

Survival Estimates of White-tailed Deer Fawns at Fort Rucker, Alabama

by

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Abstract

Decreases in recruitment of white-tailed deer (*Odocoileus virginianus*) fawns have been noted at several locations across the Southeast. Understanding the reason for these decreases is important for management of deer populations. We monitored fawns from birth until 6 months to examine age- and cause-specific rates of mortality, at Fort Rucker, Alabama, a location that has experienced substantial decreases in fawn recruitment, deer population density, and hunter success. This study, like other recent studies in the Southeast, has found that low fawn recruitment seems to be driven by greater levels of coyote (*Canis latrans*) predation than originally believed. Coyotes are a recent addition to the predator community of the Southeast, but how their addition will ultimately affect deer populations remains unknown. Predator-prey theory predicts a variety of future scenarios concerning predation rates, deer density, and responses to alternative management strategies. We describe these alternative theories in regard to the current state of knowledge.

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Chapter I: Literature Review

FAWN SURVIVAL

Overall mortality rates

In the late 20th century Linnell et al. (1995) reviewed studies of neonatal mortality in ungulates, including 19 studies on white-tailed deer (*Odocoileus virginianus*). Across these 19 studies the average percentage of mortality was 46% with a standard deviation of $\pm 28\%$. This large standard deviation indicates that these studies varied greatly in the percent mortality reported, and a small selection of the reviewed studies demonstrates this variation (71%, Cook et al. 1971; 90%, Bartush and Lewis 1981; 85%, Epstein et al. 1983; 27%, Huegel et al. 1985). Since the review published by Linnell et al. (1995), mortality of white-tailed deer fawns continues to be examined: reports of fawn mortality published soon after the review include Sams et al. (47%, 1996) and Long et al. (74%, 1998). Pusateri Burroughs et al. (2006), Ricca et al. (2002) and Vreeland et al. (2004) reported mortality rates of 16%, 59%, and 49%, respectively, to approximately 6 months of age. The most recent studies on white-tailed deer fawn survival have used VITs to locate very young and stillborn individuals, and thus were able to calculate more accurate mortality estimates (66.7%, Saalfeld and Ditchkoff 2007; 53%, Carstensen et al. 2009; 77%, Kilgo unpublished data).

Temporal patterns

As a hider species, white-tailed deer fawns remain still and hidden when presented with stressful stimuli (Lent 1974). This response, known as the prone

response, wanes as the fawn ages, and white-tailed deer demonstrate a decrease in this response as early as 10 days of age (Downing and McGinnes 1969). Young of hider species also become more active as they age and may require activity to develop muscles which allow them to outrun predators (FitzGibbon 1990). This increase in activity causes fawns to become more visible at a time when they are unable to outrun predators and thus become more vulnerable to predation (Litvaitis and Shaw 1980, Byers and Byers 1983, Aanes and Andersen 1996). The time of vulnerability to predators is not constant across white-tailed deer fawn mortality studies. Bartush and Lewis (1981) found the age at which predation occurred to range from 3 to 78 days with an average age of 21, while 73% of canid-killed fawns were 27-47 days old in a study by Nelson and Woolf (1987). In the extremes of variability, however, within days of being marked 14 of 20 fawns were killed by predators in a study by Carroll and Brown (1977), while the canid-killed fawns studied by Nelson and Woolf (1987) were all over 20 days of age. It seems as though most fawns can elude predators by 8 weeks (Nelson and Woolf 1987, Long et al. 1998). Approximately 90% of all mortality occurred within 30 days of birth in two studies (Cook et al. 1971, Bartush and Lewis 1981), indicating that during this time white-tailed deer fawns are most vulnerable to mortality.

Studies on other ungulate hider species have shown similar results in the timing of mortality. Trainer et al. (1981) determined that the greatest mortality occurred within 45 days of age for mule deer (*Odocoileus hemionus*) fawns. The median age in days for fawns killed by predators was 20, while non-predatory mortality occurred at a median age of 13 days (Trainer et al. 1981). Another study found that mule deer fawns were most susceptible to predation by coyotes between 45 and 105 days of age (Hamlin et al. 1984).

This variation is similar to that found in white-tailed deer fawns. Pronghorn (*Antilocapra americana*) may have an earlier window of susceptibility as studies have found them to be most susceptible to mortality within three weeks of age (Von Gunten 1978) and susceptible to predators between 11 and 20 days old (Barrett 1978, 1984).

Differences in the survival of the sexes

Most studies on white-tailed deer fawn mortality have found no difference in the survival of male versus female fawns (Cook et al. 1971, Bartush and Lewis 1981, Nelson and Woolf 1987, Decker et al. 1992, Sams et al. 1996, Long et al. 1998, Ricca et al. 2002), with similar results in mule deer (Zwank 1978, Trainer et al. 1981). However, a study by Carstensen et al. (2009) determined that three times as many males as females died between 5 and 12 weeks of age. This time interval is when fawns are considered to be most susceptible to predation due to an increase in activity, and males are more active than females (Jackson et al. 1972), potentially making them more visible to predators. Another reason for greater rates of mortality in males may be due to increased nutritional demands in males versus females of polygynous mammals. Male fawns have a higher birth weight and growth rate than female fawns (Wauters et al. 1995, Birgersson and Ekvall 1997) which places greater nutritional demands on the mother (Clutton-Brock et al. 1981). The effect of nutritional demands on the mother and the survival of her offspring can be seen in a study by Verme (1962) which showed decreased survival in fawns whose mothers were fed restricted diets.

Predation

Predators can substantially increase rates of mortality, and predation has been reported to account for 89% of mortalities (Kilgo unpublished data). A review by Linnell

et al. (1995) found that an average of 54% of mortality was due to predation, but high variability in the percentage of mortality due to predation is seen across studies (88%, Bartush and Lewis 1981; 63%, Epstein et al. 1983; 57%, Ricca et al. 2002; 17-70%, Vreeland et al. 2004; 86%, Carstensen et al. 2009). The type and density of predators in an area has a strong influence on rate of predation.

Potential predators on my study site, Fort Rucker, Alabama, include coyotes (*Canis latrans*), domestic dogs (*Canis lupus familiaris*), bobcats (*Lynx rufus*), black bears (*Ursus americanus*), red foxes (*Vulpes vulpes*) and grey foxes (*Urocyon cinereoargenteus*). Coyotes can cause significant mortality in white-tailed deer fawns, and it has been suggested that they have effectively filled the niche of wolves (*Canis lupus*) in some areas as a fawn predator (Ballard et al. 1999). Coyotes have been found to be a significant predator of white-tailed deer fawns (60% of predation due to coyotes, Cook et al. 1971; 70%, Huegel et al. 1985; 66.7%, Sams et al. 1996; 80%, Long et al. 1998; 100%, Saalfeld and Ditchkoff 2007; 90%, Kilgo unpublished data). Other studies have noted incidents of coyote predation but to a lesser extent (Mathews and Porter 1988, Decker et al. 1992, Vreeland et al. 2004). Nelson and Woolf (1987) were unable to distinguish between coyote and domestic dog kills and attributed 69% of mortalities to a combination of the species. Domestic dog predation has also been noted in other studies (Huegel et al. 1985, Decker et al. 1992, Long et al. 1998, Ricca et al. 2002). Lowry and McArthur (1978) reported incidences of domestic dogs chasing white-tailed deer and mule deer, with 39 reported chases resulting in 12 deaths.

In some studies bobcats have also been reported to be significant predators of white-tailed deer fawns (46% of predation due to bobcats, Epstein et al. 1983; 75% of

predation by known predators due to bobcats, Ricca et al. 2002; 90% of predation due to bobcats, Roberts 2007; 38% of predation due to bobcats, Carstensen et al. 2009).

However, bobcats are considered to be a less significant predator in most studies (Cook et al. 1971, Decker et al. 1992, Sams et al. 1996). Bobcats, an ambush predator, may be a less significant predator of white-tailed deer fawns, in comparison to coyotes, because they sit and wait for prey and would be less likely to encounter hiding white-tailed deer fawns. Other predators of white-tailed deer fawns include black bears (Mathews and Porter 1988, Kunkel and Mech 1994, Vreeland et al. 2004, Carstensen et al. 2009), both red and grey foxes (Epstein et al. 1983, Sams et al. 1996, Ricca et al. 2002), and alligators (*Alligator mississippiensis*; Epstein et al. 1983, Roberts 2007).

