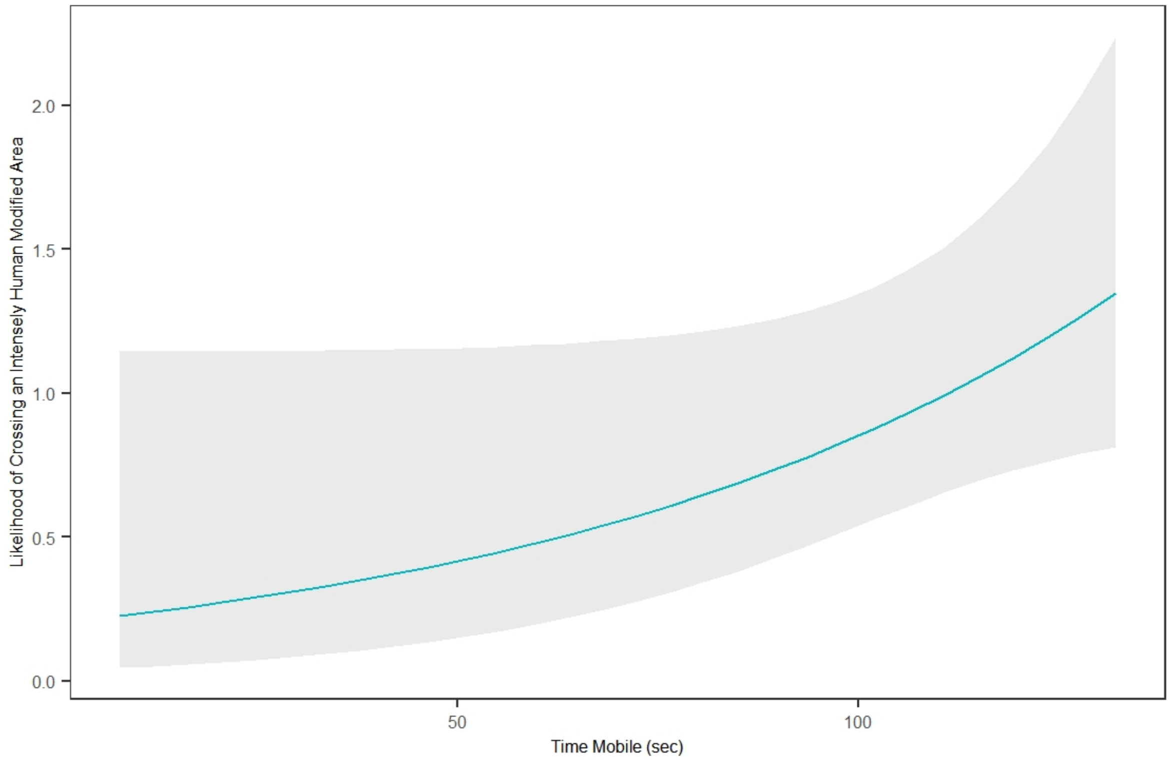

Figure 7 Effects of personality on likelihood of crossing an intensely human modified area; y= 0.0143x-1.593. A y-axis value of 0 indicates no crossing, a value of 1 indicates one crossing, and a value of 2 indicates multiple crossings. Likelihood of crossing a human modified area increases with activity. Results were obtained from generalized linear mixed models. Confidence intervals are shown at 95%.

DISCUSSION

Overview

Through a field experiment conducted in Maine, this study found that two key behavioral traits are related to a gray squirrel's decision to disperse a nut across an intensely human modified area: anxiety and activity. Anxiety is positively related with dispersal distance, suggesting that cache distance increases with anxiety. Activity was found to be positively related with likelihood of carrying a nut across an intensely human modified area, indicating that active individuals are more likely to cache across these areas.

