Density-Dependent Seasonal Home Range Size Change in Female Columbian Black-Tailed Deer
A Master's Thesis

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ABSTRACT
Northern California has seen a marked decrease in migratory deer numbers since the early 1900's due to anthropogenic suppression of the natural fire regime on both their summer and winter ranges. Deer numbers were on the rebound until the 1980's due to increased logging that more or less replaced the natural fire regime as a disturbance on the summer ranges, thus creating habitat and increased forage for deer. Logging however, has been greatly reduced due to concerns over threatened or endangered species. Residential development has further degraded or destroyed much of the winter range that is critical to their survival and may be blocking traditional migration corridors.

In this study, twelve resident female Columbian black-tailed deer (*Odocoileus hemionus columbianus*) were radio-collared and monitored to estimate home range size changes in response to seasonal increases in population density. Winter range population density increase is due to the presence of migratory deer from the East Tehama Deer Herd. This research took place over a two year period (2005 – 2007) on the Big Chico Creek Ecological Reserve in Butte County, California. After two years of data collection the sample size decreased to eight due to four mortalities, three to mountain lion predation and one roadkill. All eight remaining collared females maintained smaller winter home range sizes when the migratory deer were present than in summer when migratory deer were absent during both years (2005-06, $P < 0.008$ and 2006-07, $P < 0.008$). Mean percent change between winter and summer home range size was 64.5% for the year 2005-06 ($t = 7.23$, $d.f. = 7$, $P = 0.0002$) and 57.8% in 2006-07 ($t = 6.61$, $d.f. = 7$, $P = 0.0003$).

It has been reported that Columbian black-tailed deer exhibit territorial behavior in a dominance hierarchy social system, especially when available resources are discrete and defendable. Considering these factors, these data suggest a high level of competition between resident and migratory deer on the winter range. With reduced quantity and quality of forage on summer range and in migration corridors, migratory deer may be showing up on winter range in compromised condition. Once there, migratory deer may be limited in their access to quality resources by the resident deer, thus increasing winter mortality. Therefore, efforts should be made to preserve and then restore the remaining winter range habitat.

INTRODUCTION
Migratory Columbian black-tailed deer (*Odocoileus hemionus columbianus*) of the East Tehama Deer Herd (ETDH) in Northern California are declining due to numerous anthropogenic causes (Dave Walker, CDFG, pers. comm.). Sedentary black-tailed deer that reside year round on the ETDH winter range may be threatened with reduced numbers as well. However, decline of resident deer numbers does not appear to be proportionate to that of the migratory subpopulation.

Since the human population is steadily increasing in Northern California, developers are seeking inexpensive land on the outskirts of established communities for new housing developments that degrade or reduce the amount of critical wildlife habitat. One such area of concern is the southern portion of critical winter range for the ETDH, located in Butte County, California. Currently, it is estimated that forty percent of the ETDH critical winter range in Butte County has been lost or severely impacted by

residential development since the mid 1960's (Butte County, 2005). This portion of the ETDH winter range includes the Big Chico Creek Ecological Reserve (BCCER), the study area for the research in this manuscript. Currently, the ETDH winter range in Butte County is zoned for 40 or 160 acre (16.19 or 64.75 hectares) minimum parcels in undeveloped areas (Butte County, 2005). At these minimums, developers cannot afford to build the infrastructure required for housing subdivisions; densely-packed residential development is, thus out of the question. However, in the future, with a different political climate, developers might be able to push a zoning ordinance through that would allow for smaller minimum parcels making residential development feasible. Some researchers have identified specific growth management policies that protect critical habitats and migration corridors from degradation or destruction. This is accomplished by encouraging future growth to be clustered near existing communities (Gude *et al.*, 2007) or by establishing areas of ecological land-use (ELU) such as wildlife corridors (Bender *et al.*, 2004).

Winter range quantity and quality, for most North American Cervids, is the limiting factor affecting survival and herd productivity (Davis, 1977). According to Van Horne (1983), population density is not always a good indicator of habitat quality due to assessment on the summer range when deer at northern latitudes, or high altitudes in the case of the ETDH migratory deer, may depend disproportionately on the winter range for condition and fitness. Hewison and Gaillard (1996) found roe deer (*Capreolus capreolus*)*,* females with poor diet quality tend to produce more male than female offspring and suggest this maybe a strategy to reduce localized resource competition in the future since females are philopatric and don't disperse like males. They also suggest that the North American roe deer relatives (*Odocoileus spp.*) may employ the same evolutionary strategy under similar diet stress. In addition, the ETDH winter range is approximately half the size of the summer range (Ramsey *et al.*, 1981), and there are resident deer occupying most of the winter range year round (Henry Lomeli, CDFG, pers. comm.). Even if the ETDH summer range was the highest quality deer habitat, which it's not (Ramsey *et al.*, 1981), the migratory population could be in jeopardy if the habitat on the winter range was degraded further or lost completely (Van Horne, 1983).

Home Range Size

Dasmann and Taber (1956) define the home range of a deer as ". . . the area normally occupied in the feeding, resting, and escape activities of the animal."
Home range size variation in animals has been investigated in relation to many different factors such as population density (Dasmann and Taber, 1956; Sanderson, 1966; Schoener and Schoener, 1982; Gavin *et al.*, 1984; Riley and Dood, 1984; Erlinge *et al.*, 1990; Wahlstrom and Kjellander, 1995; Bertrand *et al.*, 1996; Henderson *et al.*, 2000; Kilpatrick *et al.*, 2001; Kjellander *et al.*, 2004; Porter *et al.*, 2004), intraspecific competition, territoriality, and social structure (Burt, 1943; Dasmann and Taber, 1956; Miller, 1974; Schoener and Schoener, 1982; Riley and Dood, 1984; Erlinge *et al.*, 1990; Bertrand *et al.*, 1996; Weckerly, 1992; Mysterud, 1999), and anthropogenic disturbance (Dasmann and Taber, 1956; Loft *et al.*, 1984; Vogel, 1989; Bertrand *et al.*, 1996; Nicholson *et al.*, 1997; Bender *et al.*, 2004).

