DISPERSAL, HOME RANGE FIDELITY, AND VULNERABILITY OF WHITE-TAILED DEER IN THE MISSOURI RIVER VALLEY

by

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GRADUATE COLLEGE
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DISPERSAL, HOME RANGE FIDELITY, AND VULNERABILITY OF

WHITE-TAILED DEER IN THE MISSOURI RIVER VALLEY

Kurt C. VerCauteren, Ph. D.

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I radiotracked 76 female white-tailed deer (*Odocoileus virginianus*) in the Missouri River Valley (MRV) of Nebraska and Iowa for 43,555 deer-days from February 1991 to February 1998. Seventy-one percent ($n = 54$) were residents of DeSoto National Wildlife Refuge (DNWR) and 29% ($n = 22$) were transients. Of transients, 10 returned to DNWR seasonally and 12 established permanent home ranges away from the refuge. Fecundity was similar on and off the refuge ($\bar{x} = 1.2$ fawns/doe). Winter densities were higher on the refuge (19 deer/km^2) than off (5 deer/km^2). The onset of female dispersal took place at the same time each year ($\bar{x} = 13$ May, $F_4 = 0.24$, $P = 0.91$) and is likely related to photoperiod. Spring green up, agricultural activities, and availability of protective winter cover did not stimulate deer to leave DNWR. Deer population structure and dynamics appear to be driven more by social interactions than first expected. The external stimuli I examined played a role in initiating these behaviors and, along with social behavior, warrant further investigation. Survival was high (≥ 0.75) for adults and juveniles, residents and transients. DNWR allowed muzzleloader deer hunting, which accounted for 77% of the mortality on the refuge. Away from the refuge, hunting was the

cause of 58% of the deaths. Human-related mortality factors (hunting, vehicles, and poaching) led to 82% of resident deaths and 100% of transient deaths. This new information on environmental and human-related factors that impact deer movements and survival will facilitate wise and timely management decisions that will aid in the fulfillment of local and regional population goals.

INTRODUCTION

My overall goal has been to learn new information about the movement dynamics, behaviors, and demographics of white-tailed deer (*Odocoileus virginianus*) in the Midwest and eastern Great Plains. Results related to the environmental, socio-biological, and human-related factors that influence deer movements will facilitate wise and timely management decisions. Improved management will consider the movement characteristics of deer and lead to the fulfillment of local and regional population goals. I also hope that my findings can be used to foster an appreciation for deer and their habitats.

This dissertation consists of 4 chapters. Chapter 1 is a theoretical review of the literature on mammalian, primarily cervid, emigration. It was conducted to aid in the development of research goals and the interpretation of findings. To remain philopatric or become transient impacts not only the individual, but others in the population. I examined the wide variety of factors that may stimulate an individual to emigrate.

In chapter 2, I examined differences in movements between resident and transient female white-tailed deer relative to extrinsic stimuli. From my previous work, and that of others, I surmised that deer emigration was based primarily on a combination of interrelated factors, namely; population density, daylength, spring green up, springtime agricultural activity, and protective cover. Though these stimuli played a role in movement behaviors, it appears that deer socio-biology and population dynamics are the primary underlying stimuli for movement. The relationship between these factors and movement warrant further investigation.

In chapter 3, I evaluated differences in survival and cause-specific mortality between resident and transient female white-tailed deer. Information on the vulnerability and fates of radiomarked deer will be useful to managers in the region.

Chapter 4 is a simulation model I developed to aid in my understanding of deer population dynamics. I determined inputs through my research and am confident they are the best I can derive from the data. The model will be important for adaptive management in planning future research. DNWR, Nebraska, and Iowa biologists can use the model as a tool for managing deer in the region.

During 1991-1997 I captured and marked 174 deer and became proficient at handling deer in traps. I co-wrote a chapter on deer trapping for an international book on mammal trapping (Appendix A). No research project is complete until the findings are shared. I developed an extension and education based component (Appendix B) to outline my progress to this end. Besides publishing and presenting results to scientific audiences, an effort was made to learn how to teach effectively and use the major types of media.

This dissertation is the cumulative product of 8 years of thought and work. I hope that managers are able to use the findings to facilitate their efforts. I also hope that other researchers can build off of these results and begin to answer questions that I did not, as well as those new ones that I have raised.

ACKNOWLEDGMENTS

Dr. Scott Hygnstrom, my advisor and mentor, earns my deepest thanks. Scott taught me more, professionally and otherwise, than I will realize for quite some time to come. Scott's positive enthusiasm, clear thinking, and sound advice has been invaluable. A graduate student could not ask for a better role model and friend.

