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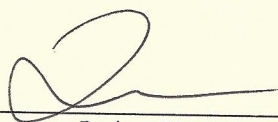
A Manipulation Study: The Effect of Predation Risk on the Space Use of the Chilean Rodent, *Octodon degus*

Erin Myers

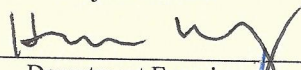
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The University of Tennessee at Chattanooga
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Project Director: Dr. Loren Hayes

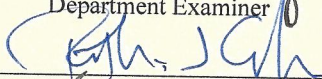
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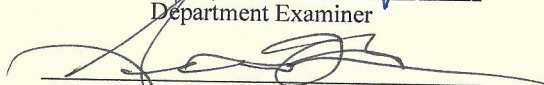
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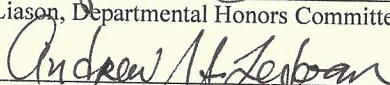
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GLOSSARY

Arboreal – refers to animals living in trees

Camera traps – trapping method that captures animals on film when researchers are not present

Dispersal – “a sequential three-step process, in which individuals leave the natal site or social group, move across unfamiliar territory, and arrive or settle into a new home range or social group” (Belichon et al, 1996)

Distance interval (DI) -- analysis indicates the distance between successive captures

Gregarious behavior – “living in groups in contrast to solitary life” (Gautier et al, 2006)

Home range – area traversed by the individual in its normal activities of food gathering, mating, and caring for young (Stickel, 1954) (Burt 1943)

Kernel -- analysis that weights the number of points (number of times an animal was caught in a specific trap) which generates a polygon with a density dependent shape.

Lek – a group of displaying males that females interact with primarily for the purpose of mating (Apollonio et al, 2014)

Live trapping – capturing a live animal in a trap

Minimum convex polygon (MCP) – analysis that represents each capture as a data point, and connects all points in order to form a polygon that represents the range of that animal

Natal philopatry – “tendency of an organism to stay in, or return to, its home area” (Lawrence & Henderson, 1989)

Obligate – symbionts that require each other in order to survive

Radio telemetry – method used wherein animal is fitted with a radio collar and readings of the animal's position are taken with a radio tower

Range area – patterns of space use within an inhabited area

Spatial Ecology – patterns and the nature of how animals utilize the space in which they inhabit (Tilman 1997)

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ABSTRACT

Predation has significant effects on animal behavior and space use across species. In small mammals, the home range areas are shown to be influenced by predation risk. This project incorporates trapping data to analyze how predation risk influences the space use of *Octodon degus*, a social rodent endemic to Chile. We compared range size of degus living in four predator exclusion enclosures versus four control, non-predator exclusion enclosures in Parque Nacional Bosque de Fray Jorge, Chile through grid trapping methods. For each enclosure (NP and P) 95% MCP, 95% Kernel, 95% Distance Interval, and average captures was measured. There were significantly more captures in NP enclosures than in P enclosures. ANOVA and nested ANOVA tests did not yield any significant difference in MCP, kernel, and distance interval between successive captures. F-tests indicated that variance in MCP and total captures—but not distance interval and kernel, was greater in P than NP enclosures. This experiment provides a better understanding of the effects of predation and contributes to over 25 years of research community ecology of social rodents.

INTRODUCTION

The distribution of living organisms has been described as neither uniform nor random, but as aggregations of patches, gradients, or other spatial patterns (Legendre & Fortin, 1989).

Spatial ecology defines patterns and the nature of how animals utilize the space they inhabit (Tilman, 1997). Animals use a given space to collect other resources, avoid predators, find shelter and mates, breed, and rear offspring (Carbone et al., 2005; Burt, 1943). Spatial ecology exhibits complexities in scale, and can be analyzed at local, regional, or global scales. For example, the tree in the genus species *Acacia* (*A. drepanolobium* and *A. seyal*) are

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the home of up to 9 species of ants, four of which are **obligate** plant dwelling ants (Young et al., 1997). Certain species have even been associated with different sized trees, suggesting a progression of ant inhabitants each with defined microhabitats (Young et al., 1997). On a larger, regional scale, studies have shown that a total of 101 species of birds exhibit long-scale migrations (at least 200 km) which are further described by 19 distinctive patterns of migration (Griffioen and Clark, 2002). Furthermore, because different populations adapt to the environment at specific scales, it is even possible to observe different responses based on the scale considered (Bellier et al., 2007). These examples emphasize the breadth of space use, but it is also important to note that spatial ecology is a dynamic element that is influenced by extrinsic factors. Energetic constraints, resource availability, and predation risk can also affect the manner in which animals use space (Hayes et al 2007; Mysterud & Ims 1998).

It is well known that predation risk can alter the way in which an animal uses space, as has been observed among species of insects (Yagi & Hasegawa, 2011; Kohler & McPeck, 1989), amphibians (Gautier et al., 2006), reptiles (Sato, et al., 2014), fish (Kelly et al., 2011), birds (Hua et al., 2013), and mammals (Boinski et al., 2005). For example, there is considerable evidence that small mammal home ranges are reduced on clear nights with full moons—when risk is the greatest—when compared to home ranges measured on dark nights (Kaufman & Kaufman, 1982). Predator-induced changes in spatial ecology can also have effects at multiple scales, including the population, community, and behavioral level. In bird populations, predators influence the abundance of individuals and therefore the degree of detection probability of the population— therefore defining the composition of the population (Hua et al., 2013). Likewise, at the behavioral level, there is theoretical (Brashare & Arcese, 2002) and empirical (Apollonio et al., 2014) evidence that predation risk influences animal social and mating systems. Specifically, **lek** formation in fallow deer populations occurs far

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from areas with higher predation risk (Apollonio et al., 2014). Finally, it is important to note the influence of ecological factors in conjunction with predation risk. For example, in various species of birds, flight distance (from an oncoming predator) has been shown to be proportional to predation risk as well as to the cost of lost foraging opportunity (Ydenberg & Dill, 1986). The significance of predation is emphasized by its effects across species, at multiple scales, and in conjunction with ecological factors which suggests the need for further research on this subject.

Specifically, predation risk seems to have a particularly strong influence on the **home range** size of small mammals (Hayes et al., 2007). Studies have indicated that overhead plant cover decreases the risk of predation while affecting the movement between shrubs in *Octodon degus* (Ebensperger & Hurtado, 2005). Long term studies also suggest that predation risk influences the dynamics of degus populations as well (Previali et al., 2009). Even the type of predator can elicit different behavioral changes in some species. *Octodon degus* have been shown to utilize different alarm calls for aerial versus terrestrial predators (Ebensperger et al., 2006).

Much of this current understanding about the effects of predation risk on animal behavior comes from observational studies of animals in a natural habitat. One limitation to observational studies is that there is no specific differentiation between confounding variables. Manipulative experiments are needed to understand the causal relationship between predation risk and behavior. Furthermore, relatively few studies have examined how animals use space, in relation to predation risk, in the natural environment. Understanding how predation risk influences animal behavior in the wild is necessary for generating new theory to better describe the link between animal behavior and predation risk.

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In order to gain a better understanding of animal behavior, it is necessary to first determine space use patterns. This study compiled three years of trapping data on the social, diurnal rodent *Octodon degus* in predator exclusion and non-predator exclusion plots. Degus are a social small mammals endemic to central Chile. Degus are diurnal, and they forage above ground in groups during the day and at night they reside in burrow systems with different social groups. These burrow systems incorporate an elaborate system of entries, tunnels, and chambers that generally exist under terrestrial shrubs or rocks.

There are a number of ways that researchers use to define and quantify space use, but typical measurements of space use are based on **live-trapping**, **radio telemetry**, and direct observation (Griffioen & Clark, 2002; Swihart & Slade, 1985). Most frequently, researchers estimate an individual's use of space by measuring its home range i.e., the area which an animal carries out "normal activities" including foraging, finding mates, caring for young (Burt, 1943). There has been some debate about whether trapping data is an effective measure of home range, and therefore measures of **range area** in this study is meant to describe a pattern of space use within an inhabited area (Kelt et al., 2014). Trapping is not a direct indication of home range, as telemetry methods would provide, because these coordinates are not definitive of the activities of an animal at a multitude of instances. This is because trapping coordinates are indicative of only a sequestered point, whereas telemetry allows for free movement of the animal and hourly readings can be made to determine changes in location. To strengthen this measure, distance interval between successive captures based on live-trapping was also can also be used to analyze linear movements.

Conceptual Framework

Predation has been shown to affect the manner in which animals use space, specifically within small mammals this can be observed through changes in home range and the number

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of captures (Previtali et al., 2009; Hayes et al., 2007). Additionally, it is important to note that additional factors like distribution of food and other resources have also been shown to alter space use (Previtali et al., 2010; Previtali et al., 2009). These changes are important given that variations in spatial ecology can alter social structure by affecting the distribution of mates, and in turn the mating systems can be altered via changes in mate selection (Apollonio et al., 2014; Brashare & Arcese, 2002). This conceptual framework is depicted in **Figure 1** with the focus of this study, the effect of predation on space use, bordered in red.

