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## **Territoriality and Spatial Structure in the Green Anole, *Anolis carolinensis***

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Territoriality and Spatial Structure in the Green Anole, *Anolis  
carolinensis*

A Thesis

Submitted to the Graduate Faculty of the  
University of New Orleans  
in partial fulfillment of the  
requirements for the degree of

Master of Science  
In  
Biological Science

by

William David Weber Jr.

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## **Abstract**

*Anolis carolinensis* has been a model organism for ecology and evolutionary biology since the seventies, yet there are still understudied aspects of their ecology. A five-year study has provided microsatellite genotypes to be used in building a pedigree and assess relatedness, enabling us to evaluate the spatial distribution of an urban population of *A. carolinensis*. Results indicate no correlation between a male's size and the distance others keep from it; however, males belonging in the heavyweight morph are dictating the spatial distribution in this population. In addition, juvenile dispersal of male offspring and partial philopatry of female offspring are key in this dynamic, where a single heavyweight male will actively defend a small area that contains multiple females, some of which are be daughters, and multiple unrelated males, most likely sneaker males.

## **Introduction**

Both the spatial distribution of an organism within its habitat and the factors driving that distribution are vital components of an animal's ecology. To date, the majority of work examining the influence of demographics on spatial distribution has been conducted on charismatic and threatened species. Relatively little attention has been paid to the factors influencing the distribution, behavior, and population structure of more cryptic species. The spatial distribution of an organism can be affected by its age, sex, size, mating system and seasonal environmental effects on food abundance or nesting site quality. (Seymour, 1991; Kesler & Haig, 2007; Clausen & Jesper, 2016). Demographics specifically impact community behaviors like home-ranging, territoriality, dispersal, philopatry, and relatedness interactions.

Although males of sexually dimorphic species will generally maintain larger home-ranges than females, home-range size does not necessarily correlate with body size among conspecifics (Schoener & Schoener, 1982). In many cases once an individual has established a home-range it will defend all or part against other individuals and other species (Subrahmanyam & Sambamurty, 2006). These defended areas constitute territories. When home-ranges and territories are established communication curtails boundary violations (Orrell, 2003; Subrahmanyam & Sambamurty, 2006; Bateman, et al., 2015), and while home-ranges may overlap depending on the species in question, territories usually will not (Hojnowski, et al., 2012). Territorial disputes may entail costs to individuals ranging from simple eviction, to injury and even mortality (Smith, 1982; Tokarz, 1985; Lovern M., 2001; Jenssen, 2005). Although in most species territorial behavior is sex-specific, usually being exhibited mainly by males (Bateman, et al., 2015), territoriality can also be influenced by size. In some species, for example, individuals may not possess the physical capability of territoriality until reaching a

certain size threshold (Stamps & Krishnan, 1997; Lailvaux S., 2004; Kaneko, et al., 2014).

Along with territorial conflict, an individual's response to conflict potential is another component of spatial distribution. For instance, individuals avoiding physical confrontation may achieve higher fitness through sneak copulations within the realm of a territory holder (Ambrosio & Baeza, 2016).

In some cases, individuals are required to leave their natal areas as resources become insufficient. However, dispersal is a multifactorial behavior motivated not only by resource availability, but also by mate location and population ecology (e.g. inbreeding avoidance, and resource availability)(Myers & Krebs, 1971; Gilroy & Lockwood, 2012). Costly in the form of predation, competition, energy expenditure, and habitat loss, dispersal is mostly male-biased, and in most cases females will not venture far from their natal home-range (Alonso & Alonso, 1992). In some instances, individuals remain in their natal home-range serving in its social hierarchy before dispersing at a later time (Kesler & Haig, 2007). In cases of natal philopatry, we expect individuals to show a pattern of spatial genetic structure and isolation by distance (IBD) (Broquet, et al., 2006). Philopatry is chiefly influenced by resources and thus can be seasonal, as in migratory bird species. Again, age and size may also dictate when and if an animal will disperse or remain (Podgorski, et al., 2014; Fatterbert, et al., 2015; Clausen & Jesper, 2016). Some monogamous species display a high level of philopatry, and thus high relatedness in close population clusters (Keane, et al., 2015). One of the most important ecological reasons for dispersal is inbreeding avoidance, and a lack of dispersal has been shown to elevate the inbreeding coefficient in some species (Zhang, et al., 2002; Huisman, et al., 2016).

In this way, patterns of relatedness can impact the way individuals establish themselves within a territory. Cougars (*Puma concolor*) share home ranges that overlap to a varying degree



between males and females, although none of the individuals involved are related, indicating offspring dispersal (Elbroch, et al., 2016). Patterns of relatedness also underlies the phenomenon of kin discrimination, which has shown to be important to inbreeding avoidance and indirect fitness conferred upon relative males (Waser, et al., 2012). The relatedness structure of a populations can thus have important implications for mating ecology, dispersal and territorial behavior. Furthermore, the practices of male-biased dispersal and female philopatry in a species may result in take-over of the mother's territory by her daughters (Pitt, et al., 2008).

Additionally, in some avian species daughters may even establish a new territory within their mothers' (Komdeur & Edelaar, 2001). The majority of territorial inheritance work thus far deals with the inheritance of a territory or resources from the mother to the female offspring, most of which has been studied in mammals (Ratnayeke, et al., 2002; Marino, et al., 2012; Mosser, et al., 2015). Few studies have examined male territory inheritance (Charnov & Berrigan, 1993), even though the fitness benefits of, in the form of the of a higher quality territory, could be substantial.

Here we describe a multi-year study investigating home-range establishment, territoriality, and spatial genetic structure in an urban populations of the green anole lizard, *Anolis carolinensis*. Green anoles exhibit a polygynous, female defense mating system whereby females will establish a home-range, and males will begin to defend a territory containing multiple females, leading to a high degree of territoriality (Jenssen & Nunez, 1998; Losos, 2009). Although the green anole is a model organism for investigating ecology and evolutionary biology, little is known regarding the factors that influence the spatial distribution of males and females. Home range, dispersal, and mating system have been extensively studied in several anole species, but, despite some careful investigations by Jenssen and colleagues (Jenssen, 1995 & 2005; Jenssen & Nunez, 1998), little is known about the relationship between population

structure and behavior in green anoles (Tokarz, 1998; Stamps, 2001; Calsbeel, 2007 & 2009). In addition to a marked sexual dimorphism, green anole populations in southeastern Louisiana often exhibit an intrasexual male dimorphism whereby large “heavyweight” males can be distinguished from smaller and younger “lightweight” males by head morphology and bite force. Heavyweight males rely more on physical combat involving biting to settle territorial disputes in the laboratory, whereas lightweights bite both less forcefully and less often (Lailvaux S., 2004). Thus, territory ownership might be expected to skew heavily towards heavyweight males, but this prediction, as well as the impact of relatedness on territoriality and territory inheritance within populations of male green anoles, has never been explicitly tested.

There is a wealth of genomic resources available in the literature to facilitate molecular ecology studies of green anoles. The green anole was the first reptile to have its genome sequenced (Aldolfi, 2011) and over seventy microsatellite markers currently exist, providing a set of neutral markers ideal for parentage analysis (Wordley, 2011). Anoles can be easily captured and marked and exist at high densities in nature, making it an ideal organism for addressing questions regarding relatedness, territoriality, and population structure.

In the present study, we marked, and genotyped every individual captured over a five-year period within an urban population of *Anolis carolinensis* lizards in Washington Park, New Orleans. We used these markers both to examine relatedness and to build a pedigree encompassing individuals sampled over the entire 5-year period. In addition, we used sample locations of capture sites, to construct spatial distribution maps to explore drivers of spatial distribution in the green anole. Here we tested three hypotheses looking at the spatial distribution of the green anole. First, because of the sexual dimorphism in green anole males will maintain larger home ranges than females. Second, due to the territoriality of heavyweight males and the

danger imposed on lightweights by them, lightweight males found neighboring a heavyweight will be related to it, and unrelated lightweight males will avoid them. Lastly females will inherit the territories of their mothers, and males will not inherit from their fathers.

## **METHODS**

### Study site

We conducted this study on a population of free-ranging green anole lizards in Washington Square Park (N29.965005°, W90.057302°) in New Orleans, LA. The park is one hectare in area and is surrounded by an iron fence, the exterior of which is bordered by concrete side walk adjacent to major roads of travel. Green anole habitat is made up of bushes of the common cast iron plant (*Aspidistra elatior*) which fringe the interior of the park fence, stretching on average two meters into the park. The interior of the park comprises open lawn and live oak trees (*Quercus virginiana*) established on the edges of the park, where green anoles have been observed, but it does not serve as the primary habitats.

### Animal sampling

We sampled the population in the spring (mid-April to early May) and the fall (mid-September to early October) of each year from 2010 to 2014. We captured lizards either by noose or by hand, and marked, with tape, each specimen's location and gave it a unique identification number. After GPS coordinates of the capture site were recorded, we transported each specimen to the lab at UNO where they were permanently marked with a unique identification tattoo with a visual implant elastomer (VIE) tag (Northwest Marine Technology, Inc., Shaw Island, WA, USA) (Losos, 2009). In the lab we removed a tail tip of no more than five centimeters from each individual with sterilized scissors and placed it into a vial of 95% ethanol. We sexed the lizards and then weighed them to the nearest 0.01g, with a Type XS107 Mettler-Toledo scale (Mettler-Toledo, LLC, Columbus, OH, USA). To measure SVL to the nearest 0.01 mm we used Rok digital calipers (Rok International Industry Co., Limited, Shenzhen, PRC), and finally, individuals were marked with a permanent marker just above the

dorsal tail-base to facilitate visual identification on subsequent collection days preventing recapture within the same sampling period. The marking is eliminated on the individual's next molting. Finally, we released lizards the morning after collection at the exact point of capture as indicated by the tape marker placed at the capture location. All methods were approved by the University of New Orleans's (UNO) IACUC protocol (UNO-11-004).