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I acknowledge all of the other graduate students I have had the opportunity to work and play with during my tenure. I am grateful for their friendship and look forward to their futures. Most notably, I will miss Martha Jeanne Desmond and Jennifer Delisle. MJD and JD were always willing to give me advice, solicited or not -- I will be in touch.

Besides bringing me my degree, the experience at UNL allowed me to meet my wife, Tammy. Thank you, Tammy, for putting up with me when absent due to tracking and hunting (no, graduation will not change this). Tammy has greatly enhanced my life and I look forward to many future adventures with her.

A special thanks goes to my parents. Mom was always there to give me support and encouragement to follow my dreams. Dad has always had an interest in my endeavors and takes with him fond memories of deer trapping and stuck trucks.

Lastly, if any canine deserves a honorary degree it is my dog, Buck-In-Rut. Buck has been on this project, accompanying me through every aspect, since the beginning. His care-free, day-to-day attitude helped me keep my responsibilities and goals in perspective. If only he could have learned to open gates.

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CHAPTER 1:

A REVIEW OF THE BASIS FOR MAMMALIAN EMIGRATION: EMIGRANT AND RESIDENT PERSPECTIVES

INTRODUCTION

The life histories of many species are characterized by permanent or seasonal movement away from the natal range. Scientists and other observers of nature have long examined movement phenomena. Studies have shown movements to be adaptive in both stable (Hamilton and May 1977, Comins et al. 1980) and variable (Cohen 1967, Levins 1968) environments and in both *r*-selected (Gaines and McClenaghan 1980) and *K*-selected (McCullough 1979, Rogers 1987) species. Female emigration, male emigration, and the extent of parental care, in combination, explain much of the variation in mammalian mating systems (Clutton-Brock 1989). To emigrate or remain philopatric affects an individual's fitness as well as the fitness of those with which it relates. This prompts many questions. Why do only some members of a population emigrate? What are the advantages and disadvantages of being an emigrant? How does the emigration of individuals affect the population and its social structure?

The risks associated with movement also invoke many questions. Will the emigrant individual be able to find a vacant, yet suitable, area within which to establish a new home range? Will it be able to find a mate(s)? Will it have less competition to contend with than it had in its' natal range? Will its' fitness be higher in the new area?

The fitness of an individual is contingent upon its' ability to reproduce and pass on genetic material. Emigrants put energy and time into moving, and may thereby sacrifice current reproduction and risk future reproduction. Emigrants take this risk in return for uncertain rewards. The benefits of moving may not exceed the costs. Dispersal also has significant implications for the population and the perpetuation of the species. Lineages ultimately persist only through the success of their disseminules (Anderson 1989). Individuals can help to ensure the perpetuation of an allele, gene combination, or chromosomal arrangement by transmitting genetic material to new locations (Van Valen 1971).

Much work has been done regarding mammalian movement and many theories have developed that postulate why some members of a population emigrate. Two categories of animal movement theory predominate: innate (Burt 1949, Howard 1960, Bengtsson 1978, Moore and Ali 1984, Waser 1985, Berthold and Terrill 1991) and environmental (Howard 1960, Sparrowe and Springer 1970, Kammermeyer and Marchinton 1976, Nelson and Mech 1984, VerCauteren and Hygnstrom 1994). Further, movement due to innate or environmental reasons may be due to proximate or ultimate stimuli. My goal was to examine the findings of past research and discuss the advantages and disadvantages of moving, for both emigrants and residents.

In the scientific literature, the definitions of terms related to animal movements are often vague and sometimes contradictory. Efforts have been made to develop clear, consistent, and unambiguous definitions (Chepko-Sade and Halpin 1987, Anderson 1989). The term *migration* defines a seasonal movement away from an area and the

eventual return to the area. Migration may have evolved in response to predictably changing food supplies or seasons, and animals may move to maintain optimum conditions for as long as possible (Sanderson 1966, Putman 1988). *Emigration*, or *dispersal*, refers to the departure of an individual from either its natal range or an established home range. An *emigrant* is an individual that removes itself, and its genetic makeup, from a local population or gene pool and establishes itself in a new area outside of the boundaries of its previous home range. The term *effective dispersal* goes one step further by referring to the movement of an individual to a new area where it produces offspring that subsequently breed. Unless a dispersal movement is followed by the production of fertile offspring the individual has not effectively dispersed, and is "dead" in an evolutionary sense (Anderson 1989). Gene flow does not occur unless the emigrant becomes a member of the breeding population in an area distinct from its former home range.