Anxiety Increases Dispersal Distance

No previous studies have examined grooming in gray squirrels specifically; however, this behavior has been associated with anxiety in many other rodents (deer mice, southern red-backed voles, northern short-tailed shrews, Brehm *et al.* 2019; prairie voles, O'Leary *et al.* 2013; lab mice, Wardwell *et al.* 2020). Thus, time spent grooming was considered a proxy for anxiety in this study. These results study suggest that the more an anxious individual is, the farther they cache a food item from the parent tree. This literature supports this hypothesis, with many studies showing that gray squirrels actively consider distance from parent tree during their caching process (Bartlow *et al.* 2018; Hopewell *et al.* 2008). Gray squirrels have been shown to preferentially cache far outside the safety of their foraging radius, thereby protecting their cache from pilferage by reducing the chance a naïve conspecific happens upon it while foraging at the same food patch (Leaver *et al.* 2017). Though Alpern *et al.* (2012) and Hopewell *et al.* (2008) proposed that gray squirrels respond to conspecifics at the food patch primarily as competitors rather than potential pilferers and respond by returning to the food patch more frequently, Hopewell *et al.* (2008) also found that gray squirrels who are being observed by a conspecific while caching increase distance between caches in an effort to reduce pilferage. Perhaps anxious individuals may more readily regard conspecifics at the same food patch as potential pilferers and increase distance to cache to decrease the likelihood of pilferage by spacing the cache farther from these potential pilferers. Alpern *et al.* (2012)'s model also predicted that scatter hoarders should increase distance to cache in response to a decrease in food availability; it may be the case that anxious individuals interpret food availability differently than less anxious individuals. Anxious individuals may more readily perceive food availability as limited, and therefore begin increasing distance to cache sooner than calm individuals.

Activity Relates to Seed Dispersal Across Intensely Human Modified Areas

Time mobile is a direct measure of activity in all animals (Boon *et al.* 2008; Haigh *et al.* 2017; Perals *et al.* 2017). Research by Boon *et al.* (2008) found that activity in female North American red squirrels (*Tamiasciurus hudsonicus*) is associated with risk-taking; highly active individuals were more likely to enter traps and other individuals' territory as well as travel farther outside their own territory. Taken together with research by McGregor *et al.* (2008), which proposed that small mammals avoid roads due to their inherent danger rather than due to noise or traffic levels, the results of this study suggests that active gray squirrels are more prone to cross roads due to their higher affinity to take risks. In accordance with Haigh *et al.* (2017), which showed that squirrels with high activity rates moved more in the wild, it is also possible that a higher activity level simply correlates to more distance covered in the field. It may be the case that urban gray squirrels who move more are simply more likely to cross intensely human modified areas due to a higher encounter rate with them. This hypothesis is supported by Uchida *et al.* (2020), which found that Eurasian red squirrels (*Sciurus vulgaris*) residing in urban areas exhibit higher activity levels than those in rural areas, possibly due to abundant resources and a perceived reduction in predation risk.

High Activity and Anxiety Predict Dispersal Across Intensely Human Modified Areas

Taken together, these results suggest that anxious and active individuals are more likely to cache a nut across an intensely human modified area. Anxious individuals show a greater tendency to move a food item farther away from its parent tree. This phenomenon may be due to anxious individuals' propensity to regard conspecifics at a food patch as potential pilferers or perceive food availability as low, which in turn drives them to increase distance to cache in an effort to protect the food item from pilferage (Alpern *et al.* 2012; Bartlow *et al.* 2018; Hopewell *et al.* 2008). High activity in squirrels is correlated with risk-taking (Boon *et al.* 2008), and thus study suggests that active individuals are more willing to accept the risk of crossing an intensely human modified area. It is also possible that active individuals simply move more, and are therefore more likely to cross these areas since they encounter them more than less active individuals.

Thus it stands to reason that a combination of high activity levels and high anxiety levels would interact to produce a high likelihood of the individual in question moving a nut across an intensely human modified area. In addition active squirrels simply moving more, active squirrels in urban areas move even more than their forest-inhabiting counterparts, causing them to encounter a greater number of intensely human modified areas than their inactive conspecifics. Perhaps inactive squirrels are more likely to perceive an intensely human modified area as an impassable boundary and are not willing to accept the risk of crossing it (Conrey *et al.* 2003; Goosem 2001). Likewise, less anxious individuals could be less concerned about conspecifics foraging at the same food patch and the amount of food available, thus these variables are less likely to elicit a decision to cache farther from the parent tree in an effort to reduce pilferage.