Home Range Size and Population Density

Burt (1943) stated, increase in population density may cause the reduction of home range size to include only that of the defended territory. Furthermore, individual

home ranges may overlap, where this overlap is considered neutral range and is not part of the defended territory.

Dasmann and Taber (1956) noticed an increase in tagged deer home range size during the year following a 20% mortality rate in their study area population. Malnutrition was cited as the cause of mortality due to high population density. However, the authors attributed the observed increase in home range size to increase in available habitat. Nevertheless, conflict and aggression were at elevated levels with high population density, and decreased considerably following periods of high mortality. Therefore, conspecific strife may become elevated prior to the lack of available forage. Thus, strife caused by high population density levels may be a greater contributing factor in limiting population size than forage availability (Dasmann and Taber, 1956). The increase in home range size, after a reduction in the Lake County population density, suggests a relationship with density. Dasmann and Taber (1956) stated that females tried to avoid one another, and with population density being so high the only way to do that was to decrease the size of their home range. However, with population density being so high, they couldn't avoid each other and this led to increased conflict and aggression.

Bender *et al.* (2004), while studying habitat use by black-tailed deer in urban Vancouver, Washington, found larger home ranges at low population density than those of deer in surrounding rural areas at higher densities. Riley and Dood (1984), while studying mule deer fawns (*O. h. hemionus*) in the Missouri River Breaks of north-central Montana, found that home ranges sizes decreased with increase in population density.

Kjellander *et al.* (2004), while studying the effects of population density on home range size of free-ranging roe deer in France and Sweden, found that as population density increased, home range size consistently decreased. The researchers suggested this was due to the solitary and territorial behavior of roe deer along with the possibility of dominance rank effects. Bertrand *et al.* (1996), while researching the effects of harvesting male white-tailed deer on home range size and social affiliations of 48 females in southern Connecticut, found a significant increase in both mean home range size and social affiliations among females when population density was reduced from a high of 69 deer Km^{-2} to 39 deer Km^{-2}. Henderson *et al.* (2000), after a 50% reduction in a suburban white-tailed deer population on Hilton Head Island, South Carolina, found a 30% increase in home range size the following year. Similarly, Porter *et al.* (2004) found smaller home ranges in suburban white-tailed deer at higher population density than those of surrounding rural areas in Irondequoit, New York. Also, Lesage *et al.* (2000), while studying the difference in seasonal home range size among two white-tailed deer populations, one at high density and one at low, in southeastern Quebec, found that on summer ranges with high quality forage, the population with the highest density had the smallest mean home range size.

In contrast, McNulty *et al.* (1997) found no significant difference in home range size of white-tailed deer following a population reduction, but the population was at a relatively low density to begin with. Gavin *et al.* (1984) found that mean home range size of seven adult female white-tailed deer decreased one year after a population density reduction. Although the difference in mean home range size between years was not significant, the researchers suggested this may have been due to a small sample size and short duration of the study. Tufto *et al.* (1996) found that home range

size tended to increase as population density increased in Central Norway. Also, Kilpatrick *et al.* (2001), while examining the effects of population reduction on the home range size of female white-tailed deer living at high density, found that home range sizes decreased after population reduction.

Additionally, habitat quality and/or diversity seem to contribute more to the effects of density than any other factor. Wahlstrom and Kjellander (1995), while studying natal dispersal in roe deer near Stockholm, Sweden, found that those deer living in the field habitat were at the highest density and had the smallest home ranges. However, the authors attributed the smaller home range size of the field deer to a significantly higher quality forage there assessed by fecal nitrogen. Loft *et al.* (1984) found that female black-tailed deer occupying habitats with higher plant species diversity have smaller home ranges. Similarly, Kie *et al.* (2002) found that landscape heterogeneity was probably the most important factor in the spatial distribution of mule deer. To summarize, Sanderson (1966) stated that habitat quality and population density in combination, with mixed proportions, has the most profound effect on home range size.

Home Range Size and Intraspecific Competition, Territoriality, and Social Structure

Burt (1943) describes mammalian territory as,

> ". . . the protected part of the home range, be it the entire home range or only the nest. Every kind of mammal may be said to have a home range, stationary or shifting. Only those that protect some part of the home range, by fighting or aggressive gestures, from others of their kind, during some phase of their lives, may be said to have territories."

Weckerly (1992) states,

> "A territorial animal prevents other individuals from exploiting resources that are heterogeneously distributed. The evolutionary implications of defense of an area may be a means of reducing the risk of resource depletion that an individual relies on for reproduction and survival. Therefore, it would not be surprising to observe behaviors that could be interpreted as expressing territoriality (antagonism and scent-marking) during periods of resource abundance."

Territoriality is not unheard of in the genus *Odocoileus*. For example, Dasmann and Taber (1956) while studying the black-tailed deer herd in Lake County, California, found that under certain conditions adult females may compete for resources with and aggressively defend their territories against other deer. The authors stop short of calling the observed behavior territoriality, but describe certain times of the year, especially when caring for fawns, where adult females occupy evenly spaced "centers of activity" within their home ranges that are usually more than 150 yards (137 meters) apart and the distribution throughout their study area is too regular to be random. When other females came in close contact, conflict arose. Levels of aggression against other females were categorized as threatening demeanor, foot striking (stomping), and actual physical contact involving the flailing of front hooves; this threatening demeanor might also include the release of pheromones from scent glands. According to Moen (1973), metatarsal gland pheromones function as an alarm signal and also as a warning to other deer to distance themselves. Additionally, pheromones from forehead glands rubbed on tree branches, etc, are used to mark home range boundaries. Dasmann and Taber (1956) also state that females may either remember conflicts or simply avoid areas occupied by others; avoidance of areas previously occupied by females that had died was cited as evidence. Similarly, McNulty *et al.* (1997) found, after a population

reduction of white-tailed deer (*O. virginianus*) at Huntington Wildlife Forest in Newcomb, New York, that the remaining deer did not adjust their home ranges relative to the vacated home ranges. Furthermore, Dasmann and Taber (1956) found that avoidance of other females led to the spacing of home range centers that ecologically resemble defended territories. This behavior was also observed in female mule deer in Montana (Riley and Dood, 1984).