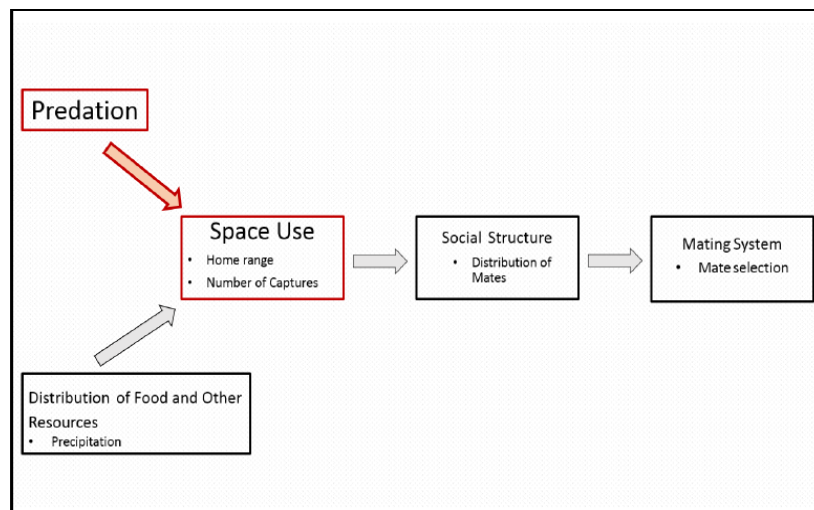


Figure 1: Conceptual Framework. The connection between predation and space use is emphasized. Additional considerations, including the distribution of food and other resources, can affect space use. This is significant due to the impact that changes in space use can have on social structure and matings systems.

Objectives

The objective of this study was to analyze the difference in space use of degus exposed to increased predation risk. For this experiment, two different measures of range areas (MCP95 and Kernel95), the distance interval between traps (MBCSC), and the total number of captures were evaluated in order to compare degu space use in predator exclusion and control enclosures ($n = 4$). Due to the connection between predation risk and reduced home ranges in small mammal populations, we predicted that animals in the predator exclusion plots would

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have smaller range areas and distance interval between successive captures, and more total captures than in the non-predator exclusion plots (Hayes et al., 2007; Kaufman & Kaufman, 1982).

MATERIALS AND METHODS

Study Site

This study was conducted at the Parque Nacional Bosque de Fray Jorge, in central Chile (30°38'S, 71°40'W), located in the IV (Coquimbo) Region, 350 km north of Santiago, Chile. This region experiences a semiarid Mediterranean climate, wherein 90% of the mean annual precipitation occurs throughout the austral winter (May-October) (Meserve et al., 1996). Frequent El Niño Southern Oscillations and La Niña Southern Oscillations impact temperature and rainfall fluctuations in this region (Meserve et al., 1996). Within the research area of the park, trapping data on *Octodon degus* within study grids were collected, as degus are the dominant small mammal in this area (Meserve et al., 1993).

Grid Trapping



Figure 1: Predator exclusion trapping grids in Parque Nacional Bosques Fray Jorge. Grids are composed of 1.8 m high fencing, a 1 m high overhang, and polyethylene netting directly above.

The study area of the park contained 75 m x 75 m (0.56 ha) grids, and this study utilized a subset of these grids that were designated as predator exclusion (n = 4) and non-predator exclusion (n = 4). The placement of the grids was randomly chosen. The predator exclusion grids have 1.8 m high fencing, a 1 m high overhang, and polyethylene netting directly

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above as shown in **Figure 1**. This design inhibits large predators from entering, while degus and other small mammals were able to freely move in and out of the enclosures through small holes in the fencing and underground tunnels. The control, non-predator exclusion plots are surrounded by low 1.0 m high fencing only. This allows small mammals and predators to enter and exit the enclosures.

Within the grids two Sherman traps with dimensions 2 x 2.5 x 9 inches were set at stations in a 5 x 5 grid at 15 m intervals between stations. Traps are placed within PVC pipe sections in order to protect animals from adverse environmental conditions. Monthly small mammals trapping has been performed continuously at this site since March 1989. Live-trap small mammal census is done in all the grids for 4 days per month, 12 months a year. Traps are baited at the time of initial set up, and then checked in the morning (approx. 0900 hrs) and again in the evening (approx. 1600 hrs) for 4 consecutive days. Any small mammal captures are marked with ear tags or leg bands and the species, sex, mass, reproductive state, and the tag number is recorded (Meserve et al., 1996).

For the analysis in this project, trapping data of adult female degus from August- November 2013, 2011, and 2010 was used. The 2012 data were omitted due to a low number of captures. Female degus were selected because they exhibit stronger **natal philopatry** and group fidelity (Ebensberger et al., 2009). Males are more likely to disperse from their natal burrow system, which could yield unreliable home range area data (Ebensberger et al., 2009). These months were selected because this fit in the reproductive window for females. Females that were pregnant or lactating were included in this study in order to analyze only those least effected by **dispersal** (Quirici et al., 2011).

The term NP represents enclosures where there were no predators (predator exclusion), whereas P represents enclosures where predators were present (non-predator

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exclusion). MCP, kernel, distance interval, and total capture means were averaged across years due to low numbers of total captures per enclosures. Nested ANOVA analysis were performed for each measure in order to determine statistical significance. F tests for equality of variances were also performed for each measure, in order to define variability.

Measurement of Range Areas

Only animals with six or more captures were used in order to provide sufficient amounts of data for range area analysis. Three measurements of range areas were included: 95% minimum convex polygon, 95% kernel, and distance interval. **Minimum convex polygon (MCP)** analysis represents each capture as a data point, and connects all points in order to form a polygon that represents the range of that animal. **Kernel** analysis was used in addition to MCP because this method weights the number of points (number of times an animal was caught in a specific trap) which generates a polygon with a density dependent shape.

Distance interval (DI) analysis indicates the distance between successive captures. This measure was included in order to represent animals that were caught in a linear progression of traps (linear captures that could not generate polygons).

Statistical Analysis

To account for variability within enclosures, and to increase statistical power, we conducted a nested ANOVA with treatment (NP and P) as fixed factors of F. Enclosures were nested within treatment and collapsed across years due to insufficient numbers of captures in some enclosures as seen in **Table 1**. All statistical analyses were performed using SAS Systems Software. For all analyses we set α at $P = 0.05$

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Table 1: Total number of captures across years. Due to low number of captures, trapping data was nested across years to increase power. Predator exclusion plots are represented by NP (no predators) and non-predator exclusion plots are represented by P (predators).

Enclosure Number	Enclosure Type	Number of Captures
1	NP	21
2	NP	26
10	NP	20
14	NP	17
3	P	8
6	P	3
11	P	8
15	P	3

RESULTS

Captures

The mean (\pm SE) number of degus captured was 19.5 ± 9.94 individuals within P enclosures and 71.5 ± 18.6 individuals within NP enclosures. There were significantly more captures in NP enclosures than P enclosures (nested ANOVA $F_{1,16} = 23.8$, $P = 0.0002$). There was not a statistically significant effect of enclosure ($F_{6,16} = 0.45$, $P = 0.83$). An F test of equality of variances indicated variability in captures can be considered was greater in P than NP, given that P is only marginally significant. ($F_3 = 0.34$, $P = 0.044$).

MCP

The mean (\pm SE) MCP range area was $0.025 \text{ ha} \pm 0.011 \text{ ha}$ in P and $0.046 \text{ ha} \pm 0.018 \text{ ha}$ in NP enclosures as shown in **Figure 1**. There was not a statistically significant difference between P and NP enclosures (nested ANOVA $F_{1,95} = 1.92$, $P = 0.17$) nor an effect of enclosure (nested ANOVA $F_{6,95} = 1.32$, $P = 0.25$). An F test of equality of variances indicated that the variability in MCP was greater in P than NP ($F_3 = 0.41$, $P = 0.02$).

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KERNEL

The mean (\pm SE) kernel range area was 0.074 ha \pm 0.029 ha in P and 0.088 ha \pm 0.032 ha in NP enclosures as shown in **Figure 1**. There was not a statistically significant difference between P and NP enclosures (nested ANOVA $F_{1,93} = 0.17$, $P = 0.69$) nor an effect of enclosure (nested ANOVA $F_{6,93} = 1.07$, $P = 0.39$). An F test of equality of variances indicated that there were no statistically difference in variability of distance interval in successive captures in P and NP ($F_3 = 0.83$, $P = 0.35$).

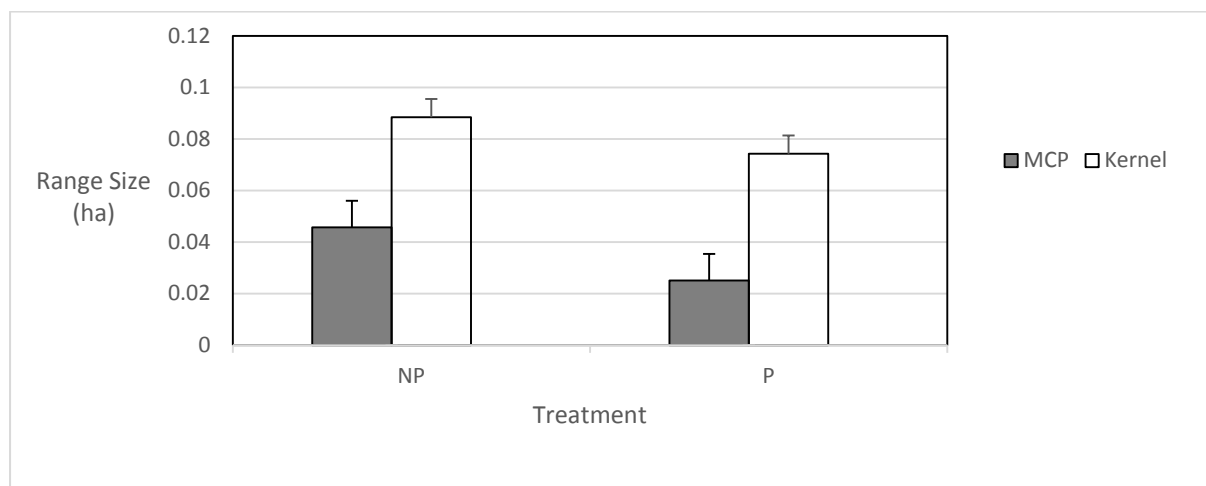


Figure 1: Comparison of MCP and Kernel analysis between NP and P enclosures.