Ecological Implications

An understanding of how different species interact with roads is crucial, especially during ecologically significant activities such as seed dispersal. Previous studies have also shown that human activity, no matter how subtle, affects the local wildlife (Forman & Alexander 1998; Oxley *et al.* 1974; Tewksbury *et al*. 2002). For example, Berger (2007) found that pregnant female moose residing in areas of Yellowstone with a local brown bear population shifted their activity and therefore their birth sites towards roads while non-pregnant females, juvenile females, and females who had lost their calf *in utero* did not exhibit the same behavioral change. Berger proposed that this shift was due to brown bears’ aversion to roads; mothers favored habitats with roads, and therefore less bears, in an effort to protect their calves. Indeed, Birnie-Gauvin *et al.* (2016) showed that urban animals experience an almost entirely different set of pressures and challenges than their rural conspecifics. More than 60% of rural fox squirrel fatalities are caused by predation whereas predation accounts for less than 5% of urban fox squirrel fatalities. Urban fox squirrels are far more likely to be killed by vehicle strikes- with more than 60% of urban fox squirrel fatalities occurring this way- demonstrating a pressure on urban fox squirrels to learn vehicle avoidance behaviors rather than predation avoidance behaviors (McCleery *et al.* 2008).

Human activity not only affects animal behavior, but the very personality ratios within wildlife populations. Brehm *et al*. (2019) showed that silvicultural methods practiced in a forest increased the proportion of bold, active, and anxious individuals within deer mouse, southern red-backed vole, and northern short-tailed shrew populations. Thus it is likely that gray squirrel populations within human modified areas exhibit different personality distributions than populations living in more pristine environments, though no studies have examined this. Since Brehm *et al.* (2019) also showed that personality type ultimately determines seed choice and cache location, it stands to reason that urbanization has affected not only the presence and distribution of gray squirrel personality types, but the role of the gray squirrel population in these areas as seed dispersers.

CONCLUSION

This study demonstrates that active and anxious gray squirrels are more likely to disperse a nut across an intensely human modified area. Active individuals are more likely to take risks, including moving across intensely human modified areas. Since active individuals also travel more within their home ranges than inactive individuals, they also may have a higher encounter rate with these areas. Anxious individuals are more likely to perceive food availability as low or regard conspecifics at a food patch as potential pilferers, thus prompting them to cache a food item farther from the parent tree in order to protect it.

These finding only raise more questions about the seed dispersal behavior of gray squirrels residing in human modified landscapes. Future studies should examine the specifics of how urbanization impacts the distribution of gray squirrel personalities. If human activity decreases the presence of anxious and active individuals, the ability of nut-producing plants to disperse across an intensely human modified area may be restricted. On the other hand, if urbanization favors anxious and active individuals, seed dispersal across intensely human modified area may be magnified. Research is also needed on how gray squirrel personality affects their seed choice. Brehm *et al.* (2019) showed that individuals of different personality types within the same species cached different proportions of seed species based on characteristics such as mass and size. If active and anxious individuals have a strong preference for or against a certain type of seed, it would impact the dispersal of plants with that seed characteristic across human modified areas.

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APPENDICES

APPENDIX A: LIST OF INDEPENDENT VARIABLES

Table 2 List of independent variables used in mixed-effects models. Behavioral variables are defined in TABLES AND FIGURES section. Response variables include distance to first cache, distance to final cache, and likelihood of crossing an intensely human modified area.

Variable	Definition
Sex	Sex of disperser
Weight	Weight of disperser (g)
Mean Distance from Center	See Appendix F
Time Mobile	See Appendix F
Distance Covered	See Appendix F
Grooming	See Appendix F
Rearing	See Appendix F
Jumping	See Appendix F
Hanging	See Appendix F

APPENDIX B: MODEL RANKINGS BASED ON AIC

Table 3 First Cache Distance. Results for the mixed-effects models with distance to first cache as the response variable. Models are ranked according to the AICc value. Variables defined in Appendix F. Where K is number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, ΔAICc is the delta Akaike Information Criterion, AICc Weight gives the probability that the model is the best choice from all the models in the set, and Cumulative Weight gives the amassed weight of all the models in the set.

