

**Resource Partitioning between Generalist Competitors  
&  
Factors Affecting the Detectability of Scat by Dogs**

by

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## Abstract

Syntopic generalist competitors like *Procyon lotor* and *Didelphis virginiana* must partition resources in order to coexist. Our study examined spatial and temporal resource partitioning using occupancy modeling to account for within-species selection for resource attributes. The presence of a competitor had a non-significant positive effect on the use of spatial and temporal resources by raccoons and opossums, indicating that resource use is independent of competitor presence. However, raccoons and opossums were never photographed together indicating they avoid direct confrontations.

Scat and its unique scent degrade over time. The ability of trained dogs to locate the scat by smell can be affected by the size, amount of rainfall, age, and location of the scat. Scat samples are less likely to be detected as they age, receive greater amounts of rainfall and decrease in size. Scat in pine is most likely to be detected, then hardwood, then clear-cut habitat types. Unequal probabilities of scat detection should be accounted for in studies using this method.

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## **Resource Partitioning between Generalist Competitors**

### **Introduction**

Competition has often been the focus of ecological research because it is an important factor in determining species co-existence (Tilman, 1994; Tokeshi, 1999). A key theory of competition states that when two species share a resource, and that resource is limited, the fitness of one species will be lowered by the presence of the other (Gause, 1932; Hardin, 1960). Moreover, in a stable environment, one of the competing species eventually will be driven to extinction if the two competitors have perfect overlap in resource use (Hardin, 1960). Consequently, if ecologically similar species are to coexist they must somehow differ in their use of resources (Gause, 1932). Indeed, partitioning of resources, such as prey items, habitat types, units of physical space, and time periods of activity, has been documented for many competing species (Bothma *et al.*, 1984; Heller and von Helversen, 1989; Litvaitis and Harrison, 1989; Fedriani *et al.*, 2000; Kamler *et al.*, 2003; Moreno *et al.*, 2006).

However, relatively few studies have been conducted on the competitive interactions of generalist species; those that have broad ecological niches. Specifically, there is a paucity of research on how resources are partitioned by medium sized (1-15kg) generalist carnivores and conclusions from past research have been equivocal (Kissell and Kennedy, 1992; Neale and Sacks, 2001; Ginger *et al.*, 2003). For example, red foxes (*Vulpes vulpes*) switched prey items in the presence of a competitor, the coyote (*Canis*



*latrans*), in one study but not another (Azevedo *et al.*, 2006; Mukherjee *et al.*, 2009). Understanding how competitive interactions amongst generalist mesocarnivores are mitigated is important for management and conservation because changes in mesocarnivore presence/absence or use of resources can have large impacts on the greater ecological community (e.g., Buskirk, 1999; Ives *et al.*, 2005; Eubanks, 2005).

Syntopic generalist species make interesting competitors because the species typically share many resources and are extremely adaptable, allowing the competitors to partition resources in a variety of ways to coexist. For example, research on coexisting generalist herbivores found that the species evolved unique biochemistry requirements to allow them to occupy different nutritional niches (Behmer and Joern, 2008). Similarly, research on generalist rodents found that competitors may coexist by exploiting different temporal niches (Abramsky *et al.*, 2001). Furthermore, generalist carnivores in Africa coexisted by partitioning habitat types (Fuller *et al.*, 1989).

Northern Raccoons (*Procyon lotor*) and Virginia Opossums (*Didelphis virginiana*) are generalist mesocarnivores and potentially strong competitors. Raccoons and opossums occur together throughout much of their distribution, have comparable expansive diets, and utilize a similarly wide range of habitats (Gardner, 1982; Kaufmann, 1982). Not only do opossums and raccoons share a variety of resources, but they are similar in body size, making them relatively equal competitors (Buskirk, 1999; Reid, 2006). Raccoons have the advantage of being slightly larger than opossums and are more aggressive in temperament (Lotze and Anderson, 1979; Gardner, 1982; Reid, 2006), facilitating dominance by raccoons in direct interactions (Stuewer, 1943). However, opossums have the advantage of numbers, producing as many as 24 young a year

(McManus, 1974). Such high reproductive rates increase the likelihood that opossums can exploit new resources before raccoons find them (Kissell and Kennedy, 1992; Chamberlain and Leopold, 2001). Thus, raccoons and opossums are well-matched competitively and provide an exciting system in which to study resource partitioning between generalist mesocarnivores.

Previous research has resulted in ambiguity over whether raccoons and opossums partition resources. Spatial association between the species is common but partitioning of spatially explicit resources (e.g. land cover type, understory density) are also prevalent (McKeever, 1959; Kissell and Kennedy, 1992; Wilson, 1996; Ginger *et al.*, 2003; Carver *et al.*, 2011). A removal study indicated that raccoons do not affect the diet of opossums, but can negatively affect the opossum's use of both macro and micro-habitats (Kasparian *et al.*, 2002; Ginger *et al.*, 2003). Sometimes the two species use separate den sites, but at other times dens are used by both species, occasionally at the same time (Shirer and Fitch, 1970; Gardner, 1982; Seidensticker *et al.*, 1987). Raccoons and opossums were observed in the same place at the same time in a study by Carver *et al.* (2011) but not by Ladine (1997); thus, avoidance of direct interactions between the two species is uncertain. Raccoons and opossums were found to have different activity patterns in studies by Wilson (1996) and Ladine (1997) but not Carver *et al.* (2011). Both species are active throughout the night. However, opossum activity peaks slightly later than raccoon activity, suggesting possible temporal resource partitioning (McManus, 1974; Lotze and Anderson, 1979). Thus, the findings from previous research have been equivocal on how raccoons and opossums partition resources to cope with the effects of competition and further study is needed.

A key limitation of previous research, which may explain differences in estimates of resource partitioning among studies, is that previous studies often didn't account for the effects of selection by the competitors for particular resource attributes—characteristics of the resource other than the presence or absence of a competitor (e.g., Kissell and Kennedy, 1992; Wilson, 1996; Ginger *et al.*, 2003). If two species mitigate competition through differences in selection for particular resource attributes (e.g., habitat characteristics, prey size, time of day) then the estimated effect of competitor presence on resource use should be negative, indicating that competing species don't use the same resource. However, consider a situation in which two competitors both select resources with the same attributes (e.g., petal color when the resource is a flower), but still attempt to decrease competitive interactions with each other by partitioning the use of the resource. A simple analysis of resource use would suggest that both species are often found together, from which a researcher could wrongly conclude that the species do not attempt to decrease their competitive interactions through resource partitioning (Gilpin and Diamond, 1982; Peres-Neto *et al.*, 2001; MacKenzie *et al.*, 2004). Yet, an analysis that examined resource partitioning between the species while accounting for selection of other resource attributes should correctly demonstrate that the species tend to avoid the resource when the species' competitor is present. Thus, research that attempts to examine partitioning of resources through analysis of resource use needs to account for the potential impact that within-species selection for resource attributes may have on estimates of competitive effects.

The purpose of this study was to examine how Northern Raccoons (*Procyon lotor*) and Virginia Opossums (*Didelphis virginiana*) partitioned spatial and temporal

resources across a large geographic area. Specifically, we estimated the effects of raccoon and opossum presence on competitor space and time use patterns across Alabama while accounting for within-species selection for other resource attributes such as habitat type and time of day. By accounting for such confounding effects, we can potentially clarify the ambiguity of previous research regarding the spatial and temporal resource partitioning of raccoons and opossums. Based on niche theory (Gause, 1932; Hardin, 1960; Buskirk, 1999), and results from the previous studies detailed above, we predicted that univariate analyses of competition between the species would reveal evidence of species attraction, but that analyses of competition that accounted for the confounding effects of selection for other resource attributes should indicate that the two species avoid each other spatially, temporally, or both.

## **Materials and Methods**

*Study Areas-* This study was conducted as part of a larger project that sampled for biodiversity across the state of Alabama (J.B. Grand, Auburn University, *unpublished data*). Eight public properties, including state parks and wildlife management areas, were selected for survey across the northern half of the state. The ecoregions of the properties surveyed included: interior plateau, ridge and valley, southwestern Appalachians, southeastern plains, and piedmont (Griffith *et al.*, 2001). Each of the eight study areas was divided using ArcGIS 9.2 (Environmental Systems Research Institute, Inc., Redlands, CA) into a grid of potential sampling units consisting of points spaced 250m apart. The potential sampling units were defined as the point and the circular area contained within a 125m radius of the point. Majority land cover type was determined for

each potential sampling unit using the 2001 National Land Cover Database (Homer *et al.*, 2004). Random selection of sampling units was stratified by land cover type in order to ensure that each land cover category was included and surveyed proportional to its availability within the eight study areas. Ultimately, 358 sample units were selected for survey.