Other causes of mortality

Mortality due to factors other than predation are common in most studies; however, predation is usually the leading cause of mortality. Other factors leading to mortality include disease, emaciation/abandonment, drowning, accidents, and poaching. Emaciation and starvation are both caused by malnutrition of the fawn. This malnutrition may be due to malnutrition in the doe (Verme 1962), leading to compromised lactation, or abandonment by the doe. Several studies have reported deaths due to malnutrition (Cook et al. 1971, Bartush and Lewis 1981, Nelson and Woolf 1987, Sams et al. 1996, Ricca et al. 2002, Vreeland et al. 2004, Pusateri Burroughs et al. 2006, Saalfeld and Ditchkoff 2007). Disease has been reported by Cook et al. (abscess, diarrhea, salmonellosis, 1971), Decker et al. (1992), Huegel et al. (acute necrotic hepatitis, 1985), Nelson and Woolf (1987), Pusateri Burroughs et al. (pneumonia and bacterial infection, 2006) and Ricca et al. (2002). Disease may also be affected by nutrition because the

immune system can be compromised in malnourished individuals (Lochmiller et al. 1983, Sams et al. 1996, Saino et al. 1997, Ditchkoff et al. 2001). Other factors of mortality including accidents, drowning, and poaching have been reported (Cook et al. 1971, Bartush and Lewis 1981, Huegel et al. 1985, Decker et al. 1992, Long et al. 1998, Ricca et al. 2002, Pusateri Burroughs et al. 2006, Saalfeld and Ditchkoff 2007).

DOE SURVIVAL

Overall survival

Adult survival is less variable than juvenile survival and has a greater impact on rate of population growth (Gaillard et al. 1998). Mortality in adults is likely to occur due to the same major factors as juveniles, but the relative importance of each mortality factor normally differs between fawns and adults. Populations in rural, exurban, and suburban areas have different rates of mortality due to differences in hunting pressure, road density, and predator ecology in these areas. Average annual mortality rates for adult does in suburban areas and other areas which are not hunted can be as low as 18% (Etter et al. 2002), but have been reported to be as high as 27% (Ricca et al. 2002) and 32% (Hansen and Beringer 2003). While average annual mortality in an exurban area where hunting was allowed, but not common, was 13% (Storm et al. 2007). Rural areas have slightly greater or equal adult doe mortality rates in comparison to suburban and exurban areas (21%, Nelson and Mech 1986; 31%, Fuller 1990; 29%, Nixon et al. 1991; 43%, DePerno et al. 2000; 32 – 39%, Hansen and Beringer 2003; 24%, Brinkman et al. 2004), however, low hunting effort can lead to very low mortality rates (13%, Campbell et al. 2005).

Hunting mortality

In most rural areas hunting is the most important source of mortality in female white-tailed deer. Mortality due to both legal and illegal firearm hunting attributed to up to 77% of deaths in a study by Hansen and Beringer (2003) and 43% of deaths in a study by Brinkman et al. (2004). Mortality from illegal hunting has been reported in suburban areas as 10% of overall mortality (Ricca et al. 2002). Hunting is normally allowed in exurban areas but only with the permission of the landowner. Therefore hunting pressure in these areas is dependent upon the landowners' view of hunting. Storm et al. (2007) found both legal and illegal hunting attributed to only 11% of mortality in an exurban area where less than 20% of landowners allowed hunting.

Disease

Death due to disease is more frequent in suburban populations in comparison to rural areas. One suburban study found that 28% of mortalities were due to disease in combination with emaciation (Ricca et al. 2002). Diseases and parasites recorded included pneumonia, *Yersinia pseudotuberculosis*, and lungworms. Of the 12 necropsied deer, 92% lacked subcutaneous body fat and had high levels of ectoparasites (Ricca et al. 2002). As previously stated, increased disease in malnourished individuals is likely due to effects of malnutrition on the immune system. In rural areas, disease caused 7% (Brinkman et al. 2004) and 14% (Hansen and Beringer 2003) of adult doe mortality.

Hemorrhagic disease is the collective name for both epizootic hemorrhagic disease and bluetongue, two viruses with identical clinical symptoms. Hemorrhagic disease is found yearly in the Southeast (Nettles et al. 1992) and has the highest prevalence in the coastal plain region (Stallknecht et al. 1991). Alabama and other states

in the southeast are considered to be endemic areas for hemorrhagic disease (Nettles et al. 1992). Deer mortality rates due to hemorrhagic disease are variable (Prestwood et al. 1974), but one study reports that mortality in endemic states is 16% (Nettles et al. 1992). Usually hemorrhagic disease outbreaks do not limit population growth of white-tailed deer (Howerth et al. 2008).

Vehicle collisions

Vehicle collisions are likely to cause greater mortality in areas with greater road densities (i.e. suburban areas) in comparison to areas with decreased road densities (i.e. exurban and rural areas). Death due to vehicle collisions was the greatest source of mortality in two suburban studies, accounting for 90% (Hansen and Beringer 2003) and 42% of all mortalities (Etter et al. 2002). In another study, vehicle collisions were reported as the second most frequent cause of death, after disease, and caused 17% of mortalities (Ricca et al. 2002). Reports of doe mortality due to vehicle collisions in exurban and rural areas have been as low as 2% (Storm et al. 2007) and 8% (Hansen and Beringer 2003), however other studies show mortality rates in rural areas due to vehicle collisions may be as great as 21% (Brinkman et al. 2004).

Predation

Predation in adult white-tailed deer is less likely than in fawns, however it does occur, and varies based on the predator ecology of the area. Coyote predation on adult white-tailed deer is thought to be minimal, and usually occurs when coyotes form packs and/or when deer are injured (Andelt 1985, Campbell et al. 2005). Additional predators of adult white-tailed deer include black bear (Campbell et al. 2005), wolf (17% annual mortality, Nelson and Mech 1986), and unidentified felid (Brinkman et al. 2004).

COYOTE FOOD HABITS

As a generalist omnivore, coyotes opportunistically prey upon small and large prey and eat fruit based on availability. The availability of these items varies based on geographic location, creating changes in the coyote diet based on its home range. In its native range in the central United States, a large diversity of small mammals, as well as other prey, is available to the coyote. This greater diversity of small mammals creates more opportunities for the generalist coyote. A food habits study in Oklahoma (Litvaitis and Shaw 1980), indicated that over 50% of scats collected in winter contained small rodents, including eastern woodrats (*Neotoma floridana*), white-footed mice (*Peromyscus leucopus*), and cotton rats (*Sigmodon hispidus*). Deer fawns may also provide an important seasonal food source in this area during fawning (Litvaitis and Shaw 1980, Andelt et al. 1987). Lagomorphs are utilized in the West, primarily in fall, winter, and spring (Litvaitis and Shaw 1980, Andelt et al. 1987). A decrease in lagomorphs in coyote diet in summer may be due to cost tradeoffs between capturing and handling lagomorphs in comparison to fawns and fruits (Andelt et al. 1987). After mammals, fruits and seeds are the most important energy source based on consumption, occurring mostly in summer and fall (Litvaitis and Shaw 1980, Andelt et al. 1987). Insects, mainly orthopterans, are another important aspect of the coyote diet during summer, being found in 26% of coyote scats (Litvaitis and Shaw 1980). The increase in fruits and insects in the coyote diet in summer decreases the importance, and therefore may decrease hunting pressure, of mammalian species (Connolly 1978, Andelt et al. 1987).

In comparison to the coyotes' native range in the West, the Southeast offers a decreased diversity of small mammals and a greater diversity of fruit. The low diversity

of small mammals leads to increased pressure on larger, more available prey items. Percentage of occurrence of white-tailed deer in coyote scat is similar in winter and spring months (40% Dec., 37% Mar., Schrecengost et al. 2008) and lower during the rest of the year. White-tailed deer fawns occurred in over 30% of scats collected in May and over 15% of those collected in June (Schrecengost et al. 2008). This occurrence coincides with fawning (29% deer fawn occurrence in scats collected during fawning, Stratman and Pelton 1997), a time when fawns are most vulnerable. Andelt et al. (1987) found increased predation on deer by coyotes when fawning was delayed to a time when fruit resources were less abundant. Unlike other white-tailed deer populations, fawning in Alabama occurs primarily in August. If fawning in Alabama is occurring when fruits are less abundant, increased predation may be seen on fawns. Other prey or carrion species found in coyote scat include wild hog (*Sus scrofa*), lagomorphs, rodents, beetles, and turkey-like egg shells (Wagner and Hill 1994, Stratman and Pelton 1997, Schrecengost et al. 2008). Studies of coyote digestive tracts from Arkansas and Tennessee have presented results that differ from other regional studies in that the diets of coyotes had greater occurrences of rodents and lower occurrences of deer (Gipson 1974, Smith and Kennedy 1983, Lee and Kennedy 1986). It should also be noted that these three studies were conducted over 25 years ago, while the other studies presented here were conducted in the last 15 years. This difference in time may account for the differences in results due to changes in coyote or prey population densities and/or habitat availability.

