University of Alberta

Habitat Availability-Preference Relationships: Moose Case Study

By

Terrance James Osko

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of **Doctor of Philosophy**

in

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DEDICATION

This work is dedicated to the memory of my late father-in-law, Edgar Evans. His deep love of hunting and the outdoors helped kindle my fondness of the same pursuits. May his spirit continue to anoint the crisp air of frosty autumn mornings.

ABSTRACT

Habitat management is driven by results from habitat selection studies that assume the habitats animals select impart fitness to their populations and are therefore required. Such assumptions are rarely tested yet often are accepted without question and generally applied, potentially leading to mismanagement of wildlife. General application also implies that observed animal preferences for habitats are assumed to be static. I used moose as a case study to investigate whether changing relative abundance of habitat classes can influence the habitat preferences of wildlife and examined how changes in relative habitat abundance might exert that influence. I tested the hypothesis that moose habitat preferences were fixed by comparing habitat use and preferences between 2 groups of moose from the same ecosystem, but which occupied areas differing in relative abundance of the same habitat classes. I used single and multiple linear regression to determine whether the observed preferences were descriptive of moose-habitat relationships that were unique for each group, or whether they were outcomes of a relationship that was common to both. I also assessed whether home range or site selection differed between the same 2 groups in response to physical features in their environment. Both habitat use and preference differed between the 2 moose groups, as did responses to environmental features, suggesting that habitat preferences were conditional upon availability. Regression results supported the hypothesis that contrasting preferences resulted from a common selection process, as well as the alternative, that moose in each group behaved according to unique selection processes. These opposing conclusions were reconciled by the possibility that unique relationships observed at specific places and times can be consolidated to describe comprehensive wildlife-habitat relationships (functional responses) that are responsive to habitat change. Wildlife

managers must challenge past generalizations about wildlife-habitat relationships by applying habitat prescriptions as experiments to test hypotheses. Such testing of assumptions that drive habitat prescriptions can improve the act of habitat management as much as the prescriptions are intended to improve habitat. Future research should also seek mechanistic understanding of habitat selection through investigation of the trade-off decisions facing animals as habitat availability changes.

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1.0 INTRODUCTION

1.1 Background

Progress often comes from "unlearning" things too readily accepted in the past; uncritically accepted dogma is a far greater barrier to progress than that which is simply not yet known (McCullough 1992). The management of wildlife commonly involves manipulation or protection of the target species' habitat based on perceived requirements (Thompson and Welsh 1993, Bookhout 1994, Krausman 1996). This habitat management is often driven by results derived from habitat selection or preference studies that commonly assume that the habitats animals select impart fitness to their populations and are therefore required (Pyke et al. 1977, Stephens and Krebs 1986, Manly et al. 1993, Garshelis 2000). Indeed, Mitchell et al. (2002) argued that this assumption underpins all studies of habitat selection in defending their testing of a habitat suitability index (HSI) for black bears (*Ursus americanus*) by determining whether high-scoring habitats were preferred. Wildlife managers equate the value of specific habitat types to the preferences expressed for those types and then manipulate landscapes such that they are comprised of more of the highly preferred, and presumably, required types. Alternatively, they quantify the abundance of the required (preferred) types on given landscapes to judge whether or not a particular species can be supported or is at risk in that landscape or region. Because these tasks are considered important enough to expend considerable capital and effort in their completion, a logical assumption would be that relationships between habitat and fitness are well understood. Otherwise, the expenditures of capital and effort will have been wasted on management prescriptions incapable of achieving desired goals, or invalid conclusions will be drawn regarding the capability of landscapes to support certain species. However, habitat use differs from what is expected from assumptions of habitat value often enough that many authors doubt the assumption that preference does in fact equate to fitness and suggest that generalizations regarding the fitness benefits of specific habitats to a particular species should not be made on the basis of preference (Van Horne 1983, Hobbs and Hanley 1990, Garshelis 2000). If habitat management strategies for the benefit of animal populations are so reliant on indications of habitat preference, why has there not been more progress in resolving the links between habitat selection and fitness?

A possibility is that habitat management has been heavily predicated on dogmatic principles established from research that has not been substantiated or correctly interpreted. Perhaps, hypotheses regarding animal behaviour, habitat use, or habitat requirements are repeated often enough in wildlife literature that they become perceived to reflect true cause and effect relationships even though many of these hypotheses have never been tested (Romesburg 1981). Furthermore habitat selection studies, which form the basis of many of these hypotheses, could have suffered from potential pitfalls (see Garshelis 2000 for review) that lead to false interpretations of habitat preferences or selection behaviour. General application of such potentially faulty information could contribute to ineffective habitat and wildlife management. As a first step, I assessed the recent wildlife literature to determine to what degree hypotheses regarding wildlife-habitat relationships are blindly accepted and broadly applied.

1.1.1 Assessment Criteria

As a benchmark, I developed criteria based on Romesburg's (1981) critique of wildlife science. Romesburg (1981) described 3 methods common to all scientific disciplines: induction, retroduction, and hypothetico-deductive (H-D). The inductive process was described as useful for finding laws of association between classes of facts. Positive correlations between game abundance and the degree of edge in a field are an example. Induction is used to declare a law of association and repeated observations add credibility to the law (Romesburg 1981). Retroduction is the process of developing hypotheses that explain why the observed associations of facts occur. For example, moose (*Alces alces*) locations may be observed to be associated with dense conifer habitat in late winter (induction) and thermal regulatory behavior may be hypothesized as a reason for this association (retroduction). Because alternative hypotheses can be developed for the same set of facts, Romesburg (1981) argued that retroduction is not always reliable. The H-D method is a means of testing the reliability of hypotheses generated by retroduction through experimentation (Romesburg 1981). The process involves predicting "test consequences" (outcomes) of an experiment that would hold true if the hypothesis is true (See Romesburg 1981 for a complete discussion).

Romesburg (1981) accused wildlife science of largely ignoring the H-D process, thereby depriving itself of a means to test the hypotheses it generates. Unreliable knowledge is produced when the hypotheses are forgotten or become dogma through repetition (Romesburg 1981, Sinclair 1991). A clear example of this is the hypothesis that mature conifer cover is essential to moose in winter. This theme has often been repeated in the literature and accepted as fact, yet this hypothesis has never been tested (see Balsom et al. 1996 for a detailed review).

Romesburg (1981) argued the reliance of wildlife scientists on induction has produced reliable knowledge, but it is of limited utility because such correlational data provides little understanding of the fundamental processes driving nature. Understanding the mechanisms which cause population responses to habitats are essential to managing habitats for populations (Hobbs and Hanley 1990, Schooley 1994).

I reviewed current literature using keywords such as "habitat use", "preference", and "selection" as search terms and applied Romesburg's (1981) criteria for reliable knowledge in the following manner: I assessed the degree to which the H-D method was employed in the reviewed wildlife-habitat studies to estimate how much of the current knowledge is being drawn from tests of hypotheses. Furthermore, because the H-D method is not infallible (Romesburg 1981), I also evaluated the reliability of inferences drawn from studies based on the strengths of their experimental design.

1.1.2 Assessment Process

I reviewed 78 papers published by The Wildlife Society (TWS), the Ecological Society of America (ESA), and the Society for Range Management (SRM) from January 1992 to July 1996 inclusive. The papers were tabulated and summarized with respect to their content. Information summarized included citation, journal, species studied, type of study, observational method, predominant scientific method, whether or not inferences or management recommendations were made, and finally, whether or not these inferences were based on tests of hypotheses.

Categories for study type included home range, preference, and habitat association. Home range studies included any studies of home range estimation, as well as movements and dispersal. Preference referred to any study that compared habitat use with availability in any way, or compared presence/absence data. Habitat association studies were those that described habitat use without comparisons with availability, correlated indices of abundance against habitat attributes, measured diet composition, or described multivariate models of habitat use.

Categories for observation methods included telemetry, direct observation, pellet group counts, and fecal analyses. Direct observations included aerial censuses, trapping of animals, ocular observations, and responses to recorded or imitated calls.

Predominant scientific methods identified were those reviewed by Romesburg (1981). Studies using statistical tests of hypotheses were sometimes classified as inductive rather than H-D if these methods were used only to establish associations between sets of facts. For example, if the primary objective of a study was to determine preference for a given habitat or to determine whether habitat use patterns were non-random, these studies were deemed inductive despite the use of H-D to establish those associations.

1.1.3 Assessment Results/Discussion

Of the 78 papers reviewed, 61 (78%) were published by TWS, 11 (14%) were published by SRM, and 6 (8%) were published by ESA (Table 1.1). Species studied were predominantly game species or some form of charismatic megafauna. However, a number of the studies did involve endangered species, as well as songbirds and other non-game animals. Thirty (39%) papers restricted study to habitat association, while 6 (8%) strictly studied preference. The remaining papers were combinations of home range and preference (15%), habitat association and preference (27%), habitat association and home range (8%), and habitat association, home range, and preference (3%).

Thirty-two (41%) studies relied strictly upon direct observations of animals, while 22 (28%) restricted themselves to telemetry. Two (3%) used only counts of fecal pellet groups, 2 (3%), used only fecal analysis, and 1 (1%) was a literature review. Sixteen (20%) of the studies used a combination of telemetry and direct observations, while 3 (4%) combined direct observations with pellet groups.

Fifty-six (72%) of the studies did not make use of the H-D process, while the remaining 22 (28%) did. Of the papers that did not use the H-D method, all but 3 made inferences or management recommendations. None of these recommendations however, were based on tests of hypotheses. Of the 22 papers that employed H-D, all made inferences or management recommendations, but only 6 restricted conclusions to evidence derived from the hypotheses tested. Twelve of the 22 H-D based papers made additional inferences or recommendations beyond what their tests of hypotheses supported, while 3 did not draw any conclusions supported by their experiments.

The strong bias towards induction and retroduction in this sample of papers is consistent with Romesburg's (1981) view that wildlife science relies heavily on these methods. These methods are not necessarily unreliable, and are in fact necessary first steps in studying species about which little is known (Gavin 1991). However, such a heavy emphasis implies little effort (and therefore little gain) in acquiring understanding of the processes underlying habitat selection and the consequences thereof. Despite the admonishment of Nudds and Morrison (1991) that "wildlife science now requires fewer of the same kinds of food habits papers about the same kinds of species", it is evident from this review that studies of habitat use have not progressed much beyond routine descriptive studies of food and habitat preferences.

At least 8 of the papers reviewed attempted to use the H-D method, but fell short in adhering to the process. The authors stated explicit hypotheses, but not in a form which would contribute to anything more than descriptive knowledge. For example, a null hypothesis presented by Robb and Bookhout (1995) was that "nest cavities used by wood ducks (*Aix sponsa*) were similar to the entire cavity population". This hypothesis lacks creativity in that it is no different than one that states habitat use by wood ducks is random. If habitat use by organisms were random, the ecological concept of niche would not exist. Tests of such rhetorical hypotheses do not bring us any closer to understanding why an organism makes the selections it does. The "test consequence" is merely a description of "what" occurs. Another null hypothesis was "nesting success is not influenced by habitat or cavity characteristics". The authors proceeded to test correlations between habitat attributes and nesting success, with no attempt to resolve true cause and effect relationships. Again, the process was inductive, despite implying that H-D was applied. This paper, and similar ones were therefore classified as having used induction and/or retroduction in Table 1.1.

Table 1.1. Summary of reviewed habitat use papers published by The Wildlife Society, The Ecological Society of America, and the Society for Range Management from January 1992 through July 1996.

Citation	Journal	Species Studied	Study Type	Observation Method	Scientific Method	Inferences Based on Hypotheses Tested?
Killbride et al. 1992	JWM	California Quail	Pref.	Tel./Dir.	I/R	No
Mellen et al. 1992	JWM	Pileated Woodpecker	Pref./HR	Tel./Dir.	I/R	No
Holzma et al. 1992	JWM	Coyote	Pref./HR	Tel.	I/R	No
Yeo & Peek 1992	JWM	Black-Tailed Deer	Pref./HR	Tel.	I/R	No
Blakesly et al. 1992	JWM	Spotted Owl	Pref.	Dir.	I/R	No
Lepitch 1992	JWM	Pheasant	Pref.	Tel.	I/R	No
Rotella & Ratti 1992	JWM	Mallard	Pref.	Tel.	I/R	No
Walsh et al.	JWM	Caribou	Pref.	Tel.	HD	Yes
Shenk and Rengelman 1992	JWM	Whooping crane	Assoc.	Dir.	I/R	No
Garrett et al. 1993	JWM	Bald Eagle	Pref./HR	Tel./Dir.	I/R	No
Bloom et al. 1993	JWM	Red Shouldered Hawk	Pref./HR	Tel.	I/R	No
Bull & Holthausen 1993	JWM	Pileated Woodpecker	Assoc./HR	Tel./Dir.	I/R	No
Conway et al. 1993	JWM	Clapper Rail	Pref./HR	Tel.	I/R	No
Gawlik & Bildstein 1993	JWM	Shrike	Assoc.	Dir.	I/R	No
Weckerly 1993	JWM	Black-Tailed Deer	Assoc./HR	Tel./Dir.	HD	Yes/No
Clark et al. 1993	JWM	Black Bear	Assoc.	Tel.	I	No
Hayes & Krausman 1993	JWM	Mule Deer	Assoc./HR	Tel./Dir.	I/HD	Yes/No
Pauley et al. 1993	JWM	White-Tailed Deer	Assoc.	Tel.	I/HD	Yes
Hayward et al.	WM	Boreal Owl	Assoc.	Tel./Dir.	I/HD	No
Gould & Jenkins 1993	WSB	White-Tailed Deer	Pref./Assoc.	Tel.	I/R	No
Mauser et al. 1994	JWM	Mallards	Pref./HR	Tel.	I/R	No
Newman & Griffin 1994	JWM	River Otter	Pref./Assoc.	PG	I/R	No
Ockenfels & Brooks 1994	JWM	Coues Deer	Pref./Assoc.	Tel./Dir.	I/R	No
Beyer & Hofler 1994	JWM	Elk	Pref./Assoc.	Tel.	I/R/HD	Yes
Adam et al. 1994	JWM	Big-eared Bat	Pref./HR	Tel.	I/R	No
Hughes et al. 1994	JWM	Snow Goose	Pref./HR	Tel.	I/R	No

Table 1.1. Continued…

Wilson et al. 1995	JWM	Breeding Birds	Assoc.	Dir.	I/R	No
Darveau et al. 1995	JWM	Breeding Birds	Assoc.	Dir.	I/R/HD	Yes
Murray & Staufer 1995	JWM	Songbirds	Assoc.	Dir.	I/R	No
DeLong et al. 1995	JWM	Sage Grouse	Assoc.	Dir.	I/R	No
Carroll et al. 1995	JWM	Gray Partridge	Pref./HR	Tel.	I/R	No
Edwards & Guynn 1995	JWM	Squirrels	Pref./Assoc.	Tel./Dir.	I/R	No
Joshi et al. 1995	JWM	Sloth Bear	Assoc./HR	Tel./Dir.	I/R	No
Krausman & Etchberger 1995	JWM	Mule Deer, Bighorn Sheep	Pref./HR	Tel.	HD	Yes/No
Beier 1995	JWM	Cougar	Assoc./HR	Tel.	I/R	No
Buchanan et al. 1995	JWM	Spotted Owl	Assoc.	Dir.	I/R	No
Chandler et al. 1995	JWM	Bald Eagle	Assoc.	Tel./Dir.	I/R/HD	Yes/No
Flores & Eddleman 1995	JWM	California Rail	Pref./Assoc.	Tel.	I/R	No
Robb & Bookhout 1995	JWM	Wood Duck	Assoc.	Tel./Dir.	I/R	No
Storch 1995	JWM	Capercaillie	Pref./HR	Tel.	I/R	No
Merendino et al. 1995	JWM	Ducks	Pref./Assoc.	Dir.	I/R	No
Coker & Capen 1995	JWM	Brown-headed Cowbird	Assoc.	Dir.	I/R	No
Baker et al. 1995	JWM	Sandhill Crane	Pref./Assoc.	Dir.	I/R	No
Trammell & Butler 1995	JWM	Ungulates	Assoc.	Dir./PG	HD	Yes/No
Mitchell et al. 1995	JWM	Small Mammals	Assoc.	Dir.	HD	No
Maxson & Riggs 1996	JWM	Ducks	Assoc.	Tel./Dir.	I/R	No
McAuley et al. 1996	JWM	Woodcock	Pref./Assoc.	Tel./Dir.	I/R	No
Squires & Ruggiero 1996	JWM	Goshawk	Pref./Assoc.	Dir.	I/R	No
Stallman & Best 1996	JWM	Birds	Pref./Assoc.	Dir.	I/R	No
Seabrook 1996	JWM	Cane Toad	Assoc./HR	Tel./Dir.	I/R	No
Shivik et al. 1996	JWM	Coyote	Assoc./HR	Tel.	HD	Yes/No
Martella et al. 1996	JWM	Rhea	Pref./Assoc.	Dir.	I/R	No
Barras et al. 1996	JWM	Wood Duck	Pref./Assoc.	Dir.	I/R/HD	Yes/No
Combs & Frederickson 1996	JWM	Mallard	Assoc.	Dir.	I/R	No
Thomas et al. 1996	JWM	Swainson's Warbler	Assoc.	Dir.	I/R	No

Table 1.1. Continued...

Krusic et al. 1996	JWM	Bats	Assoc.	Dir.	I/R	No
Clark et al. 1996	WSB	Big-eared Bat	Assoc.	Dir.	I/R	No
Lovallo & Anderson 1996	WSB	Bobcat	Pref./Assoc./HR	Tel.	I/R	No
Nelson & Buech 1996	WSB	Warblers	Pref./Assoc.	Dir.	I/R/HD	Yes/No
Robertson 1996	WSB	Pheasant	Pref./Assoc.	Lit. Rev.	I/R/HD	Yes/No
Rossell & Gorsira 1996	WSB	Red-cockaded Woodpecker	Assoc.	Dir.	I/R	No
Carey et al. 1992	EM	Spotted Owl	Pref./Assoc./HR	Tel./Dir.	I/R/HD	Yes/No
Andrén et al. 1992	Ecol.	Corvids	Assoc.	Dir.	I/R	No
Debinski & Brussard 1995	EM	Birds, Butterflies	Assoc.	Dir.	I/R	No
McGarigal & McComb 1995	EM	Birds	Assoc.	Dir.	I/R	No
Siikamäki 1995	Ecol.	Pied Flycatcher	Assoc.	Dir.	HD	Yes
Parrish 1995	Ecol.	Warbler	Pref./Assoc.	Dir.	HD	Yes/No
Welch & Wagstaff 1992	JRM	Mule Deer	Pref.	Dir.	HD	Yes
Bozzo et al. 1992	JRM	White-Tailed Deer	Assoc.	PG	I/R/HD	Yes/No
Ngugi 1992	JRM	Ungulates	Assoc.	FA	I/R	No
Schultz & Johnson 1992	JRM	White-Tailed Deer	Assoc.	Dir.	I/R	No
Wilkins & Swank 1992	JRM	Bobwhite	Assoc.	Dir.	I/R	No
Gallina 1993	JRM	White-Tailed Deer	Assoc.	FA	I/R	No
Lescourret & Génard 1993	JRM	Gray Partridge	Pref./Assoc.	Dir./PG	I/R	No
Johnson & Dancak 1993	JRM	White-Tailed Deer	Assoc.	Dir./PG	HD	Yes/No
Pollock et al. 1994	JRM	White-Tailed Deer	Pref./Assoc.	Tel./Dir.	I/R	No
Fischer et al. 1996	JRM	Sage Grouse	Assoc.	Dir.	I/R	No
Rosenstock 1996	JRM	Small Mammals	Assoc.	Dir.	HD	No

Journal Abbreviations: JWM = Journal of Wildlife Management, WM = Wildlife Monographs, WSB = Wildlife Society Bulletin, Ecol. = Ecology, EM = Ecological Monographs, JRM = Journal of Range Management.

Study Type Abbreviations: Pref. = Preference, HR = Home Range, Assoc. = Habitat Association.

Observation Method Abbreviations: Tel. = Telemetry, Dir. = Direct Observations, PG = Pellet Group, FA = Fecal Analysis.

Scientific Method Abbreviations: I = Induction, R = Retroduction, HD = Hypothetico-Deductive

Of the 22 papers classified as having used the H-D method, most attempted to study some underlying process of habitat selection. However, at least 8 either had no controls, no replication, or were generally too poorly designed to clearly demonstrate cause and effect relationships. For example, Walsh et al. (1992) tested a hypothesis that the Porcupine Caribou (*Rangifer tarandus caribou*) herd used specific habitats to avoid insect harassment. They monitored atmospheric conditions and subsequent caribou movements. During atmospheric conditions that were favorable for maximum insect activity, they observed that caribou used habitats that could potentially abate insect harassment. Although their conclusions that caribou used these habitats to avoid insect harassment are quite plausible, they did not clearly demonstrate that their observations were not simply co-varied. They did not show that the observed habitat selection was not caused by the atmospheric conditions themselves or by some other external variable. Similarly, Shivik et al. (1996) concluded that coyote movement patterns were influenced by the presence of sheep. However, lack of controls (spatial, temporal, population) substantially diminished the certainty of their conclusions. Of the studies reviewed, only one was outstanding as clearly addressing why selection of certain habitats occurs, coupled with a study design adequately controlled to measure it.