It seems logical then to conclude that Dasmann and Taber's (1956) "center of activity" within the home range is the same as Burt's (1943) "territory." In addition, Grant *et al.* (1992) found that defended home ranges were significantly smaller than undefended ranges.

As black-tailed deer in Lake County, California exhibit a tendency to aggressively defend their center of activity, avoid other deer, use scent to intimidate other deer and to mark home range boundaries, and occupy spaced home range centers that ecologically resemble defended territories, their behavior could very easily be interpreted as territoriality, which sets a precedence of territorial behavior for this subspecies.

Other researchers have also documented evidence of territoriality in black-tailed deer. Miller (1974), working with black-tailed deer in the Cedar Creek deer study area near Tillamook, Oregon, found evidence of territoriality, mostly controlled top down by dominance hierarchies in closed groups or clans of females. Overlap along the periphery of individual home ranges within clans was used at different times of day, seasons or years to create a temporal and/or spatial segregation; segregation also occurs among clans. Thus, behavior seems to limit occupancy by temporal and spatial regulation. This dominance hierarchy-enforced spatial and temporal usage of habitat forces lower ranked deer to forage in more marginal areas. In addition, Koutnik (1981), while researching social behavior and organization in mule deer (*O. h. californicus*) in northwestern Los Angeles County, California, found that the dominance hierarchy among females remained intact throughout the year regardless of reproductive status; the highest ranking females gain access to the highest quality resources. Furthermore, agonistic behavior was most intense when coveted resources were discrete and defendable, and when the possibility of increased fitness was high (Koutnik, 1981).

As Miller (1974) studied deer within a fenced enclosure, the deer did not have to contend with a large number of migratory individuals as is the case with the BCCER residents. If indeed there is territoriality and dominance hierarchy among the BCCER resident deer, the migratory animals could be classed below even the lowest ranking members of the resident population and therefore, the migratory deer could be excluded even from the marginal areas of the winter range. This would not bode well for the migratory deer in the presence of more habitat degradation or loss on the winter range by human development. According to Miller (1974), the lowest ranked deer should be the first to die of malnutrition or starvation under severe habitat conditions.

Additionally, Geist (1981), states that the suspected social system of mule and black-tailed deer is that of maternally related female clans, where resource and territory defense is facultative instead of obligatory and may be exhibited by individual deer or clans.

Graf (1956) observed what he called "sign-post" marking of home range boundaries, a territorial behavior found in Roosevelt elk (*Cervus canadensis roosvelti*),

in male black-tailed deer. According to Graf (1956), although territorial behavior is present in black-tailed deer, it's not as well developed as that in elk.

Ozoga *et al.* (1982), while studying the effects of high population density on fawn-rearing success in a captive herd of white-tailed deer near Shingleton, Michigan, found that matriarchal females showed high fidelity to fawning areas, and forcefully defended them year after year.

Gavin *et al.* (1984), while studying Columbian white-tailed deer (*O. virginianus leucurus*) on a refuge with good quality habitat in southwestern Washington, observed territorial behavior in bedding areas by females that could not be attributed to the defense of fawns. Dry, well-drained bedding sites on this refuge during winter were limited in number due to standing water in low-lying areas, and when other deer approached a female's bedding area, the female would rise from her bed, walking slowly toward the intruder in a threatening posture with ears laid back. In response, the intruder would turn and run off.

Thus, it can be concluded that there is intraspecific competition among Columbian black-tailed deer cohorts for resources whether it be for space, available forage, bedding areas, or reproductive opportunities. Schoener (1983), described consumptive, preemptive and territorial competition as mechanisms that deprive individuals or populations of the same, or other species, of resources from a given area or habitat. In addition, if quality winter range is the limiting factor for survival and productivity within the ETDH, there must be a strategy to decrease competition and strife among cohorts; partial migration could be such a strategy.

Partial Migration Strategy

According to bird migration theory, evolution of a partial migration strategy, where a portion of a population becomes migratory while the other remains sedentary or resident, is thought to have resulted from intense competition for food or nesting sites on winter ranges in tropical or subtropical latitudes. Population densities became so high due to normal reproductive excess that some were forced into other habitats or even niches (Cox, 1968). Additionally, Lundberg (1988) suggests that initiation of partial migration may occur with significant intraspecific competition on winter ranges at temperate latitudes with high winter climate variability. Furthermore, individuals that comprise the resident portion of the population should have traits which make them better able to acquire and defend limited resources. It follows then that as plant phenology or insect hatch occurs at higher latitude or altitude following winter snow melts, those individuals displaced by competition would occupy these available habitats, thus initiating the migratory strategy of the subpopulation. Migrant birds leave their winter ranges, in good condition for migration and breeding, before food supplies become short (Lack, 1968). Migratory female black-tailed deer could be exhibiting the same sort of strategy; leaving the winter range before resources are depleted, already gestating, and in good condition for migration and fawning when the summer range is reached. This strategy could lead to increased fawn survival on the summer range and, thus overall fitness. Therefore, the benefits of migrating could outweigh risks such as increased vulnerability to predation (Nicholson *et al.*, 1997). Further, Lack (1968) and Kaitala *et al.* (1993) suggest that partial migration is maintained by density-dependent selection and is therefore, a mixed evolutionarily stable strategy.