*Field Surveys-* To study competitive interactions between raccoons and opossums, we first determined the presence or absence of opossums and raccoons in each of the 358 sample units. We deployed a non-invasive infrared digital trail camera at each sample unit for 72 hours (RapidFire PC85, Reconyx, Inc., Holmen, WI). Data were collected during the months of August to December in 2009 or 2010. The cameras were programmed to take photographs when triggered by the internal motion sensor and at 2 minute time-lapse intervals. Commercially available predator lures (Caven's Minnesota Trapline Products, Pennock, MN) were administered two meters in front of each camera. For each photograph, the location, time taken based on the camera's time stamp, and presence or absence of raccoons or opossums was recorded. The average temperature (°C), wind speed (kph), humidity, and rainfall (cm) at the nearest weather station to each surveyed property was determined for each hour. At each camera location, canopy and understory cover were recorded at time of camera set-up. The average percent canopy cover was estimated using point-quarter sampling (modified from Brower and Zar, 1977). Specifically, the distance from the camera to the trunk of the nearest tree was divided by the distance over which that tree's canopy extended toward the camera. This ratio was then averaged over each of the four quadrants (northwest, northeast, southeast,

southwest) to generate an index of percent canopy cover for the camera location. If there was no tree within 25 meters of the camera the percent canopy cover was recorded as zero. The percentage of 56 8cm squares visible on a 128 by 64cm profile board at 10, 15, and 20 meters from the camera in the four cardinal directions was averaged to estimate understory visibility (Nudds, 1977). The 2001 National Land Cover Database was used to assign each sample unit a majority land cover classification in one of seven general land cover classes: agriculture, developed, hardwood, pine, mixed hardwood-pine, riparian, and scrub (Homer *et al.*, 2004).

*Analysis-* To examine how raccoons and opossums partition spatial and temporal resources, we used occupancy analysis (MacKenzie *et al.* 2002; 2006) to estimate the effect of the presence/absence of one species on the probability of the presence/absence of the other species. We used occupancy analysis because it accounts for imperfect detection – instances where a species uses a resource and yet goes undetected in sampling (MacKenzie *et al.*, 2002; 2006). In occupancy analysis, a species' probability of use ( $\psi$ ) for a resource is estimated from the presence/absence history constructed from repeated samples of each resource; the repeated samples are used to estimate the probability of detection ( $p$ ) of the species for that resource (MacKenzie *et al.* 2002; 2006). The resource of interest for our analysis of spatial resource partitioning was the sample unit, and the repeated samples were 24 3-hr blocks. The resource of interest for our analysis of temporal resource partitioning was each hour on a given date, and the repeated samples were the sampling units surveyed during that date and hour combination (range 2-23 replicates).

Occupancy analysis allows for the incorporation of covariates such as competitor presence/absence or land cover type that are specific to each replicate of the resource and may affect resource use; incorporating resource attributes as covariates in the model accounts for within-species selection of particular resources attributes (MacKenzie *et al.*, 2004). Our occupancy models also included covariates (e.g., time of day, land cover type, or amount of precipitation) that could affect the probability that a species would be detected (MacKenzie *et al.*, 2002; 2006). Covariates are included in occupancy models through a logit link function:

$$\psi_x \text{ or } p_x = \exp(\beta_0 + \beta_1 x_1 + \dots + \beta_i x_i) / 1 + \exp(\beta_0 + \beta_1 x_1 + \dots + \beta_i x_i),$$

where  $\beta_i$  is a coefficient estimate and  $x_i$  is the covariate influencing occupancy or detection.

Based on preliminary analyses (*unpublished*) and results from previous studies, we always included detection covariates for average temperature (°C), wind speed (kph), humidity, and rainfall (cm) in our models for spatial resource partitioning (Ladine, 1997; Carver *et al.*, 2011). For the models of temporal resource partitioning, we always included detection covariates for land cover type, canopy cover, understory visibility, and property, since differences in population density or selection for spatially associated resources may influence detection of species across spatial replicates within any given hourly block (Kissell and Kennedy, 1992; Wilson, 1996; Ginger *et al.*, 2003).

Our spatial and temporal models included a variable accounting for the effect of competitor presence on species' resource use, an occupancy modeling approach similar to that used by Sarmiento *et al.* (2011). Where a competitor was detected at the resource the value of the competitor presence variable was always 1.0. For those resources where the

competing species was not detected, we estimated the probability of resource use ( $\psi$ ) for the competitor from a selected best model chosen from a set of *a priori* models ranked using AICc (Burnham and Anderson, 2002). The resource use covariates considered for inclusion in the spatial analysis models included percent canopy cover, percent understory visibility, land cover class, and property (Kissell and Kennedy, 1992; Wilson, 1996; Ginger *et al.*, 2003). Property was considered because the sample units were nested within the eight properties and the properties varied in opossum and raccoon densities. The *a priori* models considered for predicting single-species spatial resource use were a global model including all covariates, models with only property, land cover type or microhabitat measures (% canopy and understory visibility), and a model with land cover and microhabitat. The resource use covariates considered for inclusion in the temporal analysis included rainfall, wind speed, temperature, humidity, and time of day (hours 0-23) as raccoons and opossums are active at specific times of the day (Wilson, 1996; Ladine, 1997; Carver *et al.*, 2011). Since raccoons and opossums are known to be nocturnal, the hours from 7am to 4pm were combined to form a single daytime period (Reid, 2006). The *a priori* models considered for predicting single-species temporal resource use were a global model including all covariates, a model with only time of day, and a model with temperature, rainfall, wind speed, and humidity.

For evaluation of the effect of competitor presence/absence on a species' resource use, we ran two occupancy models for each species and resource (spatial or temporal): a model with no resource use covariates except competitor presence, which estimated the effect of the competitor's presence/absence on a species' resource use without accounting for any within-species selection for other resource attributes; and a similar model that



included all resource use covariates, which estimated the effect of the competitor's presence/absence on a species' resource use while accounting for within-species selection for other resource attributes. We choose to focus on only the global models, including all detection covariates, instead of using techniques to generate more parsimonious models such as stepwise regression or ranking by AIC (Burnham and Anderson, 2002), because the focus of our study was not on predicting species occupancy. While our models were potentially over parameterized, the estimated effects of species interaction were more accurate, if not as precise, because we accounted for potentially confounding variables. All occupancy models were evaluated using the statistical package R (R Development Core Team, 2011).

## **Results**

In the course of our study, we collected 3,125 images of opossums and 1,081 photos of raccoons. Raccoons and opossums never appeared in the same photograph but they did occur 6 times at the same sample unit within an hour of each other. Out of the 358 spatial resource sites (sample units) surveyed over 8,520 sampling occasions, opossums were detected 319 times at 120 sites and raccoons were detected 175 times at 116 of sample units. Both raccoons and opossums were detected at 28 of the 358 spatial resource sites. Thus, opossums had a naïve spatial occupancy rate of 33.5%, while raccoons were slightly lower rate at 32.4%. Given these naïve spatial occupancy rates, raccoons and opossums should occur in the same space 10.9% of the time if they occur independently of each other. We found that raccoons and opossums used the same space

7.8% of the time. However, we note that these estimates do not account for detectability of the species.

The AICc scores for the *a priori* models considered to predict single-species spatial resource use for raccoons were 1609.8 for the global model including all covariates ( $k = 21$ ), 1607.0 for the model with only property ( $k = 13$ ), 1617.3 for the model with only land cover type ( $k = 12$ ), 1610.6 for the model with microhabitat measures (% canopy and understory visibility) only ( $k = 8$ ), and 1614.7 for the model with land cover and microhabitat measures ( $k = 14$ ). The AICc scores for the *a priori* models considered to predict single-species spatial resource use for opossums were 2271.7 for the global model including all covariates ( $k = 21$ ), 2280.1 for the model with property only ( $k = 13$ ), 2329.9 for the model with only land cover type ( $k = 12$ ), 2319.1 for the model with microhabitat measures only ( $k = 8$ ), and 2314.9 for the model with land cover and microhabitat measures ( $k = 14$ ). The best model among those considered for raccoon spatial use was the model with only the property covariate (Table 1). The best model among those considered for opossum spatial use was the global model that included all the covariates (Table 1). Detection of raccoons and opossums increased with increasing humidity, was not affected by wind speed, and decreased with increasing temperatures and rainfall (Table 1).

The effects of competitor presence on the use of space by raccoons and opossums, as examined in the spatial occupancy model without covariates for other resource attributes, were positive for both species; when opossums were present at a sample unit, raccoons were 2.3 (1.4 – 3.6; 95% LCL-UCL;  $p = 0.07$ ) times more likely to use a sample unit; when raccoons were present, opossums were 4.6 (2.8 – 7.4;  $p = 0.001$ )

times more likely to use a sample unit. The proportion of available sites used by each species based on land cover type was similar for all but riparian and scrub types (Figure 1) and opossums and raccoons showed similar trends in selection for percent canopy cover and understory visibility (Table 1), justifying the need to include other resource attributes in the model of competitor effects. For both raccoons and opossums, incorporating resource attributes decreased the positive effects of competitor presence on the use of space, estimates of competitive effects were still positive but were now non-significant for both species; when opossums were present at a sample unit, raccoons were 1.2 (0.5 – 2.8;  $p = 0.81$ ) times more likely to use a sample unit; when raccoons were present, opossums were 1.6 (0.8 – 3.2;  $p = 0.50$ ) times more likely to use a sample unit.