Distance Interval

The mean (\pm SE) distance interval between successive captures was 6.71 ha \pm 2.49 ha in P and 8.79 \pm 2.63 in NP enclosures. There was not a statistically significant difference in distance interval in P and NP enclosures (nested ANOVA $F_{1,101} = 1.33$, $P = 0.25$) nor an effect of enclosure (nested ANOVA $F_{6,101} = 0.89$, $P = 0.50$) when analyzing the distance interval between traps. An F test of equality of variances indicated that there were no statistically

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difference in variability of distance interval between successive captures between P and NP ($F_3 = 0.90, P = 0.4$).

DISCUSSION

Summary of Results

There were significantly more captures in NP enclosures than in P enclosures. ANOVA and nested ANOVA tests showed there were no significant differences in MCP, kernel, and distance interval between successive captures between P and NP enclosures. F-tests indicated that variance in MCP and total captures, but not distance interval and kernel, was greater in P than NP enclosures.

Although these results do not support my hypothesis that degus in predator exclusion enclosures would have larger range areas than degus in non-predator exclusion enclosures, there is still evidence that degu spatial ecology differs between enclosures. A significant difference in captures between enclosures suggests that animals are using space differently between enclosures differently affected by predation risk. There was a measurably greater capture success in NP than P, which indicates that degus are able to move more freely in NP than P enclosures. Another explanation for these results is that animals avoid those areas under high predation risk, given the alternative of a predator free environment. The effect of predation risk therefore minimizes movement as evidence by our live-trapping protocol. Furthermore, there was significantly more variability between captures in P enclosures and NP enclosures. It is possible the total number of captures could have varied due to differences in degu abundance, given that more degus were captured in NP than P enclosures. This would indicate that not only predation risk is affecting the number of animals in the

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enclosures, but also that increased density could result in smaller home range areas. In particular, other studies have found that in some small mammal density correlates negatively with home range size (Abramsky & Tracy, 1980).

Interestingly, there was greater variance in MCP ranges but not kernel ranges and distance interval between successive captures in NP and P enclosures. Variation in MCP between P and NP enclosures indicates differences in space use, although this could be due to the nature of this measure. In other species, predation risk has been shown to have effects on space use in kangaroo rats, desert rodents, and an effect on the activity of gerbils (Hayes et al., 2007; Ambramsky, 1995; Kaufman & Kaufman, 1982). Additional research has suggested that foraging movement is influenced by predation risk, as well as by additional intrinsic and extrinsic factors (Oksanen & Lundberg, 1995).

Recent trends in ecology focus on individual behavioral differences between animals, and therefore it is important to consider intrinsic differences that could affect space use in degus (Wilson et al., 1994; Sih et al., 2004). Specifically, features that we were unable to analyze, like body mass, age, sociality, and personality should be considered as factors that influence space use and need to be considered in future studies. Research suggests that the relationship in body size and home range is nonlinear in degus, and that home range is smallest for animals weighing approximately 100 grams (Kelt & Van Vuren, 1999). Age is another important variable to consider. Specifically, sub-adults or lactating might have larger energetic needs for growth and therefore forage more extensively (Lindstedt et al., 1986). Furthermore, while lactating females are the least affected by dispersal, sub-adults or lactating females experiencing increased competition are shown to disperse and could possibly live transiently until they are recognized socially (Quirici et al., 2011; Lindstedt, et al., 1986). We must also consider that dispersal has associated costs like increasing risk when

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moving through an unfamiliar environment in search of social groups (Ebensperger, et al., 2011; Quirici et al., 2011). Consequently, social interactions are important to note, because group living has been shown to be beneficial to degus in predator detection, suggesting a relationship between sociality and predation risk (Ebensperger & Wallem, 2002). Also, research in other mammals has shown reduced sociability during pre-partum, lactation, and post-partum periods, and this occurrence could have affected this study because only pregnant or lactating females were included (Betrand et al., 1996). Finally, personality of animals should be considered because individual differences are causes of variation in resting metabolic rate, stress, response, and activity levels, all of which in turn can affect space use (Careau et al., 2008). Considering this and other individual features is vital for future studies to gain a better understanding of special ecology.

It is also possible that other extrinsic factors, such as group size, rainfall, overhead cover, and food availability, had an influence on space use as well. In degus, large group size had been correlated with decreased vigilance (Vasquez, 2007). Considering that an individual animal does not have control over the size of its group, nor the death or dispersal of group members, random placement in a smaller group could require that an animal maintain higher vigilance and is therefore not able to forage as extensively. Additionally, rainfall has shown to have additive effects depending on strength and duration on population densities of degus during consecutive wet years, which could also lead to variation in crowding and abundance (Previali et al., 2009; Meserve et al., 1984). It is important to also consider that this effect could apply for low rainfall conditions as well (Meserve et al., 1984). African antelope (*Ourebia ourebi*) forage abundance and quality are responsible for variation in female dispersion, which results in larger groups with smaller home ranges during dry season forage (Barshares & Arcese, 2002). Additional evidence suggests that lack of

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overhead cover combined thermoregulation cause degus to be limited by physiological constraints—which are thought to have a larger role than predation risk in microhabitat selection (Yunger et al., 2002). Likewise, studies also show that degus in habitats with significant overhead cover travel into areas of higher food density (Jaskic, 1986). Food availability alone can also have a significant effect on space use. Research on other small mammals has show that females will change their home ranges based off seasonal variation in food availability (Schradin & Pillay, 2006). Collectively, prior research and this study suggest that predation risk interacts with numerous variables in order to affect range areas of small mammals.

Emerging research has shown that in other small mammals, home range is smaller when food quantity is high (Schradin, et al., 2010). Therefore, an alternative explanation of my observation that MCP, kernel, and distance interval measurements were not significantly larger in NP than P enclosures is that the opposite trend is true for home range area and predation risk—meaning that degus in predator exclusion plots could have a smaller home range area than degus in non-predator exclusion plots. In degus, ecological factors have been connected with space use, and therefore it is possible that this is a covariate that functions in concert with predation risk (Hayes et al, 2007; Meserve et al, 1996; Meserve et al 1993). Given this data, it is possible that other methodologies, such as radio telemetry, could indicate that degus in predator exclusion plots have smaller home ranges because they are able to forage more efficiently within small food-rich areas (Morris, 1987; Rosenzweig, 1987).

Challenges and Limitations

There are inherent problems with home range analyses based on data collected during live-trapping. First, because of the stationary nature of trap placement, the results that trapping

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data yield are not necessarily indicative of the true movement of the animal. Even when analyzing successive captures, the data is biased to trap location and distance between traps. This could also create an issue of trap determined range area, wherein animal movement is altered to specifically avoid traps (Trevor-Deutsch and Hackett, 1980). Furthermore, although the exact mechanism is not fully understood, there is also an inherent effect on animal behavior due to trapping. Trapping sequesters the animal within the trap and therefore inadvertently has an effect on the natural space use because that animal is no longer moving freely during the time in which it is in the trap. Concerns such as trap detection, and altered animal behavior due to the presence of researchers have also been reported (Bergstrom, 1988) (Trevor-Deutsch and Hackett, 1980).

The effect of these trapping constraints was noted in our experiment as well. Because degus were able to move freely in and out of either enclosure (P or NP), it is possible that some animals could have range areas that extended out past the borders of the trapping grid. In this case, their range areas might not have been properly quantified by trapping methods. Therefore, it is possible that we may have underestimated the actual area of space use, and this could have influenced any differences in range areas between NP vs P enclosures. It is also important to consider that the data that was collected from grids could be biased towards animals with range areas that were centrally located within the trapping grid because it was possible to obtain more captures of these animals. In order to account for these challenges associated with live trapping, we utilized three different measures of space use in our analysis to account for these concerns. Therefore, despite these limitations our estimates provide a reasonably useful measure of space use within enclosures.

Furthermore, given these limitations there is still some validity to using live trapping as an index of space, as it serves many functions and is a cost effective equipment choice.

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Live trapping procedures can distinguish important differences between **arboreal** and terrestrial space use of various species (Abreu & Oliveira, 2014). Furthermore, as live trapping provides additional data on abundance, it can also be considered an effective way to relate abundance to home range size (Komonen et al., 2013). Another important aspect to consider when comparing methodologies is cost. In regards to equipment cost, live trapping would be favored over camera traps or radio telemetry.

Future Research

Camera traps and/or radio telemetry could be utilized in future experiments in order to record a more accurate depiction of space use. First, camera traps enable coverage of more surface area, and are able to record without leaving out any areas that might be encompassed in a home range (Noss et al., 2003). This would be an improvement over live trapping techniques, although there is still an added concern that capture probabilities decrease from the center of the trapping grid (Noss et al., 2003). Given this information, radio telemetry should also be used, alone or in conjunction, as this method provides the most complete information regarding ranging patterns (Noss et al., 2003).

It is also important to mention that other variables could have influenced patterns in degu spatial ecology. Most likely, there are most likely differences in the vegetation within different trapping grids, as well as differences in topography. Previous research has shown that increased rainfall leads to increased amounts of vegetation, which in turn results in increased degu density and can induce behavioral changes (Previtali et al., 2010). Future studies should analyze the relationship between vegetation and home ranges, as well as variation in vegetation. My study site is located within a region that is affected by El Nino and La Nina Southern Oscillation events. Thus, the region experiences large fluctuations in rainfall, leading to considerable inter-annual variation in vegetation (Previtali et al., 2010).