### Spatial distribution assessment

We constructed maps of individual capture locations using QGIS v 2.4.0.0 (QGIS Development Team, 2015) and a "Google Maps" overlay as the template for park boundaries, coinciding with the location of the perimeter fence. After measuring the length and width of each cast-iron bush, we created a polygon shape file for each bush (Figure 1a). We then created a vector file containing each individual's capture locations and labeled it to create spatial maps for individuals within each cohort. A separate vector file was created for each sex (Figure 1b). Due to the limited accuracy of GPS devices, we were only able to assign the location of an individual to a specific bush where captured, but not precisely where in that bush. The capture location of each individual for a given bush was taken as the geographic center of the bush where the individual was recorded. Each bush was then measured from geographic center to geographic center of every other bush in the habitat, creating a matrix of distances. The average geographic distance of each individual from all other individuals within its cohort was then calculated using the average distance formula.

Formula 1; average distance  $\hat{d} = \frac{\varepsilon(d_1+d_2+d_3+\dots)}{n-1}$

Finally, we created additional maps displaying individuals caught more than once and mapped them to the bush where they were captured; these maps were used to estimate territorial home-range. For each of the individuals that we recaptured, we created a QGIS layer displaying



using the following conditions: Step 1, an initial denaturation at 95°C for 15 minutes followed by 35 cycles of step 2. Step 2, 94°C for 30 seconds, primer annealment at 55°C for 90 seconds, and an extension at 72°C for 60 seconds followed by a final 60°C extension period for 30 minutes. Microsatellite amplification products sizing was done using an ABI 3100 Genetic Analyzer (Applied Biosystems, Carlsbad, CA, USA) with the ROX-500 size standard (GeneScan, Waltham, MA, USA). Next we visually inspected electropherograms using GENEIOUS (Biomatters, San Francisco, CA, USA) and binned the genotypes with FLEXIBIN (Amos, 2001). We tested all loci for deviations from Hardy-Weinberg and linkage equilibrium using ARLEQUIN and the Holm's-Bonferroni sequential correction (Rice, 1989) with an alpha value of 0.0065 (Excoffier, 2010). Then the presence of null alleles and allelic drop out were assessed using MICROCHECKER (Van Oosterhout, et al., 2004).

For pedigree construction we used the software program COLONY (Wang, 2013). We set mating system parameters for male and female polygamy, in a dioecious, diploid population, with the possibility for inbreeding. The run was set for “Long” with a full-likelihood analysis method set at medium precision, and no sib-ship priors. Because we were unable to assess parentage through observation, the data set of 848 individuals was broken down into cohorts. For each cohort we assumed all individuals to be potential offspring, all males as potential fathers, and all females as potential mothers. We then combined cohorts in a sequential, stepwise manner in which all the previous seasons' cohorts were added to the following cohort so that the parentage of all the previous cohorts served as the known paternity and maternity priors of the next. This procedure was conducted until we constructed an entire pedigree of all cohorts and individuals. The probability of a parent being included in the candidate genotypes was set at 50% and a genotyping error rate of 1% was used in all constructions.

We used the program SpaGeDi to estimate kinship coefficients between male-male and male-female dyads (Hardy & Vekemans, 2002), then to construct spatial correlograms in order to investigate patterns of relatedness between individuals at different spatial classes (Figure S1). Relatedness analysis began by looking at each of the heavyweights (N=101) in our data set, we examined the relatedness of all the other male individuals captured within its home range. Using pairwise relatedness values (k) obtained from SpAGeDi, each heavyweight was compared to the entire male population of its cohort, and then compared to males captured within its home-range only.

Simple analyses including student t-test, box plots, and regressions were performed in the RStudio Version 0.98.953 (2009, Free Software Foundation Inc., Boston, MA, USA). Auto correlograms were built in the Microsoft Excel 2010 (Richmond, WA, USA).



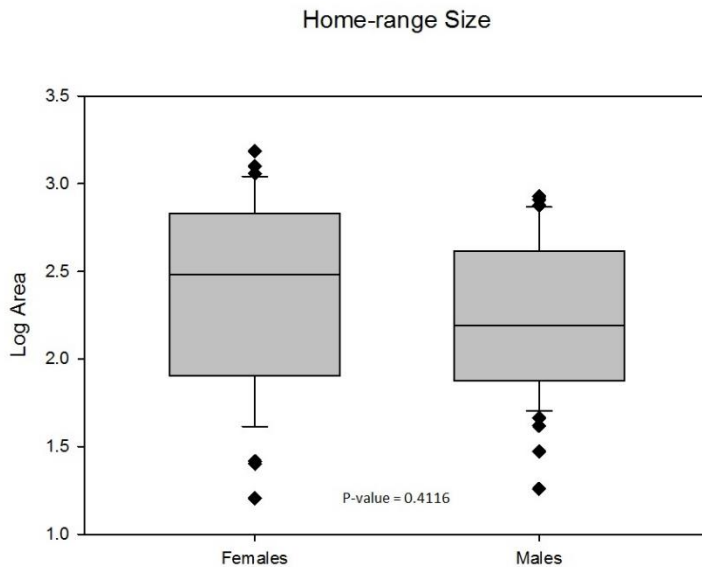
## RESULTS

### Home-range assessment

Examination of recaptured individuals shows the home ranges of females range from 16.06m<sup>2</sup> to 1537.67m<sup>2</sup>, yielding a mean female home-range size of 410m<sup>2</sup>. Male home-ranges varied from 18.15m<sup>2</sup> to 846.21m<sup>2</sup>, with a mean male home-range size of 260m<sup>2</sup>. There was no difference in home-range size between males (n = 42) and females (n = 39) (T=1.028 P<0.4116, 79 d.f.) (Figure 2).

Figure 2; Home-range area of green anoles in Washington Square Park.

"FMH"=female home-range, "MHR"=male home-range



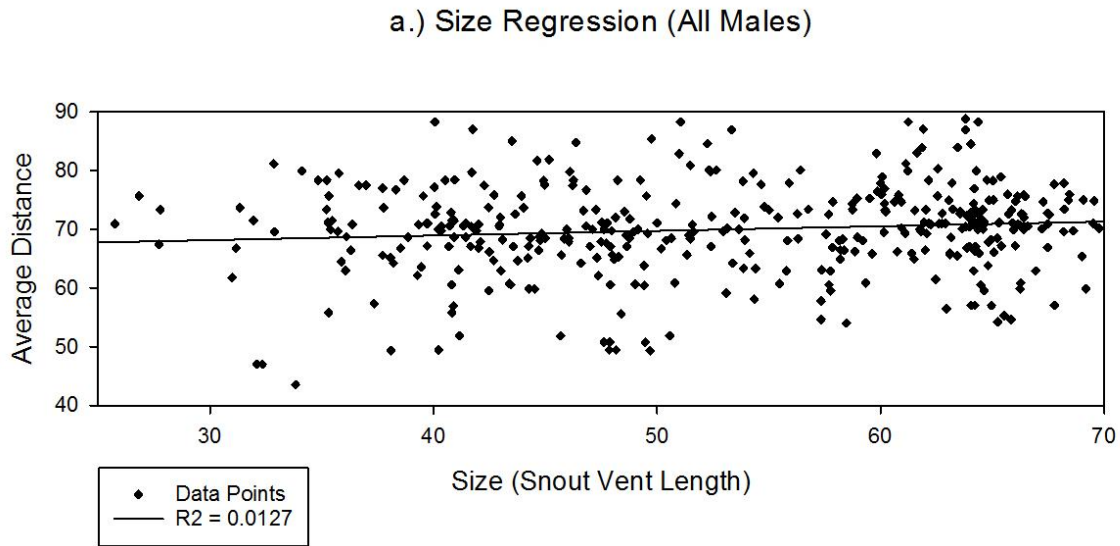
### Impact of male size on spatial distribution

The geographic average distance between lightweight males (n = 285), was 69.74m ± 8.069, was less than between heavyweights (n= 104), which was 70.60m ± 6.710, but was not significant (T=1.055, P=0.2926, 215 d.f.). Regression analysis of average distance measures and size (SVL) for all males was not significant (N=389, R<sup>2</sup>=0.0127, m=0.083). This relationship was also not significant for heavy (N=105, R<sup>2</sup>=0.0033, m=0.138), or light weight (N=285, R<sup>2</sup>=0.0142, m=0.109) males (Figure 3). Despite evidence of no correlation between size and

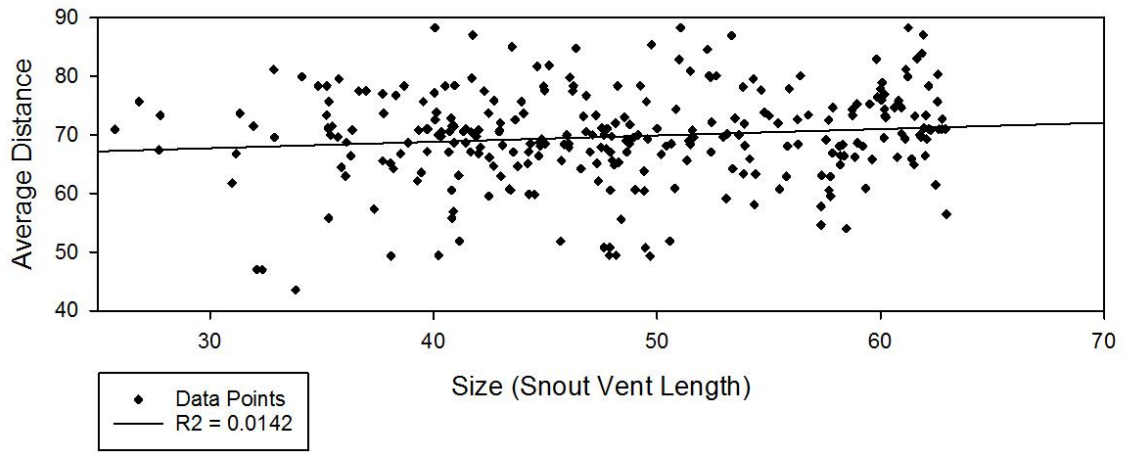
average distance, examination of QGIS spatial maps reveal a distribution pattern with heavyweight males. When the density of heavyweights is low, as it was in the Spring of 2010 (N=3), the heavyweights were captured at the maximum distance from one another (Figure 4a). When the densities of heavyweights were high (e.g. Spring 2012), usually only one heavyweight was found per bush (Figure 4b). In seasons of high heavyweight density, on some occasions we captured 2 or more heavyweights in the same bush. Since our sampling represents snapshots of animal locations at any given sampling time, this may indicate incursions as evidenced by a neighboring bush being vacant of a heavyweight (Figure 4c).