Variable	K	AICc	ΔAICc	AICc Weight	Cumulative Weight
Grooming	4	432.14	0.00	0.99	0.99
Mean Distance from Center	4	443.62	11.48	0.00	0.99
Null	3	445.60	13.46	0.00	1.00
Weight	4	446.40	14.26	0.00	1.00
Rearing	4	446.49	14.35	0.00	1.00
Sex	4	447.08	14.94	0.00	1.00
Jumping	4	447.11	14.97	0.00	1.00
Time Mobile	4	447.22	15.08	0.00	1.00
Hanging	4	447.73	15.59	0.00	1.00
Distance Covered	4	447.80	15.67	0.00	1.00

Table 4 Final Cache Distance. Results for the mixed-effects models with distance to final cache as the response variable. Models are ranked according to the AICc value. Variables defined in Appendix F. Where K is number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, ΔAICc is the delta Akaike Information Criterion, AICc Weight gives the probability that the model is the best choice from all the models in the set, and Cumulative Weight gives the amassed weight of all the models in the set.

Variable	K	AICc	ΔAICc	AICc Weight	Cumulative Weight
Grooming	4	462.58	0.00	0.91	0.91
Mean Distance From Center	4	468.82	6.24	0.04	0.95
Null	3	471.29	8.71	0.01	0.96
Jumping	4	471.42	8.84	0.01	0.97
Weight	4	471.85	9.27	0.01	0.97
Rearing	4	472.61	10.03	0.01	0.98
Distance Covered	4	473.27	10.69	0.00	0.98
Sex	4	473.45	10.87	0.00	0.99
Time Mobile	4	473.50	10.92	0.00	1.00
Hanging	4	473.59	11.00	0.00	1.00

Table 5 Likelihood of Crossing an Intensely Human Modified Area. Results for the mixed-effects models with likelihood of crossing an intensely human modified area as the response variable. Models are ranked according to the AICc value. Variables defined in Appendix F. Where K is number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, ΔAICc is the delta Akaike Information Criterion, AICc Weight gives the probability that the model is the best choice from all the models in the set, and Cumulative Weight gives the amassed weight of all the models in the set.

Variable	K	AICc	ΔAICc	AICc Weight	Cumulative Weight
Time Mobile	4	118.90	0.00	0.53	0.53
Distance Covered	4	122.07	3.17	0.11	0.64
Grooming	4	122.36	3.46	0.09	0.74
Null	3	122.84	3.94	0.07	0.81
Jumping	4	123.83	4.94	0.05	0.86
Rearing	4	124.15	5.25	0.04	0.90
Sex	4	124.73	5.83	0.03	0.92
Weight	4	124.89	5.99	0.03	0.95
Mean Distance From Center	4	124.97	6.07	0.03	0.98
Hanging	4	125.12	6.22	0.02	1.00

APPENDIX C: MODEL PARAMETERS FOR TOP RANKED MODELS

Table 6 First Cache Distance. Model parameters and standard errors for the top ranked mixed-effects models with distance to first cache as the response variable.

Variable	Slope	Intercept	Standard Error	T-value	P-Value
Grooming	1.204	10.985	0.234	5.143	0.0068

Table 7 Final Cache Distance. Results Model parameters and standard errors for the top ranked mixed-effects models with distance to final cache as the response variable.

Variable	Slope	Intercept	Standard Error	T-value	P-Value
Grooming	1.059	15.965	0.309	3.432	0.0265

Table 8 Likelihood of Crossing an Intensely Human Modified Area. Model parameters and standard errors for the top ranked mixed-effects models with likelihood of crossing an intensely human modified area as the response variable.

Variable	Slope	Intercept	Standard Error	Z-value	Pr(>|z|)
Time Mobile	0.0143	-1.593	0.00761	1.883	0.0597

APPENDIX D: OPEN FIELD TEST RESULTS

Table 9 Results from Open Field Tests. Values obtained using ANY-maze© (version 5.1; Stoelting CO, USA) tracking software. Data used to obtain AIC model rankings.