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Furthermore, it must be considered that the topography of all the trapping grids is likely not identical. Differences in landscape could lead to increased energetic constraints associated with movement, and therefore the extent of space use could be limited by this factor as well (Smith, et al., 1994; McCain, 2003). In other mammals, topography has been shown to influence home range as well as access to resources (Powell and Mitchell, 2006). These variables should be taken into account future studies of degu spatial ecology, as should different methodology to quantify space use.

Finally, it should be considered that predation risk may vary across species. Future studies should analyze the type of predators, as well as predation intensity, in order to see how these variables affect predation risk. For example, degus have evolved various strategies of predator detection such as group foraging, collective vigilance, and alarm calls that even vary between aerial and terrestrial (Ebensperger et al., 2006). Other small mammals have been shown to practice moonlight avoidance accompanied with altered microhabitat usage, including movement in more densely covered patches and varied selection of seed removal (Jacob & Brown, 2003 ; Bower and Dooley, 1992 ; Daly et al., 1992). Additionally, while predation intensity is known to effect the abundance of prey populations, there is a lack of information on the effect in small mammal space use (Navarret & Casilla, 2003 ; Lagos et al., 1995). Moreover, research has shown that even similar patterns of predation intensity can yield different consequences for different prey populations (Navarrete & Castilla, 2003). Study of these effects of these factors on predation risk will not only give insight into space use and animal behavior, but it is also necessary to better understand community dynamics.

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APPENDICES

Appendix 1: ANOVA Output of Captures

1) The SAS System	
The Mixed Procedure	
Model Information	
Data Set	WORK.DEGU_CAP
Dependent Variable	CAP
Covariance Structure	Diagonal
Estimation Method	REML
Residual Variance Method	Profile
Fixed Effects SE Method	Model-Based
Degrees of Freedom Method	Residual
Class Level Information	
Class Levels Values	
YR	3 2010 2011 2013
TRT	2 NP P

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Class Level Information

Class Levels Values

ENC 8 1 10 11 14 15 2 3 6

Dimensions

Covariance Parameters 1
Columns in X 11
Columns in Z 0
Subjects 1
Max Obs Per Subject 24

Number of Observations

Number of Observations Read 24
Number of Observations Used 24
Number of Observations Not Used 0

Covariance Parameter Estimates

Cov Parm	Estimate
Residual	862.42

Fit Statistics

-2 Res Log Likelihood 162.4
AIC (smaller is better) 164.4
AICC (smaller is better) 164.6
BIC (smaller is better) 165.1

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
TRT	1	16	23.81	0.0002
ENC(TRT)	6	16	0.45	0.8339

The SAS System

The PLM Procedure

Store Information

Item Store WORK.DEGU_CAP
Data Set Created From WORK.DEGU_CAP

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Store Information

Created By PROC MIXED
Date Created 08MAR15:13:21:14
Response Variable CAP
Distribution Normal
Class Variables YR TRT ENC
Model Effects Intercept TRT ENC(TRT)

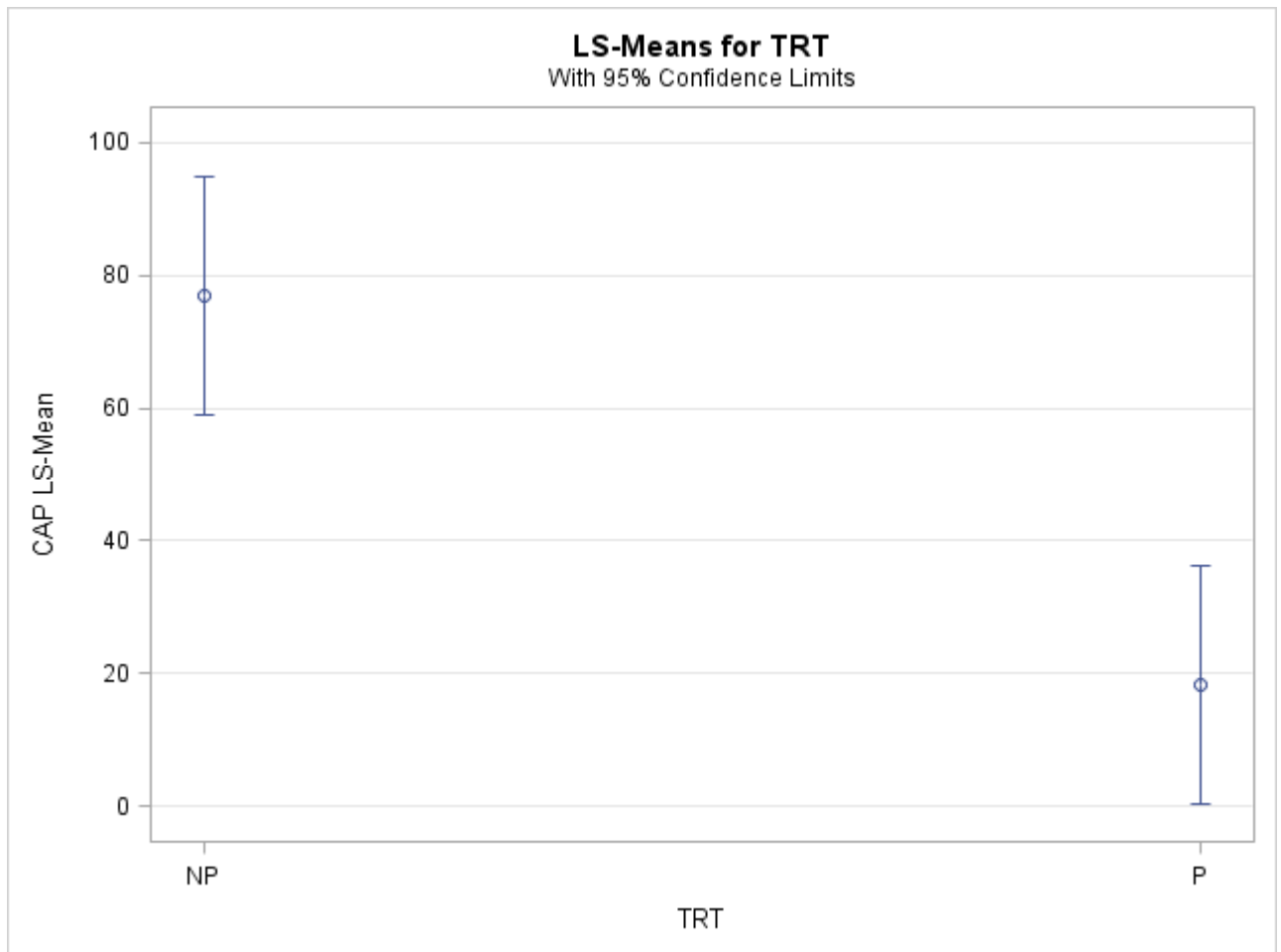
Class Level Information

Class Levels Values

YR 3 2010 2011 2013
TRT 2 NP P
ENC 8 1 10 11 14 15 2 3 6

TRT Least Squares Means

TRT	Estimate	Standard Error	DF	t Value	Pr > t	Alpha	Lower	Upper
NP	76.9167	8.4775	16	9.07	<.0001	0.05	58.9452	94.8882
P	18.4167	8.4775	16	2.17	0.0452	0.05	0.4452	36.3882



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Tukey Grouping for TRT Least Squares Means (Alpha=0.05)

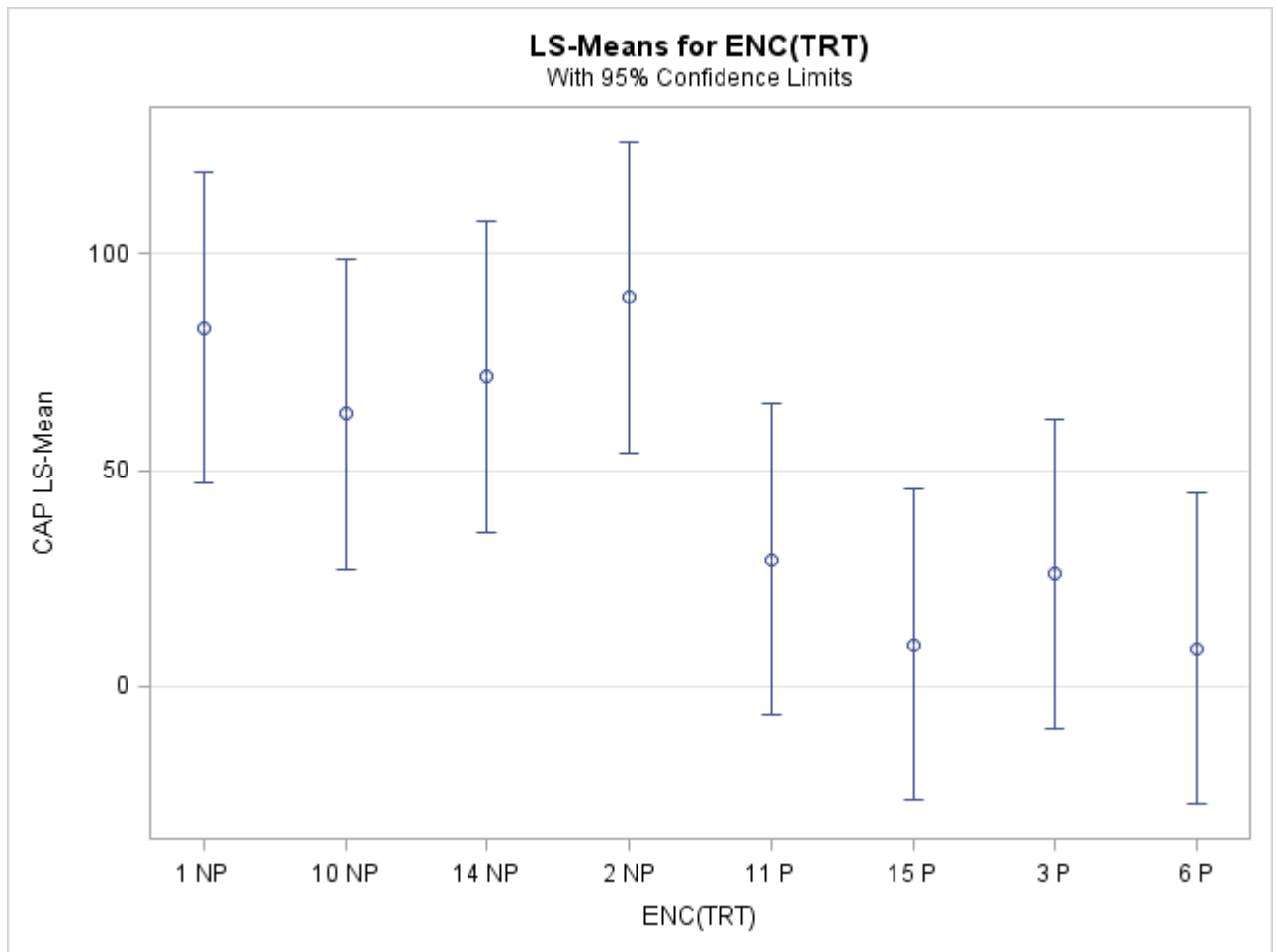
LS-means with the same letter are not significantly different.