Figure 3; Size regressions.

a.) Includes all males b.) Lightweights only c.) Heavyweights only



b.) Size Regression (Lightweights)



c.) Size Regression (Heavyweights)

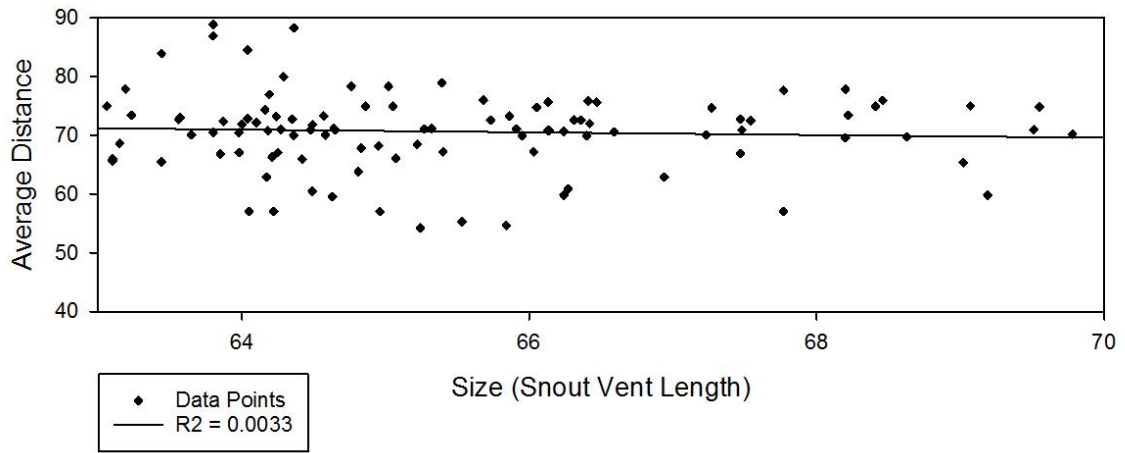


Figure 4; Examples of heavyweight spatial distributions

Individuals is indicated by a red dot, every capture season can be seen in supplemental materials



### Impact of relatedness on spatial distribution

Genotyping produced unique microsatellite genotypes for 846 individuals. Two individuals within the original data set of 848 were sampled twice as different individuals and the dataset was corrected accordingly. After Holm's-Bonferroni sequential correction we saw instances of linkage disequilibrium but with no consistent pattern between loci (Table S1). The number of alleles per locus ranged from 13 to 33 with a mean of 19.14. The average observed heterozygosity was  $0.6381 \pm 0.2455$ , and the expected  $0.7286 \pm 0.2326$ . ACAR 19 was the only locus to not show deviation from Hardy-Weinberg equilibrium, and there were no null alleles detected in the data set.

Relatedness examination reveals that a heavyweight is, on average, less related to its neighbors ( $k = -0.0144 \pm 0.0561$ ) than it is to the rest of the male population ( $k = 0.0015 \pm 0.0183$  SD), ( $T=1.6525$ ,  $P=<0.001$ , 200 d.f.). When other heavyweight males are excluded from neighbor analysis, there was no difference between the pairwise relatedness of a heavyweight's neighbor and the rest of the male population ( $T=1.9955$ ,  $P=0.4984$ , 68 d.f.).

Territory inheritance and isolation by distance

Spatial autocorrelograms revealed an inconsistent pattern of spatial genetic structure in the population. For females, there was a significant pattern of isolation by distance the Spring and Fall of 2010, Spring of 2011, Spring of 2013 and the Spring and Fall of 2014 cohorts, the female population. There was no IBD in the Spring and Fall of 2012 and Fall of 2013; the Fall of 2011 cohort yielded no discernable pattern. Spatial genetic structure of males also yielded an inconsistent pattern for IBD (Table 2). We also observed that the inbreeding coefficient ( $F$ ) of the population gradually increased with time and sampling. After the collection of ten cohorts inbreeding stabilized at  $0.3379 \pm 0.0258$  (Figure 5).

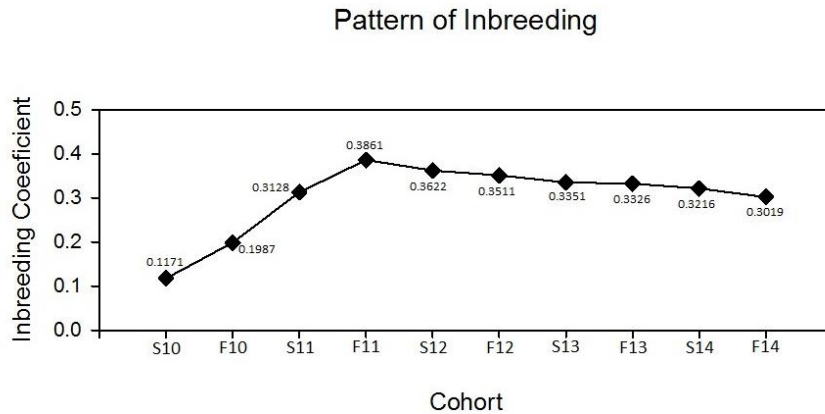
Table 1; Autocorrelogram results.

"-" is an indication of PID within that cohort, "+" indicates no PID and "?" is insignificant. The Autocorrelogram can be viewed in supplemental material

	Spring 2010	Fall 2010	Spring 2011	Fall 2011	Spring 2012	Fall 2012	Spring 2013	Fall 2013	Spring 2014	Fall 2014
<b>Female</b>	-	-	-	?	+	+	-	+	-	-
<b>Males</b>	+	-	+	-	+	+	-	?	-	-

Figure 5; The pattern of inbreeding

S=a spring collection period, F=a fall collection period, and the year follows each seasonal indicator



We had sufficient parentage and geographic information in our dataset to evaluate 16 males and 10 females for offspring territory inheritance. Results indicate that 35% of female offspring and 36% of its male offspring were found within their mother's home-range ( $\chi^2=0.707$ ) (Table S2). By contrast, 50% of female offspring and none of the male offspring were found within their father's home-range ( $\chi^2<0.01$ ) (Table S3).

## **DISCUSSION**

The causal factors underlying population spatial structure are potentially complex and poorly understood for most small, cryptic animal species. Here we used a combination of morphological, locality, and relatedness measures to test three hypotheses regarding factors influencing the spatial distribution of *A. carolinensis* in a natural urban population. Our first hypothesis, (i.e. that males maintain larger home ranges than females) was not supported, as males maintain home-ranges no larger than those of females, in this population. This is contrary to what is seen in most animals where males tend to exhibit larger home-ranges than females (Cederlund & Sand, 1994). Males will traverse larger areas looking for potential territorial take over and female acquisition, as females reside in a small area that will support them and their offspring (Said, et al., 2009). The anomaly in this population can be explained by a polygynous female defense strategy where females maintain a variable home-range, while males will stay in an area they can defend, not venturing far from its territory (Forsyth & Alcock, 1990). Leaving a territory, in this case a bush, may open the opportunity for sneak copulations, incursions from competitors, and possibly a loss of territory.

Our second hypotheses stated that due to heavyweight males' aggressive defense of their territories, lightweights close to them will be more related to them, whereas, unrelated lightweights will avoid them. We speculated that heavyweights will be more tolerant of a neighbor as a result of being more related to it, because indirect fitness can be achieved as a result of opportunistic breeding of a neighbor that one is related to (Ridley et al., 1987 & 1993). Our study however did not support this idea; heavyweights were no more related to neighboring lightweights than the rest of the population, and neighboring heavyweights in fact appear to be less related to the each other than the rest of the population. The hypothesis is also based on the

idea that the green anole is a highly territorial animal and aggressive bouts can be regularly observed between males. It would stand to reason that a lightweight male will position itself as far from a heavyweight as possible in order to avoid an encounter which could well result in an injury. Therefore, because smaller individuals are avoiding larger ones, the average distance between individuals should increase with size. We did not find evidence to support this, and the generally low  $R^2$  values in all our regressions between size and average distance between individuals suggest that male green anoles do not base their proximity to other males on those males' status as a heavyweight. However, the driver of the spatial distribution in this population is male size, as it is clearly demonstrated in the habitat mapping. The low temperature winter months in southern Louisiana cause all individuals to seek shelter (often in the leaf litter beneath their cast-iron habitat), thereby relinquishing their territories. In the spring as territories become re-established, a single heavyweight appears to actively defend a single bush. That bush will be inhabited by unrelated lightweight males and multiple females, including daughters. The same bush seems to only be inhabited by two heavyweights when there is an incursion event from a neighboring heavyweight.

Our final hypothesis was that females will inherit the territories of their mothers, whereas males will not inherit territories from their fathers. Again the data did not support the hypothesis; only 35% of a mother's daughters were found in her home-range, meaning that 2/3 of them dispersed or died. Additionally, this analysis produced two key results regarding father/offspring relations. On no occasion was a male offspring found in the territory of its father, yet 50% of a father's daughters were found within. Chi-square results indicate that the pattern seen in father/offspring interactions were not random, while mother/offspring interactions may have been. Male green anoles will mate, forcibly if necessary, with all the females it can. With the



discovery of an elevated inbreeding coefficient we can infer that there is the potential for first generation inbreeding between the fathers and daughters. Female offspring that remain in a natal bush may possibly be the offspring to the bush's occupying heavyweight. Therefore, some reproductive females are mating with their fathers. Whereas male offspring, if they have not developed adequate evasion skills, may be subject to infanticide, as is the case in other animal species (Charnov & Berrigan, 1993; Kopp, et al., 2015).