Out of the 1,696 temporal resource periods (hours of each day) surveyed over 14,776 sampling occasions, opossums were detected 393 times in 295 periods and raccoons were detected 185 times in 170 of the temporal resource periods. Both raccoons and opossums were detected in 51 of the 1,696 temporal resource periods. Thus, opossums had a naïve occupancy rate of 10.3%, while raccoons were lower at 5.9%. Given these naïve occupancy rates, raccoons and opossums should use the same hour of the same day 0.6% of the time if they are active independent of each other. We observed that raccoons and opossums used the same temporal resource period 1.7% of the time. Again, we note that these estimates do not account for detectability of the species.

The AICc scores for the *a priori* models considered to predict single-species temporal resource use for raccoons were 2021.6 for the global model including all covariates ( $k = 35$ ), 2028.7 for the model with only time of day ( $k = 31$ ), and 2105.3 for the model with temperature, rainfall, wind speed, and humidity ( $k = 21$ ). The AICc scores

for the *a priori* models considered to predict single-species temporal resource use for opossums were 3361.2 for the global model including all covariates ( $k = 35$ ), 3370.1 for the model with only time of day ( $k = 31$ ), and 3657.8 for the model with temperature, rainfall, wind speed, and humidity ( $k = 21$ ). The best model among those considered for both raccoon and opossum temporal resource use was the global model that included all the covariates (Table 1). Detection of raccoons and opossums increased with increasing canopy cover and understory density and varied amongst the properties (Table 1).

Raccoons were more likely to be detected in agriculture and riparian land cover types versus the hardwood type, and less likely to be detected in developed, scrub, pine, and mixed land cover types (Table 1). Opossums were more likely to be detected in agriculture, developed, and scrub land cover types versus the hardwood type, and less likely to be detected in riparian, pine, and mixed land cover types (Table 1).

The effect of competitor presence on temporal activity patterns of raccoons and opossums, as examined in the temporal occupancy model without covariates for other resource attributes, was significantly positive for both species; when opossums were present during a given hour and date, raccoons were  $2.9 \times 10^{10}$  ( $2.8 \times 10^7 - 3.2 \times 10^{13}$ ; 95% LCL-UCL;  $p = 0.009$ ) times more likely to also be active; when raccoons were active, opossums were 204.4 (72.3 – 577.7;  $p = <0.0001$ ) times more likely to use that hour on that date. However, raccoons and opossums appear to have very similar temporal activity patterns, with peak activity occurring from 7pm to 3am and little to no activity from 7am to 5pm (Figure 2) justifying the need to include other resource attributes in the model of competitor effects. Although incorporating temporal covariates for resource attributes decreased the positive effects of competitor presence on temporal activity patterns in both

raccoons and opossums, estimates of competitive effects were still positive but were now non-significant for both species; when opossums were present during a given hour and date, raccoons were 4.3 (0.5 – 37.6;  $p = 0.50$ ) times more likely to be active; when raccoons were active, opossums were 2.7 (0.9 – 7.7;  $p = 0.34$ ) times more likely to use that use that hour on that date.

## **Discussion**

In our study throughout the northern half of the state of Alabama, raccoons and opossums were widely distributed and fairly abundant, based on the number of photographs in all 8 study areas. Before accounting for imperfect detection, raccoons and opossums used the same spatial resource less often than predicated by independent space use, indicating that raccoons and opossums may be partitioning the spatial resource. Before accounting for imperfect detection, raccoons and opossums used the same temporal resource more often than predicated by independent space use, indicating that raccoons and opossums may be associating. When the probability of detection was accounted for, raccoons and opossums appeared to use sites or temporal periods with high probabilities of competitor presence, indicating association between the species across space and time. However, analyses of resource attributes, such as land cover type and time of day, indicated that within-species resource selection patterns were similar and thus potentially confounding with the effects of spatial and temporal resource use. Indeed, when covariates accounting for resource attributes were included in the occupancy models, raccoons' and opossums' use of sample units and temporal periods were found to be unaffected by competitor presence. Thus, our results supported the

conclusion of Carver et al. (2011), that raccoons and opossums do not partition temporal resources, contrary to results found by Wilson (1996) and Ladine (1997). All previous studies have found positive spatial associations between raccoons and opossums, (McKeever, 1959; Gardner, 1982; Kaufman, 1982; Kissell and Kennedy, 1992; Ginger et al., 2003). However, past studies of raccoon and opossum resource partitioning might have been biased because they did not account for within-species preference for other resource attributes or imperfect detections (Kissell and Kennedy, 1992; Ladine, 1997; Ginger et al., 2003). Our results concur with other synecology studies on the necessity of incorporating use covariates and detection probabilities into analyses of resource partitioning (Kroll et al., 2008; Tobler et al., 2009; Sarmiento et al., 2011).

In fact, our results may still have been affected by the limited inclusion of only a few of the many resources associated with space and time use that might be selected for by species (e.g. prey and predator densities, distance to water, etc.). Inclusion of more covariates might have allowed us to determine a negative effect of competitor presence on spatial and temporal resource use. For example, we were unable to account for differences in intensity of resource use due to differing species' abundances in various associated resources, because individual raccoons and opossums were not identifiable in the photos. We had almost three times as many photos of opossums as raccoons, suggesting that opossums were more abundant than raccoons (Jenks et al., 2011). The relative densities of raccoons and opossums can affect resource partitioning. For example, in a study by Carver et al. (2011), relative raccoon densities were greater than opossum densities and there was no evidence of temporal resource partitioning, while Ladine (1997) found temporal partitioning when opossums outnumbered raccoons. Past

studies have also found evidence of habitat partitioning after they accounted for the differing intensity of space use by raccoons and opossums due to the disparity of the species' population sizes (McKeever, 1959; Kissell and Kennedy, 1992; Wilson, 1996; Ginger *et al.*, 2003). Further research is needed to determine if spatial and temporal resource partitioning by raccoons and opossums in the presence of a competitor is being concealed by resource use covariates not included in our models.

Our results indicating that opossums and raccoons do not partition spatial and temporal resources are surprising given the amount of overall resource overlap between the species and their comparable competitive abilities (McManus, 1974; Lotze and Anderson, 1979). Based on niche theory, syntopic species with high resource overlap, such as raccoons and opossums, need to partition resources in order to continue coexisting (Gause, 1932; Hardin, 1960). Several studies suggest species with overlapping resource use can decrease their chances of competitive interactions by foraging at different peak times (Greenwood, 1978; Kronfeld-Schor and Dayan, 2003). Additionally, Buskirk (1999) suggested that mesocarnivore species, like raccoons and opossums, respond to competition through home-range displacement, habitat avoidance, and prey shifting. Previous research on other generalist mesocarnivore competitors (e.g. coyotes, foxes, and skunks) has shown strong spatial partitioning between competitors (Crooks and Vanvuren, 1995; Sovada *et al.*, 1995; Lovell *et al.*, 1998). Temporal resource partitioning amongst mesocarnivore competitors is rarer since many species already avoid each other spatially (Fuller *et al.*, 1989; De Almeida Jácomo *et al.*, 2004), however examples do exist; mink shifted from being nocturnally active to diurnally active in the presence of otters and polecats, and coyotes changed their temporal activity patterns in

the presence of wolves (Arjo and Pletscher, 2000; Harrington *et al.*, 2009). Since our study indicates that raccoons and opossums are not partitioning spatial and temporal resources, further research is needed to determine how raccoons and opossums mitigate the effects of competition.

The existence and effects of interspecific competition are difficult to establish and the difficulty is magnified for generalist species like raccoons and opossums because they often compete for many resources (Tokeshi, 1999; Townsend *et al.*, 2003). Since our study only examined two resources, space and time, raccoons and opossums might be ameliorating the effects of competition on a different scale. Competing species often appear to associate at one scale but are found to have distinct distributions at a finer scale of resolution (Townsend *et al.*, 2003). Raccoons and opossums might be avoiding each other on a very fine spatial and temporal scale. Species are able to avoid direct confrontation through sensory cues (Carver, 2011), and it is likely that opossums would avoid direct interactions with raccoons, as raccoons are known to act aggressively towards opossums (Stuewer, 1943; Ladine, 1997). Indeed, no photographs in our study contained both opossums and raccoons. Moreover, raccoons and opossums may not need to partition space or time because as omnivores they have extremely flexible diets, allowing them to potentially partition prey items (Gardner, 1982; Azevedo *et al.*, 2006). Furthermore, differences in microhabitat selection patterns might explain the lack of spatial partitioning observed at the scale of our study, similar to the use of different parts of a tree to glean insects from by warbler species when in a mixed flock (Townsend *et al.*, 2003). Indeed, we noticed that raccoons and opossums were potentially avoiding each other in land cover types where raccoon use was greater than opossum use (Figure 1).



Unfortunately, in occupancy analysis the interaction between competitors is considered the same within each resource covariate (i.e. the effect of raccoons on opossums in riparian habitats is the same as in scrub). Further research is needed to determine if raccoons and opossums are partitioning resources on a finer scale than that examined in our study (i.e. smaller than a 3.5 acre sample unit or hourly time period).