The phenomenon of partial migration has been documented in mule and black-tailed deer herds throughout California (Loft *et al.*, 1984; Livezey, 1991; Nicholson *et al.*, 1997) and in mule deer and pronghorn, (*Antilocapra americana*) elsewhere in the western United States (McCullough, 1964; Garrott *et al.*, 1987; Kufeld *et al.*, 1989; Brown, 1992; White *et al.*, 2007) and a wide range of other taxa in other parts of the world (Kaitala *et al.*, 1993). For example, blackcaps, (*Sylvia atricapilla*) in Europe and Africa (Berthold and Querner, 1982), European robin, (*Erithacus rubecula*) in Germany (Biebach, 1983), isards, (*Rupricapra pyrenaica*) in France (Crampe *et al.*, 2007), moose, (*Alces alces*) in Sweden (Seiler *et al.*, 2003), and roe deer, (*Capreolus capreolus*) in southern Norway all utilize the partial migration strategy.

As the ETDH exhibits the partial migration strategy, and as there are no other large herbivores competing for resources on the BCCER, with the exception of cattle that were removed in 2001 (Jeff Mott, ISD, pers. comm.), this is further evidence to conclude that there is a high level of intraspecific competition between the resident and migratory deer for available resources there (Cox, 1968; Lundberg, 1988). If this conclusion is correct then there should yet be other signs pointing to high levels of competition as well. These signs would include density-dependent home range size change as observed in other black-tailed deer populations as well as populations of other closely related deer taxa (Dasmann and Taber, 1956; Sanderson, 1966; Gavin *et al.*, 1984; Riley and Dood, 1984; Wahlstrom and Kjellander, 1995; Bertrand *et al.*, 1996; Tufto *et al.*, 1996; McNulty *et al.*, 1997; Henderson *et al.*, 2000; Kilpatrick *et al.*, 2001; Bender *et al.*, 2004; Kjellander *et al.*, 2004; Porter *et al.*, 2004).

East Tehama Deer Herd Natural History

The ETDH is predominantly made up of Columbian black-tailed deer (Ramsey *et al.*, 1981). Black-tailed deer are thought to have evolved during the late Pleistocene but deer in the genus *Odocoileus* appeared during the Pliocene epoch. Lack of an extensive fossil record makes estimates of the timing of their appearance uncertain. The most ancient subspecies of mule deer is the Sitka black-tailed deer (*O. h. sitkensis*) while the Rocky Mountain mule deer (*O. h. hemionus*) is the most recently evolved (Geist, 1981).

Historically, the ETDH was the largest migratory deer herd in California (Ramsey *et al.*, 1981), but that status is dependent upon the present condition of other migratory herds within the state as well as the magnitude of the current decline in ETDH numbers. However, only a portion of the ETDH is migratory; rather, some deer remain at lower elevations year round (Henry Lomeli, CDFG, pers. comm.). Partial migration in the ETDH appears to be inherited and possibly revolves around philopatric behavior where an individual born and raised on the lower elevation winter range does not migrate to the higher elevation summer range. Individuals born on the higher elevation summer range migrate to the lower elevation winter range in the fall and winter, returning in late spring and summer to their natal habitats. The ETDH is not alone in expressing philopatric behavior with strong fidelity towards summer, winter, and/or fawning areas in deer with many precedents found in the genus *Odocoileus* (Gruell and Papez, 1963; Verme, 1973; Ozoga *et al.*, 1982; Loft *et al.*, 1984; Schoen and Kirchhoff, 1985; Garrott *et al.*, 1987; Livezey, 1991; Weckerly, 1993; Main and Coblentz, 1996; Aycrigg and Porter, 1997; McNulty *et al.*, 1997; Nicholson *et al.*, 1997; McCorquodale, 1999; and Lesage *et al.*, 2000).

The EDTH migration route is the longest in the state with distances of up to 161 kilometers one way (Ramsey *et al.*, 1981); migration corridors typically follow ridge-lines of major drainages. Fall migration from the summer range near Chester, Plumas County, California, generally begins around the first of September.

Seasonal changes such as decreasing temperatures, major storms and decreasing photoperiod are the major determining factors in migration initiation (Ramsey *et al.*, 1981). Additionally, some wildlife managers believe that the onset of migration directly correlates with the opening weekend of the local archery hunting season (Henry Lomeli, CDFG, pers. comm.). One study in the west-central Cascades of Oregon suggested that slight seasonal changes in relative humidity were the most important determining factor for migration initiation, rather than temperature, precipitation, or declining habitat conditions (McCullough, 1964). Another study in Northwestern Colorado suggested that the most important migration initiation factors for mule deer were the combination of seasonal changes in diet according to energetic needs, and the quantity and quality of available forage in each of the seasonal habitats (Garrott *et al.*, 1987). Regardless of the factors thought to initiate migration, the bulk of the EDTH is on its winter range by mid-October (Ramsey *et al.*, 1981). Spring migration to the summer range typically begins around the first of April, depending upon the length and severity of the winter. Migration to the summer range is typically complete by the first of June, coinciding with the phenological development of forage plants at successively higher elevations (Ramsey *et al.*, 1981).

The total range of this herd incorporates approximately 583,443 hectares in parts of Butte, Lassen, Plumas, Shasta and Tehama Counties. The herd occupies approximately 372,800 hectares of summer range, primarily in portions of Plumas, Lassen and Shasta Counties. Habitat on the summer range varies from subalpine coniferous forest (ponderosa pine *Pinus ponderosa*, sugar pine *P. lambertiana*, incense cedar *Libocedrus decurrens*, douglas fir *Pseudosuga menziesii*, red fir *Abies magnifica*, white fir *A. concolor*, etc.), and chaparral (manzanita *Arctostapholus spp.*, mountain whitethorn *Ceanothus cordulatus*, snowbrush *C. velutinus*, deerbrush *C. integerrimus*, chinquapin *Castanopsis sempervirens*, etc.), interspersed with perennial grassland meadows at elevations above 915 meters to alpine chaparral and meadows at elevations exceeding 3,050 meters. Principal forage on the transitional and summer ranges consists of montane chaparral browse (e.g. pinemat manzanita, *Arctostaphylos nevadensis*), perennial grasses, and forbs (Ramsey *et al.*, 1981).