A greater diversity of fruit is found in the diet of coyotes in the Southeast. The summer and fall diets of coyotes in the Southeast are predominately composed of fruits

and other vegetation, with prevalence rates as great as 85% (Stratman and Pelton 1997, Schrecengost et al. 2008). Fruits included in the diet are wild plums (*Prunus spp.*), smilax berries (*Smilax spp.*), blueberries (*Vaccinium spp.*), saw palmetto fruit (*Serenoa repens*), blackberries (*Rubus spp.*), black cherry (*Prunus serotina*), poke berry (*Phytolacca americana*), and persimmon (*Diospyros virginiana*; Stratman and Pelton 1997, Schrecengost et al. 2008). The diversity of southeastern fruiting plants allows the coyote to use this as a major source of energy when available.

The studies discussed here primarily use the occurrence of a diet item in the digestive tract or scat to determine its prevalence in the diet. However, differences in the passage rate of diet items may skew these results. For example if one white-tailed deer is depredated, hair is likely to be found in multiple scats from multiple individual predators or scavengers whereas the remains of one persimmon will only be found in one scat. The results of these studies can be used to compare items in the coyote diet and perhaps even quantities of the same diet item, as the passage rate should be similar across individuals within the same species. Scat studies cannot be used, however, to determine the extent of white-tailed fawn predation, but using them to determine the timing of fawn predation is possible (Salwasser et al. 1978, Litvaitis and Shaw 1980).

BOBCAT FOOD HABITS

Unlike generalist coyotes, bobcats tend to be specialized with a strictly carnivorous diet (Litvaitis and Harrison 1989). The predominate prey species of the bobcat are lagomorphs and small mammals (Davis 1955, Dibello et al. 1990, Godbois et al. 2003). The incidence of bobcat predation on white-tailed deer is thought to be low in

most areas, and the predominance of white-tailed deer found in bobcat scats and stomachs occurs during winter (Davis 1955, Young 1958, Maehr and Brady 1986, Dibello et al. 1990). Bobcat food habit studies have demonstrated white-tailed deer fawns in the diet during fawning season, but occurrences are very low (1 of 23 stomachs during fawning period, Davis 1955; fawns occurred in 4% of scats during summer, Dibello et al. 1990). In contrast to the low incidences of white-tailed deer reported in the bobcat diet by most studies, Baker et al. (2001) found white-tailed deer hair in over 50% of the scats collected in spring and summer from bobcats released on a coastal island of Georgia. Wild hogs are another game species rarely found in the bobcat diet (Maehr and Brady 1986).

PREDATOR-PREY THEORY

Basic concepts

Predation can either be compensatory or additive. Compensatory predation is when predators remove no more individuals from a population than would have died from other causes. Therefore compensatory predation does not affect population growth. Additive predation is when predation adds to other sources of mortality. Therefore this type of predation does affect population growth and can limit or regulate a prey population. Removal studies indicating that removal of predators increases the prey population are initial indicators that predators are having an additive affect on the prey population.

Predation also relates to the numerical and functional response of the predator, which together are considered the total response (Solomon 1949). The numerical

response is the change in the size of a predator population in response to changes in prey density (there is typically a delay in this response), while the functional response is based on consumption by an individual predator (there is no or little delay in this response; Solomon 1949, Holling 1959). There are three types of functional responses (Holling 1959). The Type I functional response is based on a random search technique: as prey density increases prey killed per predator increases proportionally until no more prey can be consumed due to limitations caused by handling time (Holling 1959). This response is most common in filter and passive feeders. In the Type II response, utilization increases at a continually decreasing rate until an asymptote is reached based on searching and handling time (Holling 1959, Evans 2004). The last functional response is Type III, represented as an S-shaped curve. At low prey densities, utilization by the predator is directly density-dependent, while at high prey densities it is inversely density-dependent (Holling 1959, Evans 2004).

Limitation

Limitation is any process which reduces population growth, and includes all types of mortality and reproductive losses (Messier and Crête 1985, Sinclair and Pech 1996). If predators are limiting a prey population they are following a nonequilibrium model, and the prey population will not recover to a previous level after being disturbed (Van Ballenberghe 1987, Boutin 1992). The limitation theory is thought to occur in populations where predator and prey have been heavily manipulated and there is little, if any, density-dependent feedback between the populations (Gasaway et al. 1983). In the limitation hypothesis predators could be following Type I or Type II functional responses or have no functional response.

To determine which predator-prey theory is applicable to a population, Boutin (1992) described three experiments and the results which would identify each theory. While these experiments were originally created for moose (*Alces alces*) and wolves, they are applicable to other predator-prey systems. In the first experiment, the density and survival of the primary prey population are monitored in relation to changing predator densities and densities of alternate prey for those predators (Boutin 1992). To indicate the limitation theory, the results of this experiment would be as follows; at all prey densities the predator will take an inversely density-dependent proportion of the prey population, resulting in fluctuating prey densities (Boutin 1992). The second experiment would reduce the prey population to a low density and require a non-manipulated predator population (Boutin 1992). In this experiment a greater proportion of the prey population is taken by predators, and a continued decrease in prey density would be indicative of limitation theory (Boutin 1992). Extensive predator removal of all predatory species until prey densities are able to increase to high levels is entailed in the third experiment (Boutin 1992). This experiment will result in an increase in the density of the prey population until predators return to the system and prey populations again decline (Boutin 1992). This situation is indicative of limitation theory.

Banks et al. (2000) predicted that (1) red foxes limited juvenile recruitment of kangaroos (*Macropus giganteus*) and removal of foxes would result in increased juvenile survival, and that (2) population growth was limited by juvenile survival, so removal of foxes would result in increased population growth. They found significantly greater recruitment of juvenile kangaroos in fox removal sites versus non-removal sites, supporting their first prediction (Banks et al. 2000). Greater densities of kangaroos at

removal sites versus non-removal sites seemingly supports the second prediction; however, the investigators acknowledged the possibility that reduced predation pressure may have resulted in increased observability of kangaroos, and initial high kangaroo densities at all sites may have limited effects of fox removal (Banks et al. 2000).

Bergerud (1971) used historical data (1900 – 1967) from caribou (*Rangifer tarandus*) in Newfoundland to report on factors affecting growth of the population. This extensive amount of data allowed Bergerud (1971) to evaluate factors that were having legitimate and lasting effects on the population. Poor recruitment and high hunting pressure reduced the caribou herds from 1915 to 1930, and reduced hunting pressure, as well as the loss of a large predator (Newfoundland wolf; *Canis lupus beothucus*) did not result in a rebound of the population (Bergerud 1971). Bergerud (1971) concluded that lynx (*Lynx lynx*) were limiting the caribou population through high predation on juveniles, thus affecting population recruitment.

Regulation

Regulation occurs when a process is density dependent. The regulation predator-prey theory is based on the interaction of density dependent factors with depressive processes (i.e. predation, disease, starvation; Holling 1959, Messier and Crête 1985). Prey populations following the regulation predator-prey theory will return to a previous equilibrium level after perturbation (Boutin 1992, Sinclair and Pech 1996). Regulation theory is based primarily on the total response; however, it requires a Type III functional response.

There are two regulation theories based on the number of stable equilibrium. With the single equilibrium model the total response curve intersects the population

growth curve at one point creating a single equilibrium. If the prey population is disturbed the population will always return to this equilibrium (Boutin 1992). The equilibrium will be influenced by changes in the population growth curve and the total response curve (i.e. changes in predator density). The second regulation theory is known as the multi-equilibria or predator-pit theory (Haber 1977). According to this theory, the total response curve passes through the population growth curve three times, creating two stable and one unstable equilibrium. This allows the predator to keep the prey population at a low stable equilibrium, also known as a predator pit (Boutin 1992, Evans 2004). To escape the predator pit the prey population must increase past a threshold, the unstable equilibrium, to reach the upper equilibrium (Boutin 1992).

Boutin (1992) also gave predictions for regulation theories for his experiments. If following a Type III functional response, the first experiment will result in density-dependent proportions of the prey population being taken by predators at low to intermediate prey densities and inversely density-dependent proportions at high densities (Boutin 1992). However, the two regulation theories will differ in showing either one stable equilibrium, or two stable equilibria. The second experiment will result in a decrease in the proportion of prey taken by the predator population; however, prey density will increase with one stable equilibrium and decrease with the two stable equilibria theory (Boutin 1992). Similar to the predictions of experiment three for the limitation theory, under one stable equilibrium regulation theory the prey population will increase after predator removal and then decrease after predators move back into the system. While with two stable equilibrium regulation theory predicts that the prey population does not decrease after the reintroduction of the predatory species because the

prey population has reached an upper equilibrium (Boutin 1992).