Here we have shown that spatial observations and demography can provide evidence and support for population activities that could only be inferred by constant, continuous observations, over many years. In this study, we have established the primary driver of spatial distribution in green anole to be size. Heavyweights establish a territory and all others fit within the social framework of that territory. Without the use of morphological, locality, and relatedness measures obtained from this population we would have had to invest an enormous amount to observation time to establish this same result. This experimental design can be used in other species, with similar questions adding increasing knowledge to the ecology of animals still understudied.

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## APPENDIX

Table S1; Multiplex PCR primer information

"Exp"=Expected, "Obs"=observed, "(bp)"=base pair

	Primer	Exp. Range (bp)	Obs. Range (bp)	Forward Primer (fluorophore label)	Reverse Primer	Repeat Motif
MultiPlex 1	ACAR1	110-122**	100-110	CCAAAAACCAAAAAG GCTGA**(Blue)	TGGACACACATACA CCCACA**	(AC) <sub>38</sub>
	ACAR8	129-177**	150-180	CCCAATAGAGGAAAG GGACC** (Green)	AGAATCACGCCTTC TGCTTT**	(AAAG) <sub>76</sub>
	ACAR19	210-234**	220-260	GAAAAGTAGTGGGGC ATTGC**(Yellow)	AGTTTCCCAAGAAA ACCCGT**	(AG) <sub>42</sub>
	ACAR30	236-283**	220-280	CATCTCTTCAGGCTTT TGCC**(Blue)	CTGTCTCTTCCTCC ACCTGC**	(AAAG) <sub>48</sub>
MultiPlex 2	ACAR2	99-125**	100-110	GAATGAAGCTAAGGG GCACA**(Blue)	AGCAGATGGAAGG AAAGCAA**	(AC) <sub>28</sub>
	ACAR9	148-196**	180-200	AAAGGCAATGGCAGA GAAAA**(Green)	TAATGGGAAAGGA GGCAGTG**	(AAGG) <sub>52</sub>
	ACAR10	180-198**	160-180	GGATGTGTGTGTTTGT GTTGC**(Yellow)	GGCTGTTGAGGGAT TCTTGA**	(ACAT) <sub>28</sub>
	ACAR36	230-253**	230-310	TTGCTGCTGCTGATGT CATT**(Blue)	TCCCATTA AAAAATC ATGCTGC**	(AAAG) <sub>80</sub>

Table S2; Summary of linkage disequilibrium

Season	Linkage
Spring 2010	Acar1 ↔ Acar30
Fall 2010	Acar9 ↔ Acar36
Spring 2011	Acar2 ↔ Acar10
	Acar2 ↔ Acar19
	Acar10 ↔ Acar19
	Acar2 ↔ Acar36
Fall 2012	Acar2 ↔ Acar10
Fall 2014	Acar1 ↔ Acar10
	Acar10 ↔ Acar19
	Acar10 ↔ Acar36

Table S3; Offspring captured within the home-range of a mother

W/I=caught within the mother's home-range

Mother	Offspring							Sons W/I	Daughters W/I	% Sons W/I	% Daughters W/I	TOTAL % Offspring W/I
2	17	31	247	280	224			0/1	1/3	0.00	33	25
13	196	840	10	207	79	89	18	1/4	0/2	25	0.00	17
70	241							1/1		100		100
88	39	69						1/1	0/1	100	0.00	50
107	73	303	802	164				0/1	0/3	0.00	0.00	0.00
162	62	282	30	147				0/1	1/2	0.00	50	50
251	235	291	22					1/1	1/1	100	100	100
383	548	711							0/2		0.00	0.00
427	432							0/1		0.00		0.00
708	491	498	728					0/1	1/1	0.00	100	50
								N=10	Totals	36.11	35.38	39

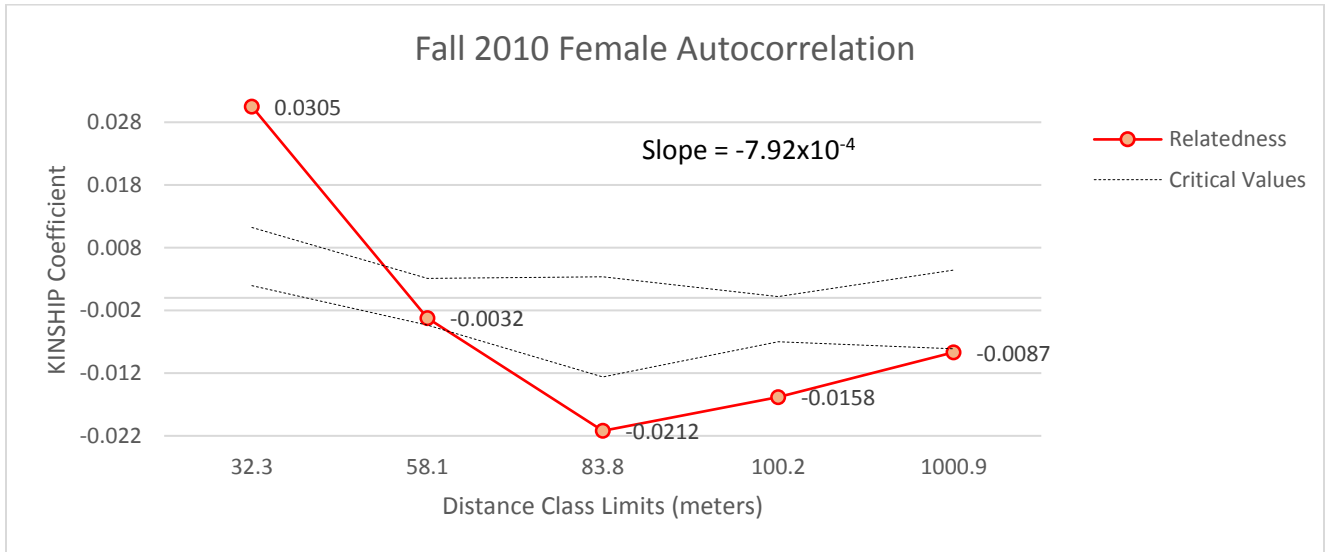
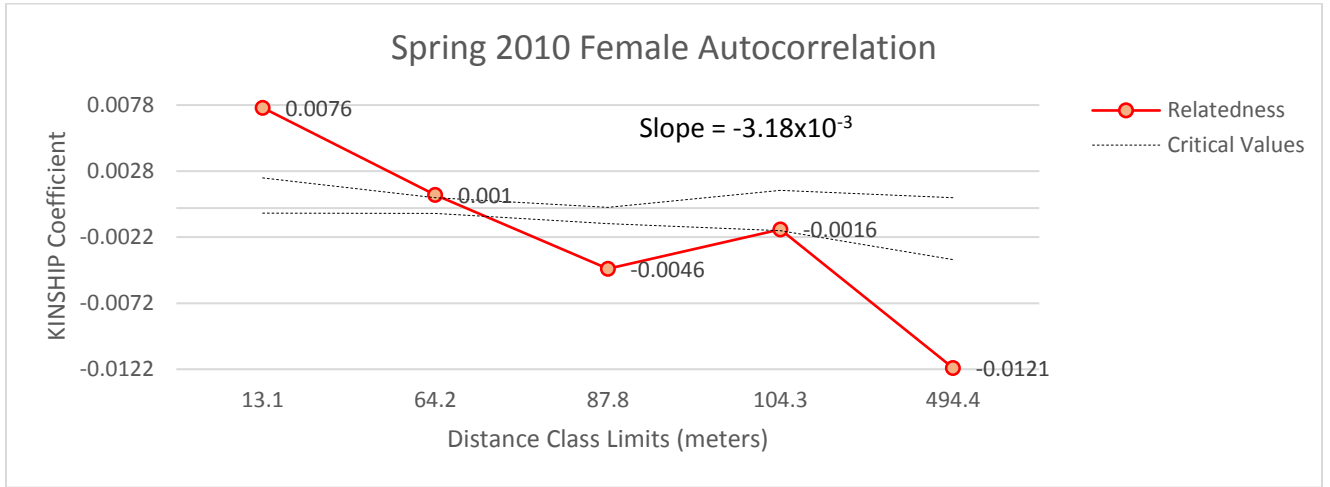
Table S4; Offspring captured within the home-range of a father