The 210,600 hectare winter range is located primarily in Butte and Tehama Counties. Winter habitat ranges from coniferous forest (ponderosa pine, douglas fir and white fir) and chaparral to blue oak woodland-annual grassland savanna and from elevations below 1,070 meters to the Sacramento Valley floor. Also included in this winter range habitat is riparian forests bounded by agricultural fields from the foothills of the Cascade-Sierra Nevada Mountain Ranges to the Sacramento River. The winter range diet includes acorns, chaparral browse, grasses and forbs (Ramsey *et al.*, 1981).

Market and unrestricted subsistence hunting to feed settlers and miners from the time of the California gold rush up to the early 1900's took a toll on the ETDH population (Ramsey *et al.*, 1981). It has been reported that throughout California deer were rare or even absent from their former ranges at the turn of the twentieth century. After that, modern game laws and their enforcement put an end to unrestricted hunting.

Widespread, large scale logging and associated slash burning along with wildfires opened up the canopy and allowed large chaparral browse areas to flourish (Ramsey *et al.*, 1981). ETDH population numbers began to improve over time and reached a high in 1963 with estimates of over 100,000 animals. From 1962 – 1971, mean population size was 64,000 deer, while from 1972 – 1981 the mean decreased to 55,800 (Ramsey *et al.*, 1981). By 1997, the population had been reduced to 26,000 individuals. Current (2006) population estimates put the total number at just under 14,000 deer (Dave Walker, CDFG, pers. comm.). Reasons for this current ETDH population decline are many and complicated. Fire suppression and encroachment by residential development into parts of the ETDH range has steadily increased, and therefore, the diversity, volume and quality of forage have been reduced. The chaparral plants deer use for browse and cover are dependent on fire to return nutrients to the soil, seed germination and regeneration by stump sprouting. Logging, which to a certain extent, replaced the natural fire regime as a source of disturbance leading to increased amounts and quality of forage, has also been reduced throughout the ETDH range due to concerns over endangered or threatened wildlife and plant species and environmental degradation. This has resulted in a dense over-story canopy depriving browse plants of needed sunlight. Following logging activities, conifer seedlings are immediately replanted and shrubs are controlled by cultivation (chaining) or herbicides (Ramsey *et al.*, 1981; Dave Walker, CDFG, pers. comm.). Residential development increases the need for fire suppression, and deer habitat is replaced by houses, commercial buildings, and supporting infrastructure.

These issues have also impacted deer migration throughout the entire ETDH range. Mysterud *et al.* (2001) indicate that the benefit of migration is not the amount and quality of forage on the summer range but rather extended availability of newly emerged, high quality forage associated with phenological development along the altitudinal gradient. With this benefit natural selection should favor migratory deer even though they have a higher risk of predation (Nicholson *et al.*, 1997). However, since much of the habitat along migration routes is in poor condition due to a lack of natural disturbance such as fire, fawn survival rates are low among migratory deer. This is due to the poor body condition of pregnant females when the summer range is reached (Henry Lomeli, CDFG, pers. comm.).

Study Area

The BCCER is managed by the Institute for Sustainable Development (ISD) and is located approximately 16 Km northeast of Chico, Butte County, California, and is within the southern-most portion of the ETDH winter range. Oriented on a North/South axis following a 7.24 Km section of Big Chico Creek, the reserve encompasses 16 Km^2 in the Cascade foothill region of the Big Chico Creek watershed. Altitude ranges from 213 m at creek level at the south end of the property to 658 m at the northeastern property line. The geology on the reserve varies depending on location. The Tuscan Formation, formed approximately 4 million years ago, is the uppermost layer made up of volcanic ash, lahars, and alluvium. The second layer, Lovejoy Basalt, is a very hard and erosion resistant volcanic rock that formed approximately 15 million years ago. The Chico Formation, formed approximately 75 million years ago is the third layer made up of an ancient sea bed. Erosion of these layers over time has given the BCCER its distinct topographical characteristics ranging from shear cliffs in some areas to gently

sloped terraces with steeper gradients between them (Guyton and DeCourten, 1978). The BCCER is comprised of several habitat types including coniferous forest (ponderosa pine *P. ponderosa*, douglas fir *Pseudosuga menziesii*, white fir *Abis concolor*), oak woodland (blue oak *Quercus douglasii,* foothill pine *P. sabiniana*, buckbrush *Ceonothus cuneatus*, etc.), chaparral (manzanita *Arctostaphylos manzanita* and *A. viscida*, deerbrush *Ceanothus integerrimus*, hoary coffeeberry *Rhamnus tomentella*, scrub oak *Q. berberidifolia*, etc.) grassland meadow (*Sitanion spp., Melica spp., Poa spp., Erodium spp., Lotus spp., Medicago spp.* etc.) and riparian forest (white alder *Alnus rhombifolia,* western sycamore *Platamus racemosa*, willows *Salix spp.* etc.)(CSU, Chico; Ramsey *et al*., 1981). Formerly two cattle ranches, the BCCER was formed by the 1999 purchase of the Simmons Ranch and the 2001 purchase of the Henning Ranch. Cattle have not been present on the BCCER since 2001 with the exception of a few strays periodically breaking through the fence from adjacent lands (Jeff Mott, ISD, pers. comm.).

The BCCER has a small, free-ranging, resident population of Columbian black-tailed deer, a subpopulation of the ETDH. Resources could be in limited supply on the BCCER during the late fall and early winter months when both the migratory and resident populations of deer are present (CDFG, 1952). Consequently, the optimal carrying capacity of the BCCER, and the ways in which these resources are partitioned among migratory and resident populations are unknown. It is important for proper management of both the BCCER and the ETDH that the optimal carrying capacity and population density be determined (CDFG, 1952).