1.1.4 Assessment Implications

The prevalence of management recommendations made without tests of hypotheses among the papers reviewed indicates there is a willingness to accept these hypotheses blindly and apply them to management without further confirmation. Such willingness no doubt contributes to the lack of observed congruency between actual habitat use and use that is expected from presumptions of habitat quality. Furthermore, general application of untested knowledge could certainly lead to mismanagement of wildlife or at least to ineffective management due to misdirected efforts. Testing of many hypotheses could be accomplished simply by monitoring the results of the habitat prescriptions upon which they were based. Apparently though, such opportunities for testing are often ignored. Broyles (1995) related how wildlife managers in the desert Southwest United States practiced water hole development to benefit desert bighorn sheep (*Ovis canadensis*) for the past 60 years with few, if any, attempts to monitor population responses of sheep or any other species. Neither was there much consideration given to water quality (which can become toxic in deserts) and its possible effects on wildlife. Similarly, Montemayor, et al. (1991) presented detailed documentation of changes in vegetation composition over 10-15 years resulting from brush management for white-tailed deer (*Odocoileus virginianus*) browse in Texas. The authors also discussed the merits of 2 methods of brush management, yet never mentioned population responses of deer or even whether deer used the improvements. Thompson and Stewart (1998) also described a habitat rejuvenation project for moose in an area of Alberta where food was considered to be a limiting factor. They reported that browse production had increased as a result of the treatments, but did not mention whether there were any measurable population effects. Quite likely, the universal application of untested concepts and subsequent lack of monitoring arise from the very fact that they are untested. If hypotheses become dogma through repetition as Romesburg (1981) suggested, the perception may be that testing is unnecessary or that it has already occurred. Thus managers continue the risky business of applying them without question.

Universal application of untested concepts implies an additional assumption to the one that preferred habitats confer fitness benefits. The second assumption seems to be that observed animal preferences for habitats are static. The assumption that habitat preferences are fixed is counter-intuitive given that optimal foraging and similar theories (Charnov 1976, Pyke et al. 1977, Rosenzweig 1981) predict that apparent preferences expressed by animals toward habitat resources should be dynamic in response to changes in the relative abundance of or increased competition for resources. Apparent preferences for resources should change as animals alter their relative use of resources in order to best address their physiological needs and constraints. Other researchers have also stated that preferences expressed for resources are likely conditional upon the relative availability of those resources (Manly et al. 1993, Arthur et al. 1996, Mysterud and Ims 1998, Boyce and McDonald 1999). If the habitat preferences of animals change as habitat availability changes, then either the whole premise that preferred habitats provide the greatest fitness benefits is flawed, or, the premise is sound but fitness benefits (and therefore preferences) are time and space-specific. Either way, general application of habitat use or preference information without regard to where or when it was collected will lead to faulty management decisions and waste of human and capital resources.

While more researchers are questioning the link between habitat preference and habitat quality, it is less clear that they are questioning the constancy of habitat preferences. Balsom et al. (1996) challenged the dogma that mature conifer cover is critical winter habitat for moose, but their concluding statements could lead to dogmatic thinking regarding habitat preferences. They stated:

> "Thus, preference for these sites has been proven, but the criticalness of mature coniferous habitat in limiting moose survival and reproduction has not."

It is uncertain whether the authors meant that preference for conifer habitats was proven only in the cases reviewed, or whether it has been proven unequivocally. If they implied the latter, the inference is no less risky to wildlife and habitat management than the assumption that conifer habitats are critical.

1.2 Moose as a Case Study

Assumptions of fixed habitat preferences that confer fitness benefits appear to be particularly common for game or other popular species. Moose are a reasonable case study because they are both charismatic and well-studied. Furthermore, some assumptions of moose-habitat relationships have recently been challenged. Observed preference for conifer cover by moose has led to acceptance that such habitats are essential to moose in late winter for thermal cover, predator avoidance, and avoidance of deep snow. Yet no evidence has been provided to substantiate these claims (Balsom et al. 1996). Moreover, retention of thermal cover for moose continues to be recommended (Thompson and Stewart 1998) despite evidence that moose are very cold-hardy (Renecker and Hudson 1986) and that the energy balance of elk (*Cervus elaphus* – a species of similar size and thermoregulatory capabilities to moose) can actually be negatively affected by thermal cover during both summer and winter (Cook et al. 1998). Thompson and Stewart (1998), as well as the Ontario Ministry of Natural Resources (1988) also advocated modified forest clearcuts in patches or strips to produce desired habitat variety, edge, and cover retention, but Rempel et al. (1997) reported that the road development required for cutting in patches resulted in less favourable population responses than in larger progressive clearcuts with less cover retention. Alternatively, while road density is negatively correlated with habitat quality in typical HSI models, moose densities in northern Alberta are higher in settled areas with high road densities than in wilderness areas that are relatively roadless (Schneider and Wasel 2000). Similarly, moose populations are increasing in Alberta's Aspen Parkland (Bjorge 1996), a highly settled agricultural region with a fixed road network and far less cover than areas typically considered suitable moose habitat. Obviously, habitat types that bestow fitness to moose in some areas may not bestow fitness (or even exist) in others. As a result, preferences for such resources probably differ between areas as well.

I used moose as a case study to investigate whether changing relative abundance of habitat classes can influence the habitat preferences of wildlife and examined how changes in relative habitat abundance might exert that influence. I also provide an example of the management (and fitness) consequences of ignoring the possibility that habitat preferences change with changing habitat availability. Finally, recommendations for future research and wildlife management emphases are provided.

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2.0 MOOSE HABITAT PREFERENCES IN REPSONSE TO CHANGING AVAILABILITY

2.1 Introduction

Motivations for conducting resource selection studies include determining the long-term resource needs of populations, developing models that predict the impacts of habitat change, and for evaluating the relative importance of resources (Manly et al. 1993). However, demonstration of preference is not equivocal evidence of its relevance to population productivity (Balsom et al. 1996). Repeated observations of habitat associations and repetition of hypothetical explanations for those associations lead to dogmatic thinking (Romesburg 1981) and further contribute to misinterpretation of habitat criticalness. For example, many authors believe mature conifer cover in close proximity to forage resources is essential to moose in winter (see Goddard 1970, Van Ballenberghe and Peek 1971, Phillips et al. 1973, Thompson & Vukelich 1981), but Balsom et al. (1996) concluded that mature conifer cover was not demonstrated to be critical in any of the literature they reviewed. The fact that scientists and managers equate the criticalness of habitat types with a species' preference for them, and that some claim these preferences are proven (Balsom et al. 1996), implies that habitat preferences often are assumed to be fixed. Evidence of this assumption in moose habitat management is the application (with minor adaptation and little testing) of the Lake Superior moose Habitat Suitability Index (HSI) model (Allen et al. 1987) to other regions and localities (e.g. Romito et al. 1996, Conoco Canada Resources, Ltd. 2001). Further evidence is the ubiquitous citations of studies, such as that of Hamilton and Drysdale (1975), despite these authors' warnings against wider application of their observations (e.g. Thompson and Euler 1987, Timmerman and McNicol 1987), which eventually become inputs for models like the one for Lake Superior. Surprisingly, such assumptions are often made even though the expectation that habitat preferences change as availability changes should be intuitive (Arthur et al. 1996, Mysterud and Ims 1998, Boyce and MacDonald 1999). Balsom et al. (1996) stated the criterion by which the criticalness of a habitat type should be measured is the population response to removal of or restriction of access to it. Since it is often assumed that a species will select resources that best satisfy its life requisites (Manly et al. 1993), the criticalness of a habitat type to a species could also be disproved by demonstrating differential preferences for a particular habitat type by members of that species. Manly et al. (1993) endorsed Johnson's (1980) definition of selection as the process by which an animal chooses a resource and preference as the likelihood that a resource will be selected if offered on an equal basis with others. I tested the hypothesis that the preferences of moose for common habitat types were fixed by comparing habitat use and preferences between 2 groups of moose from essentially the same ecosystem, but which occupied areas containing differing relative abundances of the same 9 habitat classes. To test this hypothesis, I evaluated predictions that habitat use and indices of habitat preference would be similar for respective habitat classes between these 2 groups. In addition, I compared the preference inferences derived for each group separately against the inferences drawn from treating both groups as a single sample.

2.2 Study Area

The study was located in northeastern Alberta (Fig 2.1) within the Forest Management Agreement (FMA) area operated by Alberta-Pacific Forest Industries, Inc. (Al-Pac). The study area encompassed approximately 6000 km^2 and occurred almost entirely within the Central Mixedwood sub-region of the Boreal Forest Natural Region of northern Alberta (Alberta Environmental Protection, 1994). A small portion of the study area also included the north and east slopes of the Pelican Hills, which form the eastern-most occurrence of the Lower Foothills sub-region of the Foothills Natural Region in Alberta. Topography within the Central Mixedwood portion of the study area was primarily level, sloping very gently towards the Athabasca and House Rivers, which flow almost parallel to each other from south to north through the center of the study area (Alberta Environmental Protection, 1994). Within the Pelican Hills, topography was rolling. The maximum change in elevation between the Pelican Hills portion of the study area and the remainder is approximately 400 m. The Central Mixedwood is typically vegetated with pure or mixed stands of trembling aspen (*Populus tremuloides*), often occurring with balsam poplar (*Populus balsamifera*) and white birch (*Betula papyrifera*). These species succeed to white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*). Lack of relief within the area also results in large expanses of poorly drained marshlands, as well as black spruce (*Picea mariana*) and tamarack (*Larix laricina*) forested muskegs. Occasional stands of jack pine (*Pinus* banksiana) occur on sandy soils throughout the area(Alberta Environmental Protection, 1994). Vegetation within the Pelican Hills portion of the study area is similar to that of the surrounding Central Mixedwood, except for somewhat greater abundance of birch and pine forest stands (Alberta Environmental Protection, 1994).

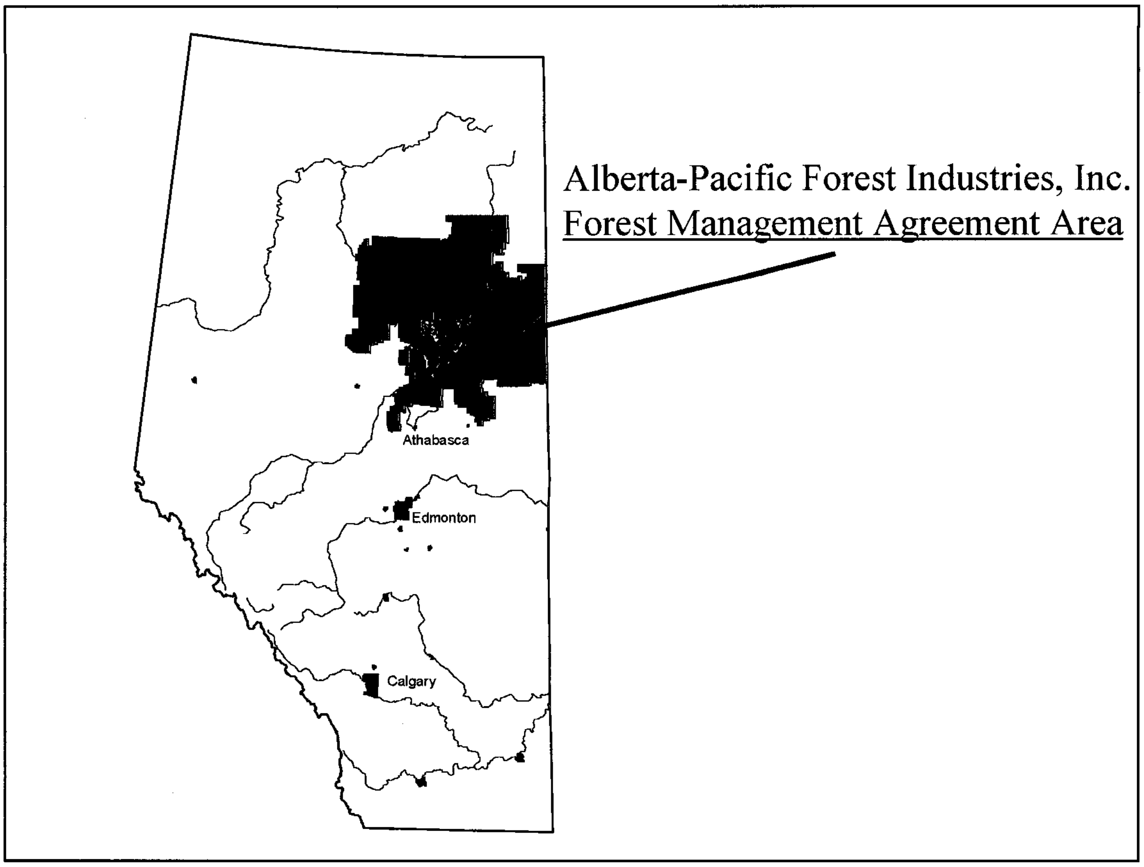

Fig. 2.1. Study area and Alberta-Pacific forest management agreement area within Alberta.

One of the major features of the study area was a central "zone" characterized by a distinctly lower abundance of upland vegetation such as poplar, white spruce, and mixedwood forests in comparison with the surrounding portions of the study area. On the other hand, this zone had a greater abundance of lowland, low to medium density black spruce forests than did the remainder of the study area. These differences in forest composition lead to the deletion of this zone from Al-Pac's FMA area due to the lack of merchantable timber. I refer to this area as the "Deletion Zone" or Zone D and to the remainder of my study area as the "Timber Zone" or Zone T (Fig 2.2).

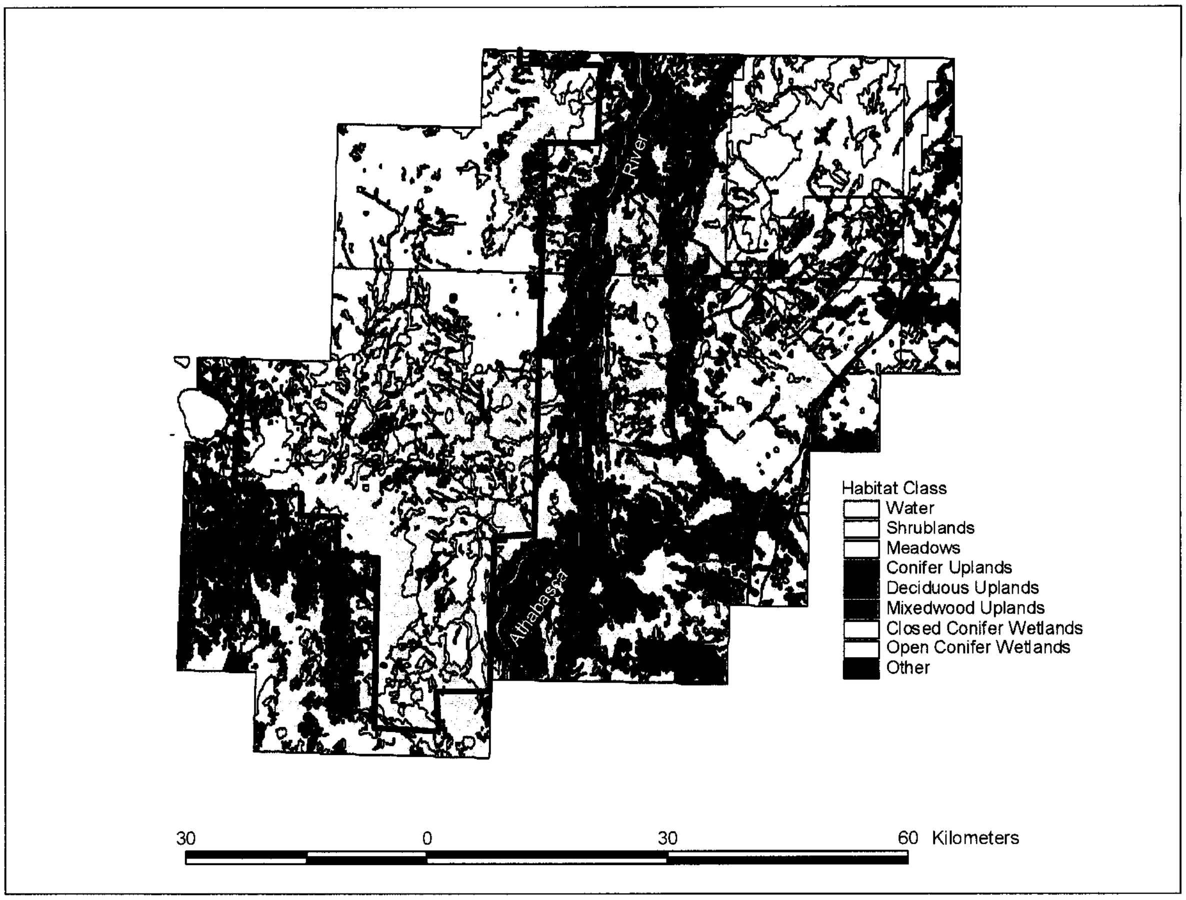

Fig. 2.2. Study area detail. The area delineated in red represents a portion of the FMA area referred to in the text as the "deletion zone" (Zone D). The remaining area is referred to as the "timber zone" (Zone T).

Moose occurred throughout the study area. Alberta's provincial wildlife service completed an extensive moose survey of northern Alberta in 1993/94 (Fish and Wildlife Division, Alberta Environmental Protection, unpublished report). Moose densities were reported by wildlife management unit (WMU), which ranged in size from about 6000 km^2 to 14,000 km^2. The study area overlapped the juncture of 4 of these units. According to the census data, there appeared to be a north-south gradient in moose densities within the study area with densities from about 0.1 moose km^{-2} in the north to 0.24 moose km^{-2} in the south. However, there did not appear to be differences in densities between Zone D and Zone T. James (1999) reported aerial grid surveys of moose within the study area completed in March of 1995 and 1997 indicated that moose were relatively more abundant in upland areas of my study area, but did not quantify those differences.

Therefore moose densities could have been higher within Zone T due to the greater occurrence of upland areas within that zone. However, proportions of radio-tagged moose locations were divided equally between upland and lowland areas from July through February, while moose locations recorded from March through June were more abundant in lowland than upland areas (67% vs 33% - James 1999). Productivity information for moose populations within the study area were not available, but mortalities among radio-tagged animals used in this study was similar between zones (0.8 moose per zone per year, N = 11 moose per zone – Osko unpublished data).

Wolf density information was not available for my study area during any recent period, however, radio-tagged wolf locations within the study area were more abundant in upland areas than lowland areas during all seasons (James 1999). Proportions of wolf pack locations within upland areas were 75% from November through February, 63% from March through June, and 57% from July through October, indicating wolf densities may have been greater within Zone T due to the greater abundance of uplands within that zone.

Primary industrial activities in the study area were forestry and oil and gas development. Forestry activity was minimal within Zone D but evidence of oil and gas development was ubiquitous throughout the study area. Despite the absence of forestry within Zone D, energy sector development in northeastern Alberta causes clearing of large volumes of timber. Human access is restricted primarily to winter in both zones, although limited parts of Zone T are accessible during summer via water craft on the Athabasca River. There was no active logging within the study area during the time of this study.

2.3 Methods

2.3.1 Analytical Approach

Few studies compare animals of the same sex and age class occupying different areas so examples of appropriate statistical procedures are scarce. Typically, habitat use observations (telemetry locations, animal tracks, etc.) are used as the sampling unit and invariably are pooled across animals to generalize to populations (Aebischer et al. 1993). The habitat composition of these observations are then compared against the composition of available habitat to determine whether use is consistent with availability and to identify which habitats are used in lesser or greater proportion than availability (avoided/preferred). However, none of the statistical models commonly used in habitat selection studies (Alldredge and Ratti 1986, 1992, White and Garrott 1990 provide reviews) adequately account for within-group between-animal variation when examining between-group differences (Aebischer et al. 1993). Furthermore, I found no examples where availability, use, or preference of specific habitat classes or resources was compared between groups of animals. Parametric techniques such as Analysis of Variance (ANOVA) and Multivariate Analysis of Variance (MANOVA) are more appropriate for making comparisons of this nature (Aebischer et al. 1993). Using individual animals rather than radio locations as the sample unit adequately accounts for within-group variation in addition to addressing problems of non-independence such as serial correlation (Aebischer et al. 1993). I therefore measured and compared habitat availability, use, and preference with individual animals used as the experimental unit.

2.3.2 Study Animals and Telemetry

Thirty-one adult female moose were captured and fitted with VHF radio transmitters between June and December of 1994 using the helicopter net-gunning technique described by Carpenter (1996). The moose were located via aerial telemetry at intervals of 2 - 3 weeks since the initial capture. Animal locations were recorded with a global positioning system (GPS) device installed in the aircraft. These positions were then transferred to an ARC/INFO geographic information system (GIS) database and plotted on a thematic map of habitat classes contained within the study area. For this study, I used 22 radio-marked moose for which complete telemetry data were available spanning the entire years of 1995 and 1996. Forty four to forty eight point locations were recorded for each moose over the 2-year period. The sample of 22 moose was divided into 2 sub-samples, or groups, of 11 animals each according to whether their radio-telemetry point distributions occurred primarily (at least 80%), if not exclusively, within the Timber or Deletion zones (Zones T or D).