Squirrel ID Code	Sex	Weight (g)	Mean Distance From Center (m)	Time Mobile (sec)	Distance Covered (m)	Time Spent Grooming (sec)	Time Spent Rearing (sec)	Jumps	Time Spent Hanging
3	Female	700	0.299	59.8	8.589	5.7	14.4	0	0
20	Female	490	0.287	54.7	11.693	10.9	15.5	3	4.7
23	Male	500	0.178	11.2	1.405	32.2	41.9	0	0
26	Male	750	0.348	7.9	0.658	0	6.2	0	0
27	Male	480	0.285	56.9	10.582	23	48.1	3	0
29	Male	460	0.273	132	11.416	0	57.9	0	0

APPENDIX E: CACHE LOCATION DATA

Table 10 Data on nuts cached by measured gray squirrels. For Nut Species, 0 indicates a hazelnut and indicates an acorn. First Cache Distance states the distance in meters the first cache was made from the parent tree. Final Cache Distance states the distance in meters the final cache was made from the parent tree. Final cache was the last time the nut was found cached, the nut may have been eaten or moved to an unknown location after this mark. For Crossing of Intensely Human Modified Area, Crossed Sidewalk, Crossed Street, and Crossed Parking Lot, 0 indicates no crossing, 1 indicates one crossing, and 2 indicates multiple crossings. Disperser indicates which measured squirrel dispersed the nut (see Appendix D for behavioral results.) Data used to obtain AIC model rankings.

Nut ID	First Cache Distance (m)	Final Cache Distance (m)	Nut Species	Crossed Intensely Human Modified Area?	Crossed Sidewalk?	Crossed Street?	Crossed Parking Lot?	Disperser
A39	19.79	51.59	0	2	2	0	0	29
B48	19.86	23.55	1	2	2	0	0	29
B51	13.3	13.3	1	2	2	0	0	29
B44	12.35	18.36	1	2	2	0	0	29
B28	10.86	23	1	2	1	1	0	29
B18	19.9	38.29	1	2	2	0	0	29
B74	19.7	11.06	1	2	2	0	0	3
B112	9.53	13.72	1	1	1	0	0	3
B76	12.7	29.79	1	0	0	0	0	3
B13	2.67	9.57	1	0	0	0	0	3
B73	9.49	62.63	1	1	0	0	1	3
A8	9.77	36.71	0	0	0	0	0	3
B24	14.15	16.6	1	0	0	0	0	26
B7	8.84	9.56	1	0	0	0	0	26
A17	11.17	9.89	0	0	0	0	0	3
B43	20.66	18	1	0	0	0	0	20
A28	19.07	16.61	0	0	0	0	0	20
B1	10.28	64.17	1	0	0	0	0	20
A36	26.62	26.62	0	2	2	0	0	3
A18	4.3	4.3	0	0	0	0	0	3
A10	20.09	20.09	0	2	1	1	0	3
A3	10.38	10.38	0	1	1	0	0	3
A42	7.57	7.57	0	1	1	0	0	3
B61	4.71	4.71	1	0	0	0	0	29
B26	1.63	1.63	1	0	0	0	0	29
B70	8.04	8.04	1	1	1	0	0	29
B110	12.9	12.9	1	1	1	0	0	3
A102	31.46	31.46	0	2	2	0	0	3
A8	4.05	4.05	0	0	0	0	0	3
A9	29.81	29.81	0	0	0	0	0	3
A20	36.62	36.62	0	0	0	0	0	3
A7	20.02	20.02	0	0	0	0	0	3
B16	30.07	30.07	1	0	0	0	0	3
B32	16.1	16.1	1	0	0	0	0	26
B17	15.85	15.85	1	0	0	0	0	3
B81	20.28	20.28	1	0	0	0	0	26
B46	3.27	3.27	1	0	0	0	0	26
A16	30.27	30.27	0	1	0	1	0	3
B29	35.82	35.82	1	0	0	0	0	20
A0	12.7	12.7	0	0	0	0	0	20
A44	18.29	18.29	0	0	0	0	0	20
B2	18.85	18.85	1	0	0	0	0	20
B118	24.91	24.91	1	0	0	0	0	20
B105	4.45	4.45	1	0	0	0	0	20
B129	15.95	15.95	1	2	2	0	0	3
B145	37.71	37.71	1	2	2	0	0	20
B143	21.23	21.23	1	2	2	0	0	20
B69	42.27	42.27	1	2	2	0	0	29
B133	9.8	9.8	1	0	0	0	0	29
B125	8.86	8.86	1	0	0	0	0	29
A130	23.33	23.33	0	0	0	0	0	27
B92	35.29	35.29	1	0	0	0	0	27
A126	81.04	81.04	0	0	0	0	0	27
A115	55.22	55.22	0	0	0	0	0	23
A101	10.56	10.56	0	0	0	0	0	20

APPENDIX F: INTERPRETIVE INFORMATION FOR OPEN FIELD TEST BEHAVIORS

Table 11 Behaviors tracked during the Open Field Test assessments and their interpretation in terms of personality traits. Included are behaviors, operational definition, units of measure, interpretive notes, and brief source lists.