Statement of Hypotheses

I investigated the hypothesis that population density affects home range size for ETDH resident does on the BCCER. Assuming that black-tailed deer exhibit facultative territorial behavior, one would expect to find resident does defending all or a portion of their home ranges against migratory deer. Therefore, the null hypothesis would predict no change in home range size in the presence or absence of migratory deer. Alternately, if the number of migratory deer migrating onto the reserve causes the overall population density to increase beyond the carrying capacity, resident females may respond by reducing the size of their home ranges to include a defendable territory with high quality forage and bedding. Additionally, this study sought to estimate the mean home range size of resident females and population density during both the summer and winter seasons.

METHODS

Deer Capture

Yearling and adult resident does were captured using Clover Traps and oak mistletoe as bait (*Phoradendron villosum*) (Henry Lomeli, CDFG, pers. comm.) or immobilized by tranquilizer dart gun (Pneu-Dart, Inc., Williamsport, PA) using a combination of the drugs Telazol and Sedazine (Fort Dodge Animal Health, Fort Dodge, IA) in a mixture of 100 milligrams Telazol to 100 milligrams Sedazine per deer on the BCCER. Tolazoline (Sigma-Aldrich Co., St. Louis, MO) was used as an antagonist to counter the effects of the Sedazine in a dose of 200 milligrams per deer when it came time for their release. Captured females were fitted with Telonics MOD-500NH radio telemetry collars equipped with mortality sensors (Telonics, Inc., Mesa, AZ) and numbered metal ear tags (CDFG) during 1, July to 15, October in 2004 and 2005.

Capture and collaring was done only during these time periods to insure that there were no migratory deer present on the BCCER and to avoid any complications during gestation or fawning.

A total of eight Clover Traps were placed in highly used travel corridors around the BCCER and moved periodically to avoid the possibility of animals habituating to the traps and to increase the likelihood of trapping additional does that might otherwise be excluded from an area due to home range defense. Oak mistletoe was used in small bunches to bait deer into traps. Female deer were immobilized by tranquilizer dart from the access road during early morning hours to have plenty of daylight to recover immobilized deer and to avoid the heat of the day. The telemetry study was done according to the CDFG telemetry protocol and under their FCC license for frequencies between 159 and 160 MHz (CDFG, 2003).

Home Range Size Data Acquisition

Collared resident deer were tracked at least once a week with a Telonics TR-5K scanning radio telemetry receiver (Telonics, Inc. Mesa, AZ) at different times throughout the day to determine diel use of the home range during a period from 16, April 2005 – 15, April 2007. When a study animal was visually located or located by triangulation with the receiver in dense cover, a Garmin 12XL GPS unit (Garmin International, Inc., Olathe, KS) was used to mark the location. Data points were then transferred from the GPS unit to ArcView GIS 3.2a software (Environmental Systems Research Institute, Inc., Redlands, CA). The data maps generated by the GIS software were then overlaid onto California Digital Ortho Quarter Quad maps (The California Spatial Information Library). A 95% minimum convex polygon (MCP), as suggested by Mohr (1947), home range was calculated for each female during each of the four periods of the study (16, April 2005 – 15, October 2005 – migratory deer absent; 16, October 2005 – 15, April 2006 – migratory deer present; 16, April 2006 – 15, October 2006 – migratory deer absent; 16, October 2006 – 15, April 2007 – migratory deer present) using ArcView Extension tools. These time periods were chosen to ensure the presence or absence of migratory deer on the BCCER (Ramsey *et al.*, 1981).

Population Estimates

Population density was estimated using a combination of results from spotlight censuses taken by this researcher using the methods set forth by Maichak and Schuler (2004), and hunter harvest and observation frequency data obtained from the BCCER hunt program collected during the two general deer seasons during the years (2004, 2005, and 2006) and using the analysis method set forth by Lancia *et al.* (1996). The hunt zone C4 season typically runs from the third weekend in September through the first weekend in October, while the hunt zone G1 season typically runs from the last weekend in October through the first weekend in November. Spotlight censuses were performed from November 2006 through February 2007 (2000 to 0200 hours), with the presence of migratory deer on the BCCER, and from July through August 2007 (2200 to 0400 hours) during their absence. Differences between winter and summer observation hours are due to seasonal changes in photoperiod. A transect was established by GIS (Maichak and Schuler, 2004), with a perimeter out to the maximum range of visibility, along both sides of the BCCER access road, incorporating an area of 67.62 ha (about 4.2% of the BCCER) with a mixture of habitat types including oak woodland, grassland, chaparral, and riparian. The driver and one observer each continuously operated a

twelve volt, hand-held, three million candle power spotlight (The Brinkmann Corporation, Dallas, TX) to view both sides of the road at the same time. When deer were spotted, the tracking vehicle was stopped and binoculars were used to help determine group size, age of individuals and sex of deer. Those that were not aged or sexed were categorized as unknowns. No spotlight census efforts were made during rainy or foggy conditions.

Statistical Analysis of Data

Statistical analysis of change in home range size for each of the eight collared, resident females, in response to the presence or absence of migratory deer was performed using the Wilcoxon Signed-Rank test (Daniel, 1990), and student's t-test for distribution of percent change in home range size using JMP-IN, version 5.1.2 (Thompson Corporation, Stamford, CT). Student's t-tests for differences between summer and winter population estimate means for the years 2004 – 2007, and between methods in acquiring population estimate means for those same years, were also performed using JMP-IN, version 5.1.2 (Thompson Corporation, Stamford, CT).

RESULTS

Forty-six total animals were captured in 2004 and 2005 combined. Forty-one deer and one bear cub (*Ursus americanus*) were captured by Clover Trap. Of the 41 deer, 29 were bucks, 8 were females and 4 were fawns. Two of these deer, one male and one fawn were trap mortalities due to predation. Four females were immobilized using tranquilizer darts during the last 2.5 months of the 2005 capture season.

The original twelve collared female deer was reduced to eight before the study could be completed due to four mortalities, three to mountain lion (*Puma concolor*) predation and one to roadkill. I obtained 716 location data points during the two year period for the eight surviving females. Winter home range size for each remaining collared female was smaller than summer home range size in 2005-06 ($P < .008$, $d.f. = 7$), and in 2006-07 ($P < .008$, $d.f. = 7$). For individual home range size data on eight surviving collared female deer see appendix 1.