2.3.3 Habitat Availability

I used LANDSAT thematic satellite imagery to establish habitat classes because cover classes derived from such data are commonly used in wildlife habitat studies as descriptors for habitat types (Leckenby et al. 1985, Oosenberg et al. 1988, Palmeirim 1988, Aspinall and Veitch 1993, August 1993, Herr and Queen 1993, Rempel et al. 1997, Glennon and Porter 1999, Peery et al. 1999, Swindle et al. 1999). In addition, many studies of habitat selection by moose and other ungulates also use gross cover classes as habitat descriptors (Krefting 1974, LeResche et al. 1974, Cairns and Telfer 1980, Hauge and Keith 1981, Pierce and Peek 1984, Oosenberg 1988, Schwab and Pitt 1991, Rempel et al. 1997). Habitat is a concept that is understood to indicate a place where an animal resides and which contains resources that an animal may use (Morrison 2001). As such, cover classes can not necessarily be equated to habitat per se, but this is a connection that has often been made. The point of this study was not to define habitat, but to explore animal use of and preferences for it in a manner commonly described in the wildlife literature. The LANDSAT imagery was preferable to other sources of cover class information because no other imagery of finer resolution was available that encompassed the entire study area, due to lack of economic interest of the deletion zone to forestry. A commercial service provider produced a supervised classification of 17 land cover classes for Alberta-Pacific's FMA area from imagery produced on 28 May 1990. The classification was ground truthed with a minimum of 50 ground observations per cover class (Taylor et al. 1991). Overall operational accuracy of the classification was reported as 85% - 95%. However, accuracy for individual classes ranged from 40% - 100% (Taylor et al. 1991). I further classified the study area into 9 habitat classes by eliminating land cover classes that were absent from the study area and by combining others, some of which individually formed a very small portion of the study area, into single classes (Table 2.1). The reduction from 17 to 9 classes reduced errors in distinction between the remaining 9 classes. For instance, the original classification produced 2 classes for deciduous uplands differentiated by age, and which were most often confused with each other. Combining these into a single class reduced the likelihood that the new class would be confused with other classes. Classes with the lowest reported accuracy were also most commonly confused with each other (Taylor et al. 1991). These formed the combined **Disturbance** class described in Table 2.1.

Table 2.1. Forest cover classification derived from LANDSAT Thematic Mapper imagery.

Cover Class Descriptors	Abbreviation	Generic Description
Water	Wat	Any permanent flowing or non-flowing water bodies
Shrublands	Sh	Complex of shrubs and herbaceous flora, often riparian
Wet Meadows	WM	Meadow complexes of mosses and herbaceous flora, non-forested
Conifer Upland	CU	Open and closed canopy upland coniferous forests (white spruce, balsam fir, jack pine)
Deciduous Upland	DU	Upland deciduous forests (aspen and balsam poplars, white birch)
Mixedwood Upland	MU	Upland forests with mixtures of species in the 2 classes immediately above
Closed Conifer Wetland	CCW	Coniferous closed canopy forests occurring on wet organic soils (black spruce, tamarack)
Open Conifer Wetland	OCW	Coniferous open canopy forests occurring on wet organic soils (black spruce, tamarack)
Disturbance	Dst	Cut areas, burned areas, and industrially disturbed areas in early stages of regeneration.

Habitat availability and use were calculated for each moose individually using the GIS. Habitat availability was defined as the proportional habitat composition within a 25 km diameter circular buffer centered over the 2-year (1995, '96) distribution of radiolocations for each moose (Fig 2.3). The buffer size was determined from annual moose movements. I reasoned that, in the absence of formidable barriers to travel, all moose in the study should be capable of traveling a distance at least equal to the greatest distance between telemetry points for any individual within either year. A circle of such diameter would define the habitats that were likely accessible to each moose. This approach, which incorporated observations of moose movement as a defining criteria, was more reasonable than using an arbitrarily defined "study area" common to all moose because habitats within each buffer were more likely to be accessible to the respective moose than would habitats within a common "study area". The maximum distance between radiolocations observed for the annual point distribution of any moose was 22 km. The mean distance moose traveled between telemetry flights was 2.5 km. Therefore, a 25 km diameter buffer was selected to encompass potential travel beyond the 22 km maximum distance observed. This distance is consistent with annual travel distances reported for Alberta moose by previous researchers (Lynch 1976, Lynch and Morgantini 1984).

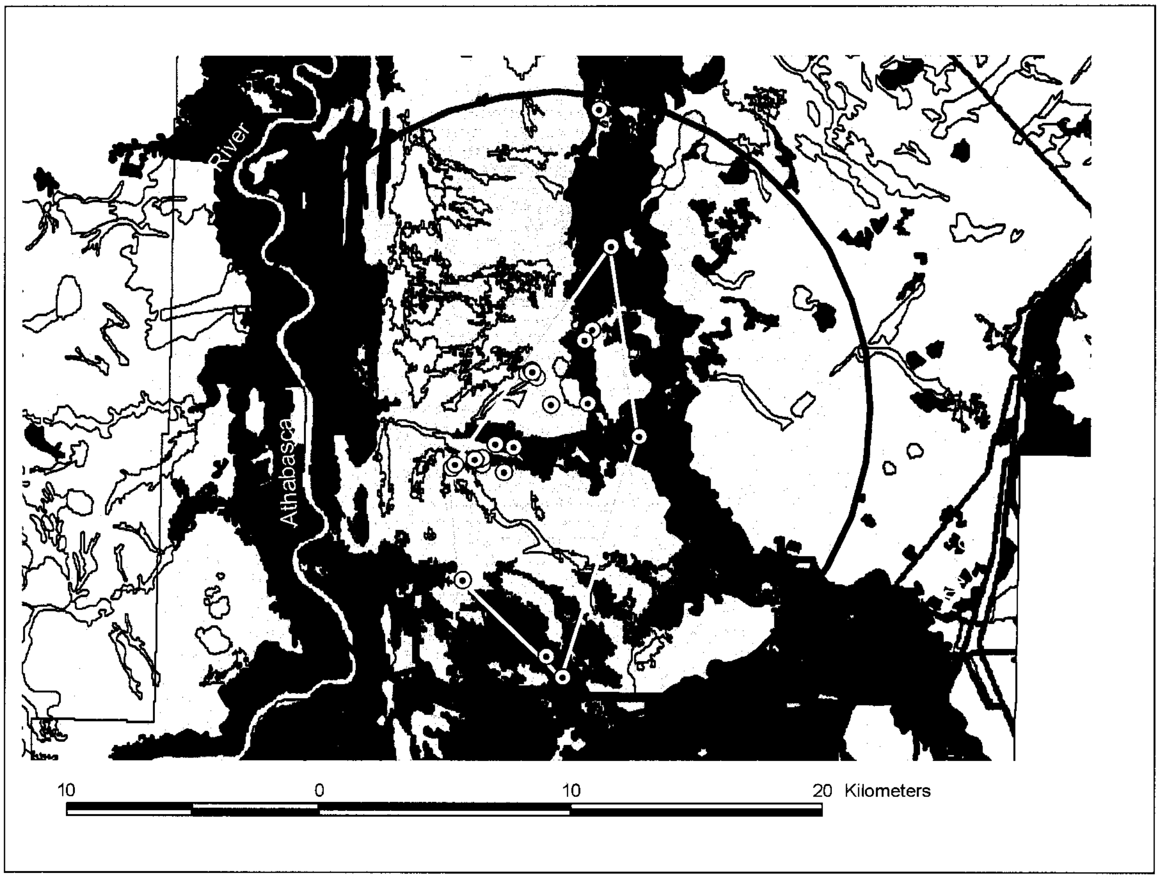

Fig. 2.3. Example 25 km availability buffer, 95% MCP home range, and 117 m radius buffered radio telemetry locations for moose.

2.3.4 Habitat Use and Preference

I attempted to use Johnson's (1980) hierarchical approach to evaluating habitat use and preference where "orders" are defined for relative scales of selection. Johnson (1980) described 2nd order selection as selection of a home range from habitat generally available and 3rd order selection as selection of sites (or telemetry locations) within a home range. However, I was unable to use home ranges as the unit of availability for comparison against telemetry locations because some of the home ranges did not contain all 9 of the habitat classes. Therefore, two estimates of habitat use were calculated, but each used the 25 km circular buffers of availability to calculate preference. I realized that my calculation of 3rd order selection tended to mix scales by comparing telemetry locations to general habitat availability, but believed the analysis would provide some insight despite this mixing. The first use estimate was represented by the proportional habitat composition of 95% minimum convex polygon (MCP) home ranges calculated for each moose. The second estimate was represented by the habitat composition within buffers of 117 m radius around each telemetry point for each moose (Fig. 2.3). The 117 m radius was the average error recorded in location of VHF radio transmitters during a test of pilot error. Data for each moose were divided into 4 periods. These were winter 1995, summer 1995, winter 1996, and summer 1996. Winter months included October through March, while summer months included April through September. Home ranges were calculated for each of these periods for each moose. Habitat use based on buffered point locations was also calculated from points recorded during each of these periods.

Home ranges were calculated using the program CALHOME (Kie et al. 1996). Preliminary analysis of home range sizes using all points for each moose indicated MCP home range sizes reached an asymptote (see Harris et al. 1990) using between 8 and 10 location points (Table 2.2). Of the home ranges calculated for this analysis (88), one was calculated using only 9 points while the remainder used 10 or more locations each.

Table 2.2. Change in lsmean MCP home range size with increasing number of telemetry locations.

Number of Telemetry Locations[1]	lsmean MCP Area (ha)[2]
3	0^{a}
6	1496^{b}
8	1648^{bc}
10	2727^{bcd}
12	3040^{cd}
14	3114^{d}
16	4067^{d}
18	3209^{d}
20	3044^{d}
22	3010^{d}
24	3586^{d}
26	3607^{d}
28	3851^{d}
30	3642^{d}

[1] Telemetry locations were randomly added from a sample of at least 44 telemetry points recorded for each of 10 randomly selected moose.

[2] Values followed by the same letter superscript do not differ ($P < 0.05$).

I measured the relative preferences expressed by moose for the 9 habitat classes by calculating Resource Selection Functions (RSFs) for each moose following Manly's et al. (1993, p. 40) description for the case of a single classed habitat variable such as "cover type", using the equation

$$B_i = \hat{w}_i / (\sum_{i=1}^{I} \hat{w}_j)$$

The equation represents the ratio of the proportional use of cover type *i* to the proportional availability of cover type *i* divided by the sum of ratios for all cover types. The expected probability for habitat use in proportion to availability (i.e. no selection) is equal to 1 divided the number of habitat classes. Manly et al. (1993) claimed this RSF represents the probability of a habitat being selected if all habitats could somehow be made equally available. This pretext makes the method attractive, particularly for comparing selection of specific habitat classes between 2 groups of animals because it is akin to offering subject animals an identical menu and comparing the choices made by each group. Absolute preferences cannot be interpreted from the RSF values because they will change as habitat classes are added or deleted. However, the RSF provides a means to measure the relative preference among a group of resources. The method was useful in this case, where the same habitat classes were available to both groups of moose and differences in indices calculated for specific habitats could be compared statistically between groups.

2.3.5 Statistical Analyses

To confirm that moose were assigned properly to their respective sub-sample groups, I performed a cluster analysis using composition of habitat classes within the 25 km buffer for each moose as the clustering criterion. Differences in availability of habitat classes between groups were then tested for by multivariate analysis of variance (MANOVA). Zone was the only factor tested because availability was not defined by season. Multi-factor MANOVAs were used to test for differences between zones, seasons, and years as main effects for home range composition, buffered telemetry point composition, and both "orders" of selection indices. In each case, zone, season, and year were entered into the models as fixed effects and moose individual was entered as a random effect. Least square means differences for individual habitat classes were compared only for main effects and interactions that were significant in the main model.

A multi-factor MANOVA was used to test for preference differences among habitat classes for the entire sample of moose as a whole. Fixed variables within the model were season and year, while moose individual was entered as a random effect. Separate analyses were run for each "order" of selection. Repeated measures were used to make pairwise comparisons among habitat classes when the main model was significant. Least square means were used to compare differences in specific habitat classes between seasons and years when those effects were determined to be significant by the main model.

All analyses were run using the Statistical Analysis System (SAS Institute 1997). All proportional data were arcsine square-root transformed for analysis but the original values were used for presentation. Statistical significance was accepted at $\alpha \leq 0.05$.

2.4 Results

The cluster analysis confirmed my assignment of moose to the 2 groups. No adjustments were made from the original assignments. The relative abundance of available habitats differed between zones in 5 of the 9 habitats (Table 2.3), also confirming my initial observations of habitat differences between the 2 areas. In all tests of habitat use and preference by zone, significant differences were observed among the 9 habitat classes overall. The effects of season and the interaction between zone and season were significant for both calculations of habitat use and both calculations of preference. The effect of zone was significant in all comparisons except for preference calculated from buffered telemetry points. There were no significant differences observed due to year or any interaction with year in any of the analyses. An individual moose within each zone was a significant factor in all analyses, indicating a large degree of distinctiveness among individual moose.

Table 2.3. Proportional availability of 9 habitat classes between zones.

	Habitat Class								
Zone	**Wat**	**Sh**	**WM**	**CU**	**DU**	**MU**	**CCW**	**OCW**	**Dst**
D	0.0326^a	0.0230^a	0.0418^a	0.0032^a	0.0763^a	0.1023^a	0.4723^a	0.2294^a	0.0192^a
T	0.0187^b	0.0115^b	0.0344^a	0.0066^a	0.1565^b	0.1583^a	0.4764^a	0.1001^b	0.0375^b

Values within a habitat class followed by the same letter superscript do not differ ($P<0.05$) based on Least Square Means. Values presented are raw means.

2.4.1 Habitat Use Between Zones

Closed Conifer Wetlands were used to a large extent (> 31% of used habitat) by moose in both zones regardless of whether home ranges or buffered telemetry points were used to measure use (Table 2.4). Moose in Zone T used this habitat class in greater proportion than moose in Zone D during summer, but proportional use of this habitat did not differ between zones in winter. Moose in Zone T made much greater use of **Deciduous Uplands**, **Mixedwood Uplands**, and **Disturbance** during both seasons than did moose in Zone D when use was calculated using home range data, but only use of **Deciduous Uplands** and **Disturbance** differed between zones using buffered point data. While moose in Zone D did not use **Deciduous Uplands** as much as moose in Zone T, they increased use of this habitat during winter, particularly when use was determined from the buffered telemetry points. Moose in Zone T made a small but significant increase in use of **Disturbance** during winter. Moose in Zone D made far greater use of **Open Conifer Wetlands** in both seasons than did moose in Zone T, regardless of order of selection. Similarly, moose in Zone D used **Shrublands** to a greater extent than moose in Zone T during both seasons. Use of **Wet Meadows** calculated from home range data was greater by moose in Zone D than Zone T during both seasons, but **Wet Meadows** were used more by moose in Zone D than Zone T only during summer using buffered point data. In addition, use of **Wet Meadows** was greater during summer than winter within Zone D using the buffered point data. Neither group of moose used **Conifer Uplands** to any great extent, but use of this habitat by moose in Zone T was greater than use by moose in Zone D during winter when use was calculated from home range data. Winter use of **Conifer Uplands** was greater than summer use within both zones using point data, but did not differ between seasons in either zone using home range data.

Table 2.4. Moose use of 9 habitat classes by Zone and Season, as indicated by:

a) proportional composition of MCP home ranges,

		Habitat Class								
Season	**Zone**	**Wat**	**Sh**	**WM**	**CU**	**DU**	**MU**	**CCW**	**OCW**	**Dst**
Summer	D	0.0403^{a1}	0.0472^{a1}	0.0310^{a1}	0.0037^{a1}	0.0256^{a1}	0.0904^{a1}	0.3649^{a1}	0.3873^{a1}	0.0096^{a1}
	T	0.0231^{a1}	0.0085^{b1}	0.0122^{b1}	0.0065^{a1}	0.2322^{b1}	0.1600^{b1}	0.4361^{b1}	0.0640^{b1}	0.0573^{b1}
Winter	D	0.0243^{a1}	0.0308^{a1}	0.0272^{a1}	0.0039^{a1}	0.0475^{a2}	0.0963^{a1}	0.4035^{a1}	0.3645^{a1}	0.0020^{a1}
	T	0.0220^{a1}	0.0090^{b1}	0.0046^{b1}	0.0066^{b1}	0.2441^{b1}	0.2060^{b1}	0.3909^{a1}	0.0480^{b1}	0.0689^{b2}

and b) proportional composition of buffered telemetry locations.

		Habitat Class								
Season	**Zone**	**Wat**	**Sh**	**WM**	**CU**	**DU**	**MU**	**CCW**	**OCW**	**Dst**
Summer	D	0.0316^{a1}	0.0903^{a1}	0.0233^{a1}	0.0000^{a1}	0.0330^{a1}	0.1322^{a1}	0.3298^{a1}	0.3471^{a1}	0.0128^{a1}
	T	0.0255^{a1}	0.0095^{b1}	0.0064^{b1}	0.0052^{a1}	0.2346^{b1}	0.1840^{a1}	0.4346^{b1}	0.0482^{b1}	0.0520^{b1}
Winter	D	0.0234^{a1}	0.0601^{a1}	0.0058^{a2}	0.0128^{a2}	0.1547^{a2}	0.1116^{a1}	0.3088^{a1}	0.3182^{a1}	0.0046^{a1}
	T	0.0145^{a1}	0.0169^{b1}	0.0002^{a1}	0.0082^{a2}	0.2710^{b1}	0.2072^{b1}	0.3447^{a1}	0.0501^{b1}	0.0873^{b2}

Values shown are actual means but differences were determined from Least Square Means. Within a season, differences between zones ($P<0.05$) are indicated by differing superscript letters. Within a zone, differences between seasons ($P<0.05$) are indicated by differing superscript numerals.

2.4.2 Habitat Preferences Between Zones

Open Conifer Wetlands were much more preferred by moose in Zone D than Zone T regardless of season or order of selection (Table 2.5). On the other hand, moose in Zone T preferred **Disturbance** much more than moose in Zone D during both seasons using either home ranges or buffered points to calculate RSFs. Preference of moose in Zone T for **Disturbance** was also greater during winter than summer using either home ranges or points. Moose in Zone T preferred **Deciduous Uplands** far more than moose in Zone D during both seasons based on RSFs calculated from home ranges. However, preferences for **Deciduous Uplands** only differed between zones during summer when RSFs were calculated from buffered points, likely because of a substantial increase in preference for **Deciduous Uplands** by moose in Zone D during winter. Selection functions calculated for **Wet Meadows** with home range data were greater for moose in Zone D than Zone T during both seasons, but did not differ in either season when calculated with buffered point data. However, the winter RSF calculated for **Wet Meadows** from points was triple the summer RSF within Zone D. **Conifer Uplands** were slightly more preferred by moose in Zone T than Zone D during winter when RSFs were calculated from home ranges, but zones did not differ during either season when RSFs were calculated from buffered telemetry points. Like **Wet Meadows**, the winter RSF calculated from buffered points for **Conifer Uplands** was much larger than the summer RSF for Zone D. Moose in Zone D had a greater preference for **Closed Conifer Wetlands** in winter than did moose in Zone T using home ranges to calculate RSFs, but moose in Zone T preferred the same habitat more than Zone D in summer when buffered points were used to calculate RSFs. This reversal was likely caused by increased preference for **Closed Conifer Wetlands** by moose in Zone D during winter based on home range data. **Shrublands** were considerably more preferred by moose in Zone D than Zone T during summer according to RSFs calculated from buffered point data. There were no seasonal differences in preference for this habitat class within either zone using either dataset.

Table 2.5. Moose Resource Selection Function (RSF) coefficients for 9 habitat classes by zone and season calculated from: a) MCP home range data,

		Habitat Class								
Season	**Zone**	**Wat**	**Sh**	**WM**	**CU**	**DU**	**MU**	**CCW**	**OCW**	**Dst**
Summer	D	0.1236^{a1}	0.1683^{a1}	0.0948^{a1}	0.0314^{a1}	0.0341^{a1}	0.1472^{a1}	0.1087^{a1}	0.2769^{a1}	0.0150^{a1}
	T	0.0859^{a1}	0.1297^{a1}	0.0450^{b1}	0.0511^{a1}	0.1990^{b1}	0.1230^{a1}	0.1300^{a1}	0.0987^{b1}	0.1377^{b1}
Winter	D	0.0893^{a1}	0.1318^{a1}	0.0846^{a1}	0.0423^{a1}	0.0925^{a2}	0.1261^{a1}	0.1840^{a2}	0.2359^{a1}	0.0135^{a1}
	T	0.1060^{a1}	0.1163^{a1}	0.0570^{b1}	0.0655^{b1}	0.1901^{b1}	0.1184^{a1}	0.1073^{b1}	0.0654^{b1}	0.1740^{b2}

and b) buffered telemetry locations.

		Habitat Class								
Season	**Zone**	**Wat**	**Sh**	**WM**	**CU**	**DU**	**MU**	**CCW**	**OCW**	**Dst**
Summer	D	0.0861^{a1}	0.2258^{a1}	0.0401^{a1}	0.0156^{a1}	0.0566^{a1}	0.2178^{a1}	0.0834^{a1}	0.2366^{a1}	0.0380^{a1}
	T	0.1341^{a1}	0.0802^{b1}	0.0332^{a1}	0.0438^{a1}	0.2150^{b1}	0.1527^{a1}	0.1326^{b1}	0.0769^{b1}	0.1316^{b1}
Winter	D	0.0623^{a1}	0.1809^{a1}	0.0130^{a2}	0.1100^{a2}	0.2024^{a2}	0.1388^{a1}	0.1076^{a1}	0.1632^{a1}	0.0217^{a1}
	T	0.0447^{a1}	0.1475^{a1}	0.0091^{a1}	0.0534^{a1}	0.2279^{a1}	0.1403^{a1}	0.1046^{a1}	0.0661^{b1}	0.2064^{b2}

Coefficients represent the probability that a habitat would be selected if all classes were made equally available (Manly et al. 1993). Non-selection (not different than by chance) is indicated by a coefficient of 1/N or 0.1111. Values shown are actual means but differences were determined from Least Square Means. Within a season, differences between zones ($P<0.05$) are indicated by different superscript letters. Within a zone, differences between seasons ($P<0.05$) are indicated by different superscript numerals.