Behavior	Definition	Units	Interpretation	Sources
Mean Distance From Center	Average distance from the center of the apparatus floor	Meters	A measure of **boldness/timidness**, or **risk taking**. Small mammals regularly engage in thigmotaxis, the avoidance of open spaces due to anxiety or fear. Therefore the smaller an animal's Mean Distance From Center, the more time they spent in the center of the apparatus floor and the more bold they are. The larger an animal's Mean Distance From Center, the more time they spent at the perimeter of the apparatus floor and the more timid they are.	Choleris *et al.* 2001; Eccard & Herde 2013; Gracceva *et al.* 2013; Ramos *et al.* 1997; Treit & Fundytus 1989; Brehm *et al.* 2019;
Time mobile	Time spent in active motion.	Seconds	A direct measure of an animal's **activity** rate.	Gracceva *et al.* 2013; Ramos *et al.* 1997; Carter *et al.* 2013
Distance covered	Total distance the squirrel traveled.	Meters	A direct measure of an animal's **activity** rate.	Gracceva *et al.* 2013; Réale *et al.* 2007
Grooming	Time spent grooming.	Seconds	A measure of **anxiety**. Though no studies have examined grooming in grey squirrels specifically, this trait has been shown to be representative of stress-coping mechanisms in many rodents.	Brehm *et al.* 2019; Wardwell *et al.* 2020; O'Leary *et al.* 2013; Martin & Réale 2008
Rearing	Time spent rearing. A rear was defined as the squirrel lifting both front paws off the floor while in an erect, inquisitive stance (not just sitting on back limbs.) A rear could have been performed both on the floor of the apparatus or while pressing front paws against the wall of the apparatus.	Seconds	An indirect measure of **activity**; rear rate often positively correlates with locomotion.	Choleris *et al.* 2001; Brehm *et al.* 2019; Réale *et al.* 2007; Martin & Réale 2008
Jumping	Total number of times the animal jumped.	Events	An indirect measure of **activity** through locomotion and avoidance attempts.	Mazzamuto *et al.* 2019; Martin & Réale 2008
Hanging	Time spent hanging. A hang was defined as an individual grasping the top of the apparatus after jumping and was considered ended once the individual touched the floor of the apparatus.	Seconds	An indirect measure of **boldness/timidness** through avoidance. Similar to Mean Distance from Center, hanging represents an animal's unwillingness to exist in an open area. Also an indirect measure of **activity**, as avoidance attempts have been positively correlated with activity.	Mazzamuto *et al.* 2019; Martin & Réale 2008

AUTHOR'S BIOGRAPHY

Skye Cahoon was born on December 14, 1997 in Newton, Massachusetts. She grew up in Wrentham, Massachusetts and graduated from King Philip Regional High School in 2016 after establishing an A Cappella club and a Birding club. With a major in Zoology and a minor in Psychology, Skye has ambitions of establishing a career researching animal cognition and behavior. She is especially fascinated by corvids and octopuses, and believes there is much to be gained by exploring non-human intelligence. Throughout her academic career Skye cultivated her passion for ecology by participating in a wide range of natural science courses, exciting internships, and personal experiences with Maine's wilderness. Her internships at the New England Aquarium in Boston, MA and Southwick's Zoo in Mendon, MA are of particular note as they left her with octopus and parrot friends. One of her favorite pastimes is wandering around in the woods while seeking out and observing fungal structures, communing with non-human creatures, and pondering the obscure mechanisms of the natural world. Skye's love for nature extends to her home life and she has owned a variety of plants and pets including a snake, parrots, hedgehogs, fish, gerbils, and cats. Her two cats, Felix and Naava, encourage her to contemplate the non-human mind on a daily basis. Skye also enjoys listening to and making music, creating physical artwork, and writing creatively.