TRT	Estimate
NP	76.9167 A
P	18.4167 B

ENC(TRT) Least Squares Means

TRT	ENC	Estimate	Standard Error	DF	t Value	Pr > t	Alpha	Lower	Upper
NP	1	83.0000	16.9550	16	4.90	0.0002	0.05	47.0570	118.94
NP	10	63.0000	16.9550	16	3.72	0.0019	0.05	27.0570	98.9430
NP	14	71.6667	16.9550	16	4.23	0.0006	0.05	35.7237	107.61
NP	2	90.0000	16.9550	16	5.31	<.0001	0.05	54.0570	125.94
P	11	29.3333	16.9550	16	1.73	0.1029	0.05	-6.6097	65.2763
P	15	9.6667	16.9550	16	0.57	0.5765	0.05	-26.2763	45.6097
P	3	26.0000	16.9550	16	1.53	0.1447	0.05	-9.9430	61.9430
P	6	8.6667	16.9550	16	0.51	0.6162	0.05	-27.2763	44.6097

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**Tukey Grouping for
ENC(TRT) Least Squares
Means (Alpha=0.05)
LS-means with the
same letter are not
significantly different.**

TRT	ENC	Estimate
NP	2	90.0000 A
NP	1	83.0000 A
NP	14	71.6667 A
NP	10	63.0000 A
P	11	29.3333 A
P	3	26.0000 A

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**Tukey Grouping for
ENC(TRT) Least Squares
Means (Alpha=0.05)**

**LS-means with the
same letter are not
significantly different.**

TRT	ENC	Estimate
P	15	9.6667 A
		A
P	6	8.6667 A

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Appendix 2: ANOVA Output of Distance Interval between Successive Captures

The SAS System

The Mixed Procedure

Model Information

Data Set	WORK.DEGU_DIST
Dependent Variable	dist
Covariance Structure	Diagonal
Estimation Method	Type 3
Residual Variance Method	Factor
Fixed Effects SE Method	Model-Based
Degrees of Freedom Method	Residual

Class Level Information

Class Levels Values

Yr	3	2010	2011	2013
Trt	2	NP	P	
Enc	8	1	10	11
		14	15	2
			3	6

Dimensions

Covariance Parameters	1
Columns in X	11
Columns in Z	0
Subjects	1
Max Obs Per Subject	109

Number of Observations

Number of Observations Read	109
Number of Observations Used	109
Number of Observations Not Used	0

Type 3 Analysis of Variance

Source	DF	Sum of Squares	Mean Square	Expected Mean Square	Error Term	Error DF	F Value	Pr > F
Trt	1	36.367140	36.367140	Var(Residual) + Q(Trt,Enc(Trt))	MS(Residual)	101	1.33	0.2510
Enc(Trt)	6	146.023762	24.337294	Var(Residual) + Q(Enc(Trt))	MS(Residual)	101	0.89	0.5038
Residual	101	2755.634953	27.283514	Var(Residual)

Covariance Parameter Estimates

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Cov Parm	Estimate
Residual	27.2835

Fit Statistics

-2 Res Log Likelihood	639.3
AIC (smaller is better)	641.3
AICC (smaller is better)	641.4
BIC (smaller is better)	643.9

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Trt	1	101	1.33	0.2510
Enc(Trt)	6	101	0.89	0.5038

The SAS System

The PLM Procedure

Store Information

Item Store	WORK.DEGU_DIST
Data Set Created From	WORK.DEGU_DIST
Created By	PROC MIXED
Date Created	06MAR15:22:30:57
Response Variable	dist
Distribution	Normal
Class Variables	Yr Trt Enc
Model Effects	Intercept Trt Enc(Trt)

Class Level Information

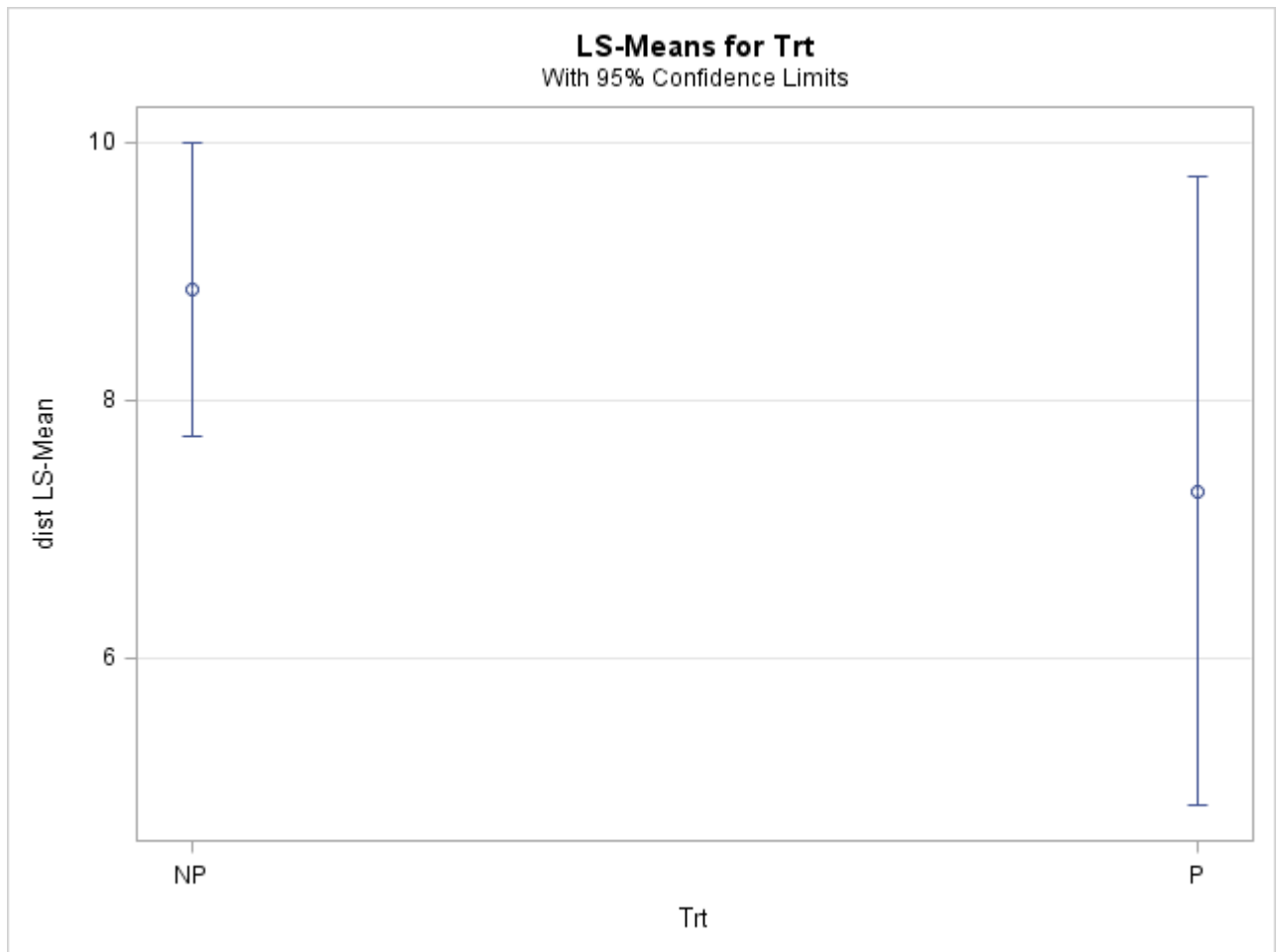
Class Levels Values

Yr	3	2010	2011	2013					
Trt	2	NP	P						
Enc	8	1	10	11	14	15	2	3	6

Trt Least Squares Means

Trt	Estimate	Standard Error	DF	t Value	Pr > t 	Alpha	Lower	Upper
NP	8.8641	0.5730	101	15.47	<.0001	0.05	7.7275	10.0007
P	7.2963	1.2312	101	5.93	<.0001	0.05	4.8540	9.7386

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**Tukey-Kramer Grouping
for Trt Least Squares
Means (Alpha=0.05)**
LS-means with the
same letter are
not significantly
different.