2.4.3. Overall Habitat Preferences

Essentially the same habitats appeared to be avoided and preferred regardless of whether home range composition or buffered telemetry point composition were used to calculate selection functions. **Wet Meadows** and **Conifer Uplands** were least preferred in both cases, followed by **Water** and **Disturbance** (Table 2.6). There were no significant differences among the remaining habitat classes in either case, but the absolute ranks of RSFs changed depending on whether they were calculated based on home ranges or buffered telemetry points. Seasonally, the trend in both cases was for greater preference of **Deciduous Uplands** in winter than summer. There was greater preference for **Disturbance** in winter than summer when RSFs were calculated from home ranges, while greater preference for **Wet Meadows** was observed in summer than winter when RSFs were calculated from buffered point composition.

Table 2.6. Resource Selection Function (RSF) coefficients for 9 habitat classes based on either home range or buffered telemetry point data for all moose and seasons combined.

Habitat Class	Home Range Data	Buffered Point Data
Wat	0.1012^{c}	0.0818^{b}
Sh	0.1365^{cd}	0.1586^{cd}
WM	0.0703^{a}	0.0238^{a}
CU	0.0476^{a}	0.0557^{a}
DU	0.1289^{cd}	0.1755^{d}
MU	0.1287^{d}	0.1624^{d}
CCW	0.1325^{d}	0.1071^{d}
OCW	0.1692^{d}	0.1357^{d}
Dst	0.0851^{b}	0.0994^{bc}

Coefficients represent the probability that a habitat would be selected if all classes were made equally available (Manly et al. 1993). Non-selection (not different than by chance) is indicated by a coefficient of 1/N or 0.1111. Values within columns followed by the same superscript do not differ ($P < 0.05$) based on differences between least square means, but values shown are actual means.

2.5 Discussion

Wildlife study designs are often constrained by the resources available to complete them, which can lead to small sample sizes and a subsequent lack of statistical power. Power is a measure of the likelihood of detecting a difference between treatments, or, 1 minus the probability of committing a Type II error (Walpole and Meyers 1989). The combination of small sample size and high variability among individual moose could have reduced the power of my tests, which may explain why some of the large differences in RSFs for some habitats between zones were non-significant. On the other hand, the differences in habitat preferences detected between zones despite the small sample size and high variability reduce doubt that the differences detected were real.

The RSF calculation presented by Manly et al. (1993) for a single categorical variable such as habitat class shares a problem common with other methods for measuring resource preferences, such as those described by Johnson (1980) and Aebischer et al. (1993). That is, once it is established that resource selection is non-random, it is not possible to determine which habitats are selected differently from random. One can only detect which habitats were selected differently from each other and infer from that analysis whether animals tend to select specific habitats differently than expected by chance. Despite this short-coming, the RSFs I calculated were useful in comparing differences in preference for specific habitat classes between groups of animals in my study because they provided values that could be compared between groups with analysis of variance techniques rather than simply comparing ranks of habitat preferences.

The differences in relative abundance of numerous habitat classes between zones despite the close geographic proximity of the zones provided an excellent opportunity for testing the hypothesis that habitat preferences of moose are fixed. Had this study measured habitat preferences in geographically distinct locations such as Alberta and Alaska, differences in observed preferences would probably have been expected because some of the habitats would not have been available in both areas as dictated by topography, soils, and climate. Moose occupying such geographically distinct areas would also have to contend with different physiological demands as a result of differences in climate and topography, and may also have evolved different strategies for coping with their environment. In the present case however, all habitat classes were available to both groups of moose and differed only in relative abundance. Furthermore, the maximum distance between individual members of the 2 groups in this study did not exceed 75 km and was generally much less. As such, environmental factors each group had to contend with were virtually the same. Given the proximity of the test groups and the lack of major barriers to dispersal, it is unlikely that these were separate populations in genetic isolation that evolved with differing adaptations to their environment. In all likelihood, if selection for habitat attributes is genetically programmed in moose, the moose in both groups would be expected to have been similarly programmed.

Factors that could possibly lead to differential habitat selection between moose groups include differential moose density and predation pressure. Population densities were similarly low within both zones, therefore habitat preferences were not likely density dependent in either zone. Caribou within the study area favoured lowland areas to upland areas, possibly because of greater predator activity within the uplands (James 1999). Therefore, differential predation pressure might explain the general occupation of Zone D by moose there, but probably does not explain differences in habitat preferences between zones. Moose within the study area generally favoured lowland areas over uplands during calving season (James 1999), but the presence of wolves apparently did not reduce the preference of moose for **Deciduous Uplands** in Zone T during other seasons.

In addition, combined human disturbances represented only a small proportion of habitats available to moose in either zone. Timing of disturbance or disturbance levels probably did not differ enough between zones to differentially affect habitat preferences. Therefore, similar habitat use patterns and preferences between the 2 groups would be a reasonable expectation. On the contrary, habitat use contrasted strikingly between zones. And, if Manly's et al. (1993) assertion that the RSFs I calculated represent the probability for selecting a habitat class if all classes were made equally available is correct, the 2 groups of moose would not have selected items similarly from the same menu of habitat classes. Neither of these observations is consistent with the hypothesis that preference for habitat resources is fixed in moose.

My observations of moose habitat preferences are contrary to a number of previous studies. For example, considering the study population as a whole, it could have been interpreted that moose in my study area avoided **Wet Meadows, Conifer Uplands** and **Disturbance**, while they seemed to prefer **Deciduous Uplands** and **Open Conifer Wetlands.** Avoidance of **Conifer Uplands**, particularly in winter, is peculiar compared to abundant reports declaring mature conifer cover in close proximity to forage resources is essential to moose (see Goddard 1970, Van Ballenberghe and Peek 1971, Phillips et al. 1973, Thompson & Vukelich 1981, for example). Similarly, while Deciduous Uplands are commonly referred to as important habitat for moose (Krefting 1974, Nowlin 1976, Peek et al. 1976, Rounds 1981, Pierce and Peek 1984, Telfer 1988), **Open Conifer Wetlands** are seldom mentioned as important moose habitat, though several authors recognized seasonal use of such habitats by moose in Alaska and Alberta (Leresche et al. 1974, Hauge and Keith 1981, Mytton and Keith 1981). Another curiosity was that **Disturbance** was avoided when that habitat class included cutblocks and burns, which are considered important food sources for moose (Peek et al. 1976, Telfer 1974, 1984). When considering the 2 groups of moose separately, the contradictions are more numerous. For instance, **Deciduous Uplands** were always important to one group of moose in my study, but not always important to the other. One group always preferred **Open Conifer Wetlands**, while the other never preferred them. **Disturbance** was strongly shunned by one group, while the other favoured it heavily. Although **Conifer Uplands** were never very important to moose in the study in general, they did increase in importance to some moose seasonally.

An important consideration for the collection and application of habitat use and availability information is the scale at which the data were collected. Despite mixing scales somewhat, my observations support the view of Johnson (1980) and others that habitat selection is hierarchical and that the scale or "order" used for measuring habitat selection must be appropriate for the questions to be answered. I witnessed moose making seasonal shifts in habitat preferences at one order of selection that were not matched at the other order. Similarly, Forbes and Theberge (1993) reported moose selected closed-canopy coniferous habitats at local scales (<100km^2), but selected areas of greater canopy disturbance at regional scales (>1000km^2). How research results can be extrapolated across scales needs to become an integral process of designing experiments and sampling protocols.

Another consideration is level of organization (individual, population, community) and how these levels relate to each other. Experimental designs also must be able to facilitate extrapolation of results among levels. A relevant question is whether to use telemetry points or individual animals as the experimental unit. White and Garrott (1990) considered that using radio locations as experimental units and pooling them from a number of animals for analysis was appropriate in some cases, but Aebischer et al. (1993) argued that many studies pool data inappropriately and recommended using individual animals as the experimental unit. By doing so, they argued concerns about serial correlation among data points are eliminated. Another question is whether measures of central tendency adequately describe habitat selection at the population level. Neither White and Garrott (1990) nor Aebischer et al. (1993) discussed what impacts averaging either sightings or individual animals may have on habitat selection inferences. I speculate that studies doing so may distort actual patterns of resource selection by averaging disregarded divergent patterns and making unwarranted generalizations.

RSF models for grizzly bears showed high variability among individuals in resource selection (Nielsen et al. 2002). As a consequence, population-level RSF models or models derived by averaging individual data were quite general and therefore not very revealing. A suggested alternative was to stratify the population into similar groups and develop separate population models for them as I did (Nielsen et al. 2002). A second alternative was to understand the functional responses (Mysterud and Ims 1998) of individual selection coefficients to availability of resources. Stratifying my sample population by relative habitat composition enabled me to better understand how moose used habitats locally, which in turn, provided better insight into how moose might use habitats over a broader area than had I pooled or averaged individuals. Senft et al. (1987) blended elements of foraging theory, landscape ecology, and hierarchy theory to solve many of the problems associated with applying traditional optimal foraging theory to large herbivores. They surmised that large-scale (regional) foraging decisions made by animals were the cumulative results of a multitude of decisions made at small scales (plants or patches). Also, Aebischer et al. (1993) claimed that radiolocations recorded for an animal approximate the trajectory of that animal's habitat use through space and time. Perhaps, in scaling up from the individual to the population level, the habitat choices of multiple individual moose culminate in a pattern or trajectory descriptive of habitat selection by the population. As such, population-level habitat use is probably described better by the collective patterns of individuals rather than some measure of their central tendency. Stratification of the sample population is a stepped approach to describing the collective pattern. Recognizing that moose habitat preferences change as availability changes provides a basis by which to stratify the sample population, and stratification provides a means by which to link individuals in the process of "scaling up".

2.6 Implications

The notion that changes in habitat availability will influence preferences (Arthur et al. 1996, Mysterud and Ims 1998, Boyce and MacDonald 1999) needs to become generally recognized in the design of resource selection studies. Absolute preferences of moose for habitat classes cannot be proven practically and relative preferences are not fixed. Apparent preferences for habitats will change as their relative abundance changes. Since the value of habitats to moose often is surmised from observations of habitat use and preference, managers must remain cognizant of the variability of habitat preferences among individuals and localities, as well as how to account for this variability when developing habitat management prescriptions.

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3.0 CONTINGENCY OF HABITAT PREFERENCES ON HABITAT AVAILABILITY

3.1 Introduction

Habitat use/availability studies are widely used to assess habitat preferences and selection behaviour and several methods have become standard (Neu et al. 1974, Johnson 1980 for example). Criticisms have been made with respect to the statistical approaches and potential misapplication of these methods (Alldredge and Ratti 1986, 1992, White and Garrott 1990, Aebischer et al. 1993). As a result, a number of improvements in use/availability data analyses have been advanced (Aebischer et al. 1993, Manly et al. 1993, Arthur et al. 1996). Despite these advances, the methods still focus primarily on interpretations of preference from disproportional habitat use. In addition to technical criticisms, a number of authors have questioned the interpretation and biological significance, as well as the application of these method's results to wildlife management (Romesburg 1981,Van Horne 1983, Hobbs and Hanley 1990, Garshelis 2000). Application of the results of use/availability analyses is of particular interest because many management decisions are based on such results and use/availability observations are often key inputs of habitat use prediction and suitability index models. Furthermore, unwarranted habitat relationship generalizations are often made based on the results of such observations (Chapter 1). As such, observations of habitat use/availability obviously carry considerable, but arguably unwarranted, weight in habitat evaluation and management.

I previously observed that differences in relative abundances of the habitat classes available between localities appeared to cause divergence in habitat preferences between moose occupying those respective locations (Chapter 2). The indication was that apparent preferences of moose for habitats would change as the relative abundance of habitats change. Mysterud and Ims (1998) argued that preference defined by habitat use in greater proportion than expected from proportional availability lacks clear biological meaning and that such approaches to assessing habitat preferences "obscure or distract attention from the processes underlying animal space-use patterns". They developed what they defined as functional responses describing habitat use (i.e. change in relative use in response to changing availability) with logistic regression models to explore the concept that preference for a habitat may be conditional on its relative availability. Statistical hypotheses regarding habitat preferences can be posed based on the nature of regression parameters (Mysterud and Ims 1998). For instance, random use of habitat is indicated by an intercept of 0 and a slope of 1 ($\alpha = 0$, $\beta = 1$), while constant use of a habitat regardless of availability would be indicated by $\alpha > 0$ and $\beta = 0$. Further examples include $\alpha > 0$ and $\beta \geq 1$ implying that a habitat is always preferred, or used in greater proportion than its availability. An $\alpha > 0$ and $\beta > 1$ imply that the strength of preference increases with availability.

Perhaps rather than questioning the value of habitat use/availability observations themselves, wildlife managers need to be more careful in the analysis and interpretation of these observations. The case where $\beta = 0$ is particularly useful in illustrating this point. Mysterud and Ims (1998) developed a scenario where an animal adjusted its home range size in order to include a certain minimum amount of some limiting habitat factor, in this case, feeding habitat (Fig. 3.1). The amount of feeding habitat in this illustration remained constant, even though the home range size increased to accommodate the minimum amount. Assuming that the animal spent equal time within each habitat (i.e. telemetry locations are split evenly between the feeding habitat and the other habitat), habitat use remained constant despite changing ratios of availability between the 2 habitat types. In this case, habitat use was not conditional upon availability because use was the same regardless of availability ($\beta = 0$, $\alpha = 0.5$), but the preference interpretation *was* conditional upon availability (Fig. 3.2). When availability of feeding habitat was less than 50%, feeding habitat appeared to be preferred because proportional use exceeded proportional availability. However, when availability was greater than 50%, feeding habitat appeared not to be preferred because use was disproportionately less than availability. Thus, while the underlying process of habitat use in this case was consistent, preference inferences were not. The preference inferences were merely 2 different outcomes resulting from the same animal-habitat relationship. Because preference inferences are conditional upon availability inappropriate preference interpretations could be made, leading to confusion and flawed management decisions.

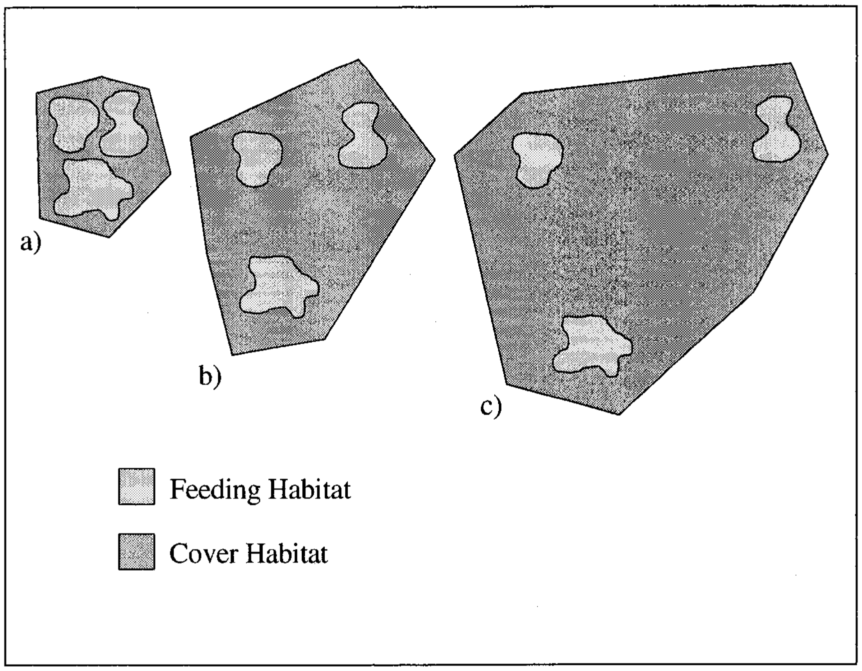

Fig. 3.1. Changes in proportion of home range occupied by feeding habitat (50, 25, and 10%, respectively), when an animal scales its home range size to include a constant amount of feeding habitat. (Adapted from Mysterud and Ims 1998).

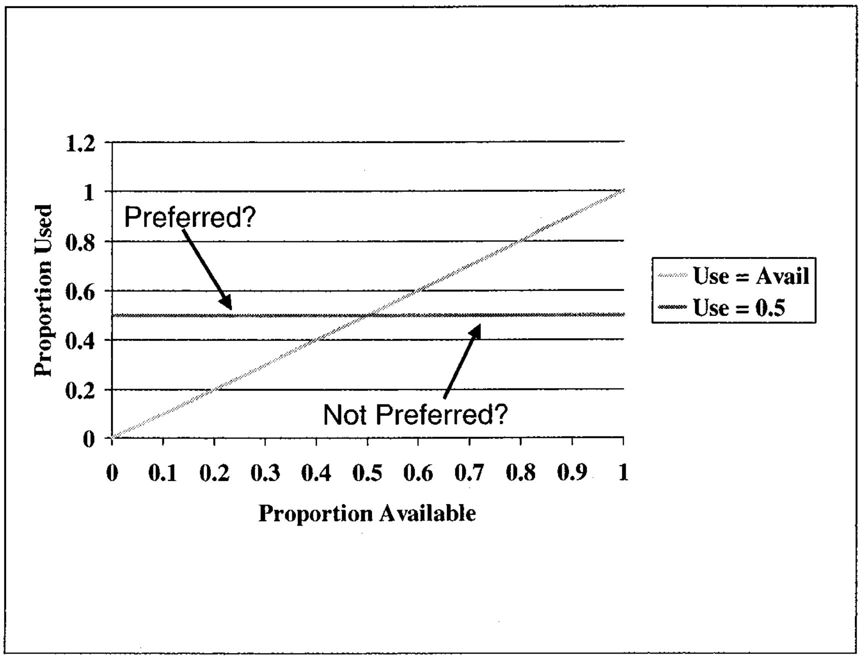

Fig. 3.2. Preference interpretations based on habitat use disproportionate with availability when habitat use is constant across all levels of availability. The light gray line represents random use or use directly proportional to availability. The darker line represents constant habitat use. When proportional availability is low, proportional use exceeds availability and the interpretation is "preference." When proportional availability is high, proportional use is less than availability and the interpretation is "avoidance."

Mysterud and Ims (1998) claimed their method could be used as an exploratory tool for evaluating changes in use patterns of arbitrarily defined habitat classes in relation to their availability. Given that the contrasts in habitat preferences of moose I observed appeared to occur as a result of differences in the relative abundance of habitat classes, exploration of my observations via some form of regression might provide some insight into why these apparent preferences differed. The goals of this investigation were to determine whether the preference inferences made in Chapter 2 were descriptive of moose-habitat relationships that were unique within each zone, or whether they were different outcomes of a relationship that was the same across both zones. Single variable regressions (use vs. availability of the same habitat) were used to test the hypotheses that 1) habitat use responses to availability were random ($\alpha = 0$, $\beta = 1$); and 2) that habitat use was constant ($\beta = 0$) regardless of availability. Single and multi-variable regressions were performed to investigate whether or not use/availability relationships were consistent between zones. This was accomplished by determining whether models could be generated that were common to both of the localities (zones) described in Chapter 2, and that described habitat use in response to availability yet yielded preference interpretations similar to those in Chapter 2 for each of the zones.

3.2 Methods

Study area, animals, and definitions of habitat class use and habitat class availability were as in Chapter 2. Linear regression was used to examine relationships between use of habitat classes and their availability, as well as between their use and the availability of other classes. **Deciduous Uplands**, **Open Conifer Wetlands**, and **Disturbance** were of interest because apparent preferences for these habitat classes were consistently different between zones in Chapter 2. **Disturbance** was removed from the analysis because this class was sparsely available (< 2.5%) among many moose in Zone D.

A total of 18 single variable regressions were performed, examining the response of habitat use to changes in habitat availability. These were completed for **Deciduous Uplands** and **Open Conifer Wetlands** using data from each of the zones independently, as well as the 2 zones combined. Regressions were calculated on both the home range and buffered telemetry point data sets. Because there was little difference in results between the 2 sets of regressions, and because the telemetry point data set represented a mixture of scales (Johnson 1980), for brevity I elected to report only on the home range regression results. There were significant zone by season interactions in use of **Deciduous Uplands** (Chapter 2); therefore regressions for **Deciduous Uplands** were completed for each zone/season combination. Comparisons were made of regression slopes, R^2, and intercepts among equations calculated for Zone D, Zone T, and the zones combined. Using mean availability as inputs, I also compared model predictions for mean use of **Deciduous Uplands** or **Open Conifer Wetlands** within a given zone using the equation generated with data from that zone, from the alternate zone, and from combined zone data.

In addition to single variable regressions, multi-variable regressions were performed on use of **Deciduous Uplands** and **Open Conifer Wetlands** against availability of **Deciduous Uplands**, **Mixedwood Uplands**, **Closed Conifer Wetlands**, and **Open Conifer Wetlands**. Selection of these classes was based on 2 criteria. First, availability of a habitat class had to exceed 2.5% of the area within the 25 km circular buffer of at least 8 moose in each zone. Therefore regressions were performed on 8 to 11 moose from each zone depending on the habitat class. Second, some biological rationale for inclusion of the class had to be made. A relationship existed between **Deciduous Uplands** and **Open Conifer Wetlands**, but the basis of the relationship was unclear (Chapter 2). Use of these habitats appeared to increase with their availability, but greater abundance (and preference) of one seemed to coincide with reduced abundance (and preference) of the other. The deciduous component of **Mixedwood Uplands** might be substitutable with **Deciduous Uplands**. Therefore, this class was included because its abundance could potentially influence use of **Deciduous Uplands**, and consequently **Open Conifer Wetlands**. **Closed Conifer Wetlands** was the most abundant class in either zone, and could provide some of the habitat features of **Open Conifer Wetlands**, so it also was retained. The remaining habitat classes failed to meet the minimum habitat availability criterion.