Alternatively, we might not be observing any effects of competitor presence on use of spatial and temporal resources because raccoons and opossums might be at a stable equilibrium where neither species can competitively dominant the other (Townsend *et al.*, 2003). There is a tradeoff between being a good competitor and other traits such as colonization ability or reproduction rates (Tilman, 1994). Two species competing over two resources can also coexist when each species holds one of the resources at a level that is too low for effective exploitation by the other species (Townsend *et al.*, 2003). Furthermore, the fitness of raccoons and opossums in the presence of a competitor, while being negatively affected in some ways, might be positively affected in others. Like a mixed flock of birds, opossums and raccoons may benefit by being active at the same time through decreasing individual predation risk (Townsend *et al.*, 2003). Putative competitors can also coexist through facilitation of prey capture, where prey is made available to the predator due to the presence of its competitor either directly or through changes in prey behavior or scavenging of carrion (Minta *et al.*, 1992; Losey and Denno, 1998). Finally, it is always possible that raccoons and opossums are not currently competing, if the environment is unstable or resources are not limited. For example, predation pressure may be holding the populations of opossums and raccoons at a level where shared resources are not scarce enough to induce competition. With the continuing

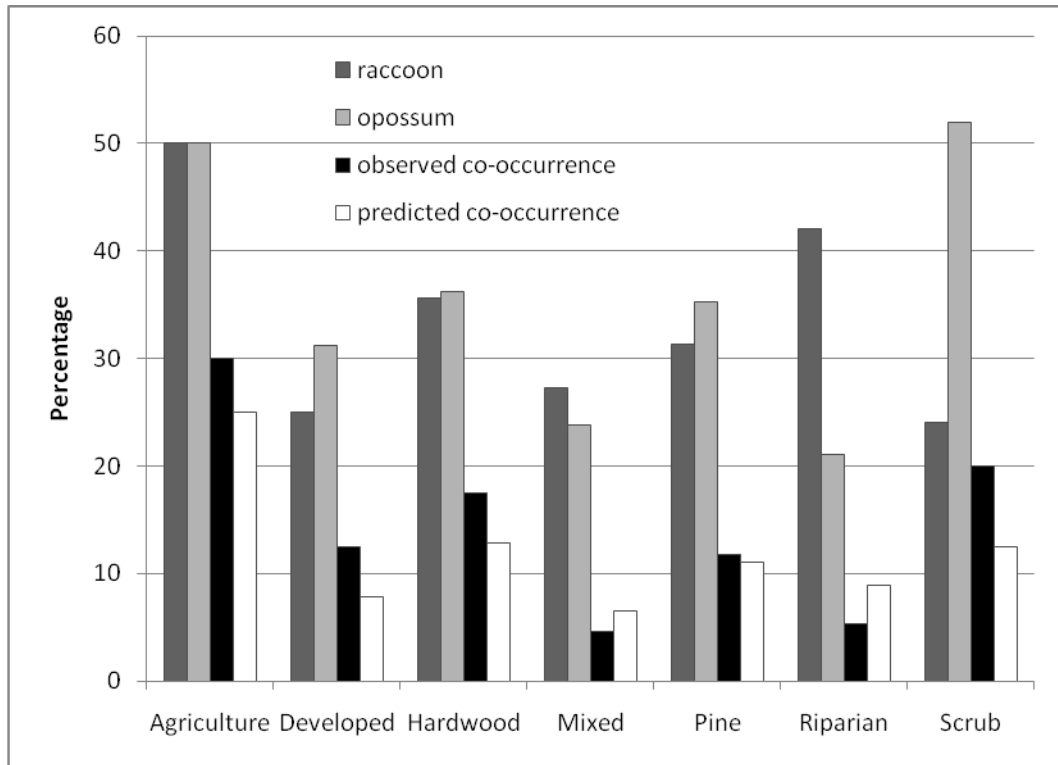
population growth in Alabama of a known raccoon and opossum predator, the coyote, it is theoretically plausible that coyotes are lessening the effects of competition (Gardner, 1982; Parker, 1995). Further studies involving more detailed data on the movement and interactions of opossums and raccoons and experimental manipulation are necessary to determine the intensity of competition between them and potential resource partitioning.

**Table 1.** Lowest AICc ranked *a priori* single species models for raccoon and opossum spatial resource use. Use covariates above divide and detection covariates below.

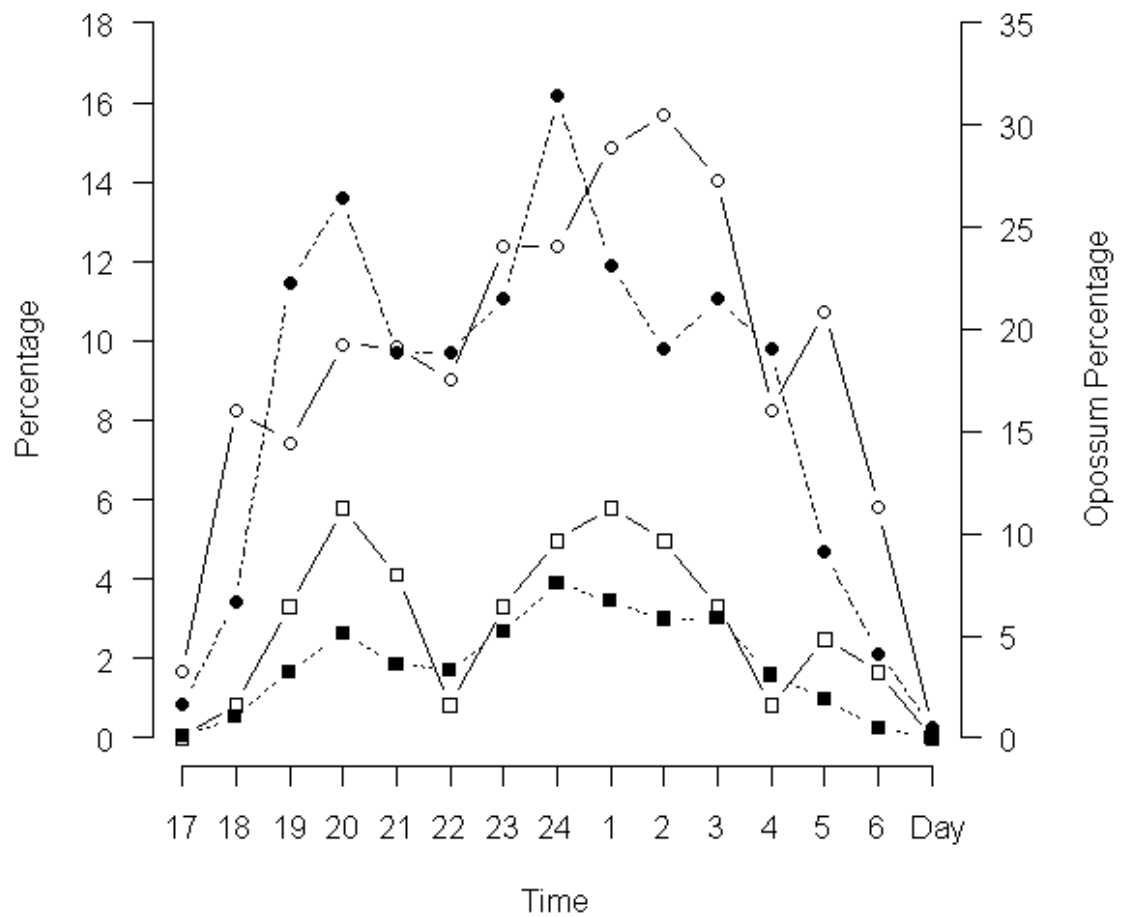
Covariate	Opossum			Raccoon		
	Estimate	SE	P-value	Estimate	SE	P-value
developed	-1.50	1.22	0.22	N/A	N/A	N/A
hardwood	-0.70	0.95	0.46	N/A	N/A	N/A
mixed	-1.35	0.99	0.17	N/A	N/A	N/A
pine	-0.61	1.02	0.55	N/A	N/A	N/A
riparian	-1.18	1.12	0.29	N/A	N/A	N/A
scrub	0.59	1.06	0.58	N/A	N/A	N/A
canopy	2.60	0.80	1.2E-03	N/A	N/A	N/A
understory	0.88	1.24	0.48	N/A	N/A	N/A
property2	1.83	0.83	0.03	1.08	0.78	0.17
property3	1.44	0.93	0.12	0.96	0.85	0.26
property4	-0.35	1.30	0.79	2.21	1.18	0.06
property5	1.49	0.80	0.06	2.20	0.76	3.6E-03
property6	4.09	1.08	1.4E-04	1.50	0.87	0.08
property7	3.75	0.92	4.3E-05	2.82	0.97	3.6E-03
property8	1.65	0.88	0.06	2.05	0.89	0.02
humidity	0.04	0.005	1.0E-12	0.04	0.007	1.6E-08
wind	-6.2E-03	6.2E-03	0.35	6.2E-03	0.01	0.45
temperature	-0.02	0.01	0.12	-0.03	0.01	0.02
rain	-0.20	0.10	0.05	-0.30	0.17	0.07

**Table 2.** Lowest AICc ranked *a priori* single species models for raccoon and opossum temporal resource use. Use covariates above divide and detection covariates below.