Type III regulation, either one or two equilibria, is likely to be caused, in at least the preferred species, when alternate species are present and also when the preferred species has a refuge (i.e. an age class that is safe from predation; Murdoch and Oaten 1975). Generalist predators with a social organization that drives selected prey are more likely to switch to alternate prey (Murdoch and Oaten 1975).

The lower equilibrium of the multi-equilibria theory is often referred to as the predator pit. Predator populations are able to keep prey regulated at this low density, with no affect to their own population density. Predator population density is maintained by switching to alternate prey when the primary prey is at a low density (Shelton and Healey 1999). Predators will still take available primary prey, while using alternate prey to help maintain energy requirements, keeping the primary prey at the low equilibrium. Generalist predators feed on a variety of animal and plant matter, and choose prey items with the greatest benefit:cost ratio. This large prey base may interfere with predator prey relationships and provide potential weakened regulatory mechanisms (Messier and Crête 1985). However it has also been suggested that switching to alternate prey may cause greater stability in a system (Murdoch and Oaten 1975).

Messier and Crête (1985) were able to show that wolves regulate moose populations in southwestern Quebec. Predation rates of wolves on moose were density dependent at low and medium moose densities and inversely density dependent at high moose densities (Messier and Crête 1985). Reduction in the wolf population allowed for increased calf survival; however, the study did not continue to monitor for wolf recovery and its effect on moose populations (Messier and Crête 1985), and therefore was not able

to determine if regulation allowed for one or two equilibria.

Using data from studies of moose and wolf interactions across the moose range, Messier (1994) determined that wolves regulate moose at a high equilibrium, in a single predator system, following what he termed the “Predation-food model (one-state)”. The “predation-food model (one-state)” is a basic regulation model where predators interact with prey populations at a high food-based equilibrium. With population growth reduced by only 5-10%, however, wolves maintain the moose population at a low equilibrium, Messier’s “predation model” (1994). A reduction in population growth is possible in populations where alternate predators [i.e. black or grizzly bear (*Ursus arctos*)] affect juvenile recruitment (Messier 1994). According to Messier (1994) the relationship curve for wolves and moose does not allow for a predator-pit to develop.

Haber (1977) modeled moose, caribou, and wolf populations and discovered that wolves were able to regulate prey populations at a low equilibrium when other disturbance (i.e. hunting, winter mortality) reduced the prey population density. If wolf populations were reduced in the model, prey populations were able to escape to a greater density (Haber 1977). Haber (1977) was able to model and describe what is now termed the predator-pit model or multi-equilibria model.

A study in Australia was able to show regulation of European rabbits (*Oryctolagus cuniculus*) by red foxes (Banks 2000). Four study sites were selected and foxes were removed from two sites. The removal sites had increased rabbit production and populations were released from fox predation for 20 months (Banks 2000). While both sites increased in rabbit density, one site had 20.3 times as many rabbits as pre-removal densities while the other had 10.3 times as many rabbits (Banks 2000). Foxes

were able to reestablish populations at the sites after 20 months of removal and were able to reach densities similar to non-removal sites in less than two years. After fox reintroduction, rabbit densities initially dropped at both removal sites. Following the breeding season, the rabbit population which had the greater density began to increase, while the lower density population slowly declined (Banks 2000). This experiment supports the predator-pit or multi-equilibrium theory, by showing that prey, rabbits, are able to escape regulation by predators, foxes (Banks 2000).

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Chapter II: Survival Estimates of White-tailed Deer Fawns at Fort Rucker, Alabama

ABSTRACT

Decreases in white-tailed deer (*Odocoileus virginianus*) fawn recruitment have been noted at several locations across the Southeast. Understanding the reason for these decreases is important for management of deer populations. We monitored fawns from birth until 6 months to examine age- and cause-specific mortality rates, at Fort Rucker, Alabama, a location that has experienced substantial decreases in fawn recruitment, deer population density, and hunter success. During 2009 and 2010, 14 fawns were captured immediately after birth and monitored: below average deer density resulted in low sample sizes during the study. Of the 14 fawns captured, 3 survived until 6 months of age. Six of 7 predation events were attributed to coyotes (*Canis latrans*) based on examination of bite patterns and remains left at the site. We determined coyote density in the study area during 2010 using DNA isolated from 44 opportunistically collected coyote scats. The median rarefaction curve estimated density of coyotes at 0.40 coyotes/km², with a 95% confidence limit of 0.32 to 0.58 coyotes/km². This study, like other recent studies in the Southeast, has found that low fawn recruitment seems to be driven by greater levels of coyote predation than originally believed. Coyotes are a recent addition to the predator community of the Southeast, but how their addition will ultimately affect deer populations remains ambiguous. Predator-prey theory predicts a variety of future scenarios concerning predation rates, deer density, and responses to alternative

management strategies. We describe these alternative theories in regard to the current state of knowledge.

INTRODUCTION

Recent changes in the predator community in the Southeast may be affecting juvenile survival and population growth in white-tailed deer (*Odocoileus virginianus*). Historically the terrestrial predator community of the Southeast consisted of red wolves (*Canis rufus*), pumas (*Puma concolor*), bobcats (*Lynx rufus*), black bears (*Ursus americanus*), and the smaller red (*Vulpes vulpes*) and grey foxes (*Urocyon cinereoargenteus*). Within the last 40 years, coyotes (*Canis latrans*) have expanded their range east into areas previously occupied by larger predators (Hill et al. 1987). Since the recent increase in the coyote population, fawn recruitment in some populations in the Southeast is thought to have decreased. Evidence of this has been documented in a recent study in west-central South Carolina (Kilgo et al. 2010) in which fawn mortality was estimated at 77%, with 89% of mortalities attributed to predation (Kilgo unpublished data). Of all mortalities, 80% were confirmed or probable coyote predation (Kilgo unpublished data). The effect of predation on fawn recruitment can also be seen in studies that have examined predator control programs. The removal of predators (e.g. coyotes and bobcats) from study areas in southwest Georgia (Howze et al. 2009) and northeast Alabama (VanGilder et al. 2009) have lead to increases in fawn recruitment. It is important to note however, that in the absence of coyotes, bobcats may also cause significant rates of mortality in white-tailed deer fawns. A study done on an island off the coast of South Carolina found overall survival to 26 weeks to be 21.1%, with 67% of

mortality attributed to bobcats (Roberts 2007).

How this change in the predator community will ultimately affect deer populations in the Southeast is unknown. It is possible to refer to areas where coyotes are non-native but have been established for longer periods (e.g. the Northeast) to understand how this new predator may affect the Southeast. While differences in climate and habitat may cause differences in survival between these areas, previous research in the Northeast provides a foundation of knowledge that can be used to predict impacts on deer populations in the Southeast. A review of research in the Northeast indicates that areas with no coyotes or other large predators have comparable or greater 6-month fawn survival (70%, Banasiak 1961) to areas with coyotes (76%, Decker et al. 1992; 65%, Long et al. 1998; 66%, Ballard et al. 1999; 45.6-58.6%, Vreeland et al. 2004). Annual survival of fawns in Northeast populations, where monitoring occurred for an entire year, was much lower than 6 month survival (26%, Long et al. 1998; 25%, Ballard et al. 1999). The large difference between 6 month and annual survival indicates that winter survival is an important aspect of juvenile survival in the Northeast. Differences in deer density and coyote density are likely to account for some differences in survival rates among these studies, but differences in climate, habitat, and available alternative prey may cause greater differences between these studies and those in the Southeast.

Recent studies in the Southeast indicate that coyotes are affecting juvenile survival (Saalfeld and Ditchkoff 2007, Howze et al. 2009, VanGilder et al. 2009, Kilgo et al. 2010), and while comparisons to the Northeast provide a foundation they will not be completely applicable due to differences in climate and habitat. This leaves managers in the Southeast ill-equipped to resolve this new management issue. To understand the

effects of this new predator in the Southeast it is necessary to understand how changes in densities of coyotes and deer affect juvenile survival and population growth. These parameters can be used in conjunction with predator-prey theory to correctly address this new problem. Understanding which predator-prey theory is most applicable in the Southeast will allow managers to implement effective and economically efficient management strategies.

Deer ecology in Alabama and other Gulf Coast deer populations differs in comparison to the Southeast and all other regions, due to differences in timing of the breeding season. Breeding in Alabama occurs primarily in January and fawns are born during August (Lueth 1955, 1967, Gray et al. 2002), while across most of North America deer breed in November and fawn during May and June (Verme and Ullrey 1984). Delayed fawning in Alabama affects alternate food availability and coincides with coyote pup independence (Harrison and Harrison 1984, Harrison et al. 1991). These factors may cause differences in fawn survival in Alabama in comparison with other populations and may result in a unique management situation.