Regressions were completed for use of **Deciduous Uplands** or **Open Conifer Wetlands** versus availability of each of the 4 selected habitat classes, as well as every possible 2, 3, and 4 variable combination. Within every combination of zone and season (if applicable) there were 15 regressions each for use of **Deciduous Uplands** or **Open Conifer Wetlands** for a total of 135 regressions. The "best" equation of each set of 15 was selected using a combination of 4 criteria: overall significance of the equation (slope *P* value), Akaike Information Criterion (AIC), R^2, and stability of the constant (intercept *P* value). The AIC is a model selection calculation that helps to prevent overfitting the model with excess parameters by applying a "penalty", which increases linearly as the number of parameters increases (Burnham and Anderson 1992). The "best" equations were those with the greatest apparent predictive ability without overfitting the model as determined from combinations of high R^2, low AIC, and a stable constant.

Best equations were compared among Zones D, T, and the zone data combined. The comparisons examined which habitat class availabilities were included as predictive parameters in the models, as well as the sign (+ or -) and magnitude of their respective coefficients. Equation predictions of habitat use were also compared using mean availability of habitat classes in each zone as inputs. Comparisons were made between predictions generated by equations derived within each zone separately and predictions generated by equations derived with zone data combined. I also used equations derived in one zone to generate predictions in the other zone. These predictions were compared to those above and all predictions were compared to the actual mean use observed. These were qualitative comparisons designed to explore apparent differences in habitat preference between zones, and to examine whether apparent preferences or preference rankings describe selection processes or whether they are outcomes of those processes. All regressions were performed using SPSS (SPSS, Inc. 1998).

3.3 Results

3.3.1 Single Variable:

Residual distributions were not perfectly normal in most regressions, however strong deviations from normal occurred only for regressions of **Deciduous Uplands** in Zone D. The assumption of constant variance was met in few cases regardless of habitat class or zone. I attempted a number of transformations to improve the residual distributions, but none were effective.

Regressions of use versus availability of **Deciduous Uplands** within the home range data set were non-significant in Zone D during both winter and summer (Table 3.1), indicating habitat use of **Deciduous Uplands** was not dependent on its availability ($\beta = 0$) within this zone during either season. The same regressions were significant with strong R^2 during summer and winter in Zone T and with data from both zones combined, implying that **Deciduous Uplands** use was neither random, nor independent of its availability in Zone T or with combined zone data. Use of Open **Conifer Wetlands** appeared to be independent of its availability in both zones (Table 3.1). There was a significant relationship between use and availability of **Open Conifer Wetlands** with zone data combined, but the R^2 was weak.

Table 3.1. Regression coefficients and their statistical significance for response of habitat use to varying availability of Deciduous Uplands (DU) and Open Conifer Wetlands (OCW) within Zones D and T, as well as with zone data combined.

Habitat Class	Season[1]	Zone	R^2	Slope	Slope *P*	Constant	Constant *P*	N
DU	Summer	D	0.038	-0.284	0.382	0.047	0.100	22
DU	Summer	T	0.859	3.063	0.000	-0.240	0.001	16
DU	Summer	Combined	0.647	2.296	0.000	-0.140	0.000	38
DU	Winter	D	0.005	0.152	0.746	0.036	0.381	22
DU	Winter	T	0.662	2.866	0.000	-0.192	0.057	16
DU	Winter	Combined	0.548	2.262	0.000	-0.115	0.012	38
OCW	Both	D	0.050	0.506	0.145	0.260	0.005	44
OCW	Both	T	0.089	-0.406	0.097	0.127	0.010	32
OCW	Both	Combined	0.133	0.858	0.001	0.086	0.125	76

[1] There were zone x season interactions effecting the use of DU, but not OCW in the analysis in Ch. 3, therefore OCW regressions were calculated with winter and summer data combined.

As expected, congruency between actual mean use of **Deciduous Uplands** or **Open Conifer Wetlands** and predicted mean use was near perfect for predictions made within the same zone the equations were generated, however, only 1 equation generated within one zone made predictions of use which were remotely similar to actual use in the other zone (Table 3.2). A reasonable prediction of winter use of **Deciduous Uplands** was made in Zone D by the model generated with Zone T data. Of greatest interest however, was that equations generated using combined zone data made reasonable predictions of

Deciduous Uplands use in either zone during both seasons. The prediction of **Open Conifer Wetland** use by the combined zone data equation was fairly reasonable in Zone D as well.

Table 3.2. Comparisons of actual proportional use of Deciduous Uplands and Open Conifer Wetlands against use predicted by simple regression equations generated within the respective zone, by combining zone data, and within the alternate zone.

	Habitat Class					
	Deciduous Uplands				Open Conifer Wetlands	
	Zone D		Zone T		Zone D	Zone T
Origin of Equation	Summer	Winter	Summer	Winter	Both[1]	Both
Same Zone	0.0255	0.0475	0.2158	0.2345	0.3761	0.0730
Zones Combined	0.0352	0.0576	0.2016	0.2216	0.2828	0.2001
Alternate Zone	-0.0063	0.0267	0.0049	0.0585	0.0339	0.3273
Actual Observed Use	0.0256	0.0475	0.2155	0.2344	0.3759	0.0731

[1] There were zone x season interactions affecting the use of DU, but not OCW, therefore OCW regressions were calculated with winter and summer data combined.

3.3.2. Multi-Variable

Combinations of variables included in "best" equations were not consistent between zones using the MCP data (Table 3.3). Equations generated from combined zone data also used different combinations of variables than either zone, except for equations defining use of **Deciduous Uplands** during summer. Variable combinations in the equation generated from combined zone data matched combinations used in Zone T. Values of the coefficients were not the same, however.

Table 3.3. Multiple regression coefficients for the "best" equations generated for use of Deciduous Uplands (DU) and Open Conifer Wetlands (OCW) versus availability of DU, Mixedwood Uplands (MU), Closed Conifer Wetlands (CCW), and OCW within Zones D and T, as well as with zone data combined.

			"Best" Equation Coefficients								
Habitat Class	**Season[1]**	**Zone**	**DU**	**MU**	**CCW**	**OCW**	**Intercept**	**R2**	**Equation *P***	**Intercept *P***	**N**
DU	Summer	D	---	---	---	0.380	-0.062	0.589	0.000	0.003	22
		T	3.063	---	---	---	-0.240	0.859	0.000	0.001	16
		Combined	2.296	---	---	---	-0.140	0.647	0.000	0.000	38
	Winter	D	---	---	---	---	---	---	---	---	22
		T	13.061	14.414	15.868	16.648	-13.439	0.902	0.000	0.011	16
		Combined	---	-3.614	-3.009	-2.799	2.503	0.577	0.000	0.000	38
OCW	Both	D	-2.197	---	-2.618	-2.307	2.309	0.415	0.000	0.000	44
		T	0.433	---	---	---	-0.009	0.154	0.027	0.786	32
		Combined	-6.832	-9.842	-7.956	-6.395	7.113	0.471	0.000	0.000	76

[1] There were zone x season interactions affecting the use of DU, but not OCW, therefore OCW regressions were calculated with winter and summer data combined.

Again as expected, congruency between predicted and actual use was excellent for predictions within the same zone that equations were generated, except for the prediction of **Open Conifer Wetlands** use in Zone T (Table 3.4). In no case did equations generated in one zone have any utility in predicting habitat use in the alternate zone. Equations generated from zone data combined varied in their ability to predict habitat use within a particular zone. Divergence between actual and predicted mean proportional habitat use ranged from 0.9 to 3.6 percentage points using the combined zone model as a predictor.

Table 3.4. Comparisons of actual proportional use of Deciduous Uplands and Open Conifer Wetlands against use predicted by multiple regression equations generated within the respective zone, by combining zone data, and within the alternate zone.

	Habitat Class					
	Deciduous Uplands				**Open Conifer Wetlands**	
	Zone D		**Zone T**		**Zone D**	**Zone T**
Origin of Equation	**Summer**	**Winter**	**Summer**	**Winter**	**Both[1]**	**Both**
Same Zone	0.025		0.216	0.234	0.376	0.055
Zones Combined	0.035	0.07	0.202	0.198	0.361	0.095
Alternate Zone	-0.006	0.345	-0.011		0.024	0.451
Actual Observed Use	0.026	0.048	0.216	0.234	0.376	0.073

[1] There were zone x season interactions affecting the use of DU, but not OCW, therefore OCW regressions were calculated with winter and summer data combined.

3.4 Discussion

Statistical power is limited by small sample sizes, which in turn, limits the detectability of relationships even if they truly exist. Therefore, while use of **Deciduous Uplands** in Zone D and **Open Conifer Wetlands** in either zone appeared to be independent of availability ($\beta = 0$), a relationship may have existed that was undetectable with the sample size available. A larger sample size may have also improved the residual distributions of the regressions.

Assuming use of **Deciduous Uplands** was independent of its availability within Zone D, the relationship between use and availability of **Deciduous Uplands** differed between zones. The uncertainty of whether or not the use/availability relationship for this habitat class differed between moose from each zone was reduced by indications from the multi-variable regressions that while summer use of **Deciduous Uplands** was dependent on its availability in Zone T, its use was dependent on the availability of **Open Conifer Wetlands** in Zone D. Different relationships also appeared to exist between zones for use of **Open Conifer Wetlands.** Use of this class appeared to be independent of its availability in each of the 2 zones, but the multi-variable equations differed considerably between zones. These differences do not support the hypothesis that the preference interpretations from Chapter 2 were different outcomes of the same behavioural responses to availability of habitat classes. On the contrary, moose in each zone appeared to be behaving according to unique selection processes that resulted in the divergent preferences observed.

Differences in habitat preference within virtually the same ecosystem may be puzzling, but many ecologists recognize this is expected (Arthur et al. 1996, Boyce and McDonald 1999). These authors argued that habitat preferences should change as availability changes. Concepts, such as resource optimization (Charnov 1976, Pyke et al. 1977, Belovsky 1978, Rosenzweig 1981), also imply that preferences may change as availability changes. Mysterud and Ims (1998) cited numerous authors that described how animals of many taxonomic groups experience "trade-off" situations that can affect habitat selection when habitat resources (forage, thermal cover, escape cover, etc.) are spatially separated. The unique regression equations observed between zones may have reflected an optimization of trade-offs faced by moose in a variable environment, with the disproportional selection of habitat classes in each zone governed by this process. Use/availability studies are a comparison of choices made versus choices possible. At any scale (feeding station or patch, community, landscape, region) an animal is faced with a finite set of possible choices defined by limits appropriate for that scale. The set of possible choices represents availability at that scale (Senft et al. 1987). The set of choices made represents use. Resource selection is presumably carried out in achievement of some goal or in provision of some habitat "service". However, since not all resources are equal in providing these services, it follows that animals faced with variable resource availability must somehow optimize resource selection from what is available to most effectively acquire necessary habitat services. As such, differences in the relative abundance of habitat classes available to moose between zones in this study could have dictated that differences in habitat use occur for moose to achieve their optimal trade-off solutions. The unique regression equations observed between zones may have been representations of those solutions.

On the other hand, regressions calculated from combined zone data adequately predicted habitat use in either zone, which in turn, could be used to infer the same habitat preferences observed in Chapter 2. The regression of combined zone data for summer use of **Deciduous Uplands** predicted that no use of **Deciduous Uplands** would occur when **Deciduous Uplands** availability was less than about 6% (Fig. 3.3). In addition, **Deciduous Uplands** appeared to be avoided when availability was less than about 11% and appeared to be preferred when availability was greater than 11%. The regression line indicated that use of **Deciduous Uplands** by moose was not random ($\alpha \neq 0$, $\beta \neq 1$) and was not independent of availability ($\beta \neq 0$). Rather, the prediction was that no use of **Deciduous Uplands** would occur at all below a certain availability ($\alpha < 0$), but would rise steeply as availability of **Deciduous Uplands** increased ($\beta > 1$). The regressions of combined zone data for use versus availability of **Deciduous Uplands** indicated that a single response function can apparently describe the selection behaviour of moose overall, yet predict the differences observed in preference between zones. Unlike the unique regressions discussed above, the regressions from combined data do support the hypothesis that the preference interpretations from Chapter 2 were simply outcomes of the same behavioural responses to availability of habitat classes.

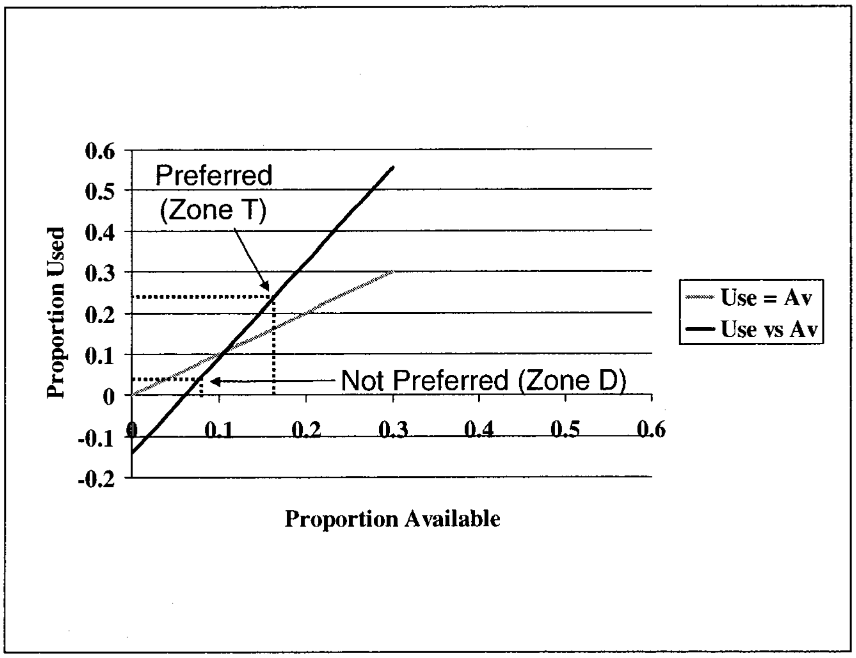

Fig. 3.3. Regression of use of Deciduous Uplands (DU) against availability for summer home range data from Zones D and T combined. The dark line represents the regression, while the gray line represents no selection. The dashed lines indicate mean availability and use of DU within the zones. These means yielded significantly different preference interpretations between zones (Chapter 2) despite being native to the same function describing use of DU in response to availability. Using disproportional use as a preference indicator, DU appear to be avoided when availability is less than 11% and preferred when it is greater than 11%.

The concept of a functional response that describes the trend of food intake by an individual against the abundance of that food is a commonly accepted ecological principle (see Caughley and Sinclair 1994, pp. 72-74 for description and discussion). This functional response is typically represented by an asymptotic curve, where at low abundance of the food item, consumption increases with increasing abundance until additional increases in the resource no longer cause increases in consumption. This may occur because the consuming animal is either satiated or cannot physically process the food beyond a given abundance level. It is conceivable that similar responses exist between use and availability of gross resources such as forest cover types or habitat classes (Mysterud and Ims 1998). Since a line can approximate short segments of a curve, the regressions of use versus availability of each habitat are possibly linear representations of short segments of the response function of moose to each habitat (Fig. 3.4). The shape of each curve and its intercept are probably better indicators of preference for a resource than is a preference index or ranking based on disproportionate use with respect to availability. For example, a common assumption is that preference for a resource will decline as availability of a resource increases. This assumption is correct when the slope of the use/availability regression line is negative. Ironically, a flat line with a positive intercept can lead to the same interpretation with methods based on use/availability ratios (Fig 3.2). Indeed, this interpretation is drawn from any line with a positive intercept and slope < 1. A positive use versus availability slope indicates use increases with increased availability. However, if the intercept is positive and the rate of increase in use does not keep up with the rate of increase in availability, then comparisons of proportions used versus available will be interpreted as preference at low availability and avoidance at high availability. Although these interpretations may describe accurate outcomes of a use response to a resource, they are not accurate depictions of the response itself. Thus, preference might be better interpreted from the slopes and intercepts of use/availability response functions than from use/availability ratios.

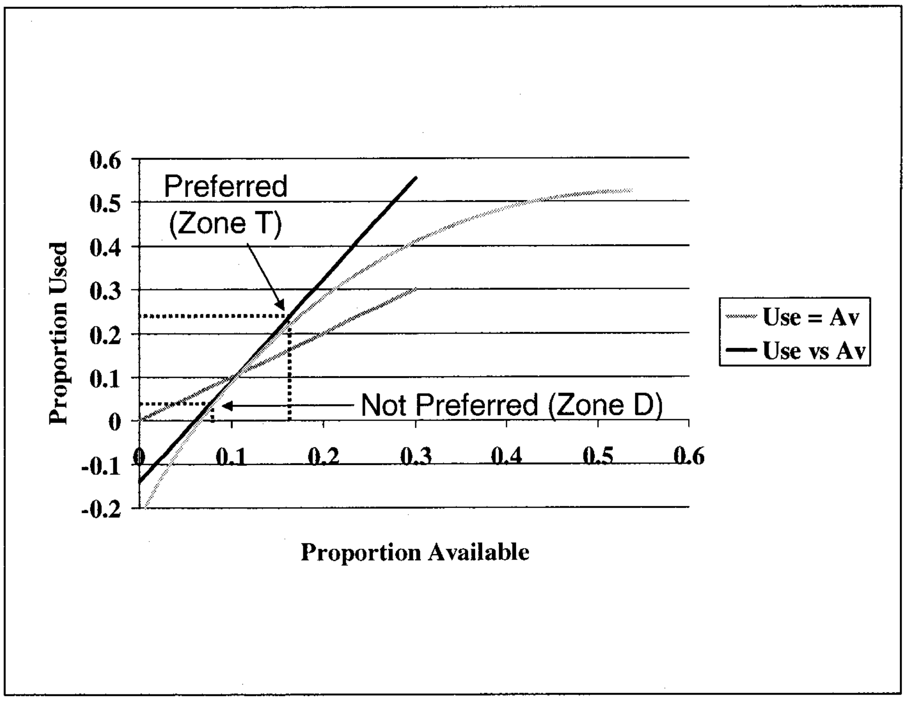

Fig. 3.4. A hypothetical functional response curve for use of Deciduous Uplands in response to availability. The regression of Deciduous Upland use appears as the dark line tangent to the light gray functional response curve, while the darker gray line represents use equally proportional to availability.

Knowing the nature of the response curve for a specific resource would enable prediction of use of that resource if its availability were known. The problem is that proportional use and availability of each habitat class are components of compositions. As such, their relationships are not independent of use and availability of other habitat classes. Therefore, it is likely difficult to ascertain the true nature of a curve describing use of a habitat resource in response to its availability without somehow accounting for the influences of other components in the habitat composition. Independence among components of a composition is constrained by the unit sum of their proportions (Aitchison 1986, Aebischer et al. 1993). Aebischer et al. (1993) demonstrated how to overcome this problem with compositional analysis so that ranks of habitat preferences could be established without influence of the unit-sum constraint. The RSF used here also addresses this problem, but perhaps such issues of non-independence are not as impeding a factor when considering functional responses in a multi-variable situation. Solving the unit-sum dilemma probably does not eliminate the effects of other possible intrinsic relationships (substitutability, complimentarity, synergy) among resources comprising the composition anyway, but these relationships may actually help explain observed resource use. For example, why was the availability of **Open Conifer Wetlands** a better predictor of summer **Deciduous Upland** use in Zone D than the availability of **Deciduous Upland** itself? Was there synergy or substitutability among habitat classes that made this so? Mysterud and Ims (1998) recognized that changing availability and spatial arrangement of habitats that provide unique resources or services can influence habitat use based on the trade-offs relating to selection between specific resources. They applied logistic regression to the data of Aebischer et al. (1993) to calculate a functional response that described habitat use by gray squirrels (*Sciurus carolinensis*) based on the trade-off between food and cover. Their approach demonstrated that learning how components within a composition interact with each other may be more enlightening in explaining habitat use or preference than simply isolating these components.

A multi-variable function extends the notion of functional response curves that describe use of a resource over its range of availability. There probably exist multi-variable functional response expressions (surfaces, polyhedrons?) that describe use of a resource over the range of all combinations of availabilities of resources within a finite set. This expression might represent an amalgam of all individual response curves for the habitat set, including the influences of the curves on each other. Furthermore, just as a regression line can approximate a segment of the functional response curve, a multi-variable regression might define a plane on a response surface, or some subsection of a response function in Euclidean space. By sampling across a range of proportional availabilities, the shape of the response function might be sketched by determining how planes or polyhedrons derived from numerous multiple regressions relate to each other in space. Once the nature of the response expression is understood, use of a resource from a given set of resources can be predicted from any combination of proportional availabilities of components within the set.

As with a univariate functional response, predictions of habitat use made by a multi-variable response function also may result in varying inferences of habitat preference if preference is based on use of habitats in disproportion to their availability. Again, such observations would not necessarily indicate differences in selection behaviour, but represent various possible selection outcomes as dictated by the response function. This point is illustrated by the multiple regression equations derived using combined zone data that adequately predicted levels of habitat use within zones, which in turn, could be used to infer the preferences observed in Chapter 2.

An obvious question is how can the optimization of trade-offs within zones that indicate unique use/availability relationships be reconciled with a global functional response that indicates a single comprehensive relationship? The matter is probably an issue of scale, or rather, a function of the range of habitat availabilities represented among the animals in the sample set. Regressions within a zone probably indicated the trade-offs and outcomes expected for the range of availabilities represented by that sample set, while the combined data represented a wider range in availabilities that was more indicative of moose behaviour overall (Fig 3.5). Any point or segment along a functional response represents the set of trade-off possibilities defined by local habitat availability. Whereas, the functional response itself represents a continuum of trade-off possibilities defined by the complete range of habitat availabilities (0 – 100%). The greater the portion of a functional response represented by a given dataset, the more powerful the potential predictability of that dataset.