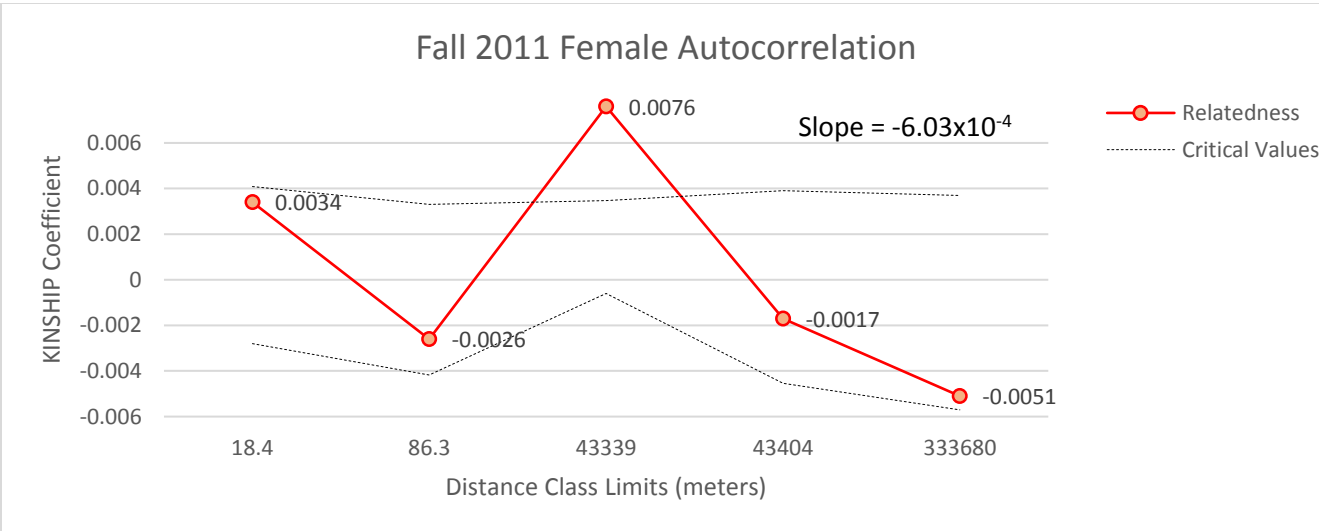
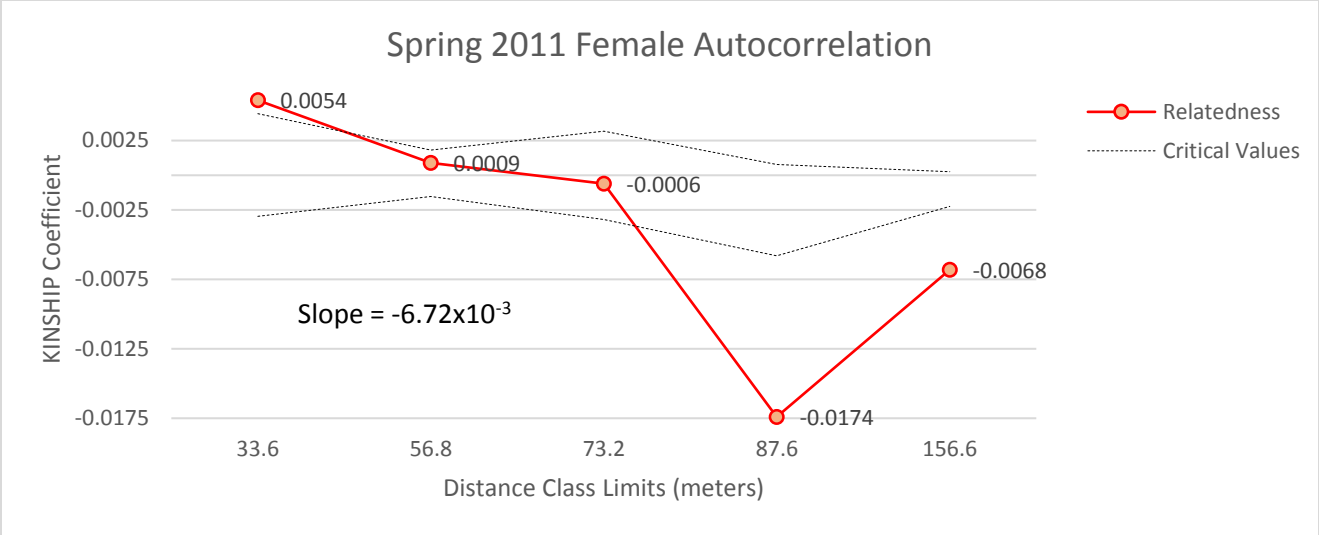
W/I=caught within the father's home-range

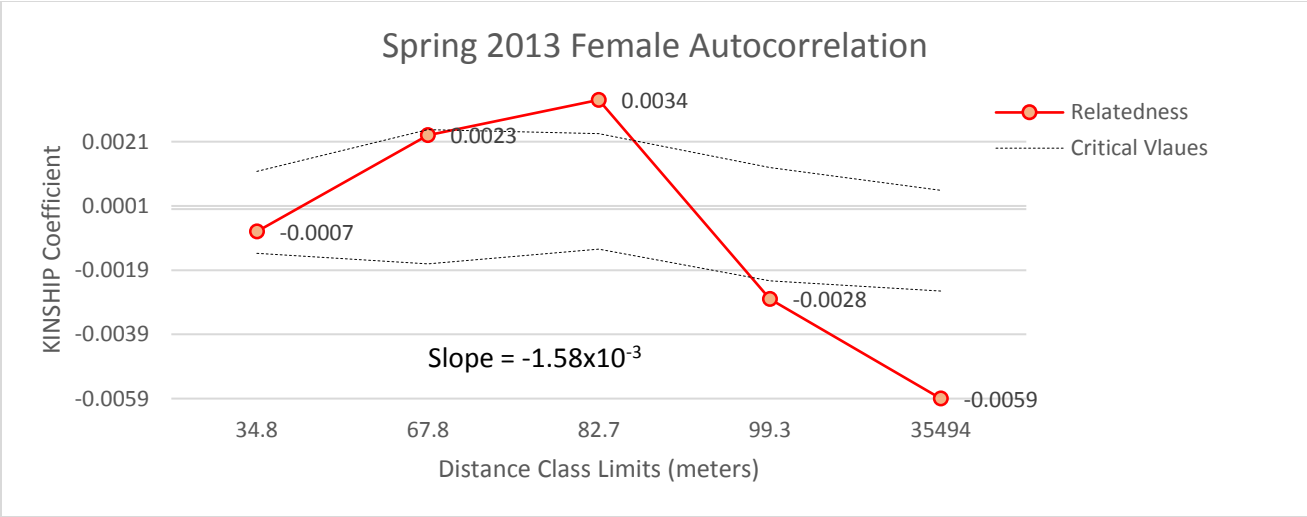
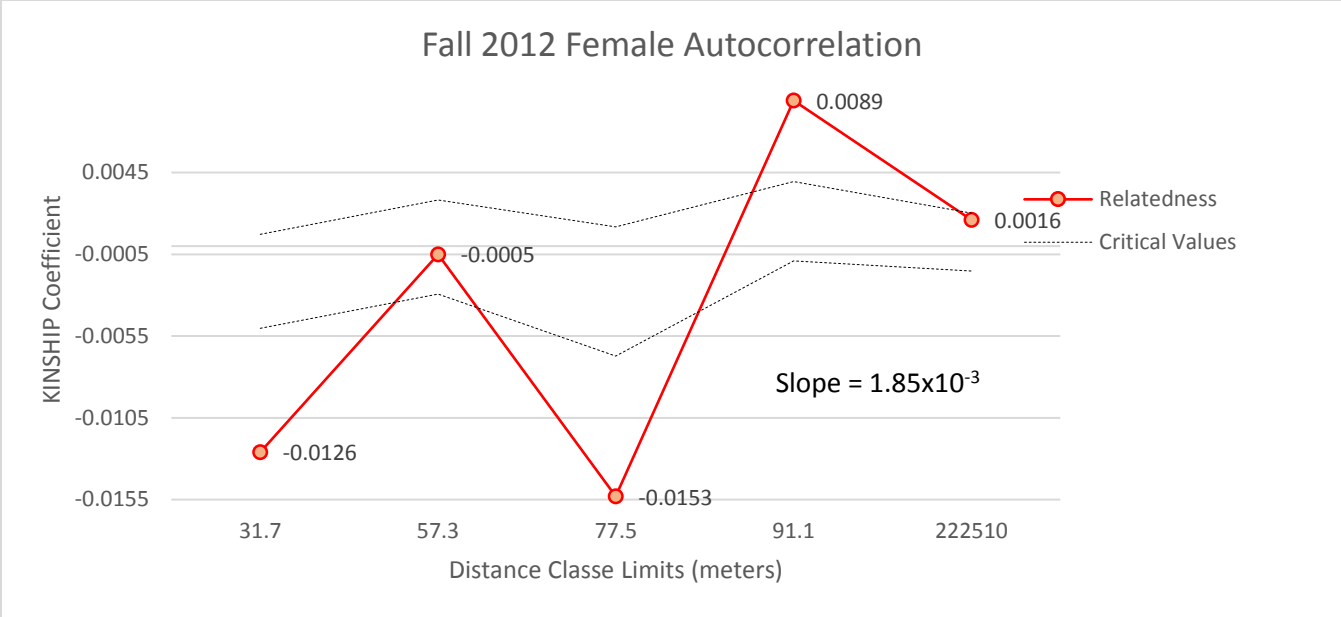
Father	Offspring					Sons W/I	Daughters W/I	% Sons W/I	% Daughters W/I	TOTAL % Offspring W/I
15	51	196	297	840		0/2	2/2	0.00	100	50
20	257	266					0/2		0.00	0.00
37	29	41	191			0/1	1/2	0.00	50	33
44	119	232	263	277	288		3/3		100	100
53	10	44	171	265	286	0/2	1/2	0.00	50	25
71	207	262				0/2		0.00		0.00
87	83	159	195	301		0/2	2/2	0.00	100	50
153	162	846					1/2		50	50
197	220					0/1		0.00		0.00
218	129	184				0/1	0/1	0.00	0.00	0.00
385	556					0/1		0.00		0.00
431	602	681				0/1	0/1	0.00	0.00	0.00
537	484	493				0/2				0.00
695	390	737				0/1	1/1	0.00	100	50
720	544					0/1		0.00		0.00
731	690	736				0/1	0/1	0.00	0.00	0.00
						N=16	Totals	0.00	50	22