Trt	Estimate
NP	8.8641 A
P	7.2963 A

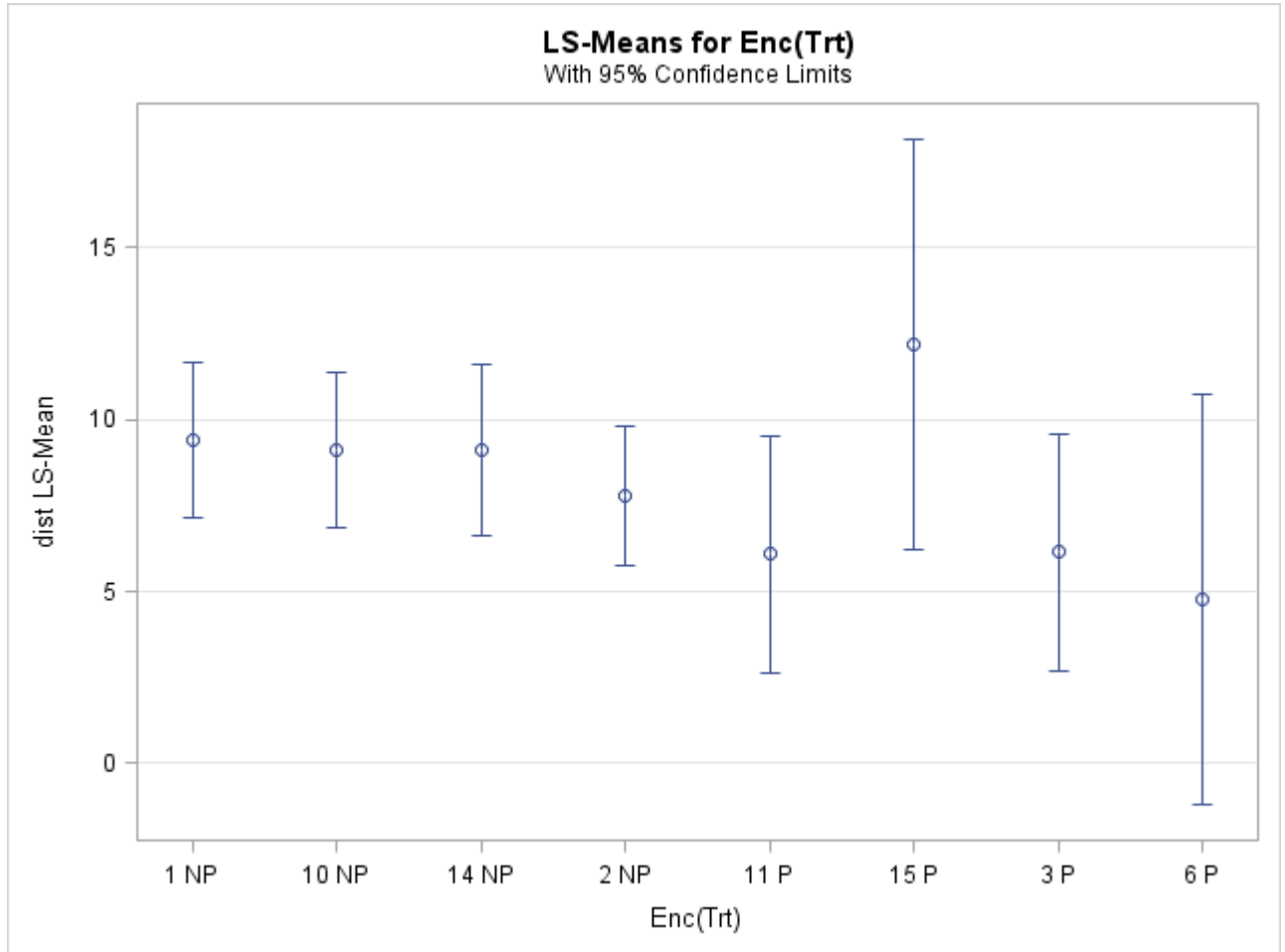
Enc(Trt) Least Squares Means

Trt	Enc	Estimate	Standard Error	DF	t Value	Pr > t	Alpha	Lower	Upper
NP	1	9.4098	1.1398	101	8.26	<.0001	0.05	7.1487	11.6709
NP	10	9.1395	1.1398	101	8.02	<.0001	0.05	6.8784	11.4006
NP	14	9.1178	1.2669	101	7.20	<.0001	0.05	6.6047	11.6309
NP	2	7.7893	1.0244	101	7.60	<.0001	0.05	5.7571	9.8214
P	11	6.0756	1.7411	101	3.49	0.0007	0.05	2.6216	9.5295

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Enc(Trt) Least Squares Means

Trt	Enc	Estimate	Standard Error	DF	t Value	Pr > t	Alpha	Lower	Upper
P	15	12.1830	3.0157	101	4.04	0.0001	0.05	6.2006	18.1654
P	3	6.1539	1.7411	101	3.53	0.0006	0.05	2.7000	9.6078
P	6	4.7727	3.0157	101	1.58	0.1166	0.05	-1.2097	10.7550



**Tukey-Kramer Grouping
for Enc(Trt) Least
Squares Means (Alpha=0.05)**

**LS-means with the
same letter are not
significantly different.**

Trt	Enc	Estimate	Grouping
P	15	12.1830	A
			A
NP	1	9.4098	A
			A
NP	10	9.1395	A
			A

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**Tukey-Kramer Grouping
for Enc(Trt) Least
Squares Means (Alpha=0.05)
LS-means with the
same letter are not
significantly different.**

Trt	Enc	Estimate
NP	14	9.1178 A
		A
NP	2	7.7893 A
		A
P	3	6.1539 A
		A
P	11	6.0756 A
		A
P	6	4.7727 A

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Appendix 3: ANOVA Output for MCP

The SAS System

The PLM Procedure

Store Information

Item Store	WORK.DEGU_MCP
Data Set Created From	WORK.DEGU_MCP
Created By	PROC MIXED
Date Created	31JAN15:23:15:08
Response Variable	MCP
Distribution	Normal
Class Variables	YR TRT ENC
Model Effects	Intercept TRT ENC(TRT)

Class Level Information

Class Levels Values

YR	3 A B C
TRT	2 NP P
ENC	8 1 10 11 14 15 2 3 6

TRT Least Squares Means

	TRT Estimate	Standard Error	DF	t Value	Pr > t 	Alpha	Lower	Upper
NP	0.04584	0.003833	90	11.96	<.0001	0.05	0.03823	0.05346
P	0.02637	0.009686	90	2.72	0.0078	0.05	0.007131	0.04562

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Class Level Information			
Class	Levels	Values	
Yr	3	2010	2011 2013
Trt	2	NP P	
Enc	8	1 10 11 14	15 2 3 6

Dimensions	
Covariance Parameters	1
Columns in X	11
Columns in Z	0
Subjects	1
Max Obs Per Subject	103

Number of Observations	
Number of Observations Read	103
Number of Observations Used	103
Number of Observations Not Used	0

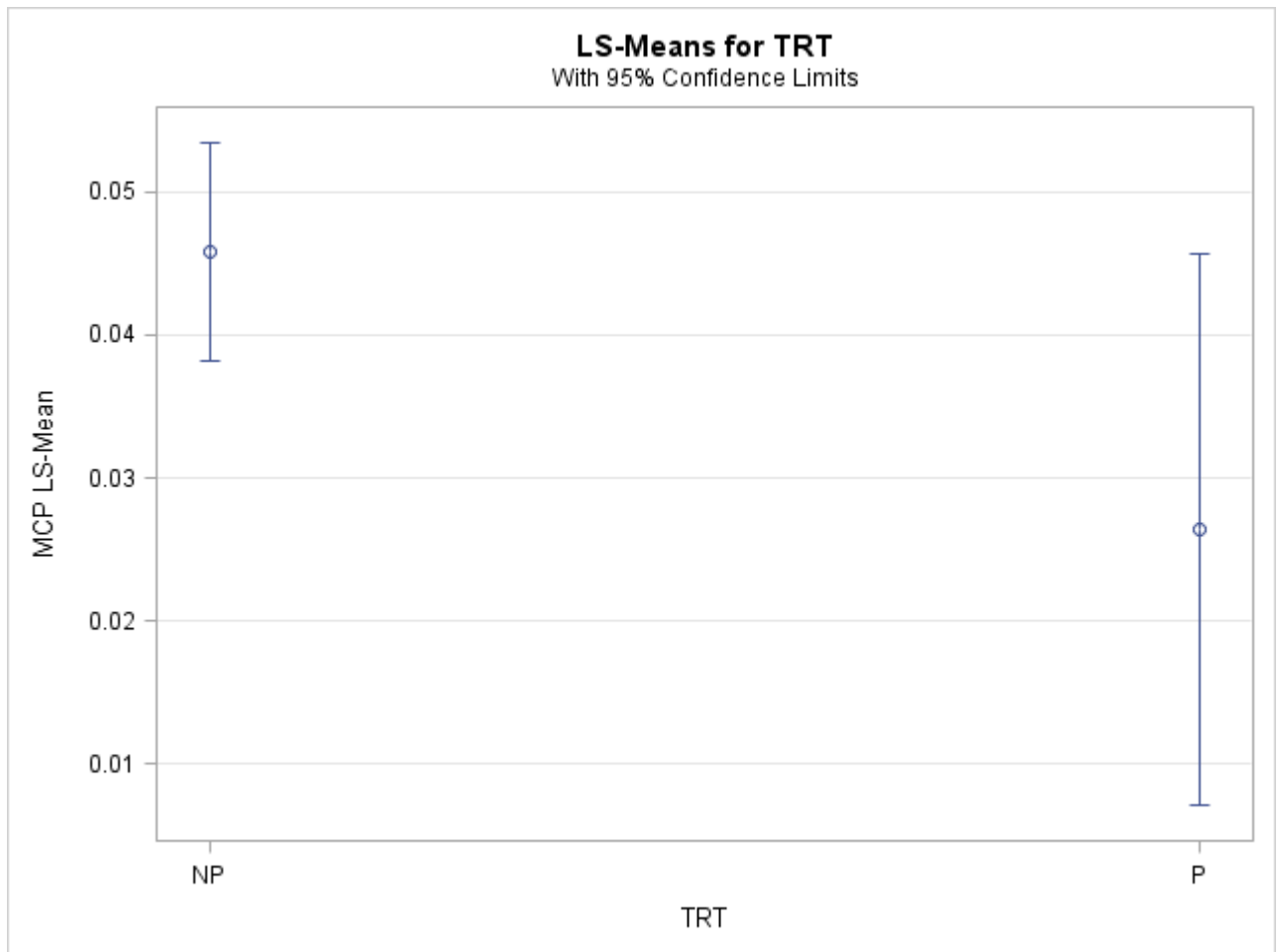
Type 3 Analysis of Variance								
Source	DF	Sum of Squares	Mean Square	Expected Mean Square	Error Term	Error DF	F Value	Pr > F
Trt	1	356652	356652	Var(Residual) + Q(Trt,Enc(Trt))	MS(Residual)	95	1.92	0.1686
Enc(Trt)	6	1464822	244137	Var(Residual) + Q(Enc(Trt))	MS(Residual)	95	1.32	0.2571
Residual	95	17608317	185351	Var(Residual)