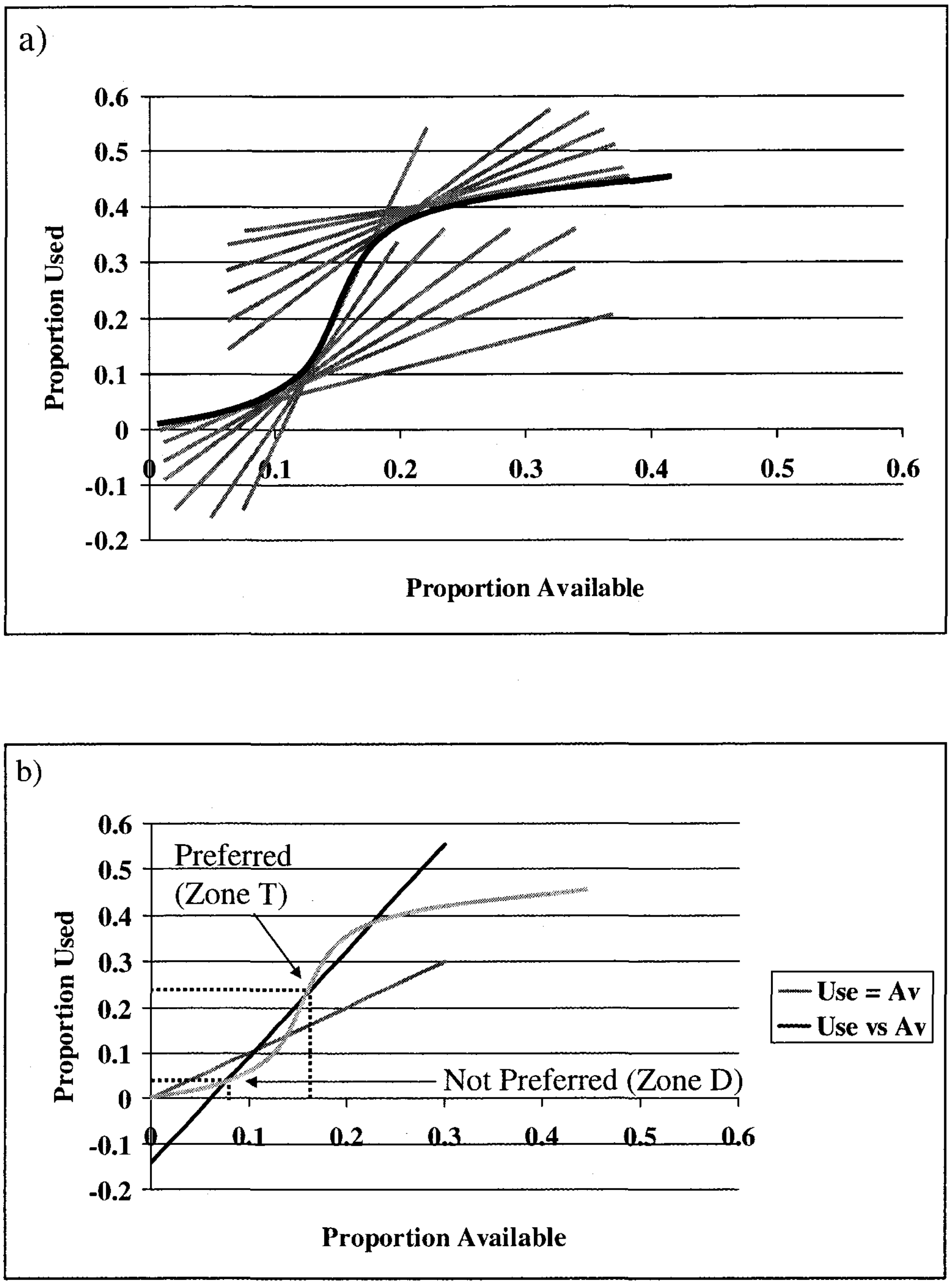

Fig. 3.5. A hypothetical function describing the response of habitat use to habitat availability where a) a family of curves representing regressions over short ranges of habitat availability are consolidated into a single descriptive function, and b) the consolidated function predicts the apparent preference "outcomes" at various points along the function.

Functional responses or regression-based techniques can help us generate collective patterns of habitat use that are more predictive and therefore more useful for effective habitat management than measurements of average patterns of use. I discussed in Chapter 2 how stratification of a sample population could be used as a stepped approach to describing the collective habitat use patterns of a population in the process of "scaling up" from the individual to population levels of organization. It may not be practical or even possible to sample populations that occupy areas representative of the entire range of availabilities for a given habitat class or classes. Therefore, another approach to generating comprehensive functional response models could be stratification of sample populations on the basis of habitat similarity, calculating functional responses or regressions for them separately, and then recombining them to estimate a curve. For example, combining the apparently flat line ($\beta = 0$) associated with use of **Deciduous Uplands** in Zone D and the sloped line describing use of **Deciduous Uplands** in Zone T with an asymptote would yield a sigmoid curve that might be more representative of the true functional response of moose in this study to use and availability of **Deciduous Uplands**. Merging the unique regressions from each zone in this way may be a step in describing the "collective pattern" of habitat use in the process of scaling up from the individual to the population level as discussed in Chapter 2. In other words, relationships from distinct areas with distinct relationships could be put together like pieces of a puzzle until the entire relationship is filled in.

Ideally, prediction of habitat use and utility would be made by mechanistic understanding of interactions between an animal's habitat and the habitat services the animal needs (Hobbs and Hanley 1990). Perhaps optimization of trade-offs based on availability and spatial arrangement of resources is the explanatory mechanism. Indeed, multi-variable response functions that integrate a combination of response curves and their interactions might be expressions of this optimization process in resource selection. Understanding how a species evaluates these trade-offs may lead to direct derivation of response functions, which could then be used to predict habitat use from availability. Regardless, it is apparent that inferences of preference based on disproportional habitat use are not meaningful measures of habitat selection behaviour because these inferences change when availability changes. Functional responses or regression-based techniques may not answer why habitat selection trade-offs are made the way they are, but they can be more descriptive of the circumstances under which these trade-offs are made than simple preference inferences can. As such, they are better predictors of habitat use under variable habitat conditions and thus provide superior opportunities for hypothesis generation towards achieving mechanistic understanding.

3.5 Implications

The present analysis provided evidence that supports both the hypothesis that preference interpretations from Chapter 2 were outcomes of the same behavioural responses to availability of habitat classes, and the alternative, that moose in each zone appeared to be behaving according to unique selection processes that resulted in the divergent preferences observed. However, these apparently opposing conclusions are not irreconcilable. In fact, an appealing possibility is that the unique relationships observed at specific places and times can be consolidated to describe comprehensive wildlife-habitat relationships that are responsive to habitat change and therefore predictive of the effectiveness of habitat management prescriptions. In any case, whether habitat relationships are absolutely unique or whether unique relationships can be merged to describe collective relationships, both options force us to recognize that habitat preferences are conditional upon habitat availability and reduce our tendency toward making generalizations about wildlife-habitat relationships. Acknowledging that managers must manage with whatever information is presently available, application of prescriptions based on habitat generalizations can not yet be completely avoided. However, such prescriptions should be applied in an experimental fashion whereby the assumptions underlying these generalizations can be tested. The information resulting from these tests will in turn enhance future management decisions.

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4.0 SPATIAL RESPONSES OF MOOSE TO NATURAL AND ANTHROPOGENIC FEATURES

4.1 Introduction

Distances from, or the presence of specific environmental features are commonly used as parameters in studies of wildlife-habitat relationships or as inputs into habitat use or suitability index models (Allen et al. 1987, Pereira and Itami 1991, Clark et al. 1993, Nadeau et al. 1995, Dyer et al. 2001, and Mitchell et al. 2002, for example). Also common are generalizations made from the results of such exercises, particularly HSI models (Bart et al. 1984, Block et al. 1994, moose examples include Romito et al. 1996, Conoco Canada Resources, Ltd. 2001). Given that the investigation in Chapter 2 indicated that moose occupying distinct localities within the study area (Zones D and T) appeared to express contrasting selectivity towards certain habitat classes, moose might also respond differentially to specific features in their environment. Transferability of results from habitat use studies or models that use distance or presence parameters to areas other than where models were generated would be limited if moose responded differentially to environmental features. Differential responses to features among moose occupying distinct areas could be influenced by the relative abundance of those features, or perhaps even the abundance of other features, between the areas. In any case, should responses to features among moose occupying distinct areas differ, generalizations of moose-habitat relationships based on the distances from or presence of environmental features would be inappropriate to make.

Boreal Alberta is subject to a number of resource extraction industries that leave various temporary and permanent marks on the landscape during exploration, production, and delivery stages of the extraction processes. Industries include, but are not limited to forestry, traditional oil and gas exploration, heavy oil extraction, surface mining, and peat extraction. Typical disturbances or features associated with these activities include road construction, seismic and pipelines, wellsites, open pits, drilling pads, compressor stations, and cutblocks. Some of these disturbances are short-lived and leave a small footprint on the landscape but can constitute a much larger footprint when considered cumulatively. Furthermore, while seismic lines or roads may only remove a small proportion of physical habitat, human activity such as automobile or off-highway vehicle traffic, as well as use of such corridors by predators, could contribute to a much larger "effective" habitat loss.

Because Al-Pac's FMA area is subject to the types of industrial disturbances described above, I was curious about the consistency of responses to such features by moose occupying distinct areas; namely Zones D and T. I wished to quantify the extent of some of these disturbances, as well as a natural feature (rivers), between zones and the responses of moose to them. I was also interested in knowing whether or not response to environmental features was consistent across spatial scales or "orders of selection" as defined by Johnson (1980). I therefore set out to answer 4 primary questions with respect to abundance of and responses to 4 environmental features (forest cutovers, seismic lines, oil/gas wells, and rivers) within the 2 zones of the study area:

1. Does the general abundance of features differ between zones?
2. Does abundance of the features within moose home ranges differ between zones?
3. Does abundance of the features within moose home ranges relative to the area available to moose differ between zones?
4. Within home ranges, does site selection differ between zones?

For the 3rd and 4th questions, I also asked whether moose locations relative to environmental features differed from what would be expected by chance.

4.2 Methods

The study area and animals used in this analysis of moose response to environmental features were the same 22 animals described in Chapter 2. Areas of habitat availability (25 km buffers) and use (MCP home ranges, telemetry point composition) were also the same as those described in Chapter 2.

Geographic databases for all environmental features were stored within an ARC/INFO Geographic Information System (GIS). The forest cutover data layer was produced by a third party by digitization of an enhanced LANDSAT thematic image. The cutover classification included both new and regenerating cutblocks. Seismic lines were linear disturbances up to 8 m wide. The seismic database was provided by an independent consultant based on aerial photo interpretation and industry records. Wellsites were typically square or rectangular clearings of up to 1 ha in size with an operational or abandoned wellhead centered in the clearing. This database was derived from industry records. Rivers included all major rivers and tributaries within the study area. Although other anthropogenic features such as roads and pipelines occurred within the study area, these features did not occur in the availability buffers and home ranges of all moose. This analysis was restricted to the 4 features described above, which did occur in home ranges and availability buffers of all of the study animals.

Abundance of each feature was measured within the 25 km diameter availability buffers and home ranges of each moose by using the GIS to calculate the density of each feature within the respective boundaries. Densities within buffers and home ranges were expressed on a per unit area basis as follows: length of seismic lines (m km^{-2}), area of cutovers (ha km^{-2}), length of all rivers (m km^{-2}), and number of wells (# km^{-2}). Density of cutovers, wells and rivers within availability buffers were compared between zones using a single factor analysis of variance (ANOVA). A non-parametric ANOVA was used due to small sample size and potential non-normality of densities. Seismic data for the FMA area is updated annually and densities of seismic lines differed between 1995 and 1996, but not between seasons within years. Therefore, YEAR was added as a factor to the above model for comparing density of seismic lines within availability buffers between zones.

Feature densities within home ranges were compared using a multi-factor ANOVA with ZONE, SEASON, and YEAR as main effects. Log transformations of feature densities + 1 were used due to non-normality of feature densities within home ranges (Zar 1984). Individual moose within ZONE was considered as a random effect in the model.

A selection index consisting of the ratio of home range densities to availability buffer densities was calculated for comparing differences in home range selection between zones. I refer to this ratio here as the "density selection ratio". Comparisons were made by entering log transformations of the ratios + 1 into a multi-factor ANOVA with ZONE, SEASON, and YEAR as main effects. Individual moose within ZONE were considered as a random effect.

Feature densities in home ranges were compared to densities in availability buffers using Wilcoxon Signed Ranks (Zar 1984). Densities were averaged across ZONE, SEASON, and YEAR unless any of these factors or their interactions were significant in the density selection ratio analysis. In cases where one or more of the main effects or interactions were significant, the test was performed on densities broken down by the significant effects.

Within home ranges, selectivity towards features was determined by comparing moose-to-feature distances (based on radio-locations) to distances between randomly generated points and the features. The GIS was used to generate random point locations within the study area. The GIS was then used again to randomly select from the population of generated points, which fell within or along the boundaries of individual home ranges. The number of random points selected was equal to the number of telemetry locations for a given moose. To compare site selection behavior relative to features between zones, I calculated the ratio of distances between moose locations and the nearest feature to distances of random locations to the nearest feature. I refer to this ratio here as the "distance selection ratio". Log-transformations of these ratios + 1 were entered into a multi-factor ANOVA with ZONE, SEASON, and YEAR as main effects. Individual moose within ZONE were entered into the model as a random effect.

Differences between moose-feature distances and random point-feature distances were compared using Wilcoxon Signed Ranks. Distances were compared within zones only, because comparisons between zones would be redundant to the density comparisons. Between zone comparisons were accomplished using the distance selection ratios described above. Distances were averaged across ZONE, SEASON, and YEAR unless any of these factors or their interactions were significant in the distance selection ratio analysis. In cases where one or more of the main effects or interactions were significant, the test was performed on distances broken down by the significant effects. I accepted statistical significance at $\alpha \leq 0.05$.

All analyses were completed using the SAS Analytical System (SAS Institute 1997). Raw densities and distances are presented for descriptive purposes. Statistical comparisons were made on least square means of transformed data, not the raw means presented below (densities within availability buffers were not transformed). Ratios presented are means of all individual ratios and are therefore not necessarily equivalent to the ratio of density or distance means.

4.3 Results

Differences between zones occurred for at least 1 of the 4 features in each of the comparisons of density within availability buffers, density within home ranges, and density selection ratios (use/availability at landscape scale). There were no significant season or year effects in any of these comparisons except for a ZONE x SEASON interaction in the comparison of cutblock density selection ratios. For each environmental feature, individual moose within zone was a highly significant ($P = 0.0001 - 0.0006$) factor in comparisons of density within home ranges and comparisons of density selection ratios. None of the overall models for any feature were significant for comparisons of distance selection ratios.

There was no difference between zones in the density of wells within availability buffers or in the density of wells within home ranges (Table 4.1a). There was also no difference between zones in density selection ratios. Since apparent selection did not differ between zones, the Wilcoxon Signed Ranks test was performed on the overall means for home ranges and availability buffers. There was no overall difference between density of wells in availability buffers and density in home ranges. Within home ranges, there was no apparent difference in site selection by moose between zones as indicated by the distance selection ratios (Table 4.1b). There was also no difference overall between moose location to well distance and random location to well distance.

Table 4.1. Summary of comparisons of density, selection ratios, and distances with respect to wells within zones, availability buffers and home ranges.

		D	T
a) Densities (wells/km^2)	Availability Buffers	0.0841	0.0766
	Home Ranges	0.0766	0.0872
	Selection Ratio	0.8297	1.1760
b) Distances Within Home Ranges (m)	Random	1838.5	1821.2
	Moose	1824.5	1891.3
	Selection Ratio	1.0360	1.0618

There was no difference between zones in the density of rivers within availability buffers (Table 4.2a). However, density of rivers within home ranges in Zone T was less than half the density of rivers within home ranges in Zone D. Density selection ratios also differed between zones. Density of rivers within home ranges differed from density in availability buffers in Zone T, but not in Zone D. Within home ranges, distance selection ratios for rivers did not differ between zones (Table 4.2b). Nor was there an overall difference between moose location to river distance and random location to river distance.

Table 4.2. Summary of comparisons of density, selection ratios, and distances with respect to rivers within zones, availability buffers and home ranges.

		D	T
a) Densities (m/km^2)			
	Availability Buffers	231.2^{a1}	201.8^{a1}
	Home Ranges	298.4^{a1}	139.4^{b2}
	Selection Ratio	1.3196^{a}	0.6169^{b}
b) Distances Within Home Ranges (m)	Random	1511.6	2770.7
	Moose	1585.1	2562.0
	Selection Ratio	1.1179	0.9681

Values within rows followed by the same letter superscript do not differ significantly ($\alpha \leq 0.05$) between zones.
Values within columns followed by the same number superscript do not differ significantly ($\alpha \leq 0.05$) within zones.

Density of seismic was greater in Zone D than Zone T within both availability buffers and home ranges, but density selection ratios did not differ between zones (Table 4.3a). Nor was there a difference overall in densities of seismic between home ranges and availability buffers. There was no difference between zones in distance selection ratios within home ranges (Table 4.3b), but Moose location to seismic distance was greater than Random Location to seismic distance overall. Overall mean moose distance to seismic was 455 m, while mean random distance to seismic was 408 m (P=0.0147).

Table 4.3. Summary of comparisons of density, selection ratios, and distances with respect to seismic within zones, availability buffers and home ranges.

		D	T
a) Densities (m/km^2)			
	Availability Buffers	1226.4^{a}	1022.1^{b}
	Home Ranges	1281.9^{a}	919.3^{b}
	Selection Ratio	1.0535	0.9069
b) Distances Within Home Ranges (m)	Random	288.5	528.1
	Moose	366.8	543.5
	Selection Ratio	1.3522	1.1936

Values within rows followed by the same letter superscript do not differ significantly ($\alpha \leq 0.05$) between zones.

Density of cutblocks within availability buffers was greater in Zone T than Zone D (Table 4.4a). Cutblock density within home ranges of moose in Zone T was almost 7.5 times the density of cutblocks in Zone D, but this difference only approached significance ($P = 0.1371$). Density selection ratios for cutblocks were also higher in Zone T than Zone D during both winter and summer (Table 4.4b). Density selection ratios did not differ between seasons within Zone D, but the winter ratio in Zone T was greater than the summer ratio in that zone despite trending in the same direction. Within home ranges, distance selection ratios for cutblocks did not differ between zones (Table 4c). There was also no difference overall between moose location to cutblock distances and random location to cutblock distances.

Table 4.4. Summary of comparisons of density, selection ratios, and distances with respect to cutblock within zones, availability buffers and home ranges.

		D	T
a) Densities (ha/km^2)			
	Availability Buffers	1.251^{a1}	2.708^{b}
	Home Ranges	0.569^{2}	4.220
b) Selection Ratio by Zone and Season	Summer	0.4587^{a1}	1.4525^{b1}
	Winter	0.0896^{a1}	1.5879^{b2}
c) Distances Within Home Ranges (m)	Random	8076.3	3687.2
	Moose	8319.6	3738.4
	Selection Ratio	1.0213	1.0450

Values within rows followed by the same letter superscript do not differ significantly ($\alpha \leq 0.05$) between zones.
Values within columns followed by the same number superscript do not differ significantly ($\alpha \leq 0.05$) within zones.

4.4 Discussion

The combination of small sample size and high variability among individual moose could have reduced the power of the above tests. There was a large difference in density of cutblocks within home ranges between zones, as well as a large difference in density of cutblocks between home ranges and availability buffers in Zone T, but neither of these differences was statistically significant. Significance of these differences might have been detected if a larger sample size was used.

Where responses to features differed between zones (rivers and cutblocks), selectivity appeared to occur only at the second order of selection (Johnson 1980) and not the third. That is, moose appeared to select or avoid these features when establishing home ranges, but once established, moose locations within home ranges did not appear to be influenced by the features. The features examined here probably represented a relatively coarse physical scale that also represented moose behaviours at a coarser scale. As such, differences were not detectable at the third order of selection. By comparison, studies that examine relationships between specific vegetation characteristics and specific behaviours, such as bedding or nesting sites for example (Ockenfels and Brooks 1994, Pollock et al. 1994, Buchanan et al. 1995), have both a finer spatial and behavioural resolution that probably lend themselves better to detection of differences at the third order of selection.

Moose from both zones appeared to avoid seismic lines to some degree overall. While statistically significant, it seems doubtful that the difference between moose-to-seismic distance and random point-to-seismic distance of about 50 m was biologically significant. Nevertheless, this difference could indicate an effective loss of a linear band of habitat at least 100 m wide for the length of every seismic line in a moose's habitat. Calculating from the density of seismic lines within availability buffers, this loss translates to a 12% potential loss of available habitat in Zone D and a 10% potential loss in Zone T.

While differences in selectivity toward features were detected between zones, it is uncertain whether these differences were conditional upon availability since four different availability-response combinations were observed. First, wells were equally available between zones, and moose in each zone appeared to respond to them in proportion to availability. Second, seismic abundance differed between zones but moose responses to them did not differ. Third, abundance of rivers did not differ between zones but moose responded differentially toward them. Finally, cutblock abundance differed between zones and moose responses toward them also differed.