	Opossum			Raccoon		
Covariate	Estimate	SE	P-value	Estimate	SE	P-value
humidity	0.02	0.01	0.08	0.04	0.03	0.12
wind	-6.2E-03	0.02	0.71	0.06	0.04	0.07
temperature	0.13	0.03	8.7E-05	-0.08	0.06	0.18
rain	-0.22	0.59	0.71	-14.4	7.83	0.07
hr1	6.30	1.04	1.3E-09	38.87	587.45	0.95
hr2	5.50	0.85	1.1E-10	24.02	42.34	0.57
hr3	5.48	0.82	2.7E-11	6.35	2.72	0.02
hr4	5.13	0.76	1.4E-11	4.06	1.15	4.3E-04
hr5	3.76	0.75	5.2E-07	44.04	520.48	0.93
hr6	2.70	0.78	5.7E-04	3.46	1.26	6.0E-03
hr17	1.33	0.89	0.14	2.12	1.15	0.07
hr18	3.42	0.77	8.4E-06	5.97	1.87	1.4E-03
hr19	7.18	1.39	2.1E-07	4.24	1.11	1.4E-04
hr20	7.72	1.72	7.0E-06	4.55	1.29	4.2E-04
hr21	5.77	0.98	3.2E-09	5.57	2.16	9.8E-03
hr22	5.52	0.88	4.3E-10	4.36	1.25	4.8E-04
hr23	6.27	1.08	5.8E-09	17.74	22.81	0.44
hr24	14.45	68.67	0.83	14.49	6.72	0.03
understory	0.01	0.01	2.5E-01	0.04	0.01	5.8E-03
canopy	1.38	0.31	8.1E-06	0.32	0.39	0.41
agriculture	0.79	0.23	6.1E-04	0.10	0.40	0.81
developed	0.24	0.22	0.29	-0.66	0.41	0.11
riparian	-0.54	0.36	0.13	0.27	0.31	0.38
pine	-0.21	0.18	0.25	-0.46	0.26	0.08
mixed	-0.09	0.16	0.56	-0.26	0.21	0.21
scrub	0.62	0.20	2.0E-03	-0.47	0.38	0.22
property1	-2.90	0.42	6.5E-12	-1.26	0.68	0.06
property2	-2.12	0.25	1.5E-17	-0.23	0.44	0.60
property3	-1.79	0.32	2.2E-08	-0.42	0.49	0.39
property4	-2.39	0.58	4.1E-05	0.46	0.46	0.32
property5	-1.94	0.21	3.5E-20	0.35	0.37	0.35
property7	-0.61	0.21	4.2E-03	0.62	0.41	0.13
property8	-1.52	0.30	4.5E-07	0.89	0.42	0.04



**Figure 1.** Percentage of sampled units used by raccoons, opossums, or both by land cover type without accounting for imperfect detection. Predicted co-occurrence calculated by multiplying individual species' probability of use. Most types are used equally by both species with the exception of riparian and scrub types. Observed species co-occurrence is greater than predicted except in types (mixed and riparian) where raccoon use is greater than opossum.



**Figure 2.** Percentage of available hours on given dates used by hour of the day without accounting for imperfect detection. Raccoons (solid line with open circles) and opossums (circle-dash) have similar activity patterns in our study. Predicted co-occurrence calculated by multiplying individual species' probability of use. Observed species co-occurrence (solid line with open square) is generally greater than predicted co-occurrence (square-dash).

## Factors Affecting the Detectability of Scat by Dogs

### Introduction

Throughout history humans have utilized the domestic dog's (*Canis lupus familiaris*,) remarkable scenting ability for a variety of needs, including tracking game, detecting predators, and forensic work (MacKay *et al.*, 2008). Starting as early as the late 1800's, dogs were used for wildlife research and conservation (Zwickel, 1980; Browne *et al.*, 2006). For example, dogs have been trained to detect species' scent trails (Akenson *et al.*, 2004; Gsell *et al.*, 2010), identify occupied burrows (Theobald and Coad, 2002; Reindl-Thompson *et al.*, 2006), recover carcasses (Homan *et al.*, 2001; Arnett, 2006), and locate invasive or endangered species (Engeman *et al.*, 2002; Cablk and Heaton, 2006). In the late 1990's, a systematic and replicable protocol was developed to locate scat samples from specific target species using dogs (Wasser *et al.*, 2004; MacKay *et al.*, 2008). Scat samples are valuable for wildlife research and conservation because their components, including undigested and digested food, hormones, and DNA, can provide information on individual identity, sex, reproductive state, stress levels, health, and diet; all without ever having to see or touch the animal (Kohn and Wayne, 1997; MacKay *et al.*, 2008). Additionally, the location of scat samples can provide information on animal movements, home range, habitat use, and resource selection (Wasser *et al.*, 2004). Consequently, the use of detection dogs to locate scat from various species has rapidly increased (Wasser, 2008). For example, dogs have been used to find scat from kit foxes, bears, bobcats, fishers, bush dogs, armadillos, jaguars, and right whales (Smith *et al.*,

2003; Wasser *et al.*, 2004; Harrison, 2006; Rolland *et al.*, 2006; Long *et al.*, 2007b; Dematteo *et al.*, 2008; Silveira *et al.*, 2009; Vynne *et al.*, 2010).

The use of scat-detection dogs to sample for species of interest has several advantages. Detection dogs, as an active search method, generate greater sample sizes and are more efficient (i.e., detections per unit effort) and accurate for detecting species presence than passive sampling methods like game cameras, hair snares, and track plates (Long *et al.*, 2007a; Harrison, 2006; Gompper *et al.*, 2006). The use of detection dogs is also more efficient than other active search techniques. For example, studies have determined that dogs cover up to 5 times the distance, in 70% of the time, with 2-15 times the detection rates of human searchers (Homan *et al.*, 2001; Smith *et al.*, 2001; Long *et al.*, 2007b; Nussear *et al.*, 2008). Furthermore, dogs can locate small, cryptic scat samples over a large area, while discriminating between scat of target and non-target species; as a result, the use of dogs greatly increases the detectability of target species, even if that species is rare (Kerley and Salkina, 2006; Long *et al.*, 2007; MacKay *et al.*, 2008; Vynne *et al.* 2010). Finally, dogs are a charismatic “tool” that broadens the appeal of conservation research to the public.

While the use of scat-detection dogs to sample for wildlife offers many advantages, limitations and qualifications to the technique exist. Individual dogs differ in their ability to find scat (Smith *et al.*, 2003; Long *et al.*, 2007b; Reed *et al.*, 2011). The likelihood of scat detection decreases as the dog’s distance from the scat increases (Reed *et al.*, 2011). Though detection dogs have successfully located targets in a variety of weather conditions and terrains (Reed *et al.*, 2011), survey conditions may affect the



physiological ability of the dog to smell a scat sample by drying out the dog's nose or increasing panting rates (Shivik, 2002; Gazit and Terkel, 2003; MacKay *et al.*, 2008). Potentially important and little-studied limitations to the use of scat-detection dogs are how a dog's ability to locate individual scat samples may be influenced by the attributes of the scat sample, its history, or its location. For example, scat and its unique scent degrade over time at varying rates as they are affected by environmental variables such as temperature, light, and moisture (Syrotuck, 1972; Harrison, 2006; MacKay *et al.*, 2008). The amount of precipitation a scat sample is exposed to should negatively affect the period the sample is available for detection as the mechanical action of falling rain breaks apart the scat and washes away the bacteria involved in scent production (Syrotuck, 1972; Smith *et al.*, 2005; Harrison, 2006; Reed *et al.*, 2011). Moreover, large volumes of scat mat not only produce more scent, and thus be easier to find, but also may take longer to degrade than small volumes of scat. Furthermore, scat decay rates, and thus scat detection rates, may vary spatially depending on the surrounding habitat in part because different habitat types have different microclimates (Lehmkuhl *et al.*, 1994; Prugh and Kerbs, 2004; Telfer *et al.*, 2006; Rhodes *et al.*, 2011); areas with less vegetative cover experience greater ranges in temperature and moisture level, as well as direct exposure to precipitation (Rosenberg *et al.*, 1974). The thickness of vegetation in a habitat type can also decrease scent dispersion affecting the probability of the dog encountering the scent (Syrotuck 1972; Gazit and Terkel, 2003; MacKay *et al.*, 2008). If factors such as volume of scat, age, amount of rainfall a scat sample has been exposed to, and habitat a sample is located in can influence a dog's ability to locate samples, analyses that rely on those

samples may produce biased estimates (Gu and Swihart, 2004; MacKay *et al.*, 2008; Rhodes *et al.*, 2011).

In this study we examined the factors that influence a dog's ability to locate scat. Specifically, we studied the effects of the amount of time a scat sample was exposed to the environment, the amount of precipitation a sample experienced, scat volume, habitat the sample was located in, and the interactions amongst these factors on the ability of scat-detection dogs to locate scat. To control for other factors that might influence scat detection (e.g. species occupancy, scat abundance, scat composition due to diet) we used an experimental approach in which scat samples from a non-native species of varying sizes were placed in a variety of habitats and searched for by dogs over time. We predicted that scat detection would decrease over time as the scat sample degraded and scent production decreased (Smith *et al.*, 2005; Harrison, 2006). We also predicted that scat samples that experienced greater amounts of precipitation would have lower detection rates. We expected that large volumes of scat would be easier for the dogs to find than small volumes of scat and that detection of larger volumes of scat by dogs would be less negatively affected by time and precipitation (Syrotuck, 1972). Finally, we predicted that a dog's ability to locate scat should vary across habitats, and detection rates in each habitat should be differentially affected by time and precipitation (Lehmkuhl *et al.*, 1994; Wasser *et al.*, 2004; Reed *et al.*, 2011; Rhodes *et al.*, 2011).