Covariance Parameter Estimates	
Cov Parm	Estimate
Residual	185351

Fit Statistics	
-2 Res Log Likelihood	1440.3
AIC (smaller is better)	1442.3
AICC (smaller is better)	1442.3
BIC (smaller is better)	1444.8

Type 3 Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Trt	1	95	1.92	0.1686
Enc(Trt)	6	95	1.32	0.2571

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**Tukey-Kramer Grouping
for TRT Least Squares
Means (Alpha=0.05)**
LS-means with the
same letter are
not significantly
different.

TRT	Estimate	Grouping
NP	0.04584	A
P	0.02637	A

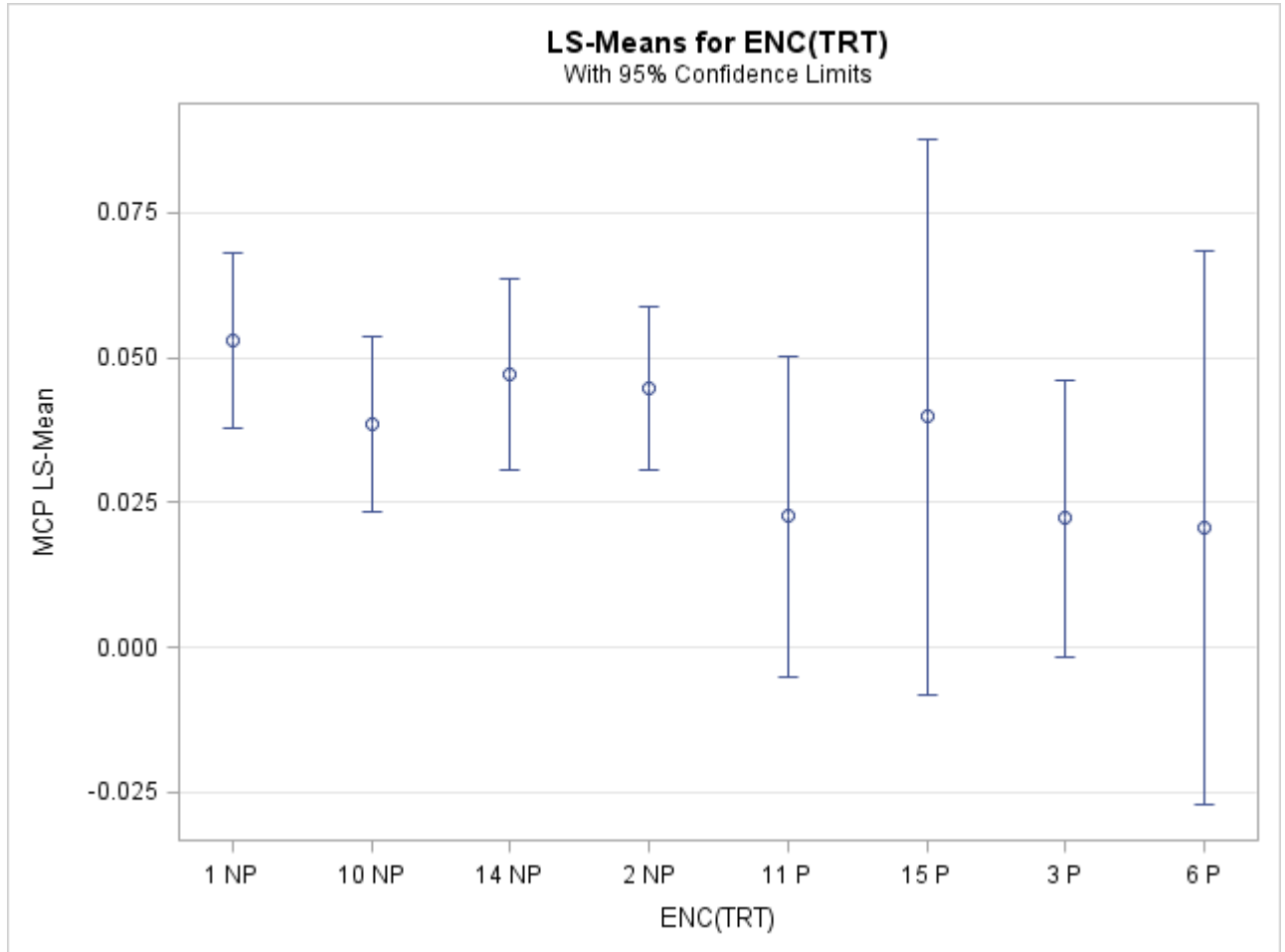
ENC(TRT) Least Squares Means

TRT	ENC	Estimate	Standard Error	DF	t Value	Pr > t	Alpha	Lower	Upper
NP	1	0.05290	0.007623	90	6.94	<.0001	0.05	0.03776	0.06804
NP	10	0.03865	0.007623	90	5.07	<.0001	0.05	0.02351	0.05379
NP	14	0.04709	0.008268	90	5.69	<.0001	0.05	0.03066	0.06351
NP	2	0.04474	0.007108	90	6.29	<.0001	0.05	0.03062	0.05886
P	11	0.02260	0.01392	90	1.62	0.1079	0.05	-0.00505	0.05025

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ENC(TRT) Least Squares Means

TRT	ENC	Estimate	Standard Error	DF	t Value	Pr > t	Alpha	Lower	Upper
P	15	0.03985	0.02411	90	1.65	0.1018	0.05	-0.00804	0.08774
P	3	0.02232	0.01205	90	1.85	0.0673	0.05	-0.00163	0.04626
P	6	0.02072	0.02411	90	0.86	0.3922	0.05	-0.02716	0.06861



**Tukey-Kramer Grouping
for ENC(TRT) Least
Squares Means (Alpha=0.05)**

**LS-means with the
same letter are not
significantly different.**

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TRT	ENC	Estimate
NP	1	0.05290 A
		A
NP	14	0.04709 A
		A
NP	2	0.04474 A
		A
P	15	0.03985 A
		A
NP	10	0.03865 A
		A
P	11	0.02260 A
		A
P	3	0.02232 A
		A
P	6	0.02072 A

Appendix 4: *ANOVA Output for Kernel*

The SAS System

The Mixed Procedure

Model Information

Data Set	WORK.DEGU_KERN
Dependent Variable	kern
Covariance Structure	Diagonal
Estimation Method	REML
Residual Variance Method	Profile

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Model Information

Fixed Effects SE Method Model-Based
Degrees of Freedom Method Residual

Class Level Information

Class Levels Values

Yr 3 2010 2011 2013
Trt 2 NP P
Enc 8 1 10 11 14 15 2 3 6

Dimensions

Covariance Parameters 1
Columns in X 11
Columns in Z 0
Subjects 1
Max Obs Per Subject 109

Number of Observations

Number of Observations Read 109
Number of Observations Used 101
Number of Observations Not Used 8

Covariance Parameter Estimates

Cov Parm **Estimate**
Residual 0.003851

Fit Statistics

-2 Res Log Likelihood -235.6
AIC (smaller is better) -233.6
AICC (smaller is better) -233.6
BIC (smaller is better) -231.1

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Trt	1	93	0.17	0.6853
Enc(Trt)	6	93	1.07	0.3871

The SAS System

The PLM Procedure
Store Information

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Store Information

Item Store WORK.DEGU_KERN
Data Set Created From WORK.DEGU_KERN
Created By PROC MIXED
Response Variable kern
Distribution Normal
Class Variables Yr Trt Enc
Model Effects Intercept Trt Enc(Trt)