Of these 4 scenarios, only the fourth appears to support the hypothesis that preferences toward habitat classes or features are influenced by their availability. Additional factors could be at play in determining selective behaviours towards features, or some features might be inert components within the environmental matrix occupied by moose that are simply ignored. Despite the difference in abundance of seismic lines between zones, both seismic lines and wellsites are ubiquitous within Al-Pac's FMA area (Dyer et al. 2001), and the persistence of their footprint is almost indefinite (Osko 2001, Osko and MacFarlane 2001). Perhaps the abundance and uniform distribution of these features precluded the ability of moose to express differences in selective behaviour toward them. Abundance of features could have been above some threshold beyond which selective behaviour is detectable. That is, seismic abundance may have been such that the asymptotic portion of a functional response curve describing moose responses to seismic lines had already been reached. Moose might have displayed a greater degree of selectivity, and perhaps differences between zones, had wells and seismic lines not been so abundant.

That moose responded differently to rivers between zones despite equal abundance of that feature could indicate that the response to rivers depended on the availability of some other feature or resource. Proportions of shrublands, which occurred primarily within riparian areas in the study area, were greater in habitats selected by moose in Zone D than Zone T (Chapter 2). This is consistent with the greater abundance of rivers observed in home ranges within Zone D in the present analysis. There was also a tendency for Resource Selection Functions for shrublands to be higher in Zone D than T in Chapter 2. Telfer (1978) suggested riparian shrublands were an important source of deciduous browse for moose. Perhaps differential use of riparian shrublands between zones resulted from moose in Zone D substituting riparian areas for deciduous forests as a source of deciduous browse, since deciduous forests were less abundant in Zone D. This in turn could have resulted in the apparently different responses to rivers in establishment of home ranges between zones in this analysis. Faced with variable environments, perhaps the moose made "trade-off" decisions (Mysterud and Ims 1998) in habitat selection that made use of certain habitat features dependent on the availability of other features.

The patterns of response towards cutblocks between zones are consistent with observations made in Chapter 2, where the habitat class that included cutblocks was differentially available, used, and selected for between zones. Use of cutblocks and burns as a browse source by moose is commonly reported (Telfer 1974, 1984, Peek et al. 1976, Wolff and Zasada 1979, McNicol and Gilbert 1980, Thompson and Vukelich 1981, Tomm et al. 1981). Most authors however, report on differential cutblock use based on cutblock morphology (Telfer 1974, Hamilton and Drysdale 1975, McNicol and Gilbert 1980, Euler 1981, Thompson and Vukelich 1981, Tomm et al. 1981, Monthey 1984, Eason 1985, Forbes and Theberge 1993) rather than based on localities occupied by moose. Although not examined specifically, cutblock morphology did not appear strikingly different between zones as indicated from the satellite imagery or during flights over the respective areas. Cutblock size and age ranges also appeared to be similar between zones. Therefore, little inference can be drawn from the "moose use of cutblocks" literature with respect to why moose in the 2 zones of our study area seemed to express different selection behaviour toward cutblocks. The answer likely lies in the processes governing selection of specific resources from the suite of resources available. Such processes are yet to be clearly defined for moose.

Individual variability was consistently the most significant factor in all analyses. The variability in resource selection behaviour expressed by moose both individually and by locality could have a variety of explanations. One could be that each animal develops its own unique strategy for acquiring requisite resources and this is expressed in differential habitat selection. A second explanation could be that moose may all use the same strategy, optimal foraging (Charnov 1976, Pyke et al. 1977) for instance, but because availability of resources differs somewhat for each individual the optimal foraging solution differs for each individual as well. This results in apparently different preferences for the same resources. Another explanation might be that some moose simply develop traditional movement patterns centered around or near their place of birth and cope as best they can with the resources available there. Moose in this study appeared philopatric to their ranges. All of these explanations suggest a moose's immediate environment strongly influences how it uses or expresses selectivity for resources. These explanations also indicate moose have a great deal of plasticity in responding to environmental variability and that making appropriate trade-off decisions probably plays a role in that plasticity.

The variety of responses to environmental features observed here also brings to bare many of the same questions raised in Chapter 2. Is scale important? Do pools or averages of data adequately describe habitat selection behaviours? Certainly, the differential responses to environmental features observed here and to habitat classes in Chapter 2 would not have been recognized if individual observations of habitat use had been pooled and compared to a single arbitrarily defined study area that represented availability for all animals. Are habitat selection behaviours better explained by the collective patterns of individual animals? If so, how should data be treated and what is the process of scaling up from individuals to populations? Before answering these questions, wildlife managers must recognize that variability in habitat between areas can change the outcomes of habitat selection behaviour, and that this will influence the models they use in making habitat management decisions. Appropriate examination of the above questions cannot proceed until it is widely acknowledged that results of habitat use studies or model outputs cannot be generalized.

4.5 Implications

In this study I demonstrated that while variable responses of moose to habitat components are generally expected to occur between landscapes, responses can be highly variable within landscapes as well. Therefore, care should be taken in making generalizations from the results of studies or models of wildlife-habitat relationships. Although scale largely is recognized to engender differences in resource selection behaviour, resource availability is not generally recognized as a driver of change in animal responses to habitat. The mechanisms by which relative abundance of habitat features drive resource selection are not understood for moose, and likely, for few if any other species. Future research should focus on the development and testing of hypotheses that investigate these mechanisms. The first steps in this process would be to recognize that responses of animals to their environment are conditional upon the composition of that environment, and to use HSI and other "habitat use" models as exploratory tools instead of for making indiscriminate predictions.

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5.0 SYNTHESIS

5.1 General Meaning Of Results

The habitat preferences expressed by moose are not fixed. Indeed, not only can preferences be expected to vary from region to region, but preferences can also differ within relatively short distances within the same ecosystem. These observations are probably not restricted to moose and quite likely are true for a number of species. Dynamic habitat preferences have 2 major consequences for the way we approach habitat management. First, reliability of the assumption that habitat preferences connote fitness benefits is reduced if preferences are not static. If preferences for habitats differ between animals or groups of animals, then obviously, a species will not always select what we perceive to be the most beneficial habitats. If they do not consistently select the best habitats, we must then question the link between habitat choices and fitness benefits. Second, since preferences are not fixed, and if the link between habitat preferences and fitness benefits is weak, generalizations cannot be made regarding either the habitats animals prefer or the fitness benefits of the habitats chosen.

5.2 Preference And Fitness

(Fagen 1988) arguments have been made that the carrying capacity (quality) of habitats will be directly proportional to preference expressed for those habitats (as determined by relative density of animals vs relative availability of habitats) whenever animals are free to choose the best habitats (i.e. animal distribution is "ideal free"). However, Hobbs and Hanley (1990) countered that habitat quality will be directly proportional to preference only when 3 conditions are met: 1) when animals are completely free to choose the best habitats; 2) after long, stable equilibria have been achieved between animal populations; and 3) when preference is measured after these equilibria have been achieved. They suggested that these conditions rarely exist and that the relationship between habitat preference and quality was therefore tenuous. Hobbs and Hanley (1990) maintained that any inferences regarding habitat value derived from use/availability data would depend on the year the data were observed and that preferences animals express for habitats would change as population density changes. In practice, availability of components within a finite set of resources can be limited by either the relative abundance of resources, or the abundance of competitors. Therefore, Hobbs and Hanley's (1990) argument with respect to preferences of animals for habitats should apply equally well to changes in relative abundance of habitat resources as to changes in population density.

Though not explicitly described, Garshelis (2000) interestingly alluded to functional responses of survival and fitness to habitat availability, with thresholds, asymptotes, and inflection points varying with the mix, size, shape, and juxtaposition of habitat components. So the assertion that preferred habitats confer fitness benefits might not be completely off the mark. However, the habitats we observe to be preferred provide the most fitness only under the prevailing conditions of our observations. In other words, both preference for and the fitness benefits of habitats are contingent upon the relative choices among the habitats available. As Mysterud and Ims (1998) suggested, animals face trade-offs that affect the selection of habitats that provide opportunities for all the essential activities required for successful reproduction. These trade-offs change as the relative abundance of resources changes, and consequently, the fitness benefits of given habitat types likely change with how they can be combined with the other habitats available. For example, optimum fitness in a given situation might dictate that less abundant high quality habitats are forgone for more abundant low quality habitats. So while animals may in fact prefer habitats that confer the most fitness, the optimal fitness solution depends on the combination of habitats available at a given place and time. Therefore, the fitness benefits conferred by specific habitat types are in a state of flux, resulting in expression of differential habitat preferences.

5.3 Preference Detection Methods and Changing Habitat Availability

There are numerous methods for measuring habitat use and preference but none of them directly address the influence of changing habitat availabilities. Some common measures of habitat use are the proportions of habitats contained within an animal's home range (see White and Garrott 1990 for detailed discussion), or simple observations of food items consumed, relative time spent within specific cover types, counts of fecal deposits and so on. Preference indices include Ivlev's electivity index (Ivlev 1961), the Chi-square analysis described by Neu et al. (1974), the ranking procedures of Johnson (1980) and Aebischer et al. (1993), and the resource selection functions (RSFs) described by Manly et al. (1993). RSFs indicate preference by computing the probability that a resource unit will be selected. The ranking methods also provide a measure of the relative likelihood of resource unit selection, but the likelihood is not quantified. The Chi-square method detects differences in habitat use from that which would be expected by chance. All of these methods, including those that do not compare habitat use to availability, are influenced by changes in habitat availability but none of them account for that influence within the techniques themselves. Previous authors have recognized this and offered solutions. Arthur et al. (1996) calculated RSFs similar to the ones I used here for moose to measure habitat selection responses of polar bears to sea ice. They addressed the issue of changing habitat availability by estimating availability for each radio-telemetry bear location and calculated repeated RSFs at 3 to 6 day intervals. Boyce and McDonald (1999) suggested modeling the responses of RSF β-coefficients to changes in availability, which can be accomplished by regressions such as those performed in Chapter 3, or by calculation of functional responses (sensu Mysterud and Ims 1998). Nielsen et al. (2002) recommended either stratifying the sample population by habitat similarity and calculating RSFs separately, or learning the functional responses of habitat use to availability. I used both the stratification method and a quasi-functional response approach in the present study and found the regression techniques more informative than stratification because they directly incorporated the influence of changing availability into the analysis and allowed for evaluating the influence of habitat availability among several classes on use of a single class. The disadvantage however, is that sampling may not always occur over a wide enough continuous range of habitat availabilities to produce a meaningful regression, in which case the stratification method may be more useful.

5.4 Availability Estimates and Scalar Issues

If the relative preferences for habitats and the relative fitness they impart are conditional upon relative availability, then it is probably quite important to accurately estimate availability if we are to understand the relationships between availability, preference, and fitness. However, previous authors agreed that habitat availability estimation could be ambiguous for a number of reasons (Johnson 1980, White and

Garrott 1990, Aebischer et al. 1993, Manly et al. 1993, Arthur et al. 1996, Garshelis 2000).

Accurate estimation of availability leads to the scale issues of "orders of selection" (Johnson 1980) and levels of ecological organization (individuals to populations). The number and types of decisions made by animals change moving from landscape to home range to community to site or patch (Senft et al. 1987). Accordingly, the habitat choices available change with each scale. For example, Senft et al. (1987) described one theory that posits the selection of diet items by an ungulate at a "feeding station" would be made from among the items immediately available when the forefeet are stationary. In contrast, home range selection would be accomplished from among the number and types of communities available across a landscape. Errors in estimating the choices available at a specific scale will lead to errors in determining preferences for resources at that scale.

Thomas and Taylor (1990) described 3 general study designs that differ on the basis of the level at which habitat use and availability are measured (population or individual level). Design I measures use and availability at the population level, Design II measures availability at the population level, but use at the individual level, and Design III measures both use and availability at the individual level. Availability estimation is particularly ambiguous for Designs I and II for 2 reasons: 1) the boundaries of predetermined study areas common to all animals in the study are typically arbitrarily defined and rarely have any biological significance, and 2) not all areas within the arbitrarily defined boundaries may be available to all animals. Clark et al. (1993) offered a solution to reduce ambiguity due to lack of biological significance for their bear study area. They created their study area boundary by circumscribing arcs, with the radius of average bear home range size, around sites where bears were trapped for affixing telemetry equipment. However, such an approach will not always address the issue of realistic availability of all habitats in the study area to all animals. Measurement of habitat availability at the individual level, as in Design III, can reduce ambiguity due to habitats not realistically being available to the individual as well as reduce ambiguity relating to issues of biological significance. Home range is often used as the estimate of availability when measuring selection at Johnson's (1980) third order of selection, but the various methods of home range calculation can be prone to errors (White and Garrott

(1990). Furthermore, readily available software programs often produce different outputs even when calculating home ranges by the same methods (Rodgers et al. 1997). Despite these errors however, using home range as an estimate of availability at least attempts to use a biologically significant boundary within which to measure availability and eliminates considerable doubt as to whether habitats contained within the home range are available. Another approach to define availability is to circumscribe a buffer of a size reasonable for the time scale examined around animal locations. For example, Arthur et al. (1996) used the maximum distance bears were expected to travel between successive radio relocations and produced circular buffers with that radius around each radio-location to define availability for the next radio-location.

I advocate measurement of habitat use and availability at the individual level because of the reduction in ambiguity discussed above, as well as the greater flexibility in questions that can be addressed. Virtually any spatial and temporal scale can be accommodated when measuring habitat availability for individuals. For instance, maximum annual travel distance could be used to define habitat availability for selection of annual or seasonal home ranges, or, daily distance buffers could be used to define availability for daily site selection. Study area boundaries encompassing all animals within a study could possibly be used to examine daily activities of animals, but if the area is larger than the expected daily movements of animals, then obviously availability will be poorly defined. Generally, using study area boundaries to define common availability among all animals in the sample limits investigation to Johnson's (1980) second order of selection (Garshelis 2000). Conversely, measurement of habitat use and availability at the individual level does not preclude addressing questions at the population level because individual use and availability measurements can still be averaged to yield population-level inferences. Another option is the "scaling up" of individual measurements in some way that describes how a multitude of individual responses culminate into a population response.

McLean et al. (1998) claimed individual measurements of availability introduced "noise" and imprecision to tests of habitat preference. They made a 2-way comparison of 6 common preference tests using 4 different measures of habitat availability to Merriam's turkeys (*Meleagris gallopavo merriami*). The 4 measures of availability were defined by a common study area encompassing all animals within the study and a sequence of 3 sizes of buffers encircling turkey poult locations. Results were more consistent among tests and with assumptions of poult feeding habits using the common study area definition of availability than any of the individual-level estimates. However, these authors mixed scales by comparing habitat use by radio-location to availability defined by a common study area. They also failed to establish any biological significance whatsoever for selection of buffer sizes. While variability among individuals may introduce "noise" into tests using individual-level availability estimates, habitat selection is not expected to be similar across scales. Moreover, since it is unclear whether their buffer sizes matched selection behaviour at any particular scale, McLean's et al. (1998) comparisons between individual and study area-based availability cannot be considered valid. For example, chipmunks (*Tamias striatus*) were more discriminating in selection of microhabitats far from their burrows than they were near their burrows (Bowers 1995). Such differences in habitat selection would not be detectable using study area to define habitat availability and preference measurements obtained with availability so defined would certainly differ from measurements using a sequence of buffer sizes around chipmunk locations. Bowers (1995) encouraged analysis of spatial usage by individuals as an alternative to population-level analyses as a more mechanistic basis for interpreting use of habitats and space. Indeed, it would not be possible to investigate functional responses as per Mysterud and Ims (1998) or use the regression approaches taken in Chapter 3 if habitat use and availability were not measured at the individual level.

5.5 Proportional Data and Habitat Class Interrelationships

If fitness is predicated on choices made given the prevailing conditions and these are governed by the trade-off decisions that animals face, then we need to understand how these trade-offs are assessed and ultimately made before we can make any generalizations about habitat preferences and any fitness benefits those preferences might confer. Such understanding will require additional hypothesis testing to determine what habitat services given habitats provide and whether there are any intrinsic relationships among habitats in the provision of those services.

For instance, while preference for a habitat can be dependent on the availability of that habitat, it can also depend on the availability of others (i.e. preference for habitat A can depend on availability of B and/or C). These relationships are governed to an extent by simple mathematics as Aebischer et al. (1993) illustrated. Because the sum of proportions must equal 1, increased proportional use of one habitat class will necessarily reduce proportional use of one or more other habitat classes. The resultant use/availability ratios are thereby unduly influenced by this constraint. However, preferences might also be influenced by additional intrinsic relationships among habitat classes that are not accounted for by addressing the unit-sum constraint.

The ranking methods of Johnson (1980) and Aebischer et al. (1993) address the unit-sum constraint by indicating the likelihood of selection if all habitat classes were made equally available, as does the RSF method used in Chapter 2. However, it is not entirely clear whether the assumption that these methods represent likelihoods of selection if habitat classes were equally available is actually true, or if it is, whether interrelationships among the habitat classes influence preference beyond this correction. If the assumption were true and there were no other influences, the RSFs calculated in Chapter 2 should not have differed between zones because the set of habitat classes "offered" in each zone were the same, and the RSF technique was to account for differences among that habitat classes within zones. Since the RSFs were not the same, either the assertion that the RSF values represent the probabilities for selection if all habitat classes were offered on an equal basis (Manly et al 1993) is false, or, preferences among habitat classes within the set are influenced by relationships among each other in addition to the unit-sum constraint. Analysis of the data from Chapter 2 with the compositional approach of Aebischer et al. (1993) yielded the same dilemma since different ranks of habitat preference were observed between zones (Table 5.1). An example of the practical implications of this dilemma is the problem it poses for predicting population densities from RSF values. Boyce and McDonald (1999) claimed that if the distribution of animals among habitats in a baseline area was known by RSF value, the density of animals by habitat type could be estimated under the assumption that all habitat units are equally available. These estimates in turn could be used to predict the population density in another area if similar use patterns can be assumed to occur there.

The dilemma presented casts doubt that one or the other of these assumptions can be made. Therefore, such density predictions could not be made without first modeling the responses of RSF β-coefficients to changes in availability, as Boyce and McDonald (1999) suggested may be necessary.

Table 5.1. Preference ranks of moose among 9 habitat classes between 2 zones as determined by compositional analysis (sensu Aebischer et al. 1993).

Habitat Preference Ranks (most to least)	
Zone D	**Zone T**
Open Conifer Wetlands	Closed Conifer Wetlands
Closed Conifer Wetlands	Deciduous Uplands
Mixedwood Uplands	Mixedwood Uplands
Water	Disturbance
Shrublands	Water
Wetland Meadows	Shrublands
Deciduous Uplands	Coniferous Uplands
Coniferous Uplands	Open Conifer Wetlands
Disturbance	Wetland Meadows

Intrinsic relationships could include synergy, complimentarity, or substitutability among habitat classes or resources. Consider a human example of 2 lunch buffets (however meagre) consisting of proportions of bread, jelly, and mustard similar between tables, but differing in proportions of peanut butter and bologna. Since jelly is a compliment to peanut butter and mustard is a compliment to bologna, more mustard and less jelly will be consumed from the table serving with a larger relative proportion of bologna and a smaller proportion of peanut butter. Simply standardizing selection indices such that preferences can be ranked under apparent conditions of uniform availability will not account for the relationships mustard and jelly have to bologna and peanut butter.

Examination of correlations of use and availability among the habitat classes from the analysis in Chapter 3 indicated that some type of intrinsic relationships might have existed among the classes. Correlations between the use of **Deciduous Uplands** and **Open Conifer Wetlands** and the availability of each of the 4 habitats considered differed between zones (Table 5.2). In addition, there were significant correlations among availabilities of the 4 classes as one might expect with proportional data, but these were not the same between zones (Table 5.3).

Table 5.2. Correlation coefficients for multiple regressions of use of Deciduous Uplands (DU) and Open Conifer Wetlands (OCW) versus availability of DU, Mixedwood Uplands (MU), Closed Conifer Wetlands (CCW), and OCW within Zones D and T using MCP home range data.

	Used Habitat Class					
	Zone D			Zone T		
	DU[1]		OCW	DU		OCW
Available Habitat Class	Summer	Winter		Summer	Winter	
DU	-0.196	0.073	-0.498	0.927	0.814	0.392
MU	0.408	0.164	0.623	-0.843	-0.901	-0.329
CCW	-0.714	-0.133	-0.377	0.599	0.728	0.244
OCW	0.767	0.025	0.223	-0.614	-0.590	-0.299

[1] There were zone x season interactions affecting the use of DU, but not OCW, therefore OCW regressions were calculated with winter and summer data combined.

Table 5.3. Coefficients with associated *P*-values (parentheses) for correlations among habitat class availabilities within Zones D and T.