To begin to understand how differences in coyote and deer population densities affect juvenile survival and population growth we estimated juvenile and adult doe survival, as well as coyote density at Fort Rucker, Alabama, where recent increases in coyote numbers and decreases in white-tailed deer density have been noted. Conducting this study in Alabama also gave us the opportunity to assess the effect of a late fawning season on juvenile survival (see Saalfeld and Ditchkoff 2007).

STUDY AREA

This study was conducted at Fort Rucker, Alabama, a 183-km² military facility that conducts helicopter training for the U.S. Army. The southeastern third of the facility, approximately 42 km², was chosen as the area most feasible for this study. After data collection, unsampled sections of the study area were disregarded and the adjusted study area consisted of 31.6 km². The vegetation on the area was mostly of forested land that was comprised of primarily pine (*Pinus spp.*) and mixed pine-hardwood forests. Dominant tree species included loblolly (*Pinus taeda*), shortleaf pine (*Pinus enchinata*), longleaf pine (*Pinus palustris*), slash pine (*Pinus elliottii*), southern red oak (*Quercus falcate*), water oak (*Quercus nigra*), laurel oak (*Quercus laurifolia*), sweetgum (*Liquidambar styraciflua*), yellow-poplar (*Liriodendron tulipifera*), sassafras (*Sassafras albidum*), dogwood (*Cornus spp.*), sourwood (*Oxydendrum arboretum*), hawthorn (*Crataegus spp.*), persimmon (*Diospyros virginiana*), and cherry (*Prunus spp.*). The study area had patches of sandhill forest which included turkey oak (*Quercus laevis*), bluejack oak (*Quercus incana*) and were dominated by longleaf pine (Mount and Diamond 1992). Plantations of loblolly pine averaging 25 years of age, slash pine averaging 30 years of age, and longleaf pine averaging 15 years of age were dispersed throughout the area. Additionally, wildlife food plots planted with a variety of wildlife crops and fruiting trees were dispersed throughout the area. Prescribed burning had occurred throughout the area since before 1980, but had recently increased in frequency and intensity.

Both firearm and archery hunting were allowed on the majority of Fort Rucker. In recent years Fort Rucker hunters have reported a total harvest of 30 to 100 deer for the

entire installation. The majority of Fort Rucker had a 2.4-m chain linked fence with barbed wire at the top; however, there were breaks over streams and for natural boundaries. This fence limited, but did not prohibit, movement of individuals to and from the population.

Camera studies on Fort Rucker have shown fawn recruitment to be as low as 0.20 fawns per doe in the last five years. Populations without coyotes in the Southeast have reported fawn recruitment estimates as high as 0.80 (Kilgo et al. 2010). Five years of data collection have shown that pregnancy rates at Fort Rucker were above 90% (Cook unpublished data), suggesting that depressed recruitment rates were not a function of low rates of pregnancy. Additionally, low recruitment was not believed to be due to changes in cover, habitat type, or yearly climate, as body weights and herd health checks had indicated that the population was in excellent physical condition.

METHODS

Doe capture and handling

From February to July of 2009 and 2010, we trapped does using cannon nets over areas baited with corn (Hawkins et al. 1968): trap sites were baited for at least a month before capture started (Ditchkoff et al. 2001). After capture, does were sedated using a combination of 125 mg of telazol to 100 mg of xylazine (1 ml/45.36 kg) injected intramuscularly. To reverse sedation, an intramuscular injection of tolazine (yohimbine hydrochloride; 3 ml/45.36 kg) was given after data collection and vaginal transmitter insertion (Saalfeld and Ditchkoff 2007). We determined age by tooth wear and replacement (Severinghaus 1949), and measured chest girth, and head, body, tail, and

right hind foot length using a flexible 2-m tape. While the deer were sedated, we inserted vaginal implant transmitters (VITs; M3960B, Advanced Telemetry Systems, Insanti, MN) approximately 20 cm into the vaginal canal with the silicone wings pressed against the cervix (Carstensen et al. 2003, Saalfeld and Ditchkoff 2007). These VITs were capable of sensing a temperature change of 34 to 30 C, and would change the pulse frequency signal emitted when expelled from the doe during parturition. All does were also fitted with VHF radio collars (M2510B, Advanced Telemetry Systems, Insanti, MN) to allow regular monitoring of survival and location before and after fawning. We monitored does approximately once a week from initial capture until more intense monitoring began in mid-July, approximately two weeks before the peak of birth in Alabama (Lueth 1955, 1967). After giving birth, does were located when their corresponding fawn(s) were located.

Fawn capture and handling

Vaginal transmitters were monitored three times a day beginning in mid-July. After the first birth of the season, we monitored transmitters every six hours. Monitoring continued until all vaginal transmitters were expelled or the doe was identified as nonpregnant. We determined if a doe was nonpregnant by examining photographs, taken by remote cameras over baited sites, for visible signs of pregnancy. Fawns were not approached until at least two hours after the VIT indicated expulsion. A precise event timer in the vaginal transmitter allowed for time of birth to be calculated to within 30 minutes.

We followed the methods of Roberts (2007) and Kilgo (unpublished data) to locate fawns that moved from the birth site. Prior to approaching the VIT, the dam was

located via VHF telemetry and approached on foot. This increased the possibility of finding fawns if they had moved from the birth site and followed the doe. If the fawn(s) were not found near the doe, we moved towards the expelled VIT. If we did not find the fawn before or when the birth site was reached, we continued to search in expanded circles around the birth site. A thermal imaging camera (Raytheon Palm IR 250D, Waltham, MA) was used to aid in conducting all searches.

We captured fawns by hand and used non-scented latex gloves to reduce scent transfer (Powell et al. 2005, Saalfeld and Ditchkoff 2007, White et al. 1972). Fawns were weighed, sexed, and fitted with expandable collars (M4200, Advanced Telemetry Systems, Insanti, MN) that were designed to fall off at approximately 6 months of age. Using a flexible 2-m tape, we measured full body length, right hind foot length, and new hoof growth. Handling was completed in an efficient manner to reduce stress, and handling times were normally less than 10 minutes per fawn.

In addition to using VITs to find fawns at the birth site, we also conducted additional searches to increase the number of fawns captured. These searches were conducted using a window-mounted thermal imager and driving slowly along dirt roads through the study area as described by Ditchkoff et al. (2005). To increase the probability of catching older, more agile individuals, fawns were approached slowly in a sporadic manner with a handheld net (Ditchkoff et al. 2005). We aged fawns that were captured with this technique using hoof growth measurements (Sams et al. 1996), and handled these fawns in the same manner as those captured with the aid of VITs.

Fawns were located at least once every day for the first 2 months, and then located once a week until they reached six months of age or the expandable collar fell off.

When we received a mortality signal, the fawn was immediately located and the cause of death determined. Cause of death due to predation was determined by assessing remains at the site for puncture wounds and evidence of predators such as hair, scat, or tracks (O’Gara 1978). All other causes of death were determined during necropsy by the State of Alabama Department of Agriculture, Thompson Bishop Sparks Diagnostic Lab, Auburn, AL.

Analysis

All analysis was conducted in Program R version 2.10.1 (The R Foundation for Statistical Computing, 2009). Age-specific survival rate of fawns was estimated until 180 days using a Kaplan-Meier survival curve without staggered entry, and any individuals with an unknown fate were right censored (Hosmer et al. 2008). To compare hazards of covariates, including sex, year, age, and age², we used a Cox proportional hazards model (Hosmer et al. 2008). In this model, entries were staggered based on date of birth (i.e. July 27) to allow the effects of age to be tested. Cause-specific mortality of fawns was analyzed using competing risks analysis; three types of mortality were used in this analysis, abandonment, bobcat predation, and coyote predation (Heisey and Patterson 2006). Annual doe survival was estimated using a Kaplan-Meier survival curve with staggered entry at weekly increments with week 1 starting on January 1st. Individuals surviving into the next calendar year were right censored and reentered in the data as a separate entry (recurrent model; Fieberg and DelGiudice 2009). We used Cox proportional hazards models to compare hazards of covariates including age and year (Hosmer et al. 2008).

Coyote density

Coyote density was estimated for summer 2010 by identifying individual coyotes within the study area using DNA extracted from scat. Scat samples were collected opportunistically on roads throughout the study area from June to September 2010. Samples were taken along the side of the fecal sample, and 0.4 mL of feces was placed into vials containing 1.5 mL DETs buffer (Stenglein et al. 2010). Genetic analyses were conducted by the Laboratory for Conservation and Ecological Genetics, University of Idaho using techniques described by Stenglein et al. (2010).