Mean home range (95% MCP) size for collared females during the summer of 2005 is 27.499 ± 7.787 hectares ($n = 8$), and in summer 2006, it was 28.842 ± 7.724 hectares ($n = 8$). No significant difference in summer home range size between years was detected ($t = 0.05$, $d.f. = 12$, $P > 0.48$).

Mean home range (95% MCP) size for winter 2005-06 was 9.120 ± 3.20 hectares ($n = 8$), and in winter 2006-07 it was 8.442 ± 2.632 hectares ($n = 8$). No significant difference in winter home range size between years was detected ($t = 0.05$, $d.f. = 12$, $P > 0.47$). However, seasonal differences in mean home range size within years were significant in (2005-06, $t = 2.01$, $d.f. = 12$, $P < 0.04$), and in 2006-07 ($t = 2.00$, $d.f. = 12$, $P < 0.04$).

Mean percent change in home range size between summer and winter for the year 2005-06 was 0.645 ($t = 7.23$, $d.f. = 7$, $P = 0.0002$) and for 2006-07 was 0.578 ($t = 6.61$, $d.f. = 7$, $P = 0.0003$).

Mean population density estimated from hunter catch-effort data obtained from BCCER hunt program records was 57.8 ± 2.2 deer Km^{-2} for winters 2004-05, 2005-06, and 2006-07. For summers 2004, 2005, and 2006, the mean was 19.8 ± 5.9 deer Km^{-2}. Differences between winter and summer means are significant ($t = 5.99$, $d.f. = 3$, $P < 0.01$). Spotlight counts were also made for winter 2006-07 and summer 2007,

generating density figures of 61.7 $\pm$ 6.5 deer Km^{-2} and 11.5 $\pm$ 3.0 deer Km^{-2} respectively. Differences between winter and summer means are significant ($t = -7.01$, $d.f. = 14$, $P < 0.01$). Differences in means using the two population density estimate methods were not significant (winter, $t = -0.36$. $d.f. = 9$, $P > 0.72$ and summer, $t = 1.39$, $d.f. = 9$, $P > 0.19$).

DISCUSSION

With significant differences between summer and winter home range size in resident females on the BCCER, the null hypothesis may be rejected, and the alternate hypothesis accepted.

The eight female Columbian black-tailed deer in this research all showed between a three and five fold decrease in the size of their home range when population density increased as much as 537% due to the presence of migratory deer. Mean difference between summer and winter home range size was at least -57% for both years of the study. These data suggests some interaction between the resident and migratory deer. Other factors could apply but are probably limited in their effect.

Home range size in female Columbian black-tailed deer with young has been investigated by few researchers (Dasmann and Taber, 1956; Miller, 1970). Both studies found maternity had little effect on home range size with the exception of females decreasing their home range size up to six weeks before parturition and remaining that way for up to eighteen weeks postpartum due to the need for imprinting by fawns thereby, lowering the risk of predation (Miller, 1970). Since parturition takes place in the early summer for this study's black-tailed deer, this would mean that home range size should decrease for at least part of the time of year that data showed actually increased. Therefore, maternity probably had little effect on the seasonal home range size differences in this research.

Seasonal changes in forage availability and quality, and energetic requirements could have an impact on home range size for the deer in this study but it is unlikely due to the direction of change during winter. McNab (1963) stated that cold temperatures increase an animal's metabolic needs, so energetic requirements increase. Taber (1956) found in his study of black-tailed deer on the North Coast Range of California, that starvation was the greatest cause of mortality, and this was augmented by unfavorable weather. Taber and Dasmann (1957), while researching black-tailed deer occupying three different habitat types in Lake County, California, found that the majority of starvation losses occurred during fall and winter. According to Taber and Dasmann (1957), the Mediterranean climate of their study area has a unique affect on deer diet. For example, the majority of shrub species in this area are evergreen but do not grow in summer or winter due to lack of moisture or low temperature, respectively. Rather, the peak growing period is spring when moisture, temperature, and photoperiod are proportional and conducive to growth. The climate and shrub species composition on the study area of Taber and Dasmann (1957) does not differ much from that found on the BCCER. Thus, quality and availability of forage during the winter months on the BCCER should be more limited than during the summer, especially with the increase in deer population density at that time of year. According to Davis (1977), winter range quantity and quality, for most North American Cervids, is the limiting factor affecting survival and herd productivity.

When water cannot be found within the home range of a deer, they will go outside of their home range to find and access water as observed in desert mule deer (Hervert and Krausman, 1986). Nicholson *et al.* (1997) noticed that during summer months, resident female home ranges were significantly farther from water than migratory, thus making the size of their home range larger, at least during summer. Regardless, water is not lacking on the BCCER even during the summer. Permanent springs can be found almost everywhere and Big Chico Creek flows year round. Therefore, water availability is not a likely factor increasing the home range size of the study's females during the summer months.

Anthropogenic disturbance is very limited on the BCCER. ISD staff and researchers are few, and reserve use is temporally and spatially segregated. Access is by permit only for visitors and hunters, with the occasional hiker trespassing from Bidwell Park, directly adjacent to the reserve's southern boundary. Hunting pressure and other forms of disturbance have been shown to cause deer to increase their movements within their home range when escape cover is light, but when dense cover is available, deer tend to stay within it, even in the presence of hunting dogs (Dasmann and Taber, 1956; Marshall and Whittington, 1968). Progulske and Baskett (1958) reported that hounds were capable of moving deer but other breeds apparently were incapable of staying on the trail of a deer for any length of time. Hunting permits are only valid for two days in all seasons except for the G1 deer season which runs nine consecutive days in late October through early November. Bird dogs are only allowed on the reserve with a permitted quail hunter; there were only three groups in fall 2006 for very short intervals. Also, tours and class field trips from California State University, Chico are few in number. Deer were located after a three day rest period following such disturbances, especially following hunts for safety and ethical concerns, and for accurate home range size assessment. Currently, the only development on the BCCER is the caretaker's house and four outbuildings. Vehicle traffic on the reserve access road is limited to ISD personnel and researchers only. Therefore, it is believed that this relatively light anthropogenic disturbance did not influence data collected during this investigation.