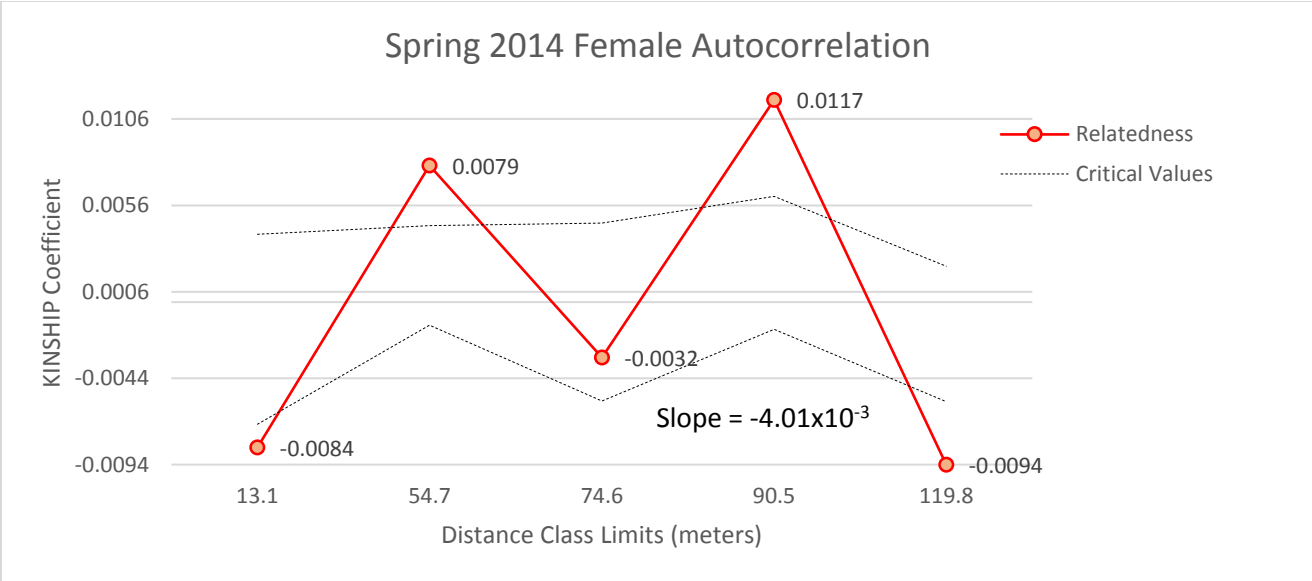
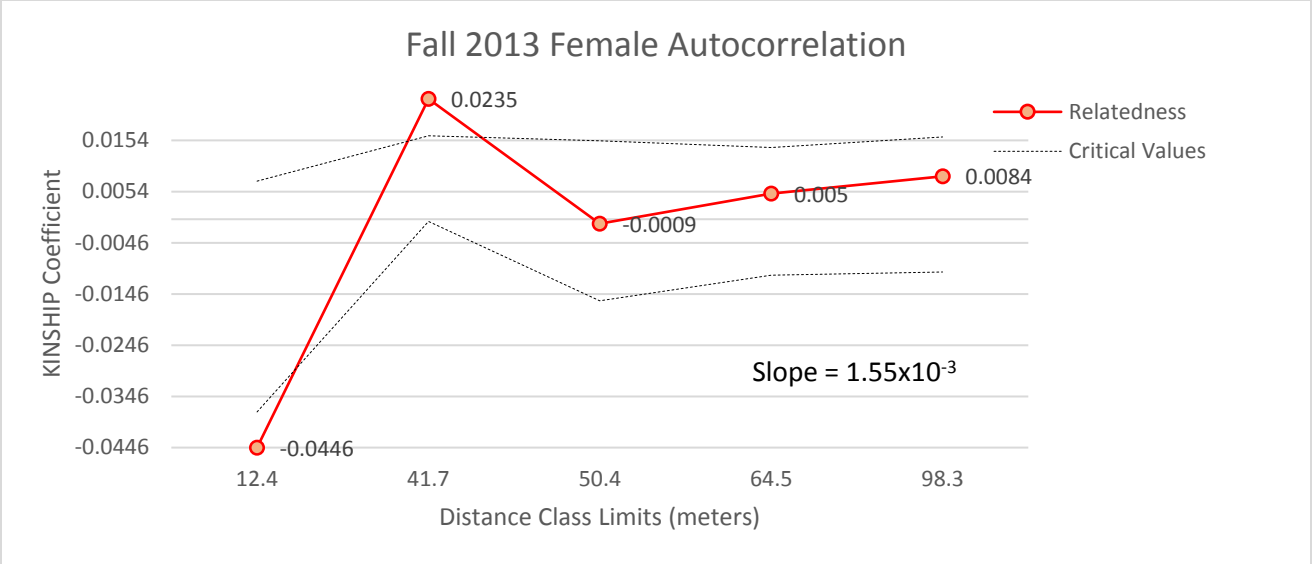


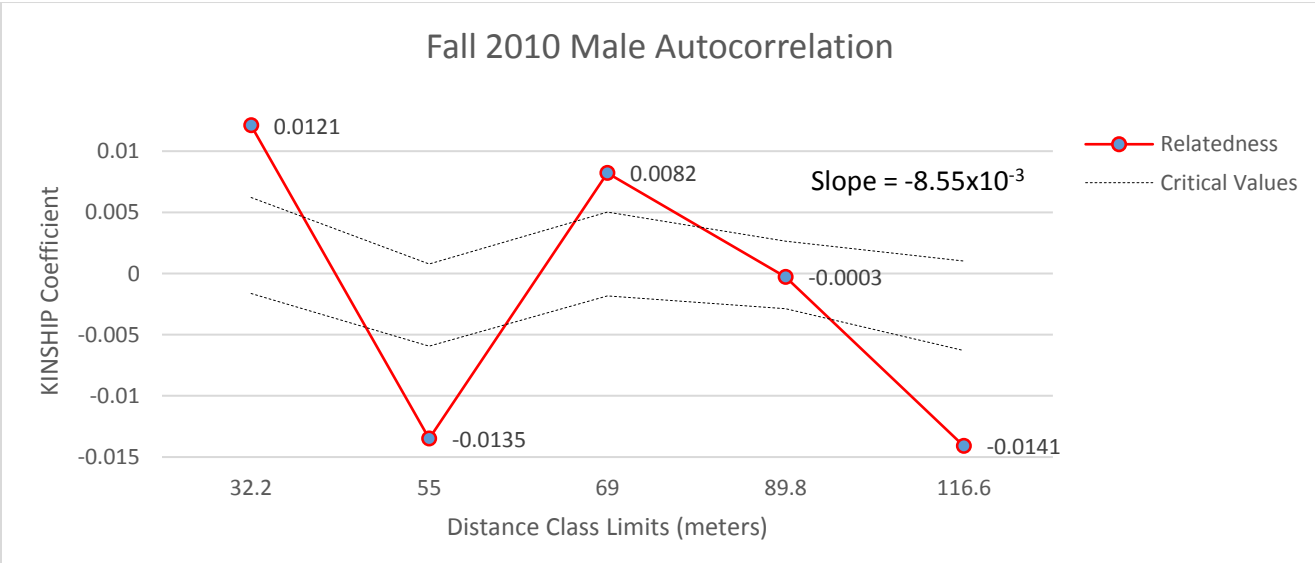
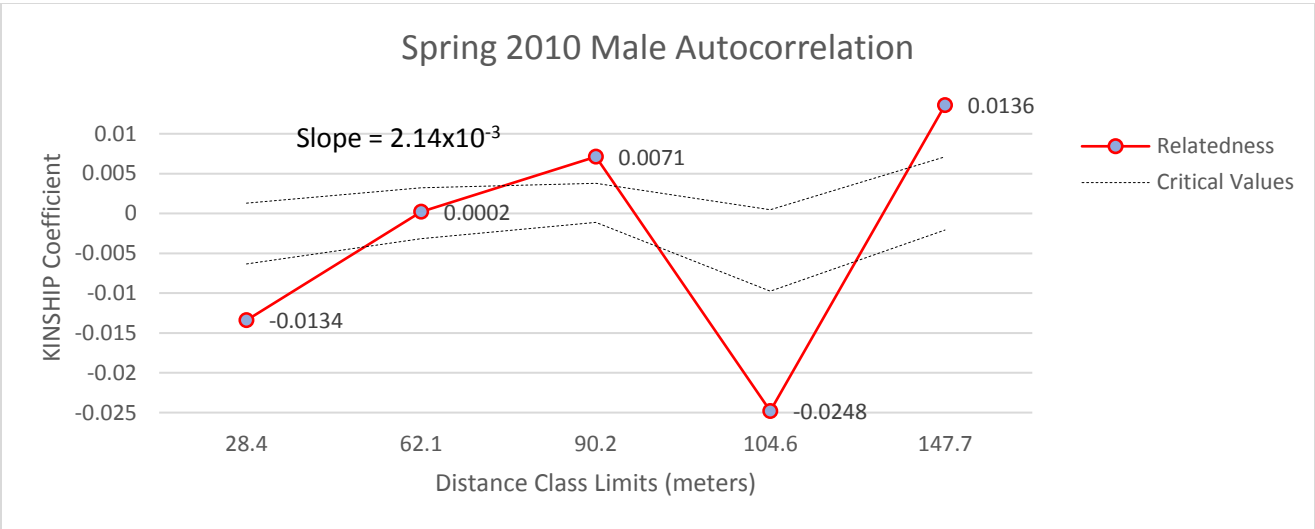
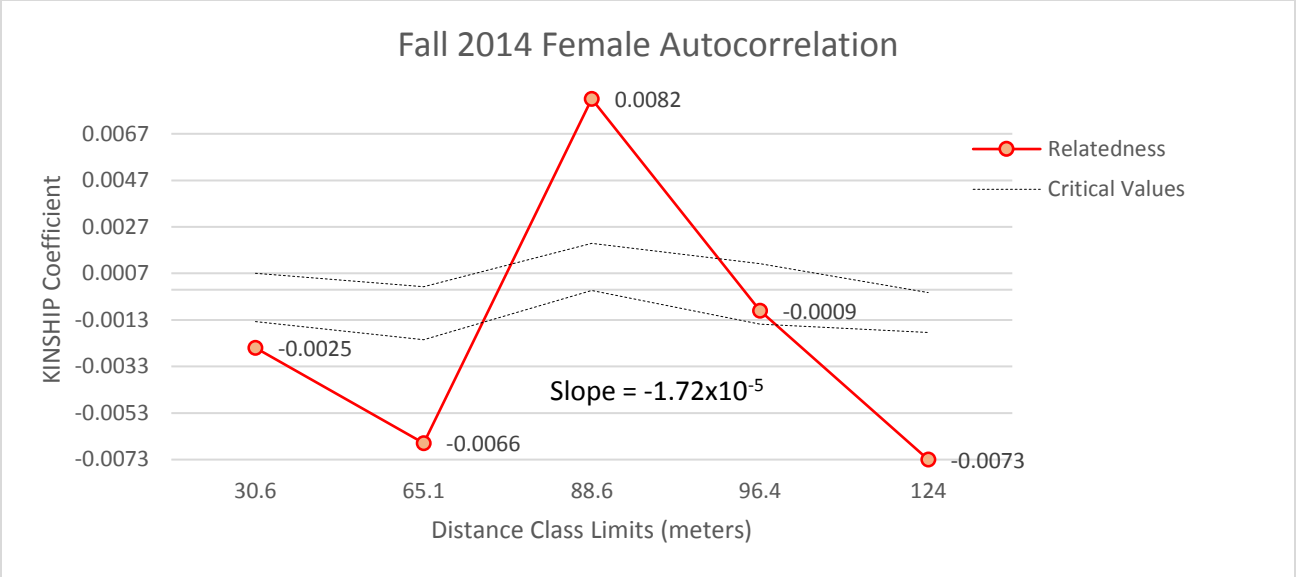
Figure S1; Autocorrelograms from Spring 2010-Fall 2014