## **Materials and Methods**

*Field Sites*- We conducted our research on properties owned by Auburn University around the town of Auburn in east-central Alabama, USA. The climatic zone is humid subtropical. The biome is classified as temperate broadleaf. Study sites were classified into three habitat types based on the majority land-cover type: clear-cut, pine, and hardwood. Clear-cut habitats had direct exposure to precipitation and a highly variable temperature and moisture regime because they consisted of areas with little canopy cover and thick vegetative ground cover. Clear-cut sites included: two-year-old regenerating sites with thick, 3.5-foot-tall herbaceous growth; a 15-year-old heavily thinned pine forest with less than 20% canopy cover and patchy grass ground cover; and mowed meadows with vegetative cover ranging from 6 inches to 2 feet tall. Pine habitats consisted of areas dominated by commercially planted loblolly (*Pinus taeda*) and shortleaf (*Pinus echinata*) pines. Pine sites ranged from a 10-year-old high-density pine forest to a mature forest with a sparse understory of deciduous trees and shrubs. Pine habitats had little direct rainfall and an observably drier microclimate because of their thick canopies, lack of vegetative ground cover, and porous substrate consisting of pine needles. Hardwood habitats consisted of areas dominated by Southern Piedmont Dry Oak Forest and Southern Piedmont Mesic Forest with canopy cover ranging from 20 to 100%, little to no vegetative ground cover, and a substrate of hardwood leaf litter. Hardwood habitats provided moderate protection from rainfall but an observably moister microclimate. All hardwood sites were generally mature hardwood stands along stream-side management zones.

*Scat Detection Dog Training-* Black bear (*Ursus americanus*) scat was collected from captive animals at the Oklahoma City Zoo and kept frozen at all times until placed in the field. Scat samples were used to train and evaluate four scat-detection dogs: Sophie, Urban, Bishop, and Holli. Dogs and professional handlers were leased from Auburn Universities' Detection Dogs for Ecological Research (EcoDogs). The dogs were trained in a manner similar to that used for other scat-detection surveys 2-3 months prior to the beginning of the field seasons (MacKay et al., 2008). Dogs were selected for specific attributes (e.g., high drive, object orientation, appropriate temperament) and trained to associate the scent of bear scat with a reward (i.e., a tennis ball). The dogs were then trained to sit and stay at the site of a located scat sample.

*Scat Surveys-* Scat surveys were conducted once a week from May to August 2010 (part 1) and February to mid-May 2011 (part 2). Prior to placement in the field, all scat was placed in a large tub and mixed well to account for any daily changes in diet. In part 1, two different sized scat samples (small and large) were used in the field trials to determine if the size of the scat sample influenced detectability. Large samples were approximately 236mL (1 cup) of scat. Small scat samples were approximately 22 mL (1.5 tablespoons) of scat. In part 2, only a medium-sized scat sample, approximately 118 mL (0.5 cup), was used. Part 1 was initialized with four scat samples, 2 of each size, placed in each of the three habitat types. Each week of the experimental trial, two additional scat samples, 1 of each size, were placed in each of the three habitats as long as there were fewer than 8 scat samples in that habitat being detected by the dogs. Part 1 had a total of

58 scats. Part 2 was initialized with 6 scat samples placed in each of the three habitat types. Six additional scat samples were placed in each of the three habitats for the following three weeks, for a total of 72 scats. Throughout both experiments, all scat samples were placed at least 80 meters apart. Each scat sample was unobtrusively marked with flagging and its GPS location was recorded. At each sample location, a 12cm rain gauge was hidden nearby to record weekly rainfall.

For each week in part 1, dog and handler teams surveyed all the scat samples found by the dogs 2 weeks previous, any new scat samples placed out the previous week, and as many as possible of the scat samples the dogs failed to detect previously (some of these samples were not surveyed each week due to time constraints), resulting in a total of 291 possible detections. In part 2, every scat sample was surveyed, whether it had been previously detected or not, every two weeks for 12 weeks, resulting in 432 possible detections. Throughout the experimental trials, dogs were rotated among scat samples and the direction of the search pattern was altered to keep the dogs from memorizing the locations of the samples. The search protocol was changed from part 1 to part 2 to limit the number of times a dog visited a scat sample to two to reduce the potential for memorization and to ensure that all scat samples would be surveyed equally. For each survey, the date, dog used, and whether or not the dog indicated on the sample was recorded. Past research has shown that the distance between the dog and target scat can greatly affect detection rates (Reed *et al.*, 2011); to control for this effect, the dogs had to pass twice within at least two meters of a scat sample before the sample was considered undetected.

*Analysis-* The amount of time in days a scat sample was in the field and the cumulative amount of rainfall in centimeters the sample received were highly correlated ( $r^2 = 0.73$ ). Therefore, principle component analysis was used to create two new independent variables; the 1<sup>st</sup> principle component had positive loadings for both the amount of time in days a scat had been exposed (0.96) and the cumulative amount of rainfall in cm (0.28) (hereafter “exposure”) and the 2<sup>nd</sup> principle component had negative loadings for time (-0.28) and positive loadings for rainfall (0.96) (hereafter “adjusted rainfall”).

The effects of the variables of interest on detection rates were analyzed using logistic mixed-effects regression with random effects for scat sample and dog. Part 1 and part 2 of the experiment were analyzed separately due to the differences in their methods. Fixed variables considered in the analysis included exposure and adjusted rainfall (first and second principle components), habitat type the sample was located in (with pine serving as the reference habitat type in the model), size of the scat sample (part 1 only), as well as interactions between habitat and adjusted rainfall, habitat and exposure, size and adjusted rainfall (part 1 only), and size and exposure (part 1 only).

An information-theoretic approach involving Akaike’s information criterion corrected for small sample sizes (AICc) was used to rank a global model, containing all the above variables and interactions, and all possible subsets of the global model based on fit to the data and the principle of parsimony (Burnham and Anderson, 2002). Multi-model inference was used to generate estimates of the effect of each variable on the dogs’ ability to detect scat samples. Such estimates are unconditional on model selection (Burnham and Anderson, 2002). The importance of each variable was also indexed by the sum of model weights for those models in which that variable was included, resulting in a

score of relative variable importance (RVI). All analysis was done using the software package R, version 2.12.2 (R Development Core Team, 2011). The R package MuMIn, version 1.0 was used for AICc model analysis (Barton, 2011).

## Results

The dogs detected the target scat samples 47.4% of the time during part 1 of the experiment and 69.2% of the time during part 2. The model with the lowest AICc score in part1 included the variables for habitat type, exposure, adjusted rainfall, size of scat sample, and the interaction between adjusted rainfall and hardwood habitat type (Table 1). However, the Akaike weight of this model suggested that the probability that this model was truly best among those considered was only 0.07, supporting the use of multi-model inference. In part 2, the model with the lowest AICc score included the variables for habitat type, exposure, adjusted rainfall, and the interaction between exposure and clear-cut habitats (Table 2). However, again the Akaike weight of this model suggested that the probability that this model was truly best among those considered was only 0.2, supporting the use of multi-model inference.

As the scat samples aged, they generally were detected less frequently (Figure 1). However, some scat samples were still being detected after 3 months in the field and might have continued to be detected if the study had continued. The average age of detected samples was 29 days (SD = 21.2) for part 1 and 44 days (SD = 24.2) for part 2. The exposure of scat samples had a relative variable importance of 1.00 for both parts of the experiment (Table 3), indicating that the variable would always be in the true best model among those considered. Model-averaged coefficient estimates from part 1 and

part 2 of the experiment suggest scat samples with the lowest observed exposure were 15.9 (2.7 – 94.3; 95% LCL - UCL) and 26.5 (3.6 – 196.0) times more likely to be detected than samples with the greatest exposure, respectively (Table 3). Our analysis provided minimal support for an interaction between exposure and habitat type in part 1 of the experiment, as evidenced by low RVI values (Table 3). However, in part 2, we observed some support for a varying effect of exposure between habitat types. The RVI for the interaction between exposure and the clear-cut habitat type was 0.80, while that for the interaction between exposure and hardwood was only 0.3 (Table 3). The model-averaged coefficient estimate for the interaction between exposure and clear-cut from part 2 indicates that the effect of exposure in that habitat type had an even greater negative effect than exposure in pine and hardwood habitat types; scat samples with the lowest exposure values in clear-cut habitats were 406 times as likely to be detected as samples with the highest exposure values (Table 3).