Interspecific competition could have caused changes in the home range size of this study's female deer. For example, Loft *et al.* (1993) studied interspecific competition between domestic cattle and mule deer on two habitat types in the Sierra Nevada, California. They found that as the level of cattle grazing increased, the home range size of the mule deer increased. However, as there are no other large herbivores present on the BCCER with the removal of domestic cattle in 2001, interspecific competition with resident deer for available resources is not an issue.

It has been demonstrated that other factors possibly influencing home range size and change therein, as found by other researchers on Columbian black-tailed deer and other deer taxa, are not likely acting on the BCCER resident deer to the same extent that population density, social structure, intraspecific competition and associated territoriality may be influencing this population.

Home Range Size, Population Density, Social Structure, Intraspecific Competition with Associated Territoriality

Miller (1974) found evidence of territoriality in female Columbian black-tailed deer, controlled top-down by a social structure consisting of dominance hierarchies in

closed groups or clans. Use of overlap in home range periphery was temporally or spatially segregated, possibly to reduce conflict. Dominant females had access to the highest quality forage and bedding sites while subordinates were forced to use more marginal areas. Koutnik (1981) found that in female mule deer, the dominance hierarchy remained constant throughout the year regardless of reproductive status, and agonistic behavior was most intense when coveted resources were discrete and defendable as they would be on the BCCER during the winter months. Moen (1973) described the use of pheromones from forehead glands in scent marking of home range (territory) boundaries by black-tailed deer. Graf (1956) reported "sign-post" marking by black-tailed males using their antlers to defoliate or de-bark brush and trees before rubbing scent from their heads onto the (territory) boundary marker outside of the breeding season. The conclusion could be reached then, that if there is a territory with territorial boundaries, there must be territorial competition among Columbian black-tailed deer. Territorial competition is a mechanism by which individuals or populations of the same, or of another species, are deprived of resources from a given area or habitat (Schoener, 1983).

Certainly habitat quality is an important variable, and according to Sanderson (1966), the combination of habitat quality and population density has the most profound effect on home range size. Of all these factors, population density is possibly the most important agent of home range size change due to its affect on Columbian black-tailed deer behavior, even in habitats of high quality (Dasmann and Taber, 1956). Evidence to this is the increase in home range size and modification in behavior towards cohorts in Columbian black-tailed deer populations, and a variety of closely related deer taxa following a population reduction (Dasmann and Taber, 1956; Riley and Dood, 1984; Wahlstrom and Kjellander, 1995; Bertrand *et al.*, 1996; Henderson *et al.*, 2000; Lesage *et al.*, 2000; Bender *et al.*, 2004; Kjellander *et al.*, 2004; Porter *et al.*, 2004).

Other evidence of intraspecific competition between the ETDH resident and migratory deer on the BCCER is provided by utilization of the partial migration strategy. Initiation of partial migration is thought to have been brought on in animals by high levels of intraspecific competition on winter ranges due to high population densities from normal reproductive excess, where the strategy benefits both the resident and migratory subpopulation's overall condition and fitness (Cox, 1968; Lundberg, 1988).

Therefore, it is likely that high population density and associated territorial competition for resources on the ETDH winter range initiated the partial migration strategy in this deer herd. With population increases between 292% (spotlight counts) and 537% (hunter harvest and sightings data) from summer to winter during the years 2004 – 2007, due solely to seasonal migration, it seems likely that the stresses placed on the environment and deer caused the observed changes in behavior and thus, the change to a smaller home range size or territory, the defended part of the home range, Burt (1943), or the "center of activity" Dasmann and Taber (1956), during winter by the BCCER resident deer. Furthermore, Grant *et al.* (1992) found that defended home ranges of ungulates were significantly smaller than undefended. Resident deer may have a better knowledge of where quality resources are located on the BCCER than do migratory, and with established home ranges ("territories" or "centers of activity"), it makes sense then that the resident deer would, in the face of increased competition for those resources, decrease the size of their home range to include those resources

needed to sustain their energetic requirements throughout the winter, and also to decrease energy expenditure during resource defense.

CONCLUSIONS

It is likely that seasonal increases in population density on the ETDH winter range increases competition for available resources and therefore, in response, resident deer decrease their home range size to only include quality resources in an area small enough to easily defend without increased energy expenditure. If indeed there is a dominance hierarchy among the BCCER resident deer, coupled with partial migration theory, the migratory animals would be classed below even the lowest ranking members of the resident population and therefore, migratory deer could be excluded even from marginal areas of the winter range. This would not bode well for migratory deer in the presence of additive habitat degradation or loss on the winter range since the lowest ranked deer should be the first to die of malnutrition or starvation under severe habitat conditions. With habitat quality decreasing on the ETDH summer range and in migration corridors where much of the growth and increase in body condition of migratory deer takes place during this time of year, mixed with a high level of competition for quality forage by resident deer on the winter range, it seems appropriate that the ETDH population is in decline.

The ETDH winter range includes critical habitat that must be preserved with minimal anthropogenic development. Prescribed burns away from development on the winter range, along migration corridors, and on the summer range can help improve habitat quality, nutrient value, diversity, and forage availability, decrease deer home range size, both resident and migratory, and possibly reduce nuisance deer intrusion into outlying residential communities.

Furthermore, estimates on mean home range size of the resident deer along with knowledge of competition between the resident and migratory subpopulations on the winter range, and population density with and without the presence of the migratory component of the ETDH will help determine an optimum carrying capacity and population density both on the BCCER and other areas of the ETDH winter range.

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