Class Level Information

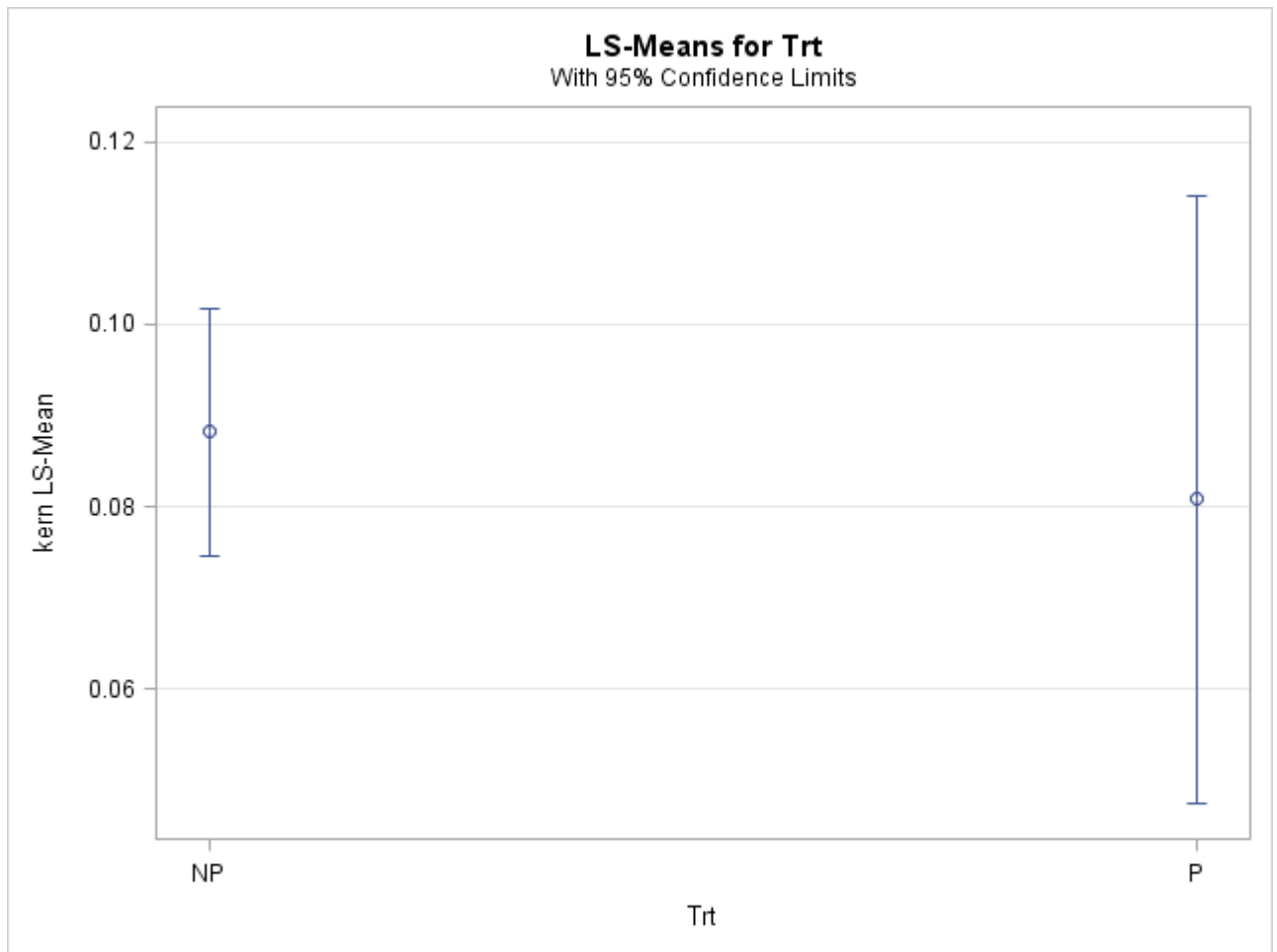
Class Levels Values

Yr 3 2010 2011 2013
Trt 2 NP P
Enc 8 1 10 11 14 15 2 3 6

Trt Least Squares Means

Trt	Estimate	Standard Error	DF	t Value	Pr > t	Alpha	Lower	Upper
NP	0.08818	0.006849	93	12.88	<.0001	0.05	0.07458	0.1018
P	0.08080	0.01682	93	4.80	<.0001	0.05	0.04739	0.1142

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**Tukey-Kramer Grouping
for Trt Least Squares
Means (Alpha=0.05)**
LS-means with the
same letter are
not significantly
different.

Trt	Estimate
NP	0.08818 A
P	0.08080 A

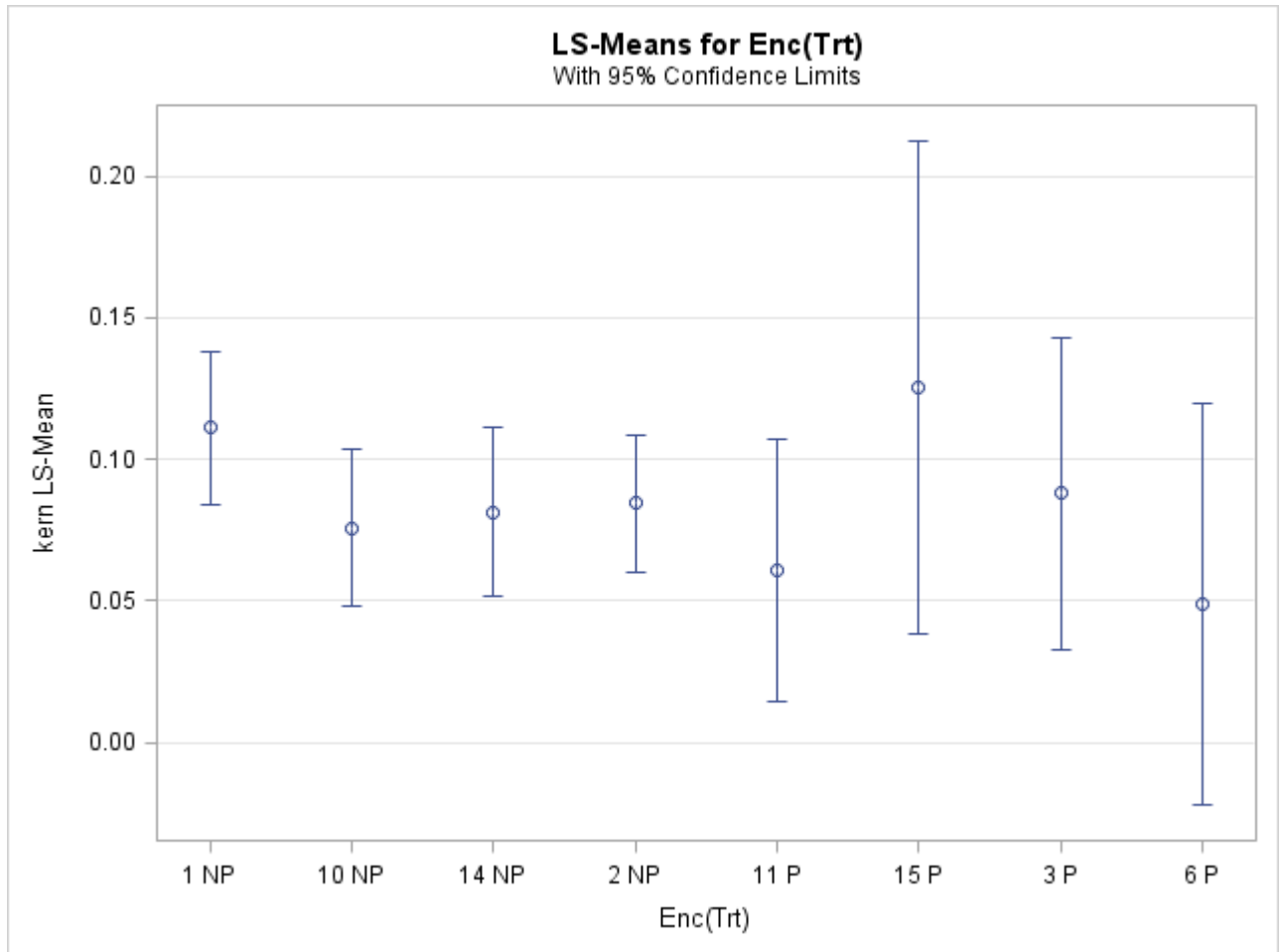
Enc(Trt) Least Squares Means

Trt	Enc	Estimate	Standard Error	DF	t Value	Pr > t	Alpha	Lower	Upper
NP	1	0.1112	0.01354	93	8.21	<.0001	0.05	0.08428	0.1381
NP	10	0.07578	0.01388	93	5.46	<.0001	0.05	0.04823	0.1033
NP	14	0.08139	0.01505	93	5.41	<.0001	0.05	0.05150	0.1113
NP	2	0.08440	0.01217	93	6.93	<.0001	0.05	0.06023	0.1086
P	11	0.06085	0.02345	93	2.59	0.0110	0.05	0.01427	0.1074

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Enc(Trt) Least Squares Means

Trt	Enc	Estimate	Standard Error	DF	t Value	Pr > t	Alpha	Lower	Upper
P	15	0.1254	0.04388	93	2.86	0.0053	0.05	0.03829	0.2126
P	3	0.08798	0.02775	93	3.17	0.0021	0.05	0.03287	0.1431
P	6	0.04895	0.03583	93	1.37	0.1751	0.05	-0.02219	0.1201



**Tukey-Kramer Grouping
for Enc(Trt) Least
Squares Means (Alpha=0.05)**
LS-means with the
same letter are not
significantly different.

Trt	Enc	Estimate	Grouping
P	15	0.1254	A
			A
NP	1	0.1112	A
			A
P	3	0.08798	A
			A

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**Tukey-Kramer Grouping
for Enc(Trt) Least
Squares Means (Alpha=0.05)
LS-means with the
same letter are not
significantly different.**

Trt	Enc	Estimate
NP	2	0.08440 A
		A
NP	14	0.08139 A
		A
NP	10	0.07578 A
		A
P	11	0.06085 A
		A
P	6	0.04895 A