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Factors Affecting Breeding Territory Size And Placement Of The Florida Grasshoper Sparrow (ammodramus Savannarum Floridanus)

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FACTORS AFFECTING BREEDING TERRITORY SIZE AND PLACEMENT
OF THE FLORIDA GRASSHOPPER SPARROW
(*AMMODRAMUS SAVANNARUM FLORIDANUS*)

by

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ABSTRACT

For most taxa, maximizing fitness depends on maintaining access to adequate resources. Territories provide exclusive use of resources for an individual or a family group, thus facilitating successful reproduction. The economic defensibility of a territory depends on the quality, abundance, and distribution of its resources as well as the amount of competition that an individual must endure to maintain exclusive access. The benefits of defense must outweigh the costs for territoriality to be profitable. Territory owners may benefit from territories with high quality resources, but they also may incur greater costs defending these resources from competitors. In contrast, territories with poor quality resources provide fewer benefits to an owner but also may have fewer competitors vying for those resources. Resource quality may change over time, especially in habitats in which periodic ecological disturbances, such as fire, occur. As a result, the cost-benefit equation of defensibility also changes over time.

The Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*), an Endangered subspecies, is a habitat specialist endemic to the Florida dry prairie, a pyrogenic ecosystem found only in south-central Florida. As a result *A. s. floridanus* has evolved with frequent fires and its demography is strongly influenced by the structural habitat characteristics, such as sparse woody vegetation and large amounts of bare ground that occur with frequent fire.

The objective of my study was to determine what factors associated with fire (i.e. habitat structure and prey abundance) affected the "decisions" of male *A. s. floridanus* to defend a territory. I hypothesized that fire and the resources resulting from fire would have an impact on

territory size and placement. I predicted that territories in more recently burned habitat would be of higher quality and that sparrows would avoid areas with a longer time since fire.

I conducted my study at Kissimmee Prairie Preserve State Park in Okeechobee County, FL. One half of my 100-ha study plot had experienced two growing seasons since the last fire and the remaining half had experienced only a single growing season since fire at the start of my study. I mapped territories of all males within my study plot twice over the breeding season; once during the early season (nest building and incubation) and once during the late season (nestling and fledgling stages). In addition, during each survey I collected arthropods and surveyed vegetation composition within territories and at random, unoccupied points within the study plot. I compared the differences between the habitat characteristics of territories and unoccupied areas, the differences between the territories of the males that occupied the two-year rough and those in the one-year rough, males that abandoned their territories mid-season and those that remained in the study plot, and the seasonal changes in territory characteristics between the early and late season territories of males that persisted.

My results indicate that *A. s. floridanus* selects certain habitat characteristics in which to place territories. Males preferred areas with fewer shrubs and more bare ground, which is consistent with previous studies. Prey biomass did not differ between territories and unoccupied areas. Nonetheless, although the mean mass of individual arthropods was larger in unoccupied areas, the numerical abundance of orthopterans, damselflies, and spiders was significantly higher in territories than in unoccupied areas. Sparrows were more likely to abandon their territories if they occurred in the two-year rough as opposed to the one-year rough. Territories in the two-year rough were significantly larger, had poorer quality habitat, and tended to have less prey than

those in the one-year rough. The sparrows that persisted throughout the season significantly

increased their territory size in the late season; however, very little spatial shift occurred,

suggesting that they merely increased their territory size rather than moved to new sites. Early-

season territories in the one-year rough were completely exclusive, but late season territories

showed considerable overlap, suggesting lack of defense and a shift toward home ranges as

opposed to exclusive territories. The habitat quality in late-season territories decreased (more

shrubs, less bare ground) from the early season. Unexpectedly, however, the biomass of prey

increased. This increase coincides with an increased demand for prey because sparrows are

provisioning young. It seems likely that the costs of defense increase at this time because time

and energy spent in defense come at the expense of time spent provisioning young. Because prey

increases in the late season, the need to defend exclusive territories may decline.

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<u>Introduction</u>

Territoriality is the mechanism through which organisms ensure exclusive access to resources that increase fitness (Brown 1964, Stamps 1994, Maher and Lott 1995). Territories vary in both function and size depending on the specific resources the territory holder requires. Some territories encompass all the resources necessary for successful reproduction and survival, including areas used to attract mates, foraging grounds, nesting sites, and areas to raise young. These territories are referred to as "Type A" territories (Mayr 1935, Nice 1941, Armstrong 1947, Hinde 1956, Brown 1969, Maher and Lott 1995). Other territories may encompass only a single resource, such as a nest site or a mate because other essential resources cannot be economically defended. These types of territories, especially, depend on the life history and ecology of different species (Nice 1941, Hinde 1956, Brown 1964).   For example, many species of seabirds defend only the area around their nest because their foraging grounds (the ocean) cannot efficiently be defended (Brown 1964).

Territorial defense of resources evolves when it is economical to do so, i.e., when the benefits of having exclusive use of those resources outweigh the costs of defending them (Brown 1964) or outweigh the benefits of adopting another strategy (e.g., a home range or non-territorial nomadism). The economic defensibility of resources depends on their relative quality, their distribution in time and space, and competition for those resources (Brown 1964, Weins 1977). The quality of resources and their abundance are not mutually exclusive and have direct effects

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on each other as well as on the costs of defending the territory (i.e., the level of competition for those resources). Although defending a territory containing high-quality resources increases the benefits of territoriality, the resulting increase in competition also may increase the costs of defense (Stamps 1990). Sanderlings (*Calidris alba*) showed a decrease in territory size with an increase in prey abundance and an increase in intruder pressure (Myers et al. 1979). Similarly, Dartford Warblers (*Sylvia undata*) showed a decrease in territory size with an increase in conspecific density and, therefore, competition for resources (Pons et al. 2008).

The costs of competition can vary among territories and among individuals. These costs may vary with territory quality; intruder pressure may increase when territory quality is high. The costs of competition may be lower for an individual in good body condition because he is more likely to win contests and expend less energy in doing so relative to individuals in poorer body condition; thus the cost-benefit ratio of maintaining a territory is reduced (Whiteman and Parker 2004, Viera et al. 2008). Individuals in poorer body condition may be forced to occupy sub-optimal habitat for which lower competition exists, thus making defense economical. When defense of a territory is no longer economical, individuals may abandon their territory for possible breeding opportunities elsewhere, or adopt an alternative mating strategy within the same habitat (Chellappa et al. 1999, Starks and Reeve 1999) by becoming a "satellite" male (Howard 1978) or a "floater" (Smith 1978, Arcese 1987, Smith and Arcese 1989, Stutchbury 1991, Zack and Stuchbury 1992, Bayne and Hobson 2001). These non-territorial individuals often are able to maintain access to some resources without the costs of territorial defense but are usually less reproductively successful than territory holders.

The spatial distribution of a resource also can affect the cost-benefit equation of territory defense. It often is not economical to defend a resource that is evenly distributed across a landscape; the cost of defending the resource is greater than the benefit of maintaining exclusive access. When resources are evenly distributed and difficult to defend, individuals can benefit from shifting energy expended in defense to attracting a mate or tending to young. It may be easier to maintain exclusive access to patchy resources, however, because an individual is able to defend a patch. Thus, the relative cost-benefit ratio changes and defense becomes more economical (Kohlmann and Risenhoover 1998). However, this may vary with the number of patches (Dell'Arte and Leonardi 2005). Few patches may result in high amounts of competition whereas many patches may reduce competition.

Resources may vary temporally, such as before and after a disturbance, and may affect the defensibility of a territory. Disturbances such as fire create early successional habitats on which some species (including species of prey) depend. James et al. (1997) found that Red-cockaded Woodpeckers (*Picoides borealis*) prefer to build cavities in longleaf pine habitats with little understory vegetation. They tend to lay larger clutches and have higher reproductive success when their territories are in habitats one year or less post-fire. These territories can be presumed to be of higher quality and, therefore, of higher economic defensibility.

In many systems, ecological succession alters the abundance and distribution of resources, especially when succession is driven by natural patterns of ecological disturbance, such as fire. As resource abundance and habitat quality change over time, the economic defensibility of territories and patterns of competition for resources also may change (Brown 1964, Brown 1969, Chamberlain and Fuller 1999, Holmes and Sherry 2001, Shriver and Vickery

2001). Haney et al. (2008) found that many forest birds tend to thrive as succession occurs after major disturbances such as severe fires. Some habitat specialists depend on periodic ecological disturbance that sets back the successional clock, and these species may not be able to persist in the absence of these natural disturbances because resources are not adequate for their life history strategy. Fire-dependent species have evolved with a landscape that was historically shaped by fire, and the persistence of these species can be threatened when fire is removed from the system. Roth and Lutz (2004) found that the abundance of Golden-winged Warblers (*Vermivora chrysoptera*) was significantly positively correlated with early successional aspen stands. In early succession habitats, the density of breeding territories was high; by 25 years post-fire, both a decline in breeding territory density and in reproduction had occurred.

The Florida dry prairie, a habitat found only in south-central Florida, is maintained by frequent fires (every 2-3 years; Orzell and Bridges 2006). The Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*), an Endangered subspecies, is a habitat specialist endemic to the Florida dry prairie (Federal Register 1986). Consequently, the ground-dwelling sparrows are dependent on frequent fires, which reduce vegetation density. Because the sparrows forage on ground-dwelling arthropods and nest on the ground, the bare ground and sparse shrub cover resulting from frequent fires facilitate foraging and enable successful breeding (Walsh et al. 1995, Shriver and Vickery 2001, Delany et al. 2002). Sparrows favor habitat burned less than one year prior to the breeding season and avoid areas that have not burned for more than two years (Shriver et al. 1996, Delany et al. 2002). In addition, reproductive success is negatively correlated with time since fire; it is highest the first year post-fire, and then declines to the point that sparrows are not able to replace themselves by three-years post-fire. This suggests that the

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resources necessary for successful reproduction in Florida Grasshopper Sparrows decline with time since fire. Therefore, we can assume that the economic defensibility of territories for *A. s. floridanus* varies with time since fire and likely declines over time. Because other resources, such as habitat structure, habitat composition, and food may depend on fire, we can also assume that time since fire may be relatively more important than individual resources when predicting whether territories are defendable or not and in explaining variation in territory size.