An *immigrant* is an individual that moves into a new home range. An *emigrant* from one area is therefore an *immigrant* into another. A *resident* is an individual of any age that has an established home range from which it will not depart long enough to establish a new home range. A *philopatric resident* is an offspring that establishes a home range overlapping that of a parent.

To my knowledge, the point at which an emigrant from 1 area becomes a resident of the area in which it has established a new home range has not been positively established. From a genetic standpoint, once the offspring of an established emigrant successfully reproduce, the emigrant has effectively dispersed and becomes a resident.

This is true, at least, from the viewpoint of those offspring carrying its genetic material. A less restrictive definition could be based on range fidelity. It may, depending on circumstances, be appropriate to reclassify an emigrant as a resident after it has remained faithful to its new range for a biologically specified period of time, even though it does not reproduce.

Dispersal theories in the literature suggest that natural selection may be acting at genetic, individual, and population levels (Gaines and McClenaghan 1980). The level at which selection takes place is a continual, driving question throughout the field of ecology. For the scope of this review I will concern myself mostly with selection among individuals, as this is the current prevailing view (Williams 1966, Maynard-Smith 1976, Hammerstein 1998).

RESIDENT AND EMIGRANT OFFSPRING FITNESS

A single litter often contains some young that emigrate and some that are philopatric. Emigration within populations is likely biased against in natural selection because emigrants have a lower chance of surviving to reproduce than do their philopatric siblings (Horn 1983). It has also been pointed out, however, that in variable environments where local populations are in danger of extinction (due to hunting, weather phenomena, etc.) only emigrants can recolonize vacated habitats, thereby reestablishing and perpetuating the species (Levins 1968, Nixon et al. 1991). Further, movement behavior can be adapted to changing environmental circumstances, favoring

whatever strategies prove successful (Sutherland 1996). For example, forage availability may decrease in an area where most individuals are philopatric to the point that those who emigrate, or pass on emigratory traits, have the highest fitness.

Individuals are thought to disperse as a means of increasing their probability of survival and reproduction, and therefore, of increasing their individual fitness (Howard 1960, Lidicker 1962, Bekoff 1977, Fairbairn 1978, Krebs 1978, Holekamp 1986). Lidicker (1962) suggested a variety of ways by which an emigrant may increase its fitness; higher probability of survival, access to higher quality habitat, possibility of more frequent matings, increased gene flow, increased fitness of offspring due to increased heterozygosity, increased probability of offspring having new and desirable gene combinations, and avoidance of competition. Many studies have found that philopatric young have a greater chance of survival than emigrant young (Errington 1963, Hawkins et al. 1971, Cockburn and Lidicker 1983, Jones 1987, Smith 1987, Putman 1988, Nixon et al. 1991). When an animal first leaves its natal range and becomes an emigrant it may be more vulnerable to environmental factors than its philopatric siblings. Dispersers are no longer being led by a parent and they are not familiar with their surroundings. Juvenile emigrants may not be adept at finding food, water, or cover for protection from weather and predators. Jūveniles also rank low in the social hierarchy because of their young age and smaller body size (Franklin et al. 1975, Franklin and Lieb 1979, Clutton-Brock et al. 1982).

Errington (1963) showed that most muskrats (*Ondatra zibethica*) taken by mink (*Mustela vison*) were emigrants. He felt that the vast majority died before locating and

establishing themselves in quality habitat. Transients also had a higher chance of accidental death or injury than philopatric siblings. Similar results have been reported for cervids (Putman 1988).

If the act of emigrating lowers survivorship, it decreases an individual's fitness as well as the fitness of the individual's parents. The emigrant individual takes a great risk from the time it departs familiar territory, as it travels through unsuitable habitat, until it finds a range in acceptable habitat where it can live and be accepted socially. The survivorship of emigrants seems inadequate for the passing of alleles that promote dispersal because only a small proportion of movers are successful in contributing to future generations (Anderson 1989). To preserve a given percentage of successful emigrants, the number of movers must increase as their survival decreases. The proportion of offspring that should become emigrants increases as their mortality rate increases (Comins et al. 1980) and may vary between genders.

After reaching a certain population density threshold, emigration increases with increasing density. An individual may disperse only when conditions in the natal range become so poor that the risks of remaining outweigh those of leaving. Emigration rates are, therefore, usually low until increasing local densities reach a level that shift the balance of risk in favor of emigration (Putman 1988).

FROM THE PARENT'S POINT OF VIEW

The fitness of a parent depends upon its success at reproducing, and the reproductive success of its offspring. Parental investment is any energy that a parent puts into an individual offspring that increases the offspring's chance of surviving at the cost