	Correlation Coefficients			
Availability Pair	Zone D		Zone T	
DU - MU	-0.699	(0.000)	-0.902	(0.000)
DU - CCW	0.236	(0.123)	0.568	(0.001)
DU - OCW	-0.131	(0.398)	-0.551	(0.001)
MU - CCW	-0.716	(0.000)	-0.795	(0.000)
MU - OCW	0.499	(0.001)	0.660	(0.000)
CCW - OCW	-0.948	(0.000)	-0.929	(0.000)

The strong negative correlation between use of **Deciduous Uplands** and availability of **Closed Conifer Wetlands** in Zone D during summer could indicate a level of substitutability between **Deciduous Uplands** and **Closed Conifer Wetlands**, which was not evident in Zone T. This substitutability was not likely based on food resources because those were scarce in **Closed Conifer Wetland** stands (Osko, unpublished data). Therefore another element common to these 2 classes probably formed the basis of the substitution. That use of **Deciduous Uplands** and availability of **Closed Conifer Wetlands** seemed unrelated in winter might indicate **Deciduous Uplands** were sought as a source of shade in summer as a substitute for shade provided by **Closed Conifer Wetlands**. **Deciduous Uplands** would not be as effective in mitigating thermal conditions in winter, therefore there was not a strong relationship between use of **Deciduous Uplands** and availability of **Closed Conifer Wetlands** during that season. Concurrent with the strong negative relationship between use of **Deciduous Uplands** and availability of **Closed Conifer Wetlands** during summer in Zone D, there was a positive relationship between use of **Deciduous Uplands** and availability of **Open Conifer Wetlands**. Availability of **Open Conifer Wetlands** might not have had any biological relationship with use of **Deciduous Uplands**, but its availability could have had an influence through its landscape dynamics with **Closed Conifer Wetlands** based on the strong negative relationship between availability of **Open Conifer Wetlands** and **Closed Conifer Wetlands** on the landscape. In other words, as the incidence of **Open Conifer Wetlands** on the landscape increased, **Closed Conifer Wetlands** decreased. As **Closed Conifer Wetlands** decreased, less shade was available and substitutes such as **Deciduous Uplands** were used, thus explaining the positive correlation between use of **Deciduous Uplands** and availability of **Open Conifer Wetlands** in Zone D during summer.

Similar interactions could explain use of **Deciduous Uplands** in response to availability of **Mixedwood Uplands**, **Closed Conifer Wetlands**, and **Open Conifer Wetlands** in Zone T. The strong negative correlations between use of **Deciduous Uplands** and availability of **Mixedwood Uplands** could indicate a strong substitutability, possibly based on food. Availability of **Mixedwood Uplands** had a strong negative correlation with availability of **Closed Conifer Wetlands**. Therefore, the relationship between use of **Deciduous Uplands** and availability of **Closed Conifer Wetlands** should be positive (which it was) because more **Closed Conifer Wetlands** on the landscape means less **Mixedwood Uplands**, which could have caused greater use of **Deciduous Uplands**. Similarly, the relationship between use of **Deciduous Uplands** and availability of **Open Conifer Wetlands** can be predicted by the landscape dynamics between **Mixedwood Uplands** and **Open Conifer Wetlands**. Availability of **Open Conifer Wetlands** and **Mixedwood Uplands** were positively related. As the proportion of **Open Conifer Wetlands** increased on the landscape, so did **Mixedwood Uplands**. Therefore, **Deciduous Uplands** use should be negatively correlated with availability of **Open Conifer Wetlands** (which it was).

While these inferences are obviously speculative, they serve to illustrate that perhaps correlations among habitat classes or resources should be exploited for their potential explanatory power even though a portion of the relationship might be explained by the unit-sum of habitat proportions. Exploring such interrelationships through appropriate hypothesis testing should provide better tools for predicting habitat use because the trade-off decisions facing animals will be better understood. More importantly, exploring these relationships will help elucidate the links between habitat use and population fitness. Defining the relationships among availability (and location) of habitat components and how these interact with habitat use is a prime example of the application of landscape ecology and should contribute to generation of better hypotheses and mechanistic understanding regarding habitat use.

5.6 Real World Consequences of Habitat Generalizations

Uncritically accepted dogma is a far greater barrier to progress than that which is simply not yet known (McCullough 1992). Obviously, not all habitat classes are equal in their capability to provide the life requisites a moose may require. Furthermore, some classes may provide multiple requisites while certain requisites might be acquirable from several different classes. As the relative abundance of habitat classes changes, animals likely make trade-off decisions in order to achieve their requisite goals. Acknowledging that trade-off decisions will occur should alert managers to the fact that preference indications will change with availability and that caution should be taken in making and accepting generalizations regarding wildlife-habitat relationships. However, ignoring the dynamic relationship between habitat use and availability and blindly applying generalized habitat relationships will lead to the waste of resources through ineffective habitat prescriptions, or worse, habitat prescriptions might actually be deleterious to wildlife.

A relevant example is the management of "Moose Zones" in northern Alberta to protect moose from the effects of industrial activities. Moose Zones were delineated by a Wildlife Habitat Committee formed by Alberta's Fish and Wildlife Division of the department of Sustainable Resource Development (SRD) during the late 1970s (G. Hamilton, pers. comm.). The areas identified as Moose Zones were selected because they were considered to be important wintering areas or areas of seasonal moose concentrations, following the literature assumptions of conifer cover in adjacency to food resources being essential to moose survival in winter. The areas delineated occur primarily within the major river valleys of northern Alberta, but include some other areas of upland habitat. Forest cover is predominantly mixed stands of trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) with balsam poplar (*Populus balsamifera*), white birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*) also occurring in the mix. Some pure stands of aspen and white spruce also occur. The purpose of the Moose Zones is to protect moose from energetically costly industrial disturbances during the critical winter period, as well as to reduce vulnerability of concentrations of moose to unregulated hunting. This is to be accomplished by limiting industrial activities within moose zones during critical periods, which may produce visual, auditory, or physical disturbances to moose or which may improve accessibility of moose to unregulated hunters. Restricted activities include timber harvest, bridge construction, stream crossings, gravel excavations, seismic activity, or any activity, that would normally require a permit from the Land and Forest Division of SRD (G. Hamilton, D. Lind, D. Moyles pers. comm.). Restrictions are in place from January 15 through April 30 in northwestern Alberta, and from February 15 through April 30 in northeastern Alberta. In addition to the different timing restrictions applied between regions of the province, specific limitations on many activities appear to be at the discretion of the local forest districts in which the activity is to occur. Moose zone locations and timing restriction periods were determined from "expert opinion" based on anecdotal observations by local biologists and literature reports of habitat utilization by moose (G. Hamilton, D. Moyles pers. comm.).

Given that Moose Zones were identified as important (if not critical) habitat for moose during a specific time of year and that restrictions in industrial activities within these areas occur during that time of year for the purpose moose conservation, moose would undoubtedly be expected to occupy these areas to a greater degree during the specified time period than during other periods. On the contrary however, I examined the occupation of Moose Zones by 8 of the moose described in Chapter 2 that included Moose Zone in their ranges and found that proportional occupation these areas was the least during the timing restriction period and the greatest during October and November (Fig. 5.1). These patterns were consistent with historic aerial surveys of river valley habitats that indicated surveys conducted in February and March often resulted in fewer counts than surveys in November and December (Lynch 1975). Recent aerial population surveys conducted in northeastern Alberta by SRD have also confirmed this pattern of river valley use (Floyd Kunnas, pers. comm.).

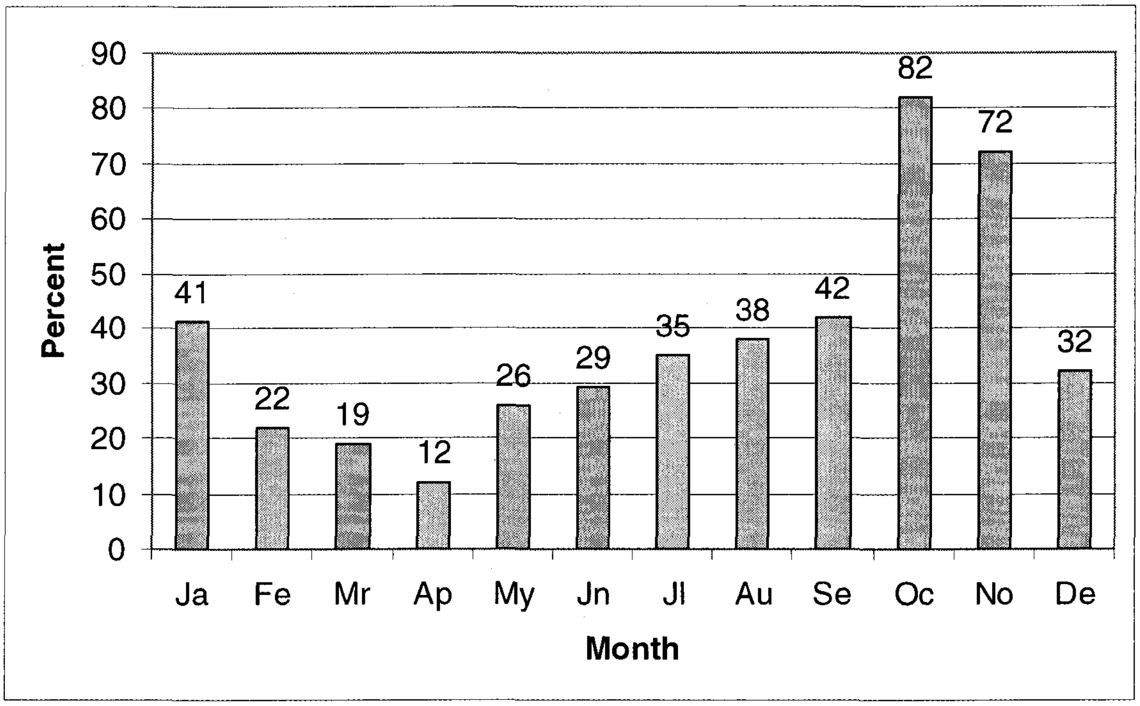

Fig. 5.1. Proportions of radio-locations occurring within river valley Moose Zones during each month (years 1995 and 1996) for 8 female moose whose ranges included river valley Moose Zones.

Furthermore, 26 of the 31 moose described in chapter 2 (including the 8 Moose Zone moose) also appeared to contradict conventional assumptions of late winter habitat selection by moose by abandoning upland forests and occupying relatively open lowland forests during the timing restriction periods. I classified the LANDSAT imagery for the study area into 2 classes, uplands and lowlands, based on the forest cover expected to occur on well-drained uplands versus lesser-drained lowlands. Uplands included areas forested by white spruce, aspen, balsam polar, balsam fir, birch, or jackpine (*Pinus banksiana*), while lowlands included black spruce (*Picea mariana*) or tamarack (*Larix laricina*) forests, willow (*Salix spp.*) dominated muskegs, or open muskegs. All 26 moose occupied upland forests in a temporal pattern very similar to the pattern of Moose Zone occupation by the 8 Moose Zone moose.

Finally, I compared the proportional monthly patterns of forest cover occupation I observed with patterns reported in 2 previous studies. The pattern I observed was similar to the pattern observed in a study conducted in the forested Bitumount area of northern Alberta (Hauge and Keith 1981), while Mytton and Keith (1981) observed a pattern more consistent with the prevailing literature in the more settled Rochester area of Alberta.

To my knowledge, the results of timing restrictions within Moose Zones in terms of moose population responses have never been monitored. It is quite likely that river valley and upland habitats are important to moose at differing times of year from region to region based on habitat use responses to varying landscape composition. Therefore a late winter timing restriction may be appropriate for other regions of the province. However, given that moose showed a low likelihood of occupying Moose Zones during this restriction period in northeastern Alberta, these habitats can hardly be described as critical during that time and managing them as such is pointless, needlessly impedes and adds costs to industry, and provides no real benefit to moose populations. Lack of monitoring precludes development of alternative plans that might actually achieve management goals for moose conservation because management remains blissfully ignorant yet self-satisfied with the results of their efforts.

5.7 Recommendations

5.7.1 Short-term:

Rather than continuing the fixation on habitat use and preference and their relationship to population fitness, perhaps wildlife management should take a more pragmatic approach that focuses less on habitat "ideals" and tries to assess and address what one or two factors might most influence a given population and allow that population to compete. The moose literature abounds with descriptions of habitat ideals for moose and how those ideals could be achieved by specialized timber harvest practices (Telfer 1974, Hamilton and Drysdale 1975, Peek et al. 1976, McNicol and Gilbert 1980, Euler 1981, Thompson and Vukelich 1981, Tomm et al. 1981, Monthey 1984, Allen et al. 1987, Forbes and Theberge, 1993), but concentration on those ideals can take attention away from some of the more fundamental factors that prevent achievement of population targets. For instance, the benefits of timber harvest in Alberta were perceived to be increases in big game numbers, but in reality, these perceptions merely arose from the fact that harvest of previously inaccessible existing game resources was enabled by the new forestry road infrastructure (Stelfox 1962). Similarly, timber harvest in Ontario patterned after the Lake Superior Moose Habitat Suitability Index (Allen et al. 1987) did not result in improved moose populations because the roading required to harvest in that manner made moose too accessible to hunters (Rempel et al. 1997). Wildlife managers should pick the "low hanging fruit" of factors that influence population fitness and address those factors that will return the most per unit of investment. Focusing on simple things like the forage production potential of forest successional stages and reducing the vulnerability of ungulates to harvest and harassment are likely to be more beneficial to wildlife and cost effective to managers than obsession with "critical" habitats (Cook et al. 1998).

For example, a pragmatic approach for addressing industrial activity within Alberta's Moose Zones described above might be to examine the conditions under which intervention would be beneficial and only apply interventions under those conditions. The rationale for enforcing timing restrictions appears to be predicated upon 4 primary criteria: that winters are severe enough to put moose at a substantial energetic disadvantage; that the mitigative effects of Moose Zone habitats are essential to moose survival or population productivity; that disturbance undermines the mitigative effects of those habitats considerably; and that moose aggregate within those habitats during timing restriction periods to take advantage of their mitigative effects. The essentialness of Moose Zone habitats to moose and the degree to which industrial activity interferes with the mitigative effects of those habitats are merely hypotheses that are yet to be proven. Assuming they are true however, the 2 remaining criteria are not likely to be met every year. Snow depths do not appreciably restrict moose movement at depths below 90 to 100 cm (DesMeules 1964, Kelsall 1969, Coady 1974, Schwab and Pitt 1991). The greatest accumulations of snow measured within open areas on Al-Pac's FMA during 1995/96 and 1996/97 (highest snowfall years during the past decade – Environment Canada, pers. comm.) was only 70 cm. And as illustrated previously, moose do not always occupy these areas during the specified time. If such is the case, then blanket enforcement of timing restrictions is meaningless, needlessly restricts activity, and wastes both government and corporate resources. A more practical, less expensive solution would be to monitor winter severity and moose occupation of areas in which activities are planned to take place, apply restrictions on an as needed basis, and monitor the results.

5.7.2 Intermediate-term:

It is time to unlearn many of things we assume to be true and bolster our pursuit for knowledge of what is simply not yet known. Both science and management must step back to reassess what we know or think we know and start challenging some of our ingrained assumptions about wildlife-habitat relationships. Much of what managers do is based on what they perceive to be critical or essential to the species they manage, but as seen here, many of those perceptions may be invalid and wildlife science has done little to challenge those assumptions. Strengthening the link between science and management by collaboratively placing more emphasis on hypothesis testing would improve both science and management. While science may never acquire complete knowledge, management will come up with the best models or plans based on whatever knowledge is available. Progress in wildlife management will only occur if wildlife scientists are more diligent in testing hypotheses rather than just generating them, and if wildlife managers can accept the limits of current knowledge, are more judicious in applying that knowledge, and embrace and implement new knowledge as it becomes available.

One mechanism for achieving such collaboration is active adaptive management, whereby management activities are conducted as experiments to test hypotheses (Sinclair 1991, Swanson and Franklin 1992). Management benefits from this approach because management does not have to wait for science to provide all the answers, yet it is provided with access to the best knowledge available in a most timely fashion. Science benefits because ample opportunities to test hypotheses in practical applications are provided, also in a timely fashion. The wildlife profession suffers from a backlog of untested principles that drive much of what it does. Many laws have been pronounced on the basis of induction and retroduction, but without testing by the hypothetico-deductive method, it is impossible to detect errors in those pronouncements (Romesburg 1981). Learning takes place in a feedback system where ideas and reality interplay and retroduction coupled with the hypothetico-deductive method presents such a feedback system (Romesburg 1981). The wildlife profession has generated many ideas and applied them, but has not been mindful of the feedback from reality. Active adaptive management provides practical opportunities to apply hypothetico-deductive methodology as a means to collect some of that feedback and test many of the ideas presently governing wildlife management practice.

Management of industrial activity within Moose Zones can again be used to illustrate the concept of active adaptive management. Once more, the essentialness of Moose Zone habitats to moose during late winter and the interference of industrial activity with habitat effectiveness are hypotheses in need of testing. Timing restrictions could be applied experimentally in certain areas within Moose Zones while not applied in others, provided the conditions of winter severity and moose occupation are met. Moose behaviour and population responses could then be measured to assess both the degree to which industry might interfere with habitat effectiveness, and whether such interference results in a population response. Management prescriptions would then be adjusted accordingly followed by further monitoring. Alternatively, simply monitoring moose occupation of Moose Zones over periods of varying winter severity could help to assess whether or not those habitats are essential to moose at all, and again, management prescriptions would be adjusted accordingly. The adaptive management approach is iterative where prescriptions are applied on the basis of hypotheses, and as these hypotheses are tested, new prescriptions are driven by the results of those tests and by new hypotheses that might be generated in the process. In the Moose Zone example, such a process might lead to abandonment of timing restrictions for industrial activities, to applying restrictions during a different time of the year, to applying restrictions to alternative habitats, or to discovery of some relationship that has a much more powerful effect on moose populations. It does not really matter what this iterative approach leads to specifically, other than the management prescriptions that arise are justifiable based on the reliability of information collected and that confidence in their ability to influence moose populations is enhanced.

5.7.3 Long-Term:

Future research should take a more mechanistic focus to understanding the relationships between habitat and wildlife. Achievement of this understanding will likely require examination of the habitat trade-offs animals face and how trade-off decisions are approached or made. I think this will require reduced obsession with habitat preferences and their perceived fitness benefits. If I had examined the habitat preferences of pine trees instead of moose I would have found that pine trees are predominantly found on sandy, xeric, low nutrient soils. Though it would appear that they " prefer" to grow there, they are not found there because that is where they grow best. Pines, like most tree species, grow best on moist, medium textured, nutrient rich soils but they predominantly occur on sandy soils because that is where they can compete (Oliver and Larson 1996). Perhaps rather than focusing on what animals prefer on the basis that what they prefer makes them more productive, we should simply look at where animals live and what allows them to live there. Returning to moose as a case study, the assumption that the best habitats will be the most densely occupied supports the notion that moose have a high dispersal tendency (Geist 1971, Waser and Jones 1983). Dispersal by moose has been demonstrated (Lynch 1976, Gasaway et al. 1980, Ballard et al. 1991) and such behaviour presumably occurs opportunistically to take advantage of favourable situations (Geist 1982) or to escape deteriorating conditions (Sweanor and Sandegren 1989). In this case, the only trade-off decision to be made is whether it is better to move on or better to remain a while longer. On the other hand, there is also considerable evidence that moose can be highly philopatric to their natal areas or to specific seasonal ranges (Cederlund et al. 1987, Sweanor and Sandegren 1988, 1989, Gasaway et al. 1989, Cederlund and Sand 1992) despite habitat deterioration (Andersen 1991). Productivity of moose philopatric to deteriorated habitat is reduced compared moose occupying superior habitat, but persistent populations are sustained nonetheless (Andersen 1991). Obviously, moose philopatric to poorer range will not have the same habitat choices as moose occupying better range and certain trade-off decisions regarding resource use will be forced upon them that moose in better ranges may never have to make. The fact that these populations persist indicates that individuals within them are making the correct decisions for use of the resources available. Mechanistic understanding should come from learning what the trade-offs are, what decisions are made, and why they are beneficial.

Pursuit of functional responses or regression techniques as an exploratory tool should aid in the examination of habitat trade-off decisions. Mysterud and Ims (1998) used functional responses to illustrate how trade-off decisions between food and cover habitats were made by gray squirrels (*Sciurus carolinensis*). Similar approaches could be taken to evaluate trade-offs between different food sources, or between foraging opportunities and intraspecific competition, or simply to explore some of the multivariable correlations between habitat classes like those discussed above. Functional responses might also be used to look for thresholds in habitat use or avoidance. For example, deciduous uplands are commonly thought to be preferred by moose (Krefting 1974, Nowlin 1976, Peek et al. 1976, Rounds 1981, Pierce and Peek 1984, Telfer 1988), but moose in Zone D avoided them where they were relatively scarce (Chapter 2). Perhaps below some threshold level of availability, it becomes inefficient for moose to seek these habitats out. Moose then adjust their selection strategies such that these habitats become avoided in deference to more abundant (though possibly lower quality) habitats simply because searching efficiency is increased. The regression of use versus availability for moose from both zones together supported the notion that such a threshold might exist (Chapter 3), which emphasizes the importance of observing habitat selection behaviour across a wide range of relative habitat abundance and habitat quality. Thresholds, asymptotes, or other inflections in functional responses will not be apparent if habitat use responses are only studied along a narrow range of availability. Obviously, understanding and applying rules such as these, if they exist, could prove fruitful in determining how certain trade-off decisions are made, and ultimately, in developing mechanistic predictive models of resource selection behavior.

5.8 Conclusion

I demonstrated that the habitat preferences of moose are not fixed, casting doubt on the widely accepted assumption that preferred habitats impart the most fitness. The wildlife profession must be prepared to challenge such assumptions as well as the many existing and new ideas relating to wildlife-habitat relationships that drive wildlife management practice. Many such ideas have been untested yet accepted as fact, leading to management practices that can be inappropriate, ineffective, or deleterious, not to mention wasteful of human and capital resources. Untested ideas and principles are far from useless information. However, this information would be much more powerful and beneficial to wildlife management if used to test hypotheses of how we perceive the world to work rather than used as hunches that seem to pan out often enough that we continue to use them. Greater collaboration between wildlife science and wildlife management in the generation and testing of ideas is a mechanism for expediting improvement in the reliability of wildlife knowledge and "unlearning what has been too readily accepted in the past."

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