The objective of my study was to determine what factors associated with fire (i.e., habitat structure and prey abundance) affected the "decisions" of male *A. s. floridanus* to defend a territory. Because *A. s. floridanus* has evolved with frequent fires, its demography is tied to the sparsely vegetated habitat that results from fires. Therefore, I hypothesized that fire was the driving factor in determining *A. s. floridanus* territory size and placement. I predicted that *A. s. floridanus* would preferentially place territories in areas that were more recently burned because fire creates more preferable habitat for the sparrows (fewer shrubs, more bare ground). Specifically, I predicted that territories in the one-year rough would be smaller, have fewer shrubs, more bare ground, and more prey. Territories in the two-year rough should be larger and have poorer resources. I also predicted that over the course of a season, as the time since fire lengthened, territories would increase in size and resources within those territories would decline (i.e., less suitable habitat structure and fewer prey).

<center>Materials and Methods</center>

Study site and focal species

      Kissimmee Prairie Preserve State Park (KPPSP; Fig 1), located in northwest Okeechobee County, Florida (27° 35'N, 81° 03'W), contains 9,200 ha of dry prairie habitat (Perkins et al. 2008). Dry prairie, found only in south-central Florida, is a fire-dependent, mostly treeless landscape characterized by poorly drained soils. Generally, this habitat has a high abundance of *Serenoa repens, Aristida beyrichiana*, and *Quercus minima*, of which presence and abundance vary by hydrological status and soil differences (UFSWS 1999, Orzell and Bridges 2006). The amount of bare ground within the habitat is highly dependent on time since fire. Litter and grass become denser and bare ground decreases with longer time since fire (Shriver and Vickery 2001). Additionally, the succession of woody shrubs increases with time since fire (Delany et al. 1985).

      The Florida Grasshopper Sparrow generally breeds from March to September (Shriver et al. 1996). The length of the breeding season depends on the frequency and severity of fires as well as the timing and amount of precipitation throughout the year. Females build the nest and incubate the eggs, but both parents take part in post-hatching care of the young (Smith 1963). Males are territorial throughout spring and summer and normally begin displays and territorial vocalizations in early March (Shriver et al. 1996). Territorial behaviors decline in late May with the appearance of nestlings (Smith 1968, Vickery 1996). With this decline in defense, other male grasshopper sparrows begin to move freely into formerly defended areas. If significant growing-season fires and moderate amounts of precipitation occur, territorial displays and nesting may resume in early to mid-June and taper through August or September (Shriver et al. 1996).

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Territorial boundaries may shift temporally and seasonally as a result of the movement of males during nesting (Smith 1963).

My study plot, located within KPPSP, was 100 ha in area (Fig 2). In February of 2007, 51.8 ha of the plot were burned as a part of a prescribed fire within the preserve. As a result, this area of the plot was two growing seasons (14 months) post-burn when my study began in April 2008. The remaining 48.2 ha of the plot were burned in August 2007; thus only a single growing season post-burn had elapsed (8 months) at the start of my study. Seasonality of fire may affect the subsequent vegetative composition in dry prairie. Fires during the dormant season (August – March) tend to favor woody and fire-resistant vegetation whereas growing season (April – June) fires encourage flowering and seeding of native grasses and forbs (Robbins and Myers 1992, Slocum et al. 2003). Although the seasonality of these two fires differed (February and August), both occurred during the dormant season, but more critically, the timing of the fires differed such that during the 2008 breeding season, one portion had experienced two growing seasons and the other portion only one. Time since fire greatly affects the vegetative structure (height and density) in Florida's dry prairie (Delany et al. 1985, Shriver and Vickery 2001). *A. s. floridanus* is sensitive to the density of vegetation because it relies on bare ground for successful foraging and nesting (Delany et al. 2002, Pranty and Tucker 2006). Therefore, frequent fires are an important aspect of its natural history.

It is estimated that fewer than 1000 individual *A. s. floridanus* exist throughout their range (Delany et al. 2005) and these occur in only three distinct populations, one at Avon Park Air Force Range (APAFR; which occurs as three distinct subpopulations), one at Three Lakes Wildlife Management Area (TLWMA), and one at KPPSP. Between 1998 and 2002, the

population of FGSPs at APAFR experienced a severe decline from nearly 200 singing males to fewer than 20. The population at TLWMA appears to be stable, but is smaller than the population at KPPSP. At KPPSP, the population appears to be stable, but the total population size is not known because only about 10% of the potential habitat is surveyed each year (P. Miller, pers. comm.). In a recent population viability analysis for *A. s. floridanus*, Perkins et al (2008) estimated a range of population sizes of the FGSP at KPPSP after 50 years and assuming a variety of different restoration and conservation scenarios. These estimated population sizes ranged from 112-703 individuals (423 ± 129 sparrows, mean $\pm$ 1SE).

Most males within my study population were marked with individual color-band combinations as well as a uniquely-numbered aluminum band. The unique band combinations allowed for easy field identification of individual birds using a spotting scope or binoculars. Males that had not been banded but were actively defending a territory were mist-netted using a recorded playback of male vocalizations, banded, and morphological measurements were taken. Required permits from USFWS, FFWCC, and FLDEP were obtained prior to the beginning of the study.

Territory Mapping

I mapped territories for each male located within the study plot. Actively defending males were found by walking transects throughout the study plot, and each male was identified by its unique color-band combination. Once a singing male was identified I conducted a series of focal observations to determine the location of individual singing perches within its territory. I began focal observations at civil twilight (30 minutes before sunrise) and continued them until the

individual bird stopped singing, usually for 3-4 hours. I did not intentionally flush males from

perches, which could have forced them outside of their territory boundaries and resulted in

mapping a larger territory than was actually being defended. I collected GPS points at each perch

location that an individual male used for display (singing) until the territory area reached an

asymptote (i.e., the area of the territory did not increase with an increase in the number of perch

locations collected; Fig. 3). Many males had preferred perches that they used regularly, and I

recorded a point at these locations each time the male visited and sang. I collected approximately

10 – 20 points each day; an asymptote of the territory area usually was reached after 4-5

mornings of field observations (~30-40 locations). However, because males tended to defend

different areas of their territory in response to the daily locations of their neighbors, I never

observed an individual male for fewer than 3 mornings to prevent daily biases. I mapped the

territories of all actively defending males within the study plot twice: once during the early

breeding season (April 1 – May 15) and again during the late breeding season (June 1 – July 15).

Territory areas were measured by creating a minimum convex polygon (Delany et al. 1995) in

ArcView 3.3 using all of the territory points collected for each male.

Arthropod abundance within territories

After an asymptote was reached for an individual male's territory size, a transect was

established as the longest distance through the center of the territory using ArcView 3.3. I

sweep-netted the length of this transect and collected all arthropods captured (Kobal et al. 1998,

Sutter and Ritchison 2005). Sweep-netting was not conducted during rainy or windy (over 10

mph) conditions. All arthropods from an individual territory were placed in a large plastic freezer

bag and frozen (Kaspari and Joern 1993), after which the prey items that are selected by *A. s. floridanus* as prey (Kobal et al. 1998, Delany et al. 2000) were separated, individual items were counted, and all prey items were weighed to the nearest 0.01g. The mass of the selected arthropods was divided by the total area of the transect (its length x 1 m width), which provided the mean mass of prey per m^2 of transect or biomass. These methods were repeated for late season territories.

Habitat composition within territories

Habitat composition within territories was measured along the same transect used for arthropod collection. Transect length varied by territory size, but all territories were sampled at a minimum of 10 points taken every $8 - 10$m along the transect. Percent cover was estimated visually for dwarf oak (*Q. minima*), saw palmetto, woody-stemmed shrubs other than *Q. minima*, grass, and bare ground within a $1m^2$ plot around each point (Weins 1969, Delany et al. 1985). These values were averaged for the entire transect for each part of the season.

Unoccupied areas

During the early and late seasons, after all territories within the study plot were mapped, 20 points were randomly selected within areas not occupied by *A. s. floridanus*, excluding wetlands or ephemeral ponds. From each random point, I extended a 50-m transect in a randomly selected direction. The length of each transect was sweep-netted and arthropods were collected and sorted using the same methods as within territories. Vegetation was measured along the 50-

m transect using the same methods as within territories. The mean percent-cover value of each transect was determined for each type of vegetation.

Body Condition

Throughout the breeding season, I captured territorial males and collected morphological and body condition indices in order to determine if body quality had an effect on the ability of a male to gain and defend high-quality territories. Once a male was captured, I took three morphological measurements; right tarsus length (mm), right wing chord (mm), and body mass (g) and gauged condition indices on their body fat (discrete score from 0 – 7), pectoral muscle shape (discrete score from 0 – 3), and amount of feather mites on their right primary feathers (discrete score from 0 – 3; Harper 1999, Green 2001, Robb et al. 2001; see Appendix B). I also regressed mass against tarsus length and used the residual of each individual from the regression line as another measure of size-corrected body condition.

Statistical Analysis

All data were tested for normality and were transformed when the data did not fit basic statistical assumptions (Gotelli and Ellison 2004). For comparison between territory and unoccupied points, I used point type as the categorical variable and tested variation in prey abundance and the five habitat variables using t-tests. For analyses testing the differences in territory characteristics between males that stayed and males that abandoned their territories, I used logistic regression with male behavior (stayed or left) as the dependent variable. To test for

differences in territory characteristics as they relate to territory size, I used linear regression. These variables were tested against the independent variables, prey abundance and the habitat variables. When comparing between males that remained from the early season to the late season, I used paired t-tests for comparison of their early and late season territory characteristics. Two-tailed tests with ($P < 0.05$) using SPSS 16.0 were used for all analyses and all reported values are means $\pm$ 1 SE.