The cumulative rainfall scat samples received ranged from 0 to 36 cm with an average of 9.2 cm in part 1 and 0 to 38 cm with an average of 17.8 cm in part 2. Adjusted rainfall had moderate support for inclusion in the true best model amongst those considered with RVI values of 1.0 in part 1 and 0.65 in part 2 (Table 3). The estimated relationship between the adjusted rainfall variable and the probability that a dog detected a sample was negative for both experimental parts, suggesting that samples receiving a disproportionately large amount of rain for their age were less likely to be detected (Table 3). Model-averaged coefficient estimates from part 1 and part 2 of the experiment suggest that scat samples with the lowest adjusted rainfall values were 83 (0.8 – 9,061) and 1.6 (0.1 – 23) times as likely to be detected as samples with the highest adjusted rainfall



values, respectively (Table 3). Our analysis showed support for variations in the effect of adjusted rainfall between habitat types in part 1; the probability that the interaction between adjusted rainfall and hardwood habitat would be in the best model amongst those considered was 0.72, while the interaction between adjusted rainfall and clear-cut had an RVI of 0.49 (Table 3). The model-averaged coefficient estimate for the interaction between adjusted rainfall and hardwood habitat from part 1 indicates that the effect of disproportionately large amounts of rain in hardwood habitats had an even greater negative effect than the effect of adjusted rainfall in pine habitats; scat samples with the lowest adjusted rainfall values in hardwood habitats were 72,812 times as likely to be detected as samples with the highest adjusted rainfall values (Table 3). The model-averaged coefficient estimate for the interaction between adjusted rainfall and clear-cut habitat from part 1 suggest that disproportionately large amounts of rain had no effect in the clear-cut habitat type (Table 3). We observed minimal support for an interaction between adjusted rainfall and habitat type in part 2 of the experiment, as evidenced by low RVI values (Table 3).

Generally, the dogs detected 62% of the large-volume scat samples and 27% of the small-volume scat samples. Our analysis provided strong support for an effect of scat-sample volume, with sample volume always being included in the true best model among those considered (Table 3). The model-averaged coefficient estimate indicated that large scats were 9.4 (3.9 – 22.7) times more likely to be detected than small scats. The interactions between scat-sample volume and exposure and sample volume and adjusted rainfall had low support for inclusion in the best model as indicated by the RVI values (Table 3).

In general, dogs were more likely to detect scat samples in pine habitat types compared to hardwood, and hardwood compared to clear-cut habitat types (Figure 2). In both parts of the experiment we observed strong support for an effect of habitat type on the probability of scat-sample detection as RVI values for habitat variables were all greater than 0.8 (Table 3). The model-averaged coefficient estimate from part 1 indicates that scat samples in pine habitats were 2.6 (0.9 – 7.6) times as likely to be detected as samples in hardwood habitats; the estimate for the difference between pine and clear-cut habitats was comparable (Table 3). Similarly, in part 2, dogs were 19.7 (6.8 – 56.8) times as likely to detect a scat sample in pine habitat as in clear-cut habitat and 4.1 (1.5 – 11.6) times as likely to detect a scat sample in pine habitat as in hardwood habitat (Table 3).

## **Discussion**

Our rate of scat sample detection was only 60%, but our study indicated that many factors could be influencing the detectability of individual scat samples by dogs, resulting in imperfect detection rates. One of the most important factors affecting a dog's ability to detect a scat sample was the amount of sample exposure. Previous field research has anecdotally noted that older scat samples are less likely to be detected, but since scat in the field is notoriously hard to age no research has previously quantified the effects of scat age on detectability by dogs (Long *et al.*, 2007; MacKay *et al.*, 2008). In our study, detection rates declined to 30% as scat samples reached 3 months of age (Figure 1). Studies examining the physical decay rates of scat typically reported scat samples visually persisting for much longer time periods than our scat samples were detectable by dogs (Lehmkuhl *et al.*, 1994; Rhodes *et al.*, 2011). However, this

discrepancy may be due to the fact that previous research on scat decay focused on herbivore pellets, while our study used loosely formed bear scat. While visual identification of scat samples was not recorded in our experiments, we observed that the majority of our scat samples were no longer visually discernable after a month in the field. The average age of scat samples detected by dogs in our study was 36 days, but some week-old scat samples went undetected. Alternatively, dogs located other target samples months after the sample was deposited, even in instances when the sample was no longer visually discernable. Thus, future research is needed to determine the differences between the physical decay rates of various species' scat and how physical decay may affect detection of scat samples by dogs.

The amount of cumulative precipitation a scat sample received affected the detection of the samples by dogs. The less rain a sample received, both in absolute terms and for a given age, the more likely it was to be detected. Rain negatively affects scat persistence in the environment and consequently its availability to the dogs, by physically deteriorating the scat and by increasing moisture content in the scat and its surroundings, thus enhancing rates of decay (Syrotuck, 1972; Smith *et al.*, 2005; Harrison, 2006; Reed *et al.*, 2011). Moisture is a commonly cited reason for greater rates of scat decay and cumulative precipitation has previously been shown to negatively affect the dog's ability to detect scat samples (Prugh and Krebs, 2004; Reed *et al.*, 2011). We found that age-adjusted rainfall (i.e. rainfall for a given age) was more important in part 1 of the study than in part 2. One potential explanation for the difference is that more down-bursts and other heavy rain events were observed in the summer session (part 1), which could potentially cause greater manual break-up of scat. The effect of age-adjusted rainfall on

scat detection also was tempered by an interaction with habitat type in part 1; specifically, rainfall decreased detection rates in hardwood habitats more than in pine and in pine habitats more than clear-cut habitat types. A difference in the percentage and type of canopy cover between hardwood and pine habitats might have allowed greater mechanical break-up of scat in the hardwoods. Furthermore, the leaf litter in hardwood habitats might have retained more moisture than the pine-needle litter in pine habitats, possibly stimulating the growth of bacteria and fungi that decay scat and interfere with the dog's ability to locate the target scent (Syrotuck, 1972; MacKay *et al.*, 2008). In clear-cut habitat types, scat samples might have been protected from mechanical break-up due to rain by the extremely thick vegetative ground cover. Also, samples in clear-cuts potentially experienced greater evaporation rates which would decrease the moisture content in scat samples and the surrounding microhabitat, thereby slowing decay by coprovores. The interactions between rainfall and habitat were not important in part 2, potentially due to the dichotomy in rainfall intensity as well as the variation in the thickness of vegetative ground cover and canopy cover between seasons. Future studies should examine the differences in rainfall events, from light to heavy, and the influences of canopy and ground cover on the detectability of scat samples by dogs.

Scat samples with large volumes were nine times more likely to be detected by dogs than those with small volumes. Large-volume scat samples probably produced much larger and stronger scent pools for the dogs to locate. Additionally, scat samples with large-volumes are probably less likely to be affected by age and rainfall than scat samples with small volumes, although we observed little support for interactions between scat size and exposure or adjusted rainfall potentially due to small sample sizes.

Overall, scats were more likely to be detected in pine habitat types than hardwood or clear-cut and hardwood habitats had higher detection rates than clear-cut habitats. Our results were probably due to the thick canopy we observed in the pine habitats we used, which provided protection from weather extremes, and less sample decay in the pine habitats caused by observably lower ground-level humidity (Gutzwiller, 1990; Wasser *et al.*, 2004; Harrison, 2006; MacKay *et al.*, 2008). Pine and hardwood habitats also had little observable understory vegetation and in pine habitats, enveloping leaf litter, which can impede scent circulation (Syrotuck, 1972). Additionally, the pine and hardwood habitats were observably cooler during search periods potentially allowing the dogs to pant less, thus improving their scenting ability (Gazit and Terkel, 2003; Smith *et al.*, 2003). Furthermore, differences amongst habitat types in the abundance of dung beetles and other saprophagous invertebrates that are known to remove scat might have contributed to our results (Tsaparis *et al.*, 2009). We did not find a difference in effect between clear-cut and hardwood habitat types on sample detection by dogs in part one potentially due to inflated rates of detection in the clear-cut sites as trails were inadvertently created to the scat samples through the thick vegetation present in the summer.

Studies on scat decay rates, which should correlate with detection rates of scat samples by dogs, showed differences in decay rates between habitat types similar to the differences in detection rates in our study (Prugh and Kerbs, 2004; Telfer *et al.*, 2006; Rhodes *et al.*, 2011). For example, Lehmkuhl *et al.* (1994) found that elk pellets decayed faster in clear-cuts compared to forest habitats. Additionally, Tsaparis *et al.* (2009) found the greatest mean time to decay was in coniferous forests, while mid-ranged values were

found in maquis shrubs (a habitat type between hardwood and clear-cut in our study), and the most rapid time to decay was observed in open areas. Further research is needed on how scat detection is affected by additional habitat types and to specifically determine why scat detection varies among habitats.

This study found that the age of a scat sample, the amount of rainfall the sample receives, the habitat the sample is located in, and the size of the sample all affect the detection probability of scat samples by dogs. The majority of studies using scat-detection dogs have previously ignored any potential differences in scat detection due to these variables (Dematteo *et al.*, 2008; Silveira *et al.*, 2009; Vynne *et al.*, 2010). However, depending on the questions asked and the study methodology, such potential biases in scat-detection rates could impact study results. For example, if scat samples decay at a rapid rate, researchers may erroneously conclude that a species was not present in an area when it was, a false-negative error (Rhodes *et al.*, 2011). However, a study by Rhodes *et al.* (2011) concluded that even a rare species will have few false-negatives at the scat decay rates we found in our study (3% a day). Additionally, false positive errors are also possible when using scat as an indirect measure of presence, since scat can also decay very slowly; for example, koala (*Phascolarctos cinereus*) scat has been known to persist for years in the environment (Rhodes *et al.*, 2011). If dogs are still able to detect an animals' scat long after the animal has left the area, researchers may erroneously conclude the animal is still present in the area. Furthermore, studies using scat detection by dogs to estimate species habitat selection or use can also be biased by differences in detection rates among habitat types (Rhodes *et al.*, 2011). Finally, studies of occupancy or population parameters including individuals that range in body size, such as different

species, genders, or age classes, may be biased if they use scat samples detected by dogs since detection rates of larger scat samples are greater.