We iterated a rarefaction curve, an accumulation of unique individuals or genotype with the asymptote representing the estimated population size [$y = (a*x)/(b + x)$], where x was the number of amplified samples, y was the cumulative number of unique genotypes, a was the asymptote, and b the rate of decline in the slope], 1,000 times to determine the number of coyotes in the study area (Kohn et al. 1999). The median, rather than the mean (Frantz and Roper 2006), number of coyotes, as determined by the rarefaction curves, was used to determine coyote density on the adjusted study area (31.6 km²).

RESULTS

We captured 15 does and recaptured one doe in year 2 of the study, resulting in 16 deployed VITs during 273 trap sessions over two field seasons: 9 VITs were deployed in 2009 and 7 in 2010. The 16 deployed VITs resulted in 11 birth events: 6 in 2009 and 5 in 2010. Twelve live fawns (4 in 2009 and 8 in 2010) and 2 stillborn fawns in 2009 were found at or near VIT birth sites. In 2009, one VIT was expelled prematurely, although a

fawn was found within 24 hours of birth near the doe. One additional fawn was found during random searches in 2009. Capture efforts resulted in a total of 15 does and 14 fawns for survival analysis.

Overall probability of fawn survival to six months of age was determined to be 0.26 (95% CI = 0.10 – 0.68) with 3 of 14 fawns surviving. All mortalities occurred between 3 and 40 days of age, but no patterns of mortality were apparent within this period (Figure 1). No covariates were found to be significant predictors of mortality, based on a full model including age ($P = 0.739$, $\beta = 0.972$, 95% CI = 0.821 – 1.15), age² ($P = 0.878$, $\beta = 1.00$, 95% CI = 0.999 – 1.001), sex ($P = 0.606$, $\beta = 0.571$, 95% CI = 0.0680 – 4.80), and year ($P = 0.762$, $\beta = 1.57$, 95% CI = 0.0847 – 29.08).

Three types of mortality were identified: abandonment, bobcat predation, and coyote predation. Vehicle collisions were not a cause of mortality for any individual within the study; however, other fawns without radio collars were noted to have died from vehicle collisions within the study area. Competing risks analysis determined that the probability of mortality by 180 days of age due to abandonment, bobcat predation, and coyote predation was 0.154 (95% CI = 0 - 0.329), 0.125 (95% CI = 0 - 0.327), and 0.649 (95% CI = 0.138 – 0.857), respectively. Since fawns were monitored daily during the time frame when all mortalities occurred we are confident that scavenging events were not misdiagnosed as predation.

Annual probability of doe survival was 0.75 (95% CI = 0.58 – 0.965) with 10 of 15 does surviving throughout the study period. No covariates were found to be significant predictors of mortality, including age ($P = 0.557$, $\beta = 1.411$, 95% CI = 0.447 – 4.45) and year ($P = 0.322$, $\beta = 0.383$, 95% CI = 0.0574 – 2.56). Causes of mortality

included poaching ($n = 1$), disease (hemorrhagic disease; $n = 2$), and unknown causes ($n = 2$). Mortality was attributed to unknown causes due to extensive scavenging or relocation of the collar by scavengers prior to discovery of the mortality event. Although hunting was allowed on the study area, no hunting related mortalities could be determined. Mortality occurred throughout the year with no apparent discernable patterns (Figure 2).

Forty-four of 60 coyote scat samples sent for analysis were used to determine coyote density within the adjusted study area. The 16 samples which were not used in analysis were due to lack of amplification ($n = 6$), incorrect species ($n = 2$), inability to determine individual ($n = 5$), or the scat was found outside of the adjusted study area ($n = 3$). Ten individuals were identified from these samples, and 1000 rarefaction curves of bootstrapped sampling taken with replacement resulted in a median number of 12.78 (95% CL = 10.21 – 18.48) coyotes in the area. When density was adjusted for the size of the study area (31.61 km²), coyote density was determined to be 0.40 (95% CL = 0.32 – 0.58) coyotes/km².

DISCUSSION

Fawn survival to 180 days in our study was 0.26, and survival of adult does was 0.75; however, confidence intervals were large for both survival rate estimates due to low sample size. We were unable to determine if any variables in our models affected survival, but whether this was due to the variables not affecting survival or a product of low sample size is unknown. Assuming our estimated rates of survival are representative of the population at Fort Rucker, fawn survival was less than historic averages for white-

tailed deer (54%, Linnell et al. 1995) and consistent with more recent studies of fawn survival in the Southeast (33.3%, Saalfeld and Ditchkoff 2007; 23%, Kilgo unpublished data). The fawn survival estimate from this study was also consistent with recruitment estimates (0.20 fawns per doe, Mayo personal communication) at Fort Rucker that were obtained using game cameras to estimate fawn:doe ratios. Survival of adult does on Fort Rucker was in the range of reported estimates of other rural white-tailed deer populations (79%, Nelson and Mech 1986; 69%, Fuller 1990; 71%, Nixon et al. 1991; 57%, DePerno et al. 2000; 61 - 68%, Hansen and Beringer 2003; 76%, Brinkman et al. 2004).

Our data suggest that low recruitment at Fort Rucker was the result of high rates of predation on fawns which has been documented in other recent studies in the Southeast (Saalfeld and Ditchkoff 2007, Howze et al. 2009, VanGilder et al. 2009, Kilgo unpublished data). Coyotes were the leading cause of fawn mortality in our study and the probability of mortality due to coyotes was estimated to be 0.649. Coyotes potentially caused up to 63% of mortalities in white-tailed deer fawns in an Alabama population (Saalfeld and Ditchkoff 2007) and 80% of mortalities in a South Carolina population (Kilgo unpublished data). These recent studies differ from previous fawn survival studies in the Southeast because coyotes are the leading predator, where prior studies found bobcats to be the leading predator (Epstein et al. 1983).

Exactly how this low recruitment affects long-term densities of white-tailed deer populations is somewhat unknown, but some researchers have begun to explore methods that could minimize impacts of predation on recruitment rates. Howze et al. (2009) removed 30 – 40% of the predator populations from January to August 2008 with most removal occurring during the fawning season and VanGilder et al. (2009) removed close

to 100% of the predator populations before peak fawning in 2007. Both of these studies reported that removal of bobcats and coyotes led to an increase in fawn recruitment. These results suggest that predation in these systems was additive. In systems where predation is compensatory, predator removal will theoretically have no effect on population growth, while additive predation will result in increased population growth following predator removal. Although these studies improved our understanding of the potential impacts of predator control programs on fawn survival and subsequent population growth, they were only conducted for one year each and did not evaluate the long term effects of predator control or contribution of increased fawn recruitment to growth of the deer population. To accurately predict the long term effects of management prescriptions such as predator control programs, population parameters (density, recruitment, etc.) must be regularly monitored. These data can then be used to definitively determine if predators are having an additive or compensatory effect on white-tailed deer populations.

Interactions of white-tailed deer and coyotes should follow basic principles of predator-prey theory, and an understanding of these theories can be useful in predicting impacts of management prescriptions (predator control programs, etc.). Mortality factors can be described as either limiting or regulating to prey populations. Limitation is any process that reduces population growth, and includes all types of mortality and reproductive losses (Messier and Crête 1985, Sinclair and Pech 1996). In limiting cases, predation may be described as either additive or compensatory. If a prey population is limited by food resources, predation is most likely compensatory, and any losses associated with predation do not measurably increase rates of mortality. If predation is

additive and predators are limiting a prey population, then the predator and prey populations can be described as following a nonequilibrium model, and the prey population will not recover to previous levels after being disturbed (Van Ballenberghe 1987, Boutin 1992) without a reduction in predation. Regulation occurs when a depressive process (i.e. predation, disease) is density dependent (Holling 1959, Messier and Crête 1985). Prey populations that are being regulated by predators will return to a previous equilibrium level after perturbation (Boutin 1992, Sinclair and Pech 1996).

To distinguish between limiting and regulating predator-prey interactions, it is essential that the functional (Type I, II, or III; Holling 1959) and numerical responses of the predator be understood. For predation to be limiting, predators can be described as following a Type I or Type II functional response, or have no functional response. The Type I functional response is based on a random search technique: as prey density increases, the number of prey killed per predator increases proportionally until no more prey can be consumed due to limitations caused by handling time (Holling 1959). In a Type II functional response, predation increases at a continually decreasing rate until an asymptote is reached based on search and handling time (Holling 1959, Evans 2004). If predation is density-dependent at low prey densities and inversely density-dependent at high prey densities (Type III functional response; Holling 1959, Boutin 1992), then predators are regulating the prey population (Pech et al. 1992).