The body condition indices were analyzed using linear regression and ANOVA. The dependent variables for the analyses were territory size and prey abundance. Because of such a small sample size (n = 8), principal component analysis and non-metric dimensional scaling were not appropriate and interpolation was not possible.

A Sorenson distance measurement was used in PCOrd (Kruskal 1964, Mather 1976) and a non-metric multidimensional scaling (NMS) was performed to reduce the five habitat variables (palmetto, oak, non-oak woody shrubs, grass and bare ground) into one axis. I determined *a priori* models that may predict *A. s. floridanus* territory size using previous literature. I also hypothesized various interactions among the principal variables (habitat axis, prey abundance, and time since fire) and included them in the models. In total, I assessed the relative support of 12 models in explaining variation in FGSP territory size. I used AIC_c, Akaike Information Criterion corrected for small sample sizes (Burnham and Anderson 2002), and selected the best model of those tested based on ΔAIC_c. I determined the weight of each model and the cumulative weight and model support for each of the three factors.

The amount of overlap of territory boundaries was calculated for the early season and the late season using ArcGIS. The area of early season territories encompassed within late season

territories also was calculated to determine the amount of spatial shift that occurred for each territory. I calculated the percentages of overlap for the early season and the late season as a proportion of total area of overlap divided by the total area of territories. To determine the amount of spatial shift for an individual from the early season to the late season, I calculated the percentage of the early season territory that was encompassed within the late season territory.

Results

I determined territory sizes for 14 males: 13 in the early season and 8 during the late season (Fig. 4). Of the 13 territories measured during the early season, four occurred exclusively within the portion of the study area that had undergone two growing seasons post-fire, eight occurred exclusively within the portion that had undergone only a single growing season post-fire, and one territory included portions of both post-fire intervals. Of the 13 males whose territories were measured during the early season, only seven were subsequently observed and their territory size measured during the late season survey. Six early season males did not defend territories during the late season survey and one male established a territory between the early and late seasons. The mean territory size for the 14 males across the entire season was 1.42 ($\pm$ 0.24) ha. The mean territory size for the early season males (n = 13) was 1.11 ($\pm$ 0.29) ha and in the late season the mean size was 1.67 ($\pm$ 0.14) ha (t-test, t = -1.44, df = 19, p = 0.022). Only 33% of the territories were within the two-year rough that encompassed 52% of the study plot. The remaining 48% of the study plot with a one-year rough contained 67% of the territories.

Variation in territory characteristics in different fire regimes

During the early season, the mean territory size of males exclusively within the two-year rough was 1.85 (± 0.63) ha whereas males within the one-year rough had significantly smaller territories (0.65 (±0.13) ha; t-test, t = 2.759, df = 11, p = 0.019). Palmetto cover was less in territories in the one-year rough than in the two-year rough, although the difference was only marginally significant (t-test, t = 1.852, df = 11, p = 0.091), but no trends existed within territories for the other four habitat variables or for prey abundance.

Habitat preferences

A. s. floridanus selected certain habitat characteristics in which to place their territories. Sampling points within territories had less palmetto (t-test, t = -2.587, df = 31, p = 0.022) and more bare ground (t = 2.302, df = 31, p = 0.028; Table 1) than unoccupied points. Territories also had fewer non-oak woody shrubs than unoccupied points (t = -2.252, df = 24.8, p = 0.033); however, neither oak (t = -0.442, df = 31, p = 0.662) nor grass (t = 0.308, df = 28.9, p = 0.760) seemed to be an important factor in placement of territories. Prey biomass (mass/area of transect) did not vary significantly between territories and unoccupied points (t = 0.871, df = 26.7, p = 0.391; Fig. 5), although prey biomass tended to be higher on territories. Variation in prey biomass appeared to be higher among unoccupied points. This high variation may have made it difficult to detect a statistical difference between territories and unoccupied points because it reduced the power of the statistical tests based on the obtained sample sizes. The mean mass of individual arthropods (total mass/number of individuals) collected was greater in unoccupied habitat than within territories (df = 32, F = 4.225, p = 0.048; Fig 6). However, the

numerical abundance of orthopterans (df = 32, F = 13.645, p = 0.001; Fig 7a), damselflies (df = 32, F = 6.441, p = 0.016; Fig 7b), and spiders (df = 32, F = 11.858, p = 0.002; Fig 7c) was significantly higher in territories than in unoccupied areas. Dragonflies (df = 32, F = 0.521, p = 0.476; Fig 7d), a miscellaneous category of other types of arthropods that sparrows prey upon such as leafhoppers (df = 32, F = 12.140, p = 0.001; Fig 7e), and lepidopterans (df = 32, F = 0.932, p = 0.342; Fig 7f) were not different (Moran 2003). However, sweep-netting may be inadequate for effectively sampling lepidopterans (Cooper and Whitmore 1990).

Ecological Correlates of Territory Size

Of the 12 general linear models tested to explain variation in territory size, the model containing only time since fire was selected as the best (Table 2a,b). Territories located in one-year rough were significantly smaller than those in the two-year rough (df = 12, F = 7.612, p = 0.019). The second (habitat and time since fire additive effects), third (habitat), and fourth (prey abundance) best models received relatively low empirical support (ΔAIC_c = 5.72, 5.80 and 7.62, respectively). The weight of the best model was over 17 times that of the second-best model, indicating little uncertainty of its selection as the best candidate model (Burnham and Anderson 2002). The remaining 8 models received no empirical support (ΔAIC_c > 7.00; w_i = 0.00).

Territory characteristics of males that stayed versus those that left

Of the six males that maintained a territory only during the early season, four had territories that were exclusively or primarily within the two-year rough (Fig. 8). In contrast, of

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the seven males that remained on the study area, only one had a territory in the two-year rough. Males that abandoned their territories were more likely to have had an early-season territory in the two-year rough than males that persisted (66% vs 14%), although the difference was only marginally significant (Fisher Exact Test, $\chi^2 = 3.75$, p = 0.086). The mean early-season territory size of the six males that left the study area was significantly larger than that of the seven birds that stayed in the study plot (t –test, t = 2.991, df = 11, p = 0.012; Fig. 9). Those six males also defended territories with more non-oak woody shrubs (df = 1, Wald = 3.47, p = 0.06) and a trend toward less bare ground (df = 1, Wald = 2.33, p = 0.13) and less prey (df = 1, Wald = 1.32, p = 0.25) than in the territories of the seven males that stayed (Table 3). Although the differences in bare ground and prey abundance were not significant, the patterns are consistent with the predicted influence of these factors on territory size and how these factors vary with time since fire.

Seasonal territory characteristics for males that remained on the study site

The mean territory size for the seven males that remained in the study area for the entire season increased from 0.571 ($\pm$ 0.069) ha in the early season to 1.717 ($\pm$ 0.155) ha in the late season (t-test, t = -11.574, df = 6, p < 0.001; Fig 10). In addition, during the early season, each of the seven males maintained an exclusive territory in which no overlap occurred with other resident *A. s. floridanus*. In contrast, during the late season, only one of these territories was exclusive. Five territories overlapped with one other territory and one overlapped with two different territories (Figs 11a, b). Interestingly, only two territories overlapped one another during the early part of the season, and these were both of males that did not maintain territories

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through the later part of the season. Total overlap increased from 8.4% in the early season to 30.7% in the late season.

The early season territories of the seven persistent males contained fewer non-oak woody shrubs (t-test, t = -.6.223, df = 6, p = 0.001), more bare ground (t = 3.890, df = 6, p = 0.008; Table 4), and less prey than their late season territories (t = -2.842, df = 6, p = 0.029; Fig 12). Relatively little spatial shift occurred in the territory locations of persistent males. As during the early season, six of the seven persistent males maintained their late season territories in the more recently burned area of the study plot. In most cases, sparrows simply enlarged their early season territory. The percent of the early season territory that occurred within the boundary of the late season territory ranged from 44% to 98% (mean = 79 ± 0.04% SE), suggesting relatively little spatial shift.

Body Condition

I captured 8 of the 13 territorial males during the early season and 5 of the 8 males during the late season. Four males were caught during both the early and the late season. The remaining birds were not responsive to playback and were never captured. As a result, my sample sizes for the influence of body condition on territory size were extremely small; however, I examined the data for evidence of any patterns, even if the very low power excluded a high probability of detecting any significant differences. Five of the eight males that were caught in the early season continued to defend their territory during the late season. Neither body size nor condition differed between males that stayed and those that left. In addition, body size and condition did

not differ from the early season to the late season for the four males that were captured twice, nor was body size or condition useful in predicting territory size.

<div align="center">Discussion</div>

My results indicate that time since fire is the most important factor influencing variation in territory size and placement in *A. s. floridanus*. Although 52% of the study area had undergone two growing seasons since the last fire, only 33% of the early season territories occurred in this two-year rough. Most territories (67%) were established in the portion of the study area that had undergone only a single growing season post-burn, even though that comprised only 48% of the study area. Although these proportions were not statistically significant (largely because of relatively low sample sizes), they suggest preference for maintaining territories in areas that had recently burned. Within the one-year rough, territories were smaller and had higher quality habitat, as indicated by more bare ground and fewer shrubs. Regardless of whether sparrows had territories in the one or two-year rough, they appeared to demonstrate preference for sites that were more open and with fewer shrubs. Furthermore, males that maintained territories in the two-year rough were more likely to have larger territories with poorer habitat quality and lower prey abundance than the territories of males in the one-year rough. Those that defended territories in the two-year rough were more likely to abandon them. Of the males that persisted throughout the season, their early-season territories were smaller with higher quality habitat than in their late-season territories. However, although their territory size increased with time since fire, prey biomass also increased, a pattern opposite of what I predicted. As territory size

increased, so did the amount of overlap of territories suggesting that the relative benefit of maintaining exclusive access to resources had declined or the cost of defending them had increased. In fact, the late-season behavior of Florida Grasshopper Sparrows suggests a shift from territoriality to a home range system.