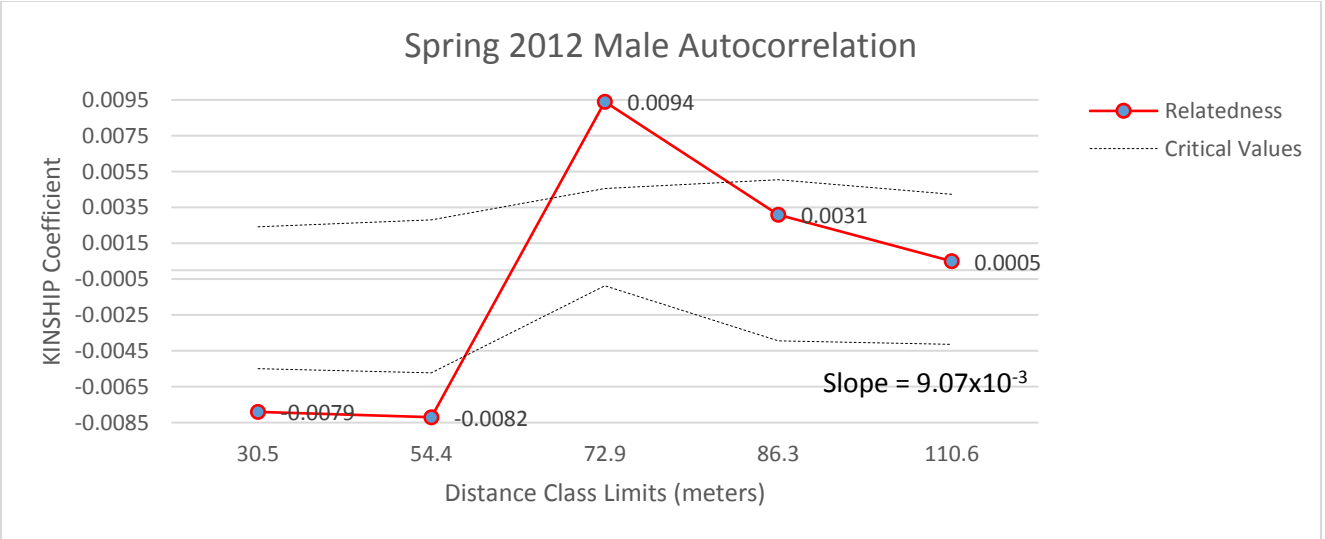
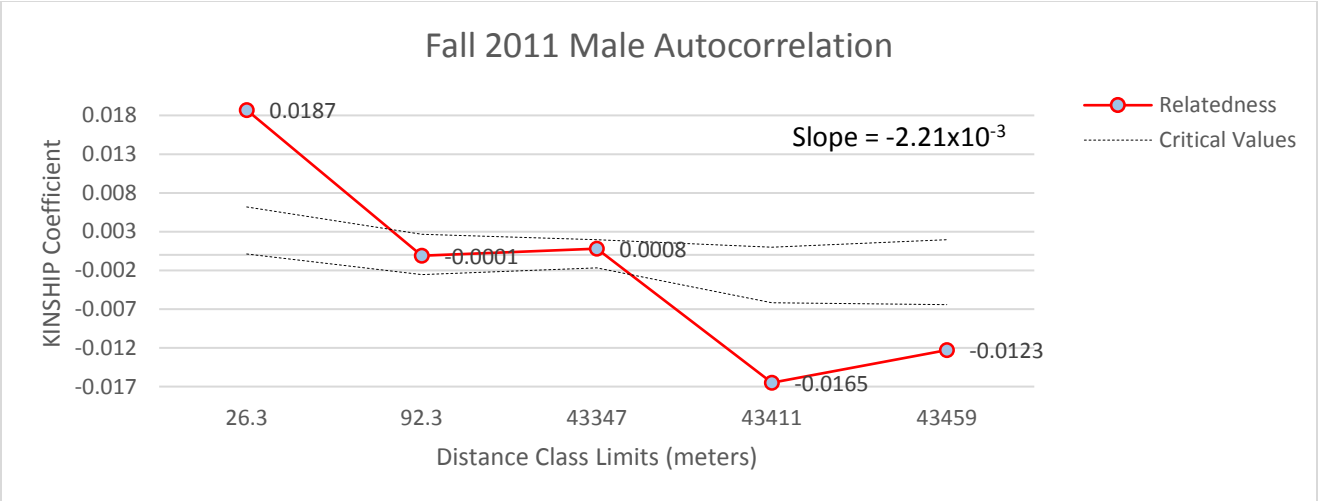
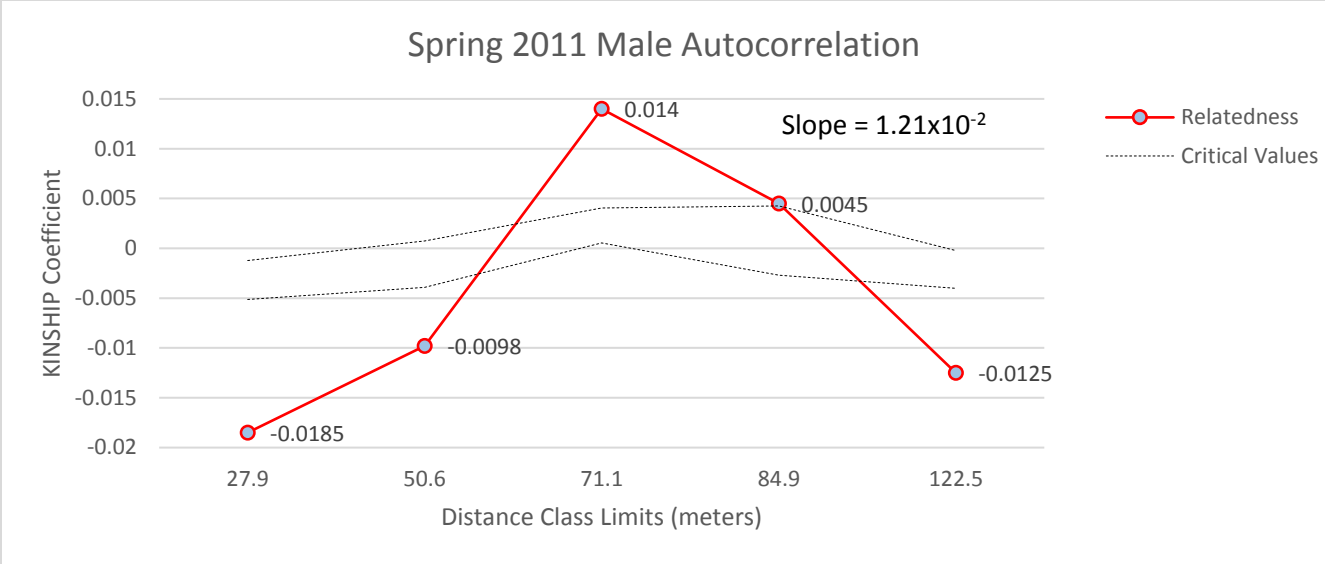