According to regulating theory, the density at which a prey population reaches equilibrium is dependent upon the interaction of the prey population growth curve in the absence of predators, and the total response (e.g., the combination of the functional and numerical responses; Solomon 1949) of the predator population. It is possible for either

one or two stable equilibria to develop depending on the relationship between these two curves (see Appendix II). If two stable equilibria develop, the model or theory is described as multi-stable state or a predator pit (Haber 1977). The predator pit refers to the lower equilibrium (e.g., density) at which prey are regulated by predation. According to theory, the prey population is unable to escape the predator pit and grow to greater densities without a reduction in predation and/or other mortality factors. Until the prey population increases above a third, non-stable equilibrium point (Boutin 1992, Evans 2004) that is located between the two stable equilibria, they will remain in the predator pit. To understand which of these theories applies to white-tailed deer and coyotes in the Southeast, a thorough understanding of the interaction between deer density and rates of predation amidst stable coyote densities is required (Boutin 1992). Additionally, the response of deer density and rates of predation must be understood in the context of changing coyote densities (Boutin 1992).

Due to the ecology of coyote and deer interactions, it is most likely that coyotes are regulating deer populations. When a predator switches between available prey species, a Type III functional response can occur (Murdoch and Oaten 1975). Generalist predators, such as coyotes, are more likely to switch prey than specialist predators and are likely to switch as a group based on their social organization (Murdoch and Oaten 1975). A Type III functional response can also arise when the prey species has an age class that is safe from predation (i.e. refuge, Murdoch and Oaten 1975); the mature adult age class in white-tailed deer is less likely to be depredated than the juvenile age class, as seen in our study. These two ecological factors strongly suggest that a Type III functional response is occurring in this system and coyotes are regulating deer.

We believe that deer-coyote interactions at our study site, and possibly in other locations across the Southeast, follow the patterns predicted of a regulation model, and the deer population at Fort Rucker is potentially in a predator pit. Prior to the mid to late 1980's, Fort Rucker had an overpopulated deer herd that exhibited signs of poor condition (e.g., low body weights, levels of parasitism; Mayo, personal communication). At this time, a substantial increase in antlerless harvest was applied in a concerted effort to reduce deer densities. In the greatest reported harvest year, 1987, over 600 deer were harvested, and between 400 and 650 deer were harvested each year from 1984 to 1991. Efforts to reduce the deer population were suspended in 1995 after harvest numbers and apparent deer densities reached a point that was considered to be below what was originally desired. Although the deer population was expected to rebound following reductions in hunting pressure, the rebound never occurred, and the annual deer harvest has been <200 deer for the last 15 years and <120 animals for the past 10 years.

All indications are that Fort Rucker currently has a deer population that is below average for Alabama and the Southeast, and there has been no apparent increase in the population despite substantial decreases in hunter harvest. However, without data on coyote densities or the proportion of deer killed by coyotes before and after the deer population decreased, it is not possible to determine with certainty if the deer population at Fort Rucker is being regulated according to a single or multi-equilibria model. If the coyote density is assumed to have been constant throughout the sequence of events at Fort Rucker, the events suggest a predator pit: a high deer population was pushed below a threshold due to intense hunting, and a lower density was established from which there has been little or no increase despite decreased hunter harvest. If coyote density

increased during these events, regulation could be occurring at a single low equilibrium as described by Messier's (1994) predation model. It is impossible to state with total confidence that this is in fact a predator pit or regulating scenario, as it is also possible, although unlikely in our opinion, to conclude that predation is not density dependent and coyotes are limiting the local deer population.

Fort Rucker is not the only property that has observed low recruitment and low deer densities in the Southeast. Two other studies have recently reported low recruitment with below average deer densities (4 - 8 deer/km², Johns and Kilgo 2005; 3.8 - 5.8 deer/km², Howze et al. 2009). A third study has also reported low recruitment of fawns following heavy doe harvest, and attributed the low recruitment to predation (VanGilder et al. 2009). Unfortunately, recent data on population growth, fawn survival, and recruitment have not been reported for other Southeastern deer populations with average or above average densities, thus preventing comparisons with these reported studies. This is the first known study in the Southeast to report both survival rates of white-tailed deer and estimated coyote densities. Presenting both of these estimates creates a baseline for comparison with future studies and could help to elucidate our understanding of the interactions between these two species.

Current views and popular practices of white-tailed deer and coyote management in the Southeast could be influenced by a more complete understanding of the predator-prey model that best describes this system. Quality deer management (QDM) is a growing practice in the Southeast and promotes densities in balance with habitat conditions and healthy buck:doe ratios (Miller and Marchinton 1995). In most cases, the management prescription that is applied to achieve these objectives is increased antlerless

harvest. Populations maintained at a low equilibrium by coyotes through single state regulation may decline even further with increased antlerless harvest because this harvest will most likely be additive (Nelson and Mech 1981, Messier and Crête 1985). However, if coyotes are regulating deer populations through multi-stable equilibria as we believe, then antlerless harvest programs that do not account for deer density could theoretically result in deer populations that are driven to a density from which they are unable to recover without help. Because of this possible outcome, deer management programs that promote high antlerless harvest should ensure efforts are in place to monitor vital deer population parameters to guarantee that deer densities are driven to and maintained at desired levels.

Coyote management in most states in the Southeast consists of hunting regulations with no bag limit and an open season throughout the year. Whereas these regulations are designed to allow managers to control coyote density, successful control programs for coyotes are expensive (Pearson and Caroline 1981). An understanding of predator-prey theory can improve the impact of predator management programs on deer populations. Using theory as a guide, managers could estimate an optimal coyote density and only remove necessary individuals, thereby reducing costs. If coyotes are regulating or limiting deer populations, it is likely that coyote densities will need to be assessed annually. However, in areas with multi-stable equilibria, it may be possible to manage deer populations without predator control if deer populations are greater than the non-stable equilibrium or threshold. After this point, assuming predator-prey dynamics do not change, only an outside event that results in increased mortality (disease, hunting pressure, etc.) should be able to drive deer densities below the non stable-equilibrium

point.

To determine the predator-prey model that defines deer-coyote dynamics in the Southeast, additional research is needed. Efforts should focus on examining the interaction of these species at varying deer and coyote densities. Determining which theory applies in the Southeast will allow managers to estimate optimal deer densities and rates of predation for specific areas. Non-hunted or minimally-hunted populations may benefit from greater coyote densities than hunted properties, while managers of hunted areas will likely need to incorporate deer harvest rates into the appropriate predator-prey model to predict the combined effects of coyotes and hunters on the local deer population.

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Figure 1. Survival of white-tailed deer fawns from birth to 180 days of age at Fort Rucker, AL during 2009 and 2010.