Territory Size

The mean territory size for all males (n = 13) for which I measured at least one territory, including both early and late-season territories, was 1.42 (± 0.24 SE) ha. This was smaller than the mean size of 1.8 ha (± 0.96 SD) determined by Delany et al. (1995). They observed territory sizes ranging from 0.6 to 4.8 ha; my estimates of territory size ranged from 0.36 to 4.1 ha. The locations of our studies differed; theirs was at Avon Park Air Force Range (APAFR), where the area is grazed by cattle at a relatively low density. In addition, at the time of their study most dry prairie was burned on a three-year rotation, so a greater proportion of their territories likely occurred in two- or even three-year roughs, whereas most of the territories I measured occurred in a one-year rough. Our methods of mapping territories also differed. They mapped territories once over a longer period of time (April through June), a time interval in which an increase in territory size occurred in my study. They also recorded locations of males at five-minute intervals rather than collecting locations of used perches. However, their sample size was larger (n = 30 territories for 21 males) and their study occurred over a span of four breeding seasons. Because fire was such an important determinant of territory size in my study, I conclude that the difference in fire history between APAFR and KPPSP likely influenced the difference in mean territory size that was observed during the two studies.

Habitat preferences

Consistent with my prediction, the sparrows preferentially selected habitat with more bare ground and fewer shrubs in which to place their territories. Tucker and Bowman (2006) reported that sites at APAFR where sparrows were most abundant and most likely to persist as the population declined were characterized by more bare ground and fewer shrubs, suggesting that these characteristics represent high quality habitat. In many studies bare ground was an important factor influencing habitat suitability for the sparrows (Delany et al. 1985, Delany and Linda 1994). Presence of bare ground allows the sparrows to forage more efficiently and provides optimal nest habitat. Tucker and Bowman (2006) introduced the importance of runways, bare spaces large enough ($\geq$ 4cm) for a sparrow to move through the habitat, which offer cover from aerial predators while foraging. In their study runways were positively correlated with the amount of bare ground within a habitat. Although I did not attempt to measure runways, it seems likely these structural features were more common both within sparrow territories and within the portion of my study area that was only a single growing season post-burn, because these areas had a greater amount of bare ground. However, prey biomass was not significantly different between territories and unoccupied areas; thus the preference for areas with more bare ground (i.e., runways) suggests a preference for habitat that facilitates safe and effective foraging rather than food abundance.

The sparrows avoided areas with a high percent shrub cover, consistent with findings from Delany and Linda (1994) and from Whitmore (1981), who studied the migratory subspecies *A. s. pratensis*. However, neither of these studies separated the shrub types as I did in my study. I found that the sparrows avoided palmetto and non-oak woody shrubs but not *Q. minima*. Delany

and Linda (1998) found that nests are primarily shielded by *Q. minima* so it may be more beneficial for sparrows to include oak within their territories than to avoid all shrub types. I also did not find a difference in grass cover between territories and unoccupied areas, which is inconsistent with findings from previous studies. Whitmore (1981) and Delany and Linda (1994) found that unoccupied areas held a higher percent cover of grass than territories. However, neither of these studies were conducted in undisturbed native dry prairie, thus other influences such as grazing might have altered habitat structure, both within territories and in unoccupied habitat, and altered the apparent preferences of sparrows.

Prey biomass was greater in unoccupied areas than in territories. However, the numerical abundance of most species of arthropods collected was higher in territories, suggesting that more but smaller arthropods occur in areas selected by sparrows. A larger number of arthropods in a habitat with an abundance of bare ground may increase the probability of capture by the grasshopper sparrows. Also, sparrows are relatively small birds averaging only about 17-18g, and virtually nothing is known about their preferred size of arthropod prey. It may be that the sparrows are selecting territories based on a size distribution of prey appropriate to their gape size and foraging abilities.

Territory characteristics of males that stayed versus those that left

The six males that abandoned their territories after the early season survey had larger territories with marginally poorer habitat than those of the males that persisted. Three of those six territories plus a majority of a fourth territory occurred within the two-year rough, which may have indicated an inability of those males to defend higher quality habitat. Two of these six

males also had overlapping territories, suggesting the territories may not been of high enough quality to make them economically defensible; i.e., the effort to maintain exclusive access to those resources may have been greater than the benefit. Six of the seven males that persisted had territories in the one-year rough. Those males had smaller territories with higher quality habitat (more bare ground, fewer shrubs). Consistent with my prediction, as the season progressed and time since fire increased, habitat quality decreased and the seven males that persisted increased their territory sizes. As the habitat quality decreased, it is likely that the cost-benefit equation of defense shifted and the territory was less economically defensible. Bare ground decreased, which may have reduced the ability of the sparrows to forage successfully. Consistent with a change in economic defensibility, territories became less exclusive and the amount of overlap of territory boundaries increased. Unexpectedly, the amount of prey increased as the season progressed, which was not consistent with my prediction of decreasing resources with increased time since fire. This may be a factor of the seasonality of prey species; sparrows may time their breeding so that the presence of fledglings coincides with this increase in prey biomass (Komen and Brown 1993, Schoech 1996).

The demand for resources should increase with the arrival and development of young. Changes in the demand for resources also alter their economic defensibility. The cost of territory defense is greater if the time and energy spent in defense could be better spent in provisioning young. Consistent with this idea, if prey abundance increases, the need to maintain exclusive access may decrease, thus we should expect a decrease in territoriality. This was evident in the change in male behaviors; they became less territorial during the period in which many of them were provisioning dependent young. Territories increased in size, but also markedly increased in

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overlap. Therefore, it is likely that sparrows shifted their activities from defense of their territories to provisioning their young.

Territoriality and the Demography of the Florida Grasshopper Sparrow

The results of my study are entirely consistent with what is known about sources of variation in the demography *A. s. floridanus*. The sparrows favored establishing territories in the one-year rough, and those territories were smaller and more exclusive, suggesting that the resources within were of higher quality. As time since fire increased, both between years (i.e., the one-year rough versus the two-year rough) and seasonally (early vs. late in the one-year rough), territories tended to increase in size, suggesting a decline in the relative quality of resources or an increase in the costs required to defend them. This change in the economic defensibility of territories may have been so great that most of the males in the two-year rough abandoned their territories in mid-season. During the 2008 breeding season several significant summer burns occurred in multiple sites throughout KPPSP where *A. s. floridanus* is known to defend territories. One of the males that abandoned his territory in the two-year rough was found defending a territory in a newly-burned site during the late breeding season. If a male's early-season territory was not comprised of optimal dry prairie habitat, it may have been more beneficial for him to abandon his territory and seek better reproductive opportunities in newly-burned prairie.

Consistent with this pattern of spatial use, Delany et al. (2002) found that reproductive success decreased with time since fire. Productivity was highest one year post-fire and declined at two years post-fire, but still was high enough to be self-sustaining. Productivity then declined

dramatically at three years post-fire to the point where reproduction could not replace mortality, leading to a population sink. These demographic patterns are strong evidence that the quality of resources essential to reproductive success declines with time since fire. As the quality of resources declines, the benefits associated with maintaining exclusive access decline and the profitability of maintaining territories declines as well. Thus the demographic patterns observed by Delany are consistent with the patterns of territorial behavior I observed in this study.

Management

Prescribed burning during the dormant season (December – March) at one to three-year intervals is the most commonly used management practice for dry prairie (Pranty and Tucker 2006). However, a three-year rough is not adequate to support a source population of sparrows, as reproductive success is significantly lower than in more recently burned dry prairie. Population density also declines, and this study suggests that the decline in density may occur because individual sparrows cease to defend territories in three-year roughs. As time since fire increases, resources decline and habitats are inadequate to support a source population. Therefore, a mosaic of fire regimes is optimal for a sparrow population. This mosaic would constantly provide newly-burned habitat with high quality resources and economically defensible territories into which sparrows occupying suboptimal habitats could move.