In conclusion, scat-detection dogs are an efficient way to non-invasively collect a variety of data. However, like most research methods, detection dogs have limitations that need to be accounted for in study design and data analysis. In cases where false negatives are a concern, repeat surveys coupled with analysis methods that account for detectability (i.e., occupancy analysis; MacKenzie *et al.* 2006) can be conducted, as long as the time interval between surveys is shorter than the time it takes for the scat to decay (Long *et al.*, 2007b). Conversely, researchers can overcome false positive errors by conducting repeat surveys in which all previously found scat samples are removed or marked, thus allowing one to determine the presence of new scat samples. Sampling more intensively, having larger sample plots, or statistically accounting for differences in detection rates between habitats can overcome variations in detection rates between habitats (Rhodes *et al.*, 2011). Climate and weather conditions that the scat detection study is being conducted in are also important considerations. Interestingly, our dogs occasionally located samples that they had failed to locate in previous week's trials potentially due to differences in short-term weather conditions on the scat sample and the dogs ability to detect the sample (Smith *et al.*, 2003; Cablk and Heaton, 2006; Reed *et al.*, 2011). To account for the effects of weather, scat surveys using dogs should be conducted in optimal conditions: cool and dry (MacKay *et al.*, 2008). Finally, studies that require repeated surveys of known scat locations should take into account the dog's ability to "cheat" (i.e. memorize scat sample locations or cue off slight changes in handler behavior) when designing the survey. While we believe "cheating" occurred rarely and

randomly enough to not bias our results, our study could have been improved by stricter protocol in part one of the experiment.



**Table 1.** Top ten models by AICc score and null model for part 1 of the experiment. Model weight =  $\omega$ , variables included have an “x”, cc = clear-cut habitats, hw = hardwood habitats, rain=adjusted rainfall.

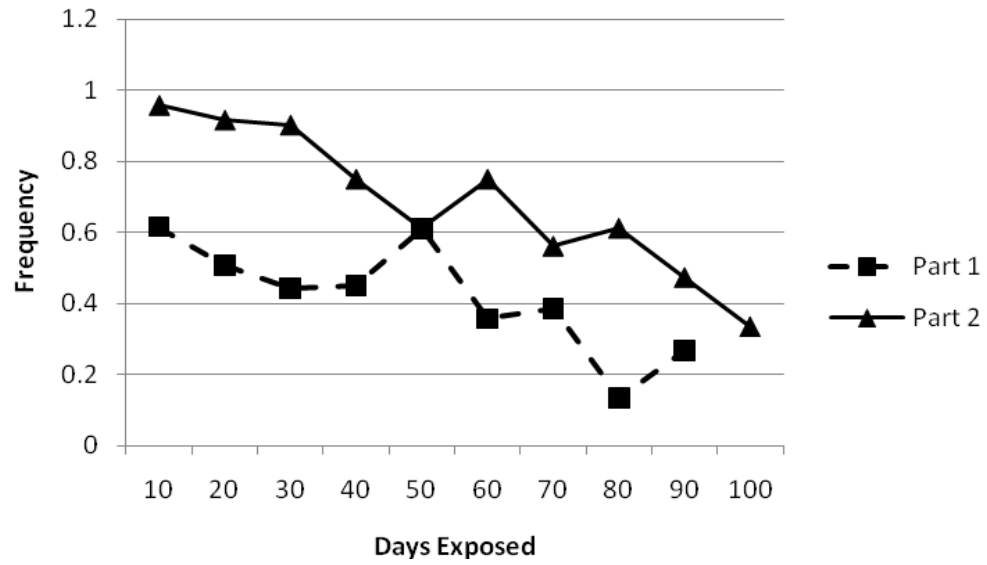
Model												
cc	hw	age	rain	size	hw*rain	cc*rain	cc*age	size*rain	size*age	k	AICc	$\omega$
x	x	x	x	x	x					7	329.5	0.068
x	x	x	x	x	x	x				8	329.7	0.06
	x	x	x	x	x						330.3	0.046
x	x	x	x	x	x		x			8	330.5	0.041
x	x	x	x	x	x	x	x			9	330.7	0.038
x	x	x	x	x	x			x		8	330.7	0.038
x	x	x	x	x	x				x	8	331.4	0.026
x	x	x	x	x		x				7	331.4	0.026
x	x	x	x	x	x	x		x		9	331.5	0.026
x	x	x	x	x	x	x			x	9	331.5	0.025
										1	379.6	8.90E-13

**Table 2.** Top ten models by AICc score and null model for part 2 of the experiment. Model weight =  $\omega$ , variables included have an “x”, cc = clear-cut habitats, hw = hardwood habitats, rain=adjusted rainfall.

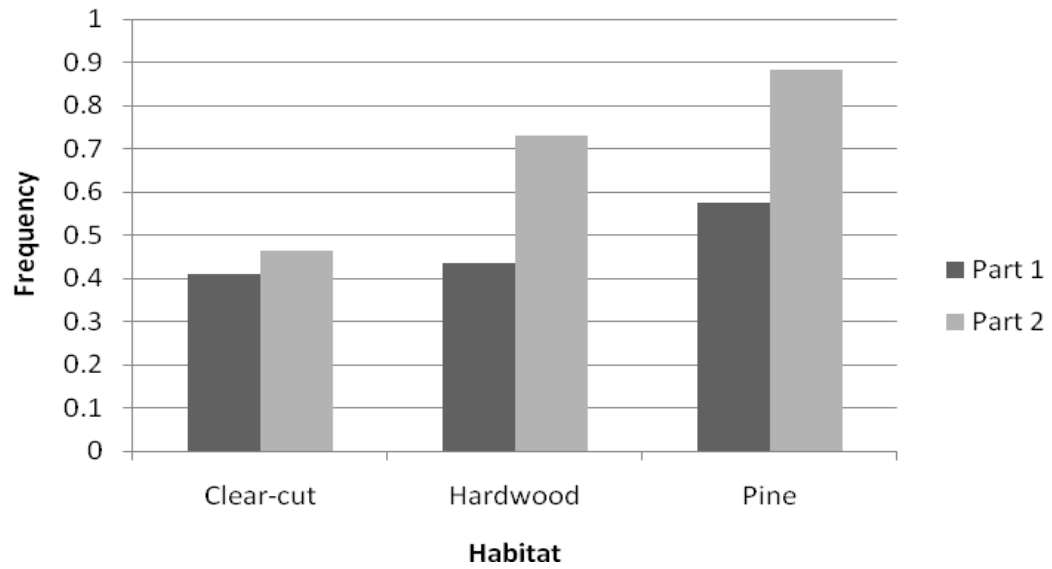
Model										
cc	hw	age	rain	cc*age	cc*rain	hw*age	hw*rain	k	AICc	$\omega$
x	x	x		x				5	405.2	0.203847
x	x	x	x	x				6	405.9	0.143342
x	x	x	x	x			x	7	406.44	0.109687
x	x	x		x		x		6	407.12	0.078112
x	x	x	x	x	x		x	8	407.73	0.057463
x	x	x	x	x		x		7	407.87	0.053692
x	x	x	x	x	x			7	407.97	0.051075
x	x	x	x	x		x	x	8	408.31	0.043089
x	x	x						3	408.83	0.033163
x	x	x	x					4	409.08	0.029284
								1	506.09	2.51E-23

**Table 3.** Odds ratios for effects of various variables on detection of scat samples. Reference habitat is pine. RVI is the probability variable is in the true best model among those considered. Coefficient estimates and their standard errors were derived using multi-model inference.

	part 1				part 2			
	Odds	RVI	Estimate	SE	Odds	RVI	Estimate	SE
age	0.969	1.00	-0.031	0.010	0.965	1.00	-0.036	0.011
rainfall	0.806	1.00	-0.216	0.115	0.983	0.65	-0.017	0.052
clear cut	0.391	0.84	-0.940	0.552	0.051	1.00	-2.980	0.530
hardwood	0.387	0.90	-0.950	0.542	0.242	0.98	-1.420	0.514
age*clear cut	0.981	0.33	-0.020	0.018	0.970	0.80	-0.030	0.014
rainfall*clear cut	1.242	0.49	0.217	0.130	0.968	0.19	-0.033	0.085
age*hardwood	1.007	0.26	0.007	0.017	1.000	0.30	0.000	0.018
rainfall*hardwood	0.717	0.72	-0.332	0.151	0.905	0.29	-0.100	0.079
large size	9.393	1.00	2.240	0.442				
age*large size	0.994	0.27	-0.006	0.015				
rainfall* large size	1.105	0.33	0.100	0.120				



**Figure 1.** As the number of days scat samples are exposed to the environment increases, the proportion of samples detected by dogs decreases.



**Figure 2.** The frequency that scat samples are detected by dogs depends on which habitat each sample is located in. The frequency of detection decreases from pine to hardwood to clear-cut habitats.

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