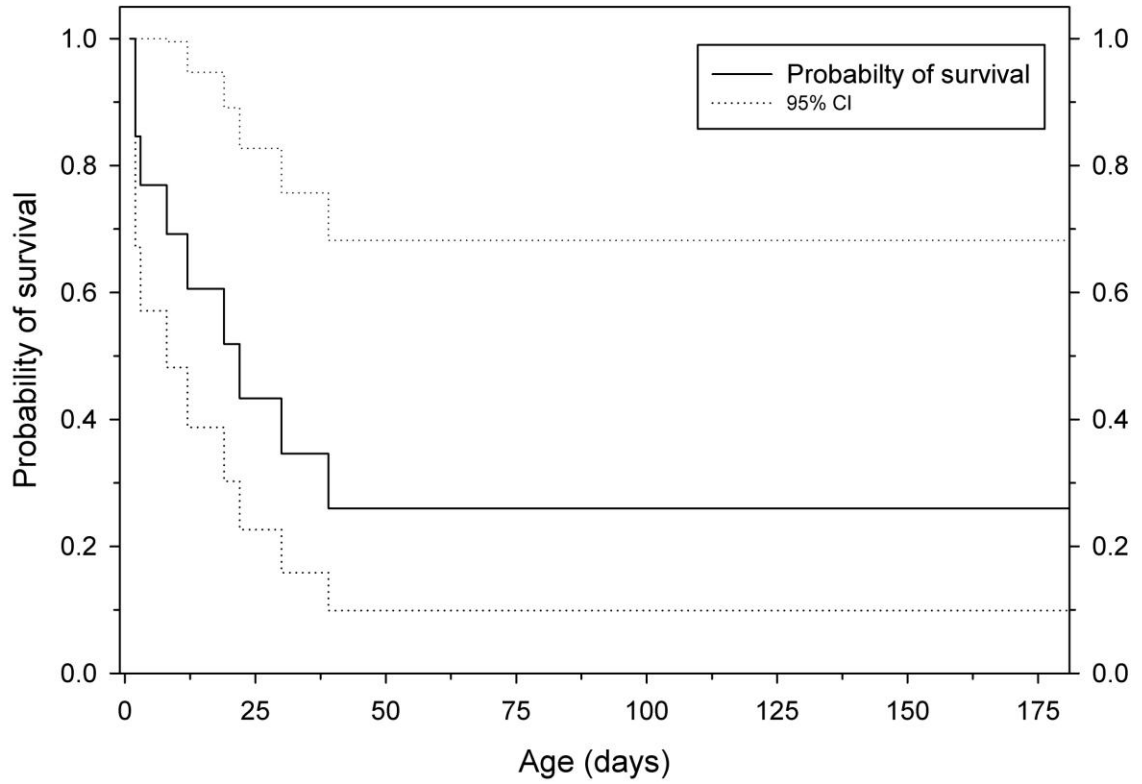
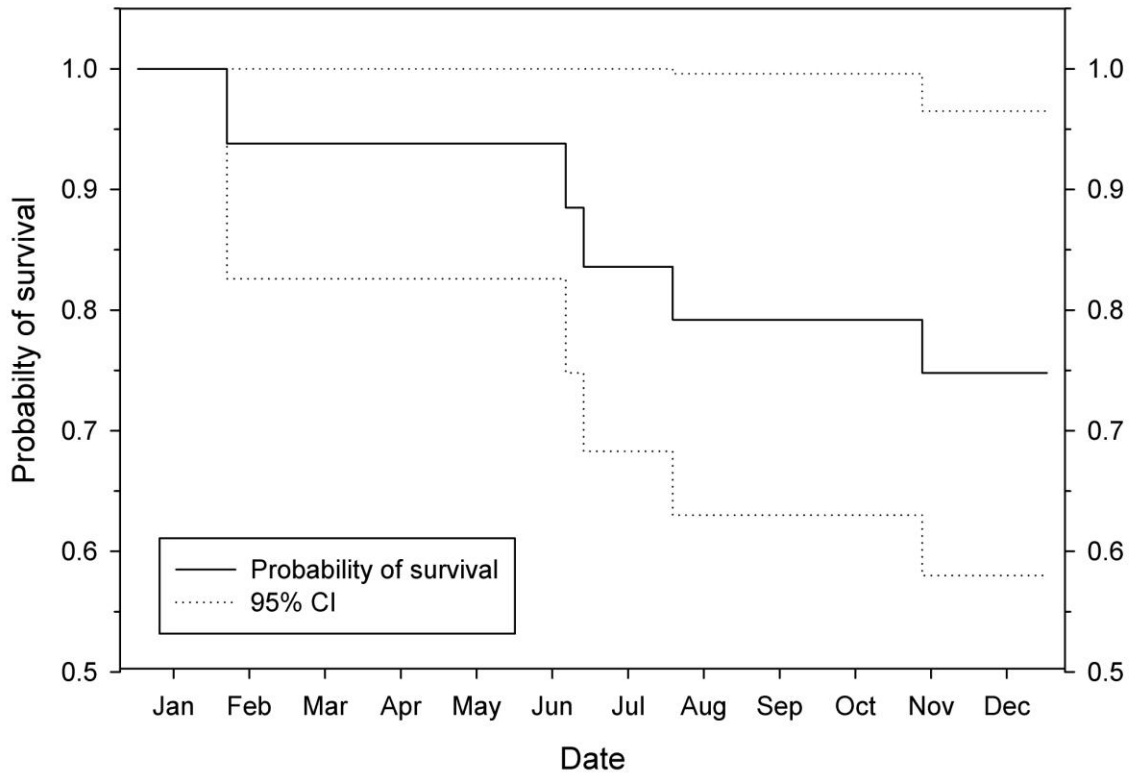


Figure 2. Annual survival of female white-tailed deer at Fort Rucker, AL. These data were determined based on survival from capture week in either 2009 or 2010 until the end of the study in February 2011.



APPENDIX I

Table 1. Doe data

Doe ID	Date of Capture	Transmitter Fate	Fawns Caught or Recovered	Date of Death	Cause of Death
D1	4/16/2009	premature expulsion	1	—————	Survived
D2	4/16/2009	successful	1	—————	Survived
D2	3/15/2010	successful	2	—————	Survived
D3	4/29/2009	successful	2 (stillborn)	11/13/2009	Unknown
D4	5/8/2009	—————	2 (fetal)	7/8/2009	Disease
D5	5/8/2009	successful	2	8/4/2010	Unknown
D6	5/20/2009	not pregnant	0	—————	Survived
D7	5/20/2009	successful	1	—————	Survived
D8	6/30/2009	not pregnant	0	2/13/2010	Poached
D9	7/13/2009	successful	0	—————	Survived
D10	2/24/2010	successful	0	—————	Survived
D11	4/27/2010	not pregnant	0	—————	Survived
D13	6/1/2010	—————	2 (fetal)	6/30/2010	Disease
D14	6/1/2010	successful	2	—————	Survived
D15	6/9/2010	successful	2	—————	Survived
D16	7/8/2010	successful	2	—————	Survived

Table 2. Fawn data

Fawn ID	Doe ID	Birth Date	Sex	Date of Death	Age (Days)	Cause of Death
F1	D1	7/27/2009	M	8/16/2009	20	Coyote Predation
F2	D5	7/31/2009	F	8/23/2009	23	Coyote Predation
F3	D5	7/31/2009	M	9/9/2009	40	Coyote Predation
F4	D2	8/1/2009	F	—————		Survived
F6	N/A	8/15/2009	F	—————	1	Right Censored
F7	D7	8/20/2009	M	9/20/2009	31	Coyote Predation
F8	D15	8/3/2010	F	8/7/2010	4	Coyote Predation
F9	D15	8/3/2010	M	—————		Survived
F10	D2	8/4/2010	F	8/7/2010	3	Abandoned
F11	D2	8/4/2010	M	8/7/2010	3	Abandoned
F12	D16	8/11/2010	M	8/24/2010	13	Bobcat Predation
F13	D16	8/11/2010	F	—————		Survived
F14	D14	9/3/2010	M	—————	11	Right Censored
F15	D14	9/3/2010	M	9/12/2010	9	Coyote Predation
	D3	8/28/2009	M	—————	0	Stillborn
	D3	8/28/2009	F	—————	0	Stillborn

APPENDIX II

Figure 1. The interaction between the population growth curve and the Type III functional response resulting in two stable equilibria, A and C, and one unstable equilibrium, B, also known as the multi-stable state or predator pit theory.

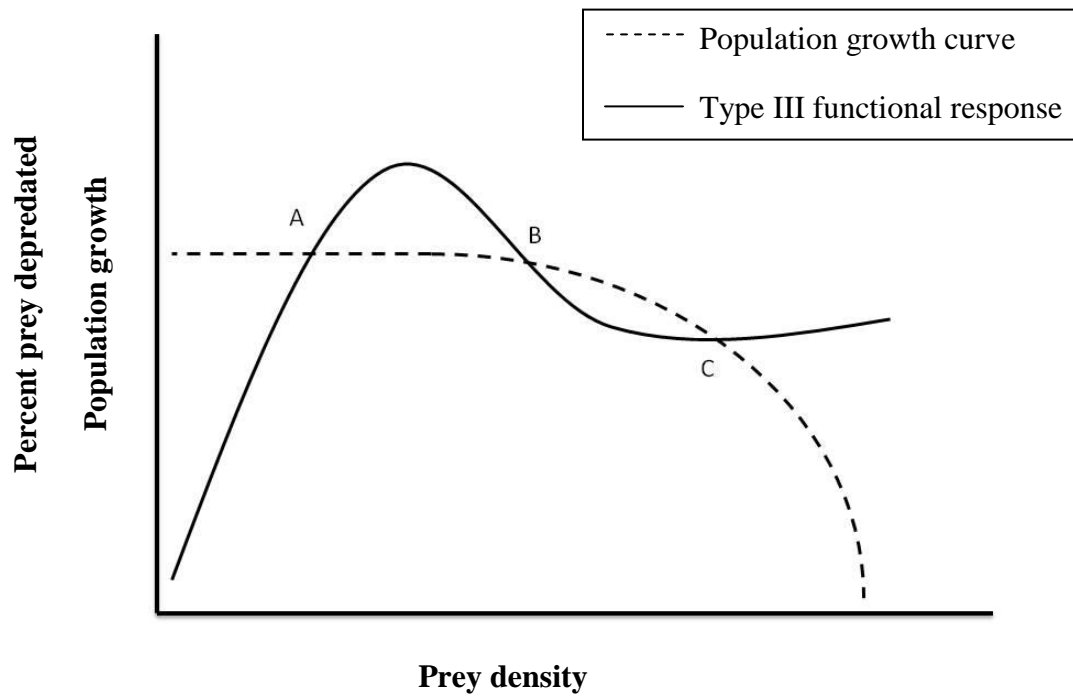


Figure 2. The interaction between the population growth curve and the Type III functional response resulting in one stable equilibrium, A, also known as the regulation theory.