APPENDIX A: FIGURES AND TABLES
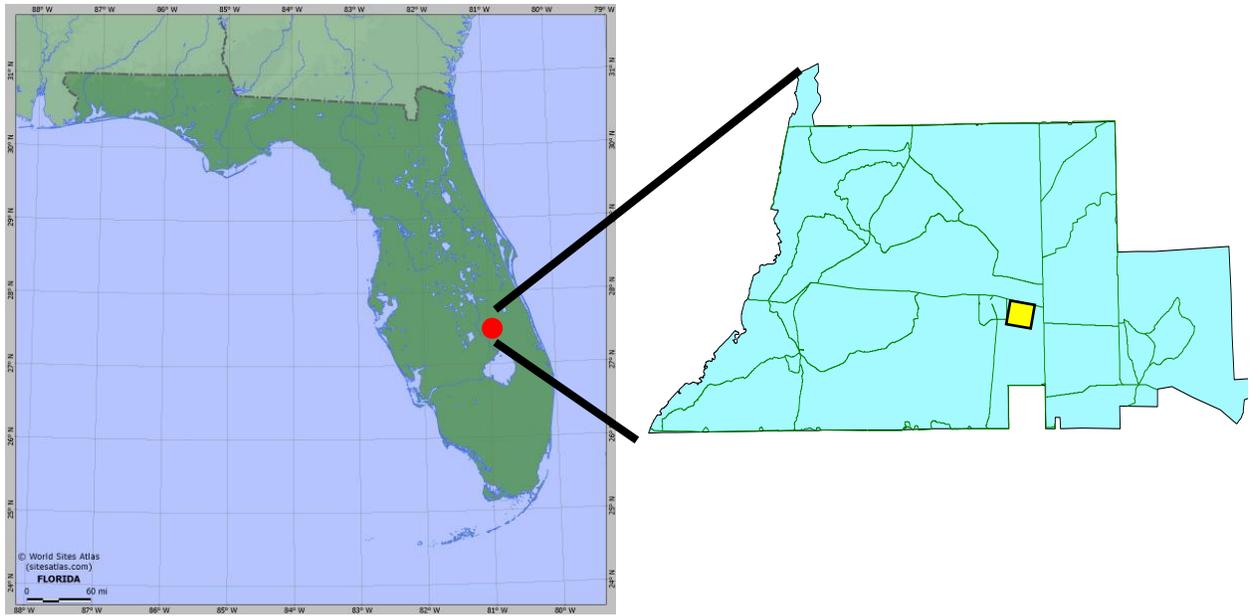
Figure 1: Location of KPPSP in south-central Florida and of the 100-ha study plot within Kissimmee Prairie Preserve State Park (yellow square)
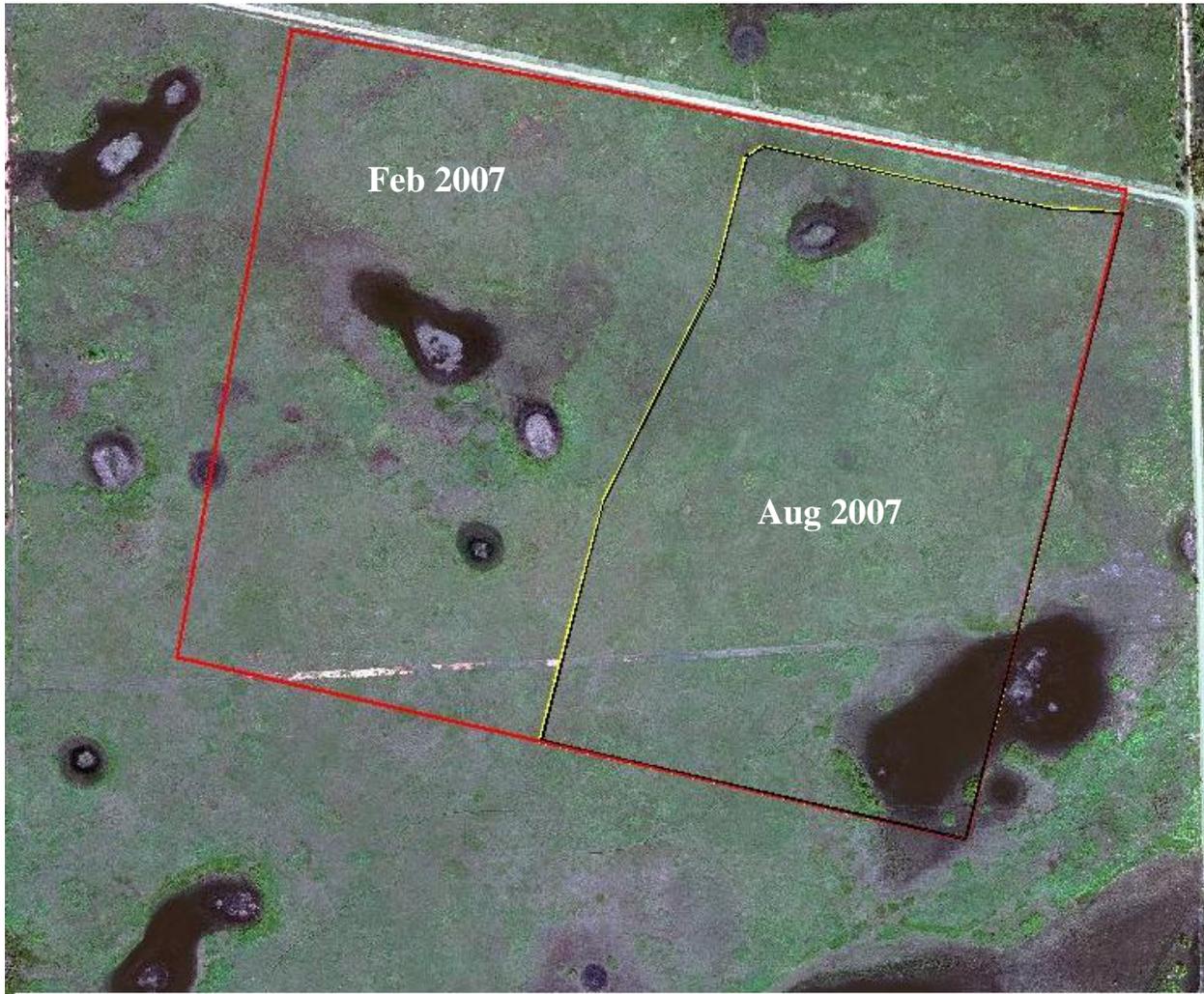
Figure 2: Study plot (red outline) and the location of fire line separating fires that occurred February 2007 and August 2007 (yellow outline).
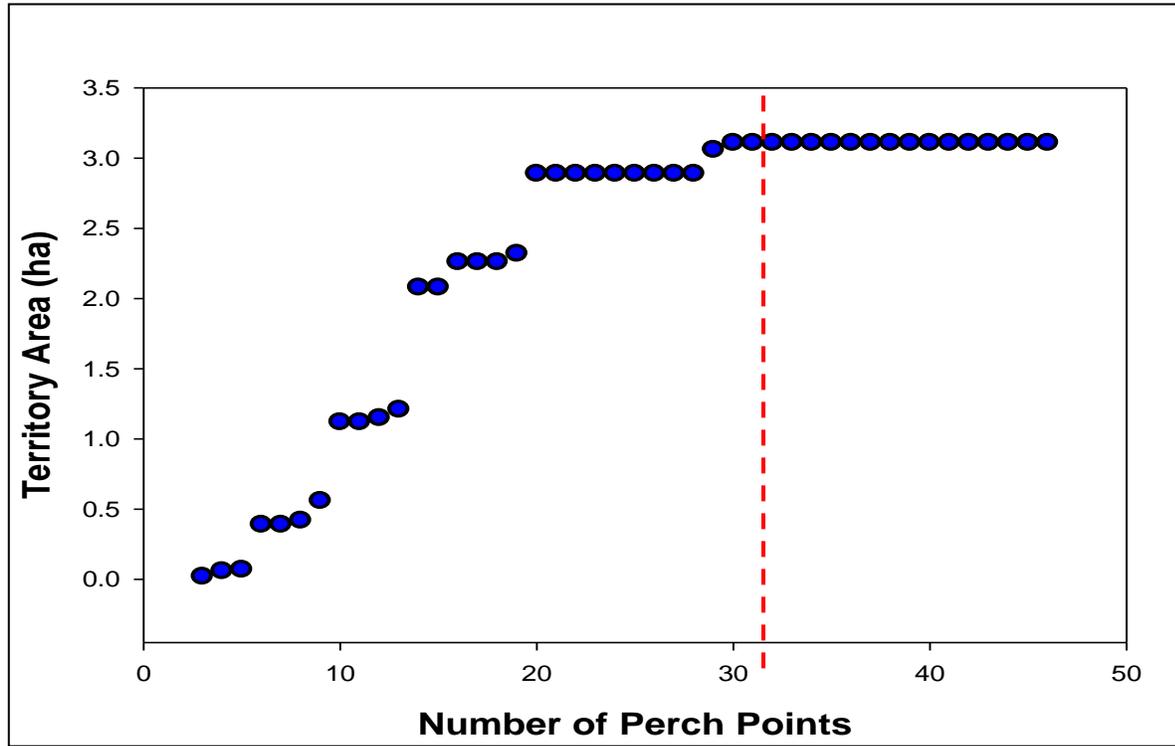
Figure 3: Asymptote of individual territory area with number of perch points. This territory reached its area asymptote at 31 perch locations.
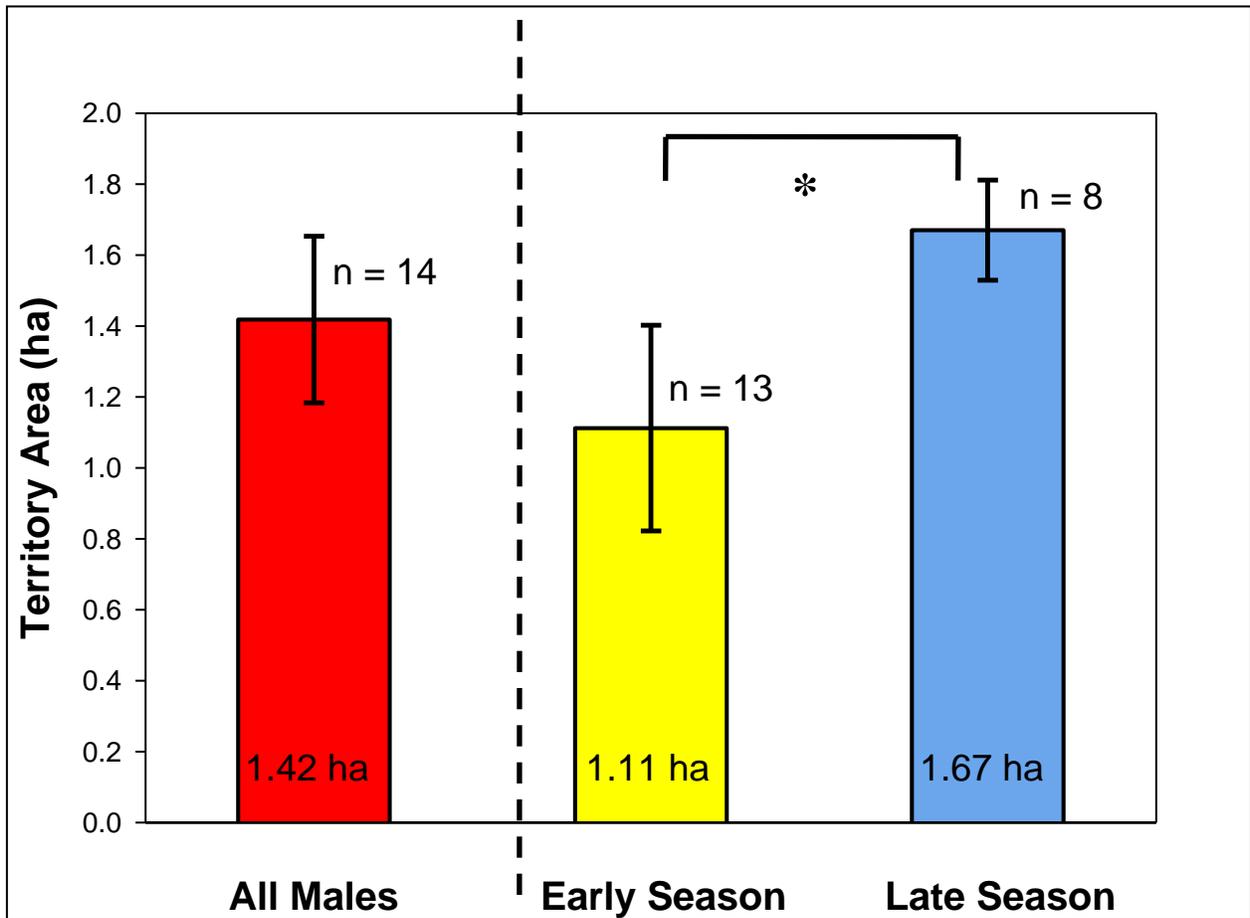
Figure 4: Territory sizes (in ha) of all males observed during the season as well as the territory sizes in the early and late seasons. Error bars denote ± 1 SE. Territory sizes increased significantly from the early to the late season.
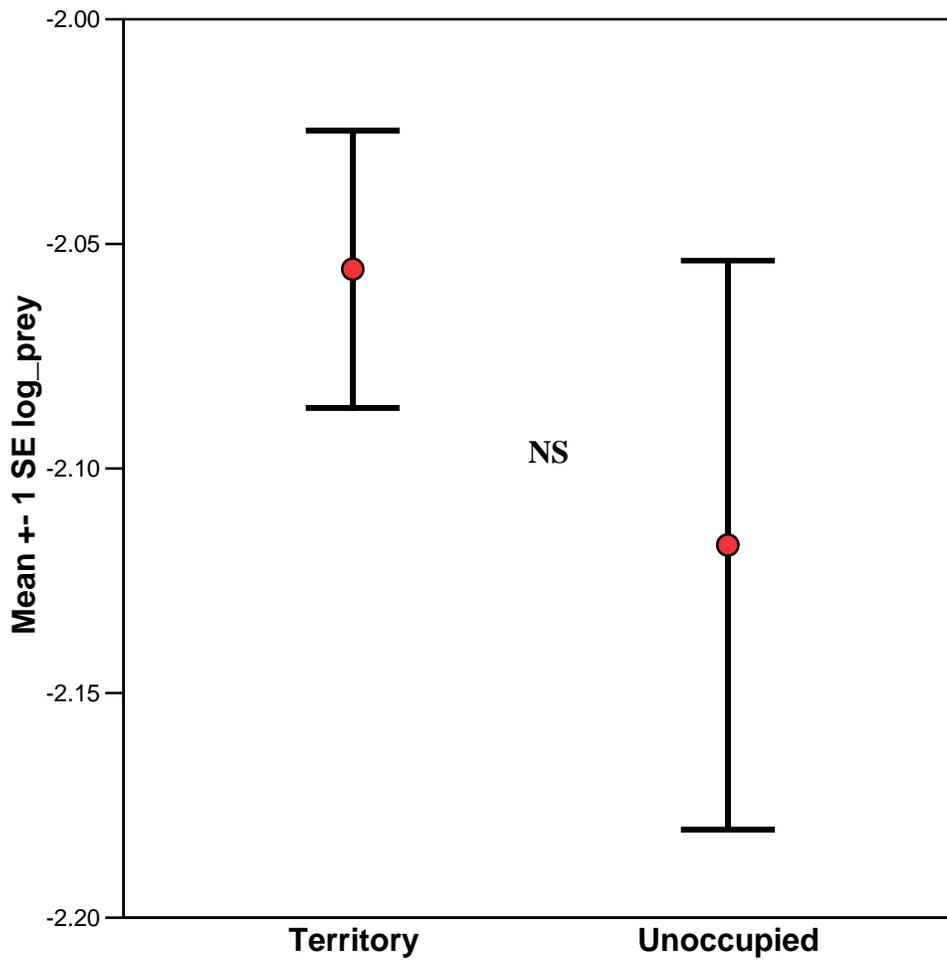
Figure 5: Territories and unoccupied areas did not hold different levels of prey biomass during the early season. Error bars denote ± 1 SE.
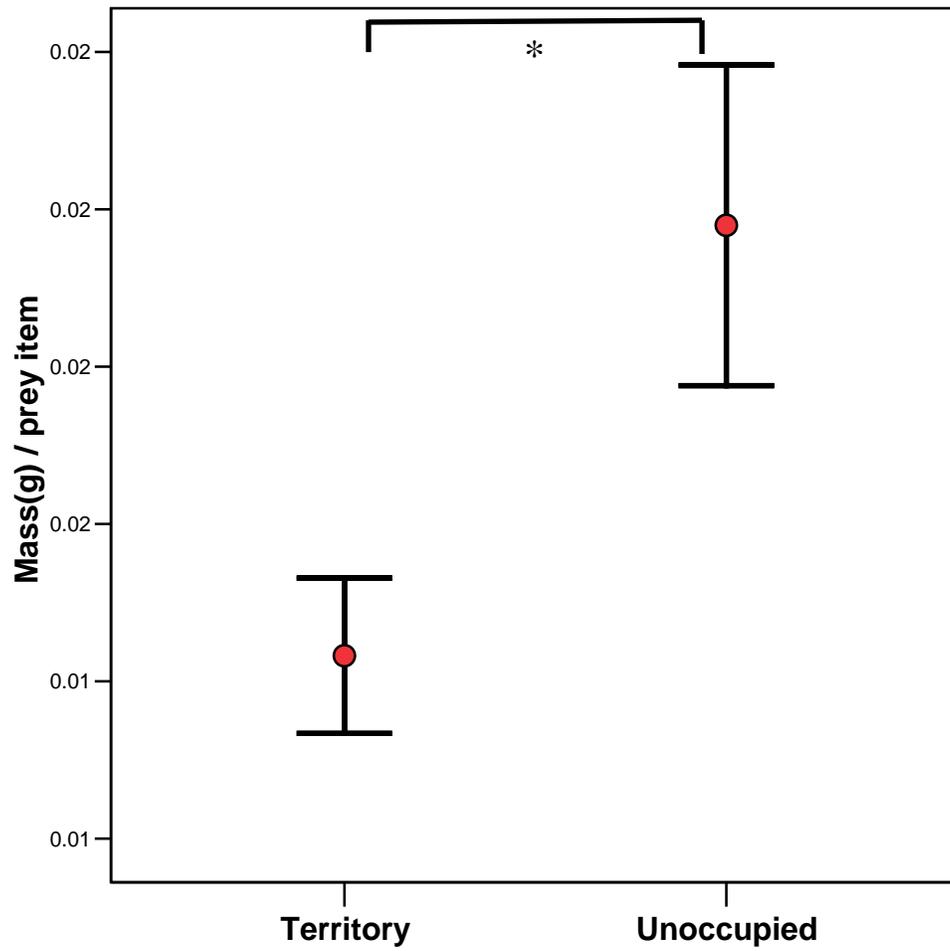
Figure 6: The mean mass per individual prey item was significantly smaller in territories than in unoccupied areas. Error bars denote ± 1 SE.