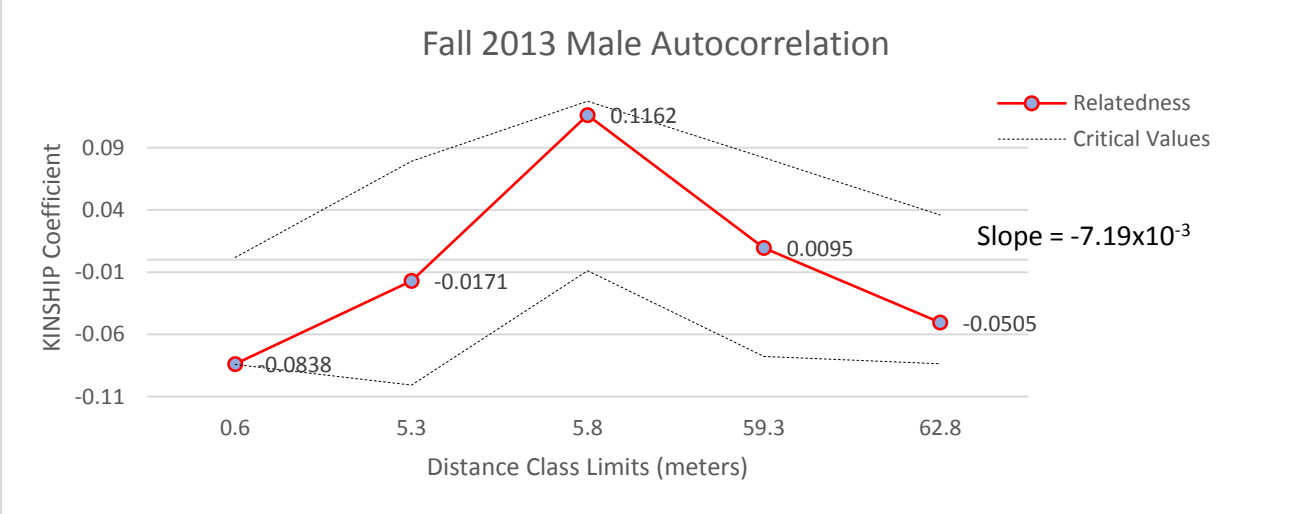
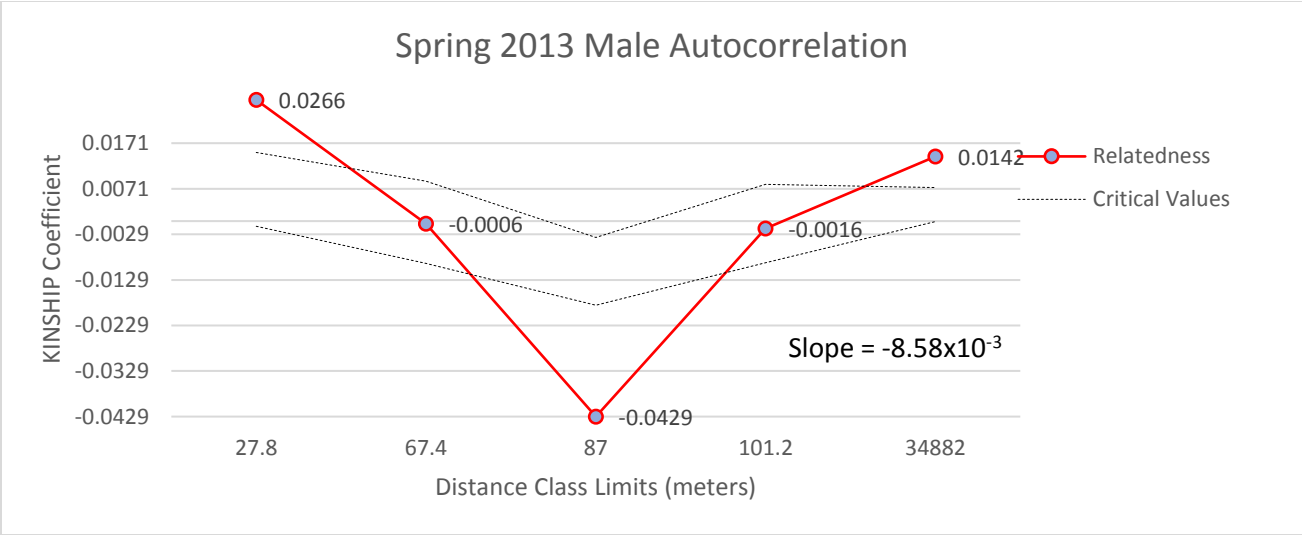
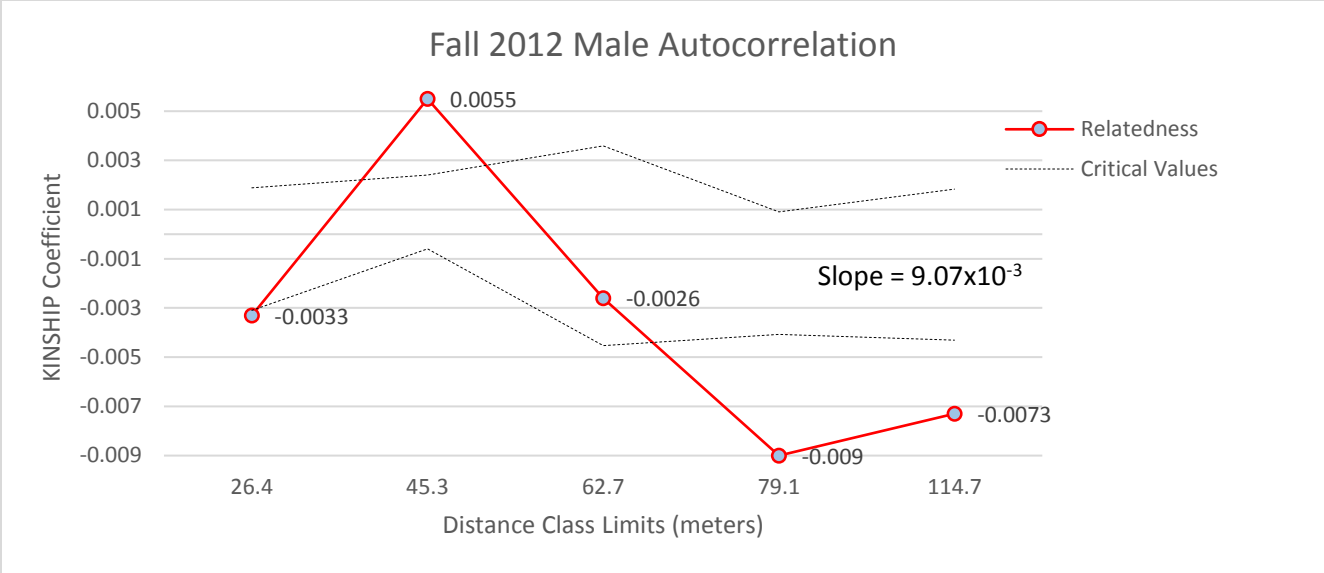


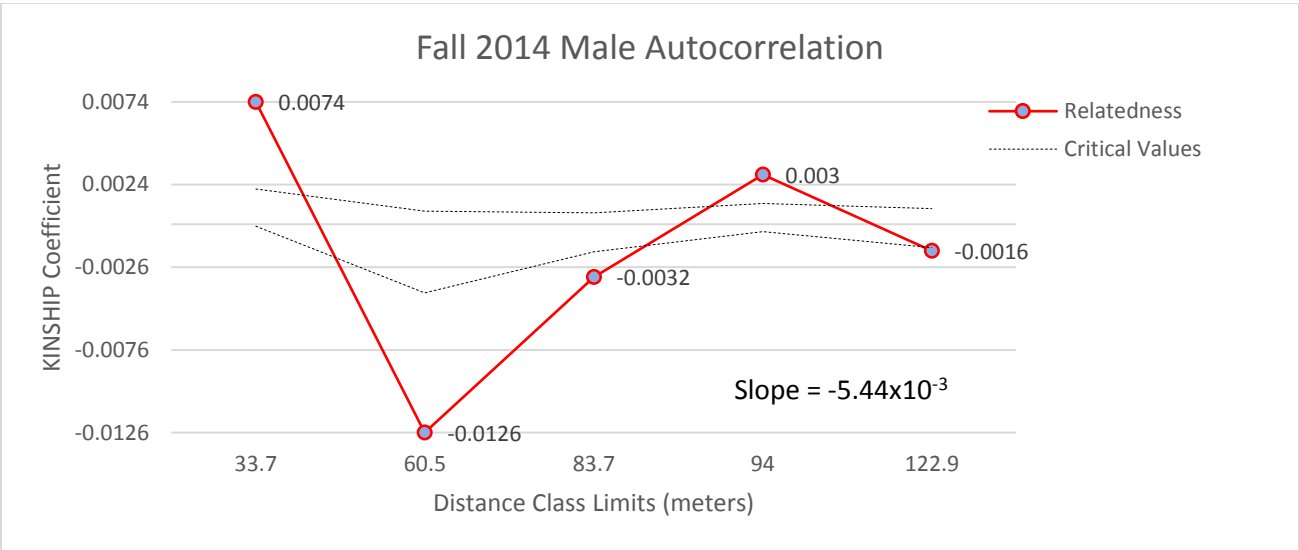
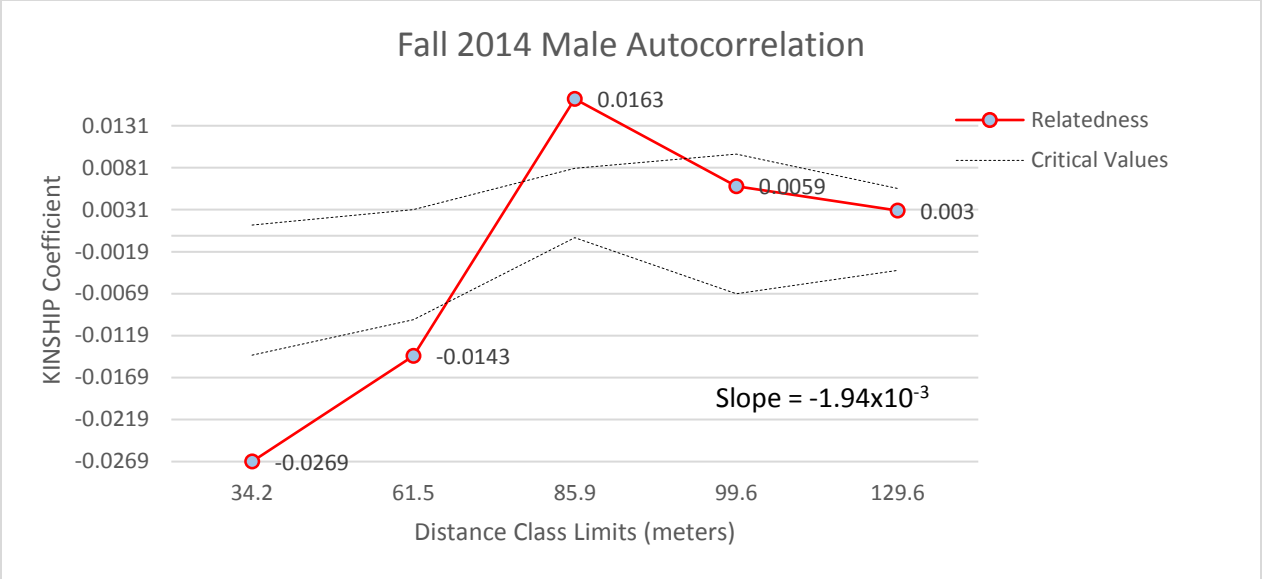














## **Vita**

The author was born in Shippensburg, Pennsylvania. In 2010 he graduated from the Baltimore City Community College with an Associate's Degree. Weber was awarded a Crescent Scholarship to complete his undergraduate work at the University of New Orleans, where he conducted research in the labs of Dr. Nicola Anthony and Dr. Jerome Howard. In 2013 he graduated with a Bachelor of Science degree concentrated in Biology. After graduation Weber was granted admission into the Graduate Program at the University of New Orleans where under the tutelage of Dr. Simon Lailvaux, and again Dr. Nicola Anthony, he worked to obtain a Master's of Science with a concentration in Biology.