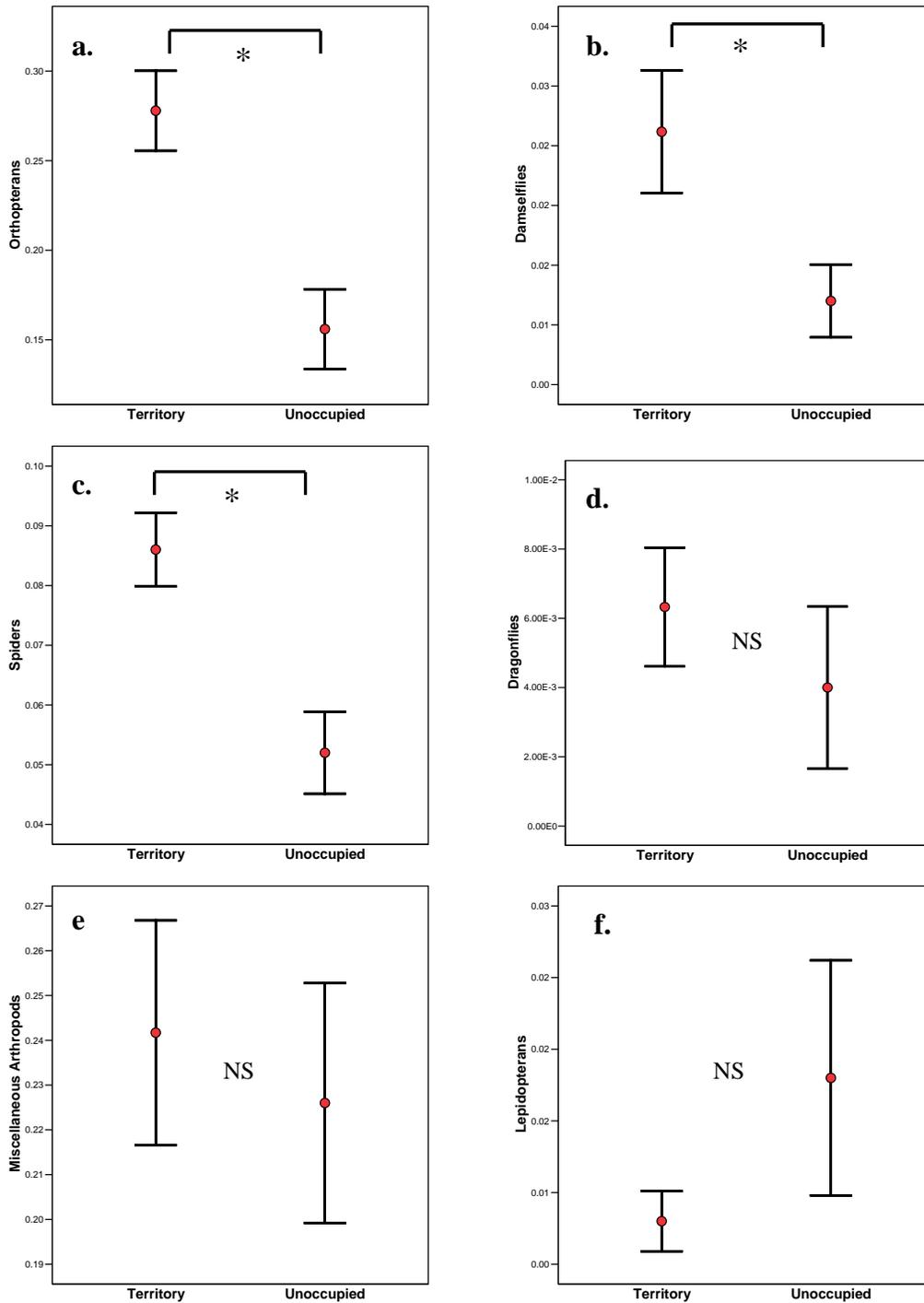
Figure 7: Numerical abundances of a) orthopterans, b) damselflies, and c) spiders were significantly higher in territories than in unoccupied areas. d) Dragonflies, e) miscellaneous prey items and f) lepidopterans did not differ. Error bars denote ± 1SE.
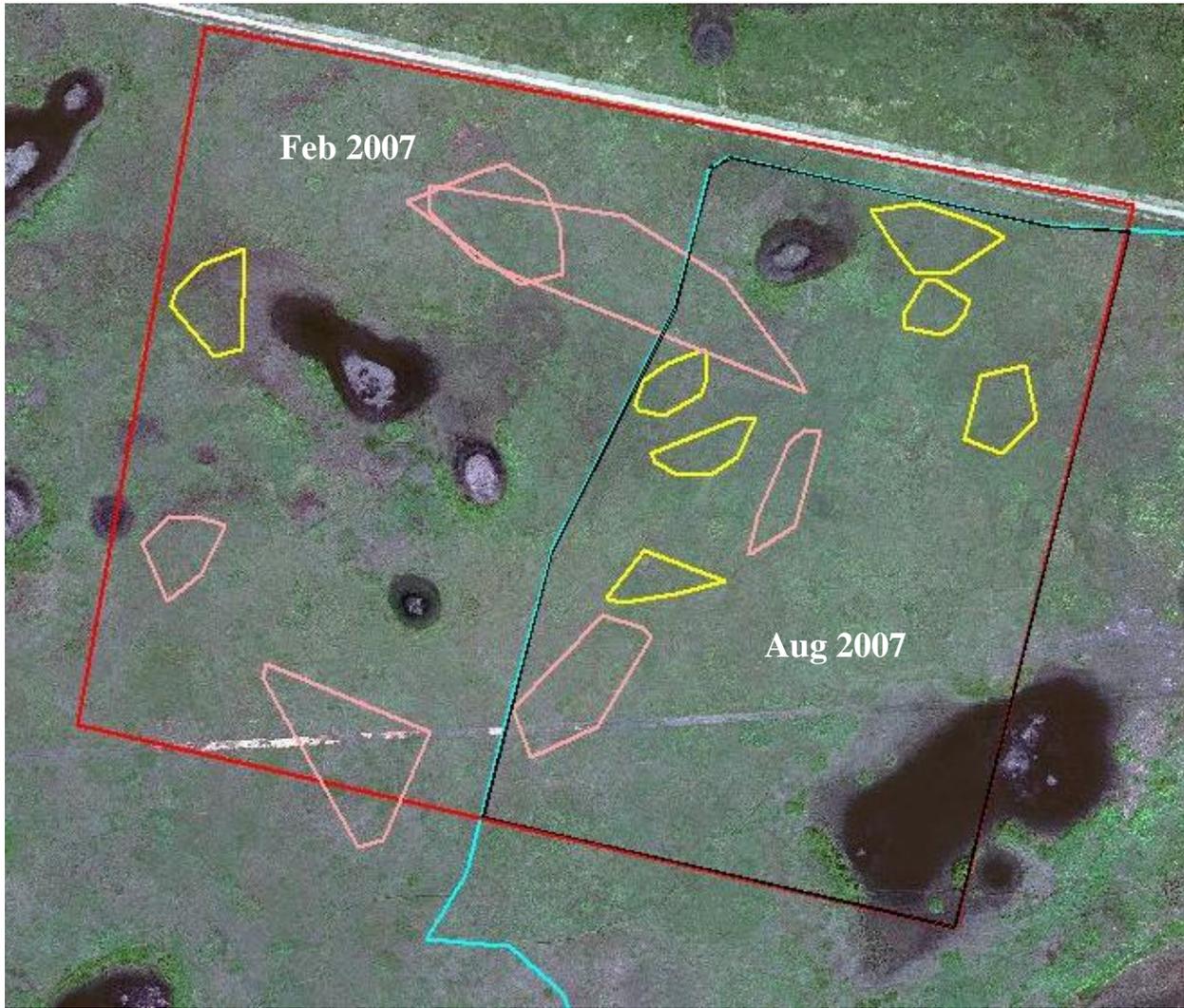
Figure 8: Locations of early season territories of males within the study plot (red outline). Males that stayed throughout the season are outlined in yellow and males that abandoned their territories after the early season are outlined in pink. Six of the seven males that remained throughout the season held territories in the more recently burned area.
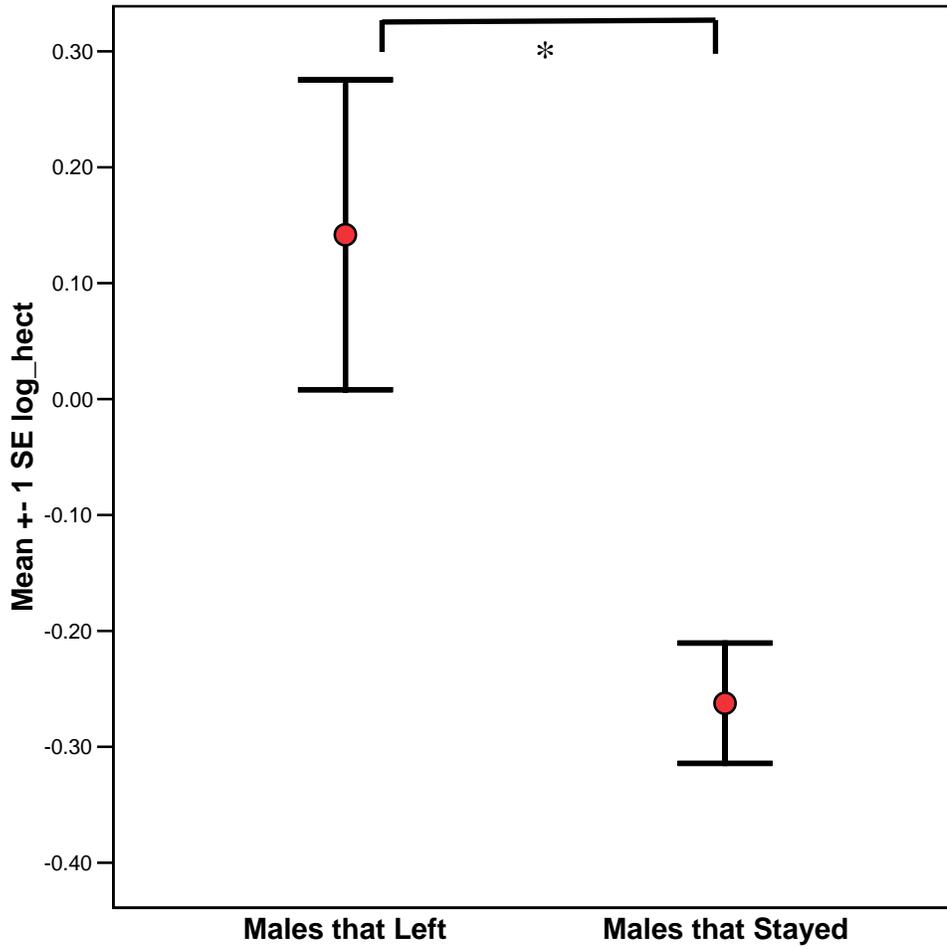
Figure 9: Males that stayed throughout the entire season had significantly smaller territories than males that abandoned their territories after the early season. Error bars denote ± 1 SE.
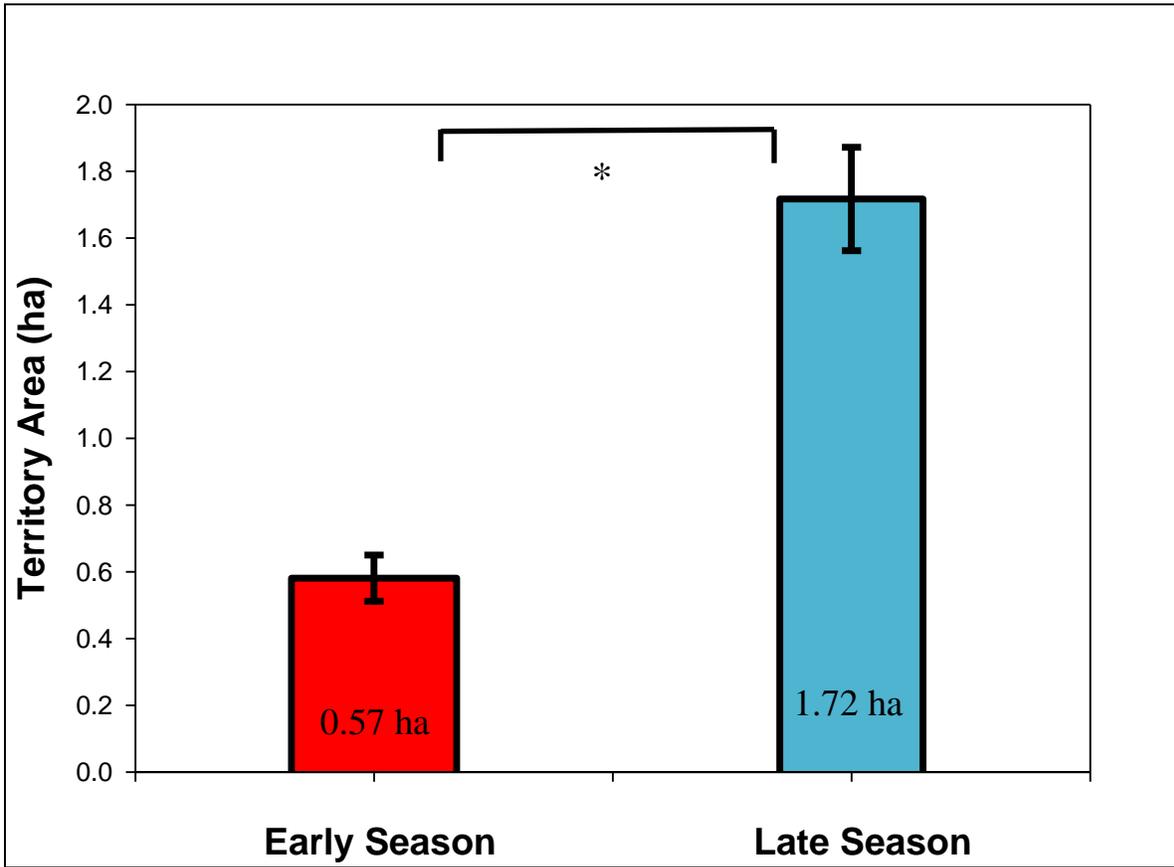
Figure 10: Territories of the seven males that stayed throughout the season increased significantly in size from the early season to the late season. Error bars denote ± 1 SE.

Figure 11: a) Early season territories of the males that stayed throughout the entire season. b) Late season territories of the males that stayed throughout the season. The size of territories significantly increased and overlap of territory boundaries developed during the late season. The solid white territory is of the male that settled a territory between the early and late surveys. His territory overlapped with the only male that remained in two-year rough.
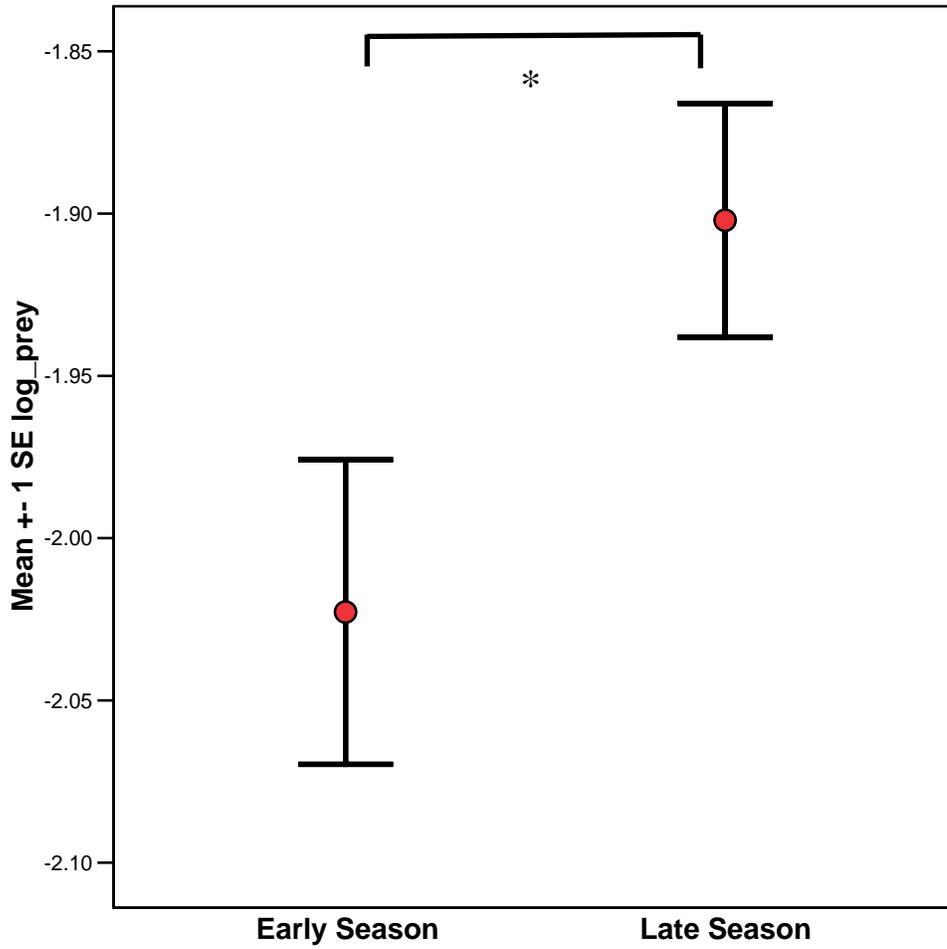
Figure 12: The early season territories of the seven males that stayed throughout the season had significantly less prey biomass than their late season territories. Error bars denote ± 1 SE.

Table 1: *A. s. floridanus* selected habitat that had less palmetto, more bare ground, and fewer non-oak woody shrubs for their territories.

	Territories (n = 13)	**Unoccupied** (n = 20)	
	Mean % (±1 SE)	**Mean % (±1 SE)**	*p* – value
Palmetto	14.7 (± 1.9)	23.6 (± 2.5)	0.015
Oak	24.1 (± 2.3)	25.9 (± 3.7)	0.662
Non-oak Woody Shrubs	2.1 (± 0.5)	5.1 (± 1.3)	0.033
Grass	31.8 (± 2.1)	30.1 (± 3.4)	0.760
Bare Ground	38.5 (± 2.9)	30.4 (± 2.2)	0.028

Table 2: a) AICc values for all models ranked in ascending order relative to ΔAIC_c; Deviance is the difference in the -2log-likelihood between each model and the global model, K is the number of parameters in the model, ΔAIC_c is the adjusted AIC_c relative to the top model; and wi is the normalized weight of the model. b) Cumulative weights for each variable are shown below.

a.

Model	Deviance	K	$\Delta AIC_c{}^a$	wi	Model Likelihood
Fire	65.40	2	0	0.88	1.00
Fire + Habitat	64.57	3	5.72	0.05	0.06
Habitat	64.57	2	5.80	0.05	0.05
Prey	64.54	2	7.62	0.02	0.02
Prey + Fire	64.53	3	12.30	0.00	0.00
Habitat * Fire	64.52	4	18.82	0.00	0.00
Prey + Habitat	64.52	3	23.52	0.00	0.00
Prey + Habitat + Fire	64.52	4	24.45	0.00	0.00
Prey * Habitat * Fire	64.52	5	27.40	0.00	0.00
Prey * Fire	64.52	4	37.62	0.00	0.00
Prey * Habitat	64.52	4	58.66	0.00	0.00
Prey + Habitat +Fire +(Prey * Habitat) + (Habitat * Fire) + (Prey * Fire)	64.52	7	58.74	0.00	0.00

[a] The lowest $AIC_c = 64.52$

b.

Cumulative Weight	
Fire	0.93
Habitat	0.10
Prey	0.02

Table 3: Males that stayed had fewer non-oak woody shrubs than males that left after the early season. They also showed a marginal trend towards more bare ground.

	df	Wald	p – value
Palmetto	1	0.13	0.72
Oak	1	0.00	0.99
Non-oak Woody Shrubs	1	3.47	0.06
Grass	1	1.96	0.16
Bare Ground	1	2.33	0.13

Table 4: Late season territories of the males that stayed had more non-oak woody shrubs and more bare ground than the early season territories of the same males.

	t	df	*p* – value
Palmetto	-0.998	6	0.357
Oak	-0.397	6	0.705
Non-oak Woody Shrubs	-6.223	6	0.001
Grass	-1.611	6	0.158
Bare Ground	3.890	6	0.008

APPENDIX B: BODY CONDITION INDICES

Fat Scoring (from MAPS protocol):

0 – none: No fat in the furculum or anywhere on the body

1 – trace: A very small amount of fat in the furcular hollow (<5% filled) but not enough to cover the bottom of the furculum and no fat or just a trace of fat is present under the wing, on the abdomen, or anywhere else on the body; or, if there is not fat in the furcular hollow, at least a trace of fat is present under the wing, on the abdomen, or both

2 – light: The bottom of the furculum is completely covered by the furcular hollow, is less than 1/3 filled, and a small amount of fat may be present under the wing, on the abdomen, or both; or, if there is no fat in the furcular hollow, a covering pad of fat is definitely present under the wingpit and, usually, on the abdomen.

3 – half: The furcular hollow is about half full (from 1/3 to 2/3 filled), and a covering pad of fat is definitely present under the wingpit and, usually, on the abdomen; or, if there is no fat in the furcular hollow, a thick layer of fat under the wing as well as on the abdomen is well rounded.

4 – filled: The furcular hollow is full (from 2/3 full to level with the clavicles) and a thick layer of fat also occurs under the wing and on the abdomen; or, if the fat in the furcular hollow is not full, the fat under the wing as well as on the abdomen is well rounded.

5 – bulging: The furcular hollow is more than full that is, the fat is bulging slightly above the furculum. The fat under the wing as well as that on the abdomen is also well rounded.

6 – greatly bulging: Fat is bulging greatly above the furculum. Large mounds of fat occur under the wing and on the abdomen.

7 – very excessive: The fat pads of the furculum, wingpit, and abdomen are bulging to such an extent that they join. Nearly the entire ventral surface of the body is thus covered with fat, and fat even extends onto the neck and head.

Feather Mites Scoring (Harper 1999):

0 – none: no mites visible

1 – light: some mites visible but not obviously exceeding 20 mites

2 – moderate: more than 20 mites visible, along up to half of rachis or up to half of barbs

3 – heavy: mites along most of rachis or between over half of barbs

Pectoral Muscle Scoring:

0 – Sternum sharp, muscle depressed

1 – Sternum easy to distinguish but not sharp, muscle neither depressed, sharp nor rounded

2 – Sternum still distinguishable, muscle slightly rounded

3 – Sternum difficult to distinguish, muscle rounded (full)

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