

Benefits of using marginal opportunistic wildlife behavior data:

Constraints and applications across taxa – a
dominance hierarchy example relevant for wildlife
management



Diploma Thesis in Biology

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Summary

This study is a new approach on collecting, handling and examining wildlife behavior data across mammal species in order to provide new and unique conclusions from efficient data collection schemes.

Sophisticated dominance hierarchy patterns and the ability of individual recognition are well described in many large mammals such as monkeys and cetaceans through the effort of detailed long-term studies. Their implications are well known as important topics regarding management strategies, especially for endangered species. However worldwide, for other large mammals, e.g. bears, detailed long-term wildlife behavior studies are virtually not available.

This is due to the inaccessibility and inefficient observation abilities for many animal species in the wild, especially long-term studies. Up to now, it is believed that long-term studies are necessary to describe the existence of social structures like dominance hierarchies and individual perception abilities reliably and to present results in a sophisticated 'significant' manner.

To accomplish more detailed behavior investigations on species where we lack such long-term data, here a new approach to this discipline 'behavior modeling' is presented, concentrating on the use of marginal opportunistic samples. This statistical approach has never been conducted to behavior analysis so far.

Marginal behavior data for six species were investigated and compared: Howling monkeys (*Alouatta palliata*), Humpback whales (*Megaptera novaeangliae*), Muskoxen (*Ovibos moschatus*) and Spotted seals (*Phoca largha*) are described as social species through long-term data; Brown bears (*Ursus arctos*) and Polar bears (*Ursus maritimus*) are described to be non-social.

Algorithmic models are built to discover underlying pattern via 'data-mining' in short-term data which could not be sufficiently revealed otherwise and through traditional statistics usually used for behavior data analysis so far. Here fore, the program TreeNet is used due to its efficiency in uncovering underlying pattern, and its sufficient performance even when working with very limited data.

Results using these marginal data confirm that sociality exists across all four species, which have been described previously as social through the use of long-term data and revealing very

similar findings. These results confirm the applicability of the analytical approach as such. In the two bear species, described and managed as 'non-social animals' so far, very similar patterns of sociality and individual perception abilities were found. This supports that close similarities between monkeys, cetacean and bear species exist, what should force us to re-think some of the bear management strategies world-wide.

With implementing a new approach for behavior data analysis which one believed to be not sufficiently analysable so far, many new opportunities and perspectives looking at behavior studies and broader data are presented. Data investigating social traits in animals can be collected for many species world-wide and where no long-term studies are applicable, as the case for many endangered animal species. Further, already existing marginal data sets can now be re-investigated for underlying patterns.

It appears that global cooperation and data exchange plays a key role for future research and the forthcoming of wildlife management. This is supported here by providing thesis data-sets and results via globally available Metadata (NBII) online.

Zusammenfassung

Diese Studie stellt eine neue Herangehensweise zur Erhebung, Handhabung und Untersuchung von Wildtierverhaltensdaten über Säugetierarten dar, um neue und einzigartige Rückschlüsse von diesem effizienten Datenerhebungsmodell zuzulassen.

Gefestigte Dominanzhierarchiestrukturen und die Fähigkeit zur Individualerkennung sind ausführlich für Großsäugerarten wie Affen und Wale mit Hilfe von detaillierten Langzeitstudien beschrieben. Gerade für ein durchgreifendes und ‚artgerechtes‘ Management einer Tierart, besonders für gefährdete Tierarten, ist das Einbeziehen von Sozialität unabdingbar. Allerdings sind detaillierte Langzeit-Freilandstudien weltweit für viele andere Großsäuger, wie zum Beispiel Bärenarten, fast nicht existent.

Begründet wird diese Tatsache durch die schwierige Zugänglichkeit und durch schlechte Beobachtungsmöglichkeiten von vielen Tierarten im Freiland, vor allem über einen langen Zeitraum hinweg. Bisher wird angenommen, dass die Existenz sozialer Strukturen, wie Dominanzhierarchie und Individualerkennung, nur durch Langzeitstudien erfasst und statistisch überzeugend ‚signifikant‘ gezeigt werden könne.

Um detaillierte Verhaltensuntersuchungen bei Tierarten durchführen zu können, für die kein detailliertes Wissen über Sozialstrukturen vorliegt, wird in dieser Arbeit eine neue Datenerfassungs- und Auswertungsmethode ‚behavior sampling‘, basierend auf opportunistischen Kurzzeit-Verhaltensdaten, präsentiert. Dieser statistische Ansatz ist zuvor bei Verhaltensdaten auf diese Weise noch nie angewendet worden.

Von sechs Arten wurden Kurzzeit-Verhaltensdaten untersucht und vergleichend dargestellt: Brüllaffen (*Alouatta palliata*), Buckelwale (*Megaptera novaeangliae*), Moschusochsen (*Ovibos moschatus*) und Larcha-Robben (*Phoca largha*) werden in Langzeitstudien als soziale Tierarten dargestellt; Braunbären (*Ursus arctos*) und Eisbären (*Ursus maritimus*) sind bisher als nicht soziale Tierarten beschrieben.

Es werden algorithmische Modellierungen („data-mining“) zum Auffinden von Strukturen und Mustern in den Datensätzen verwendet, die durch bisher traditionell angewendete statistische Untersuchungen nicht aufgedeckt werden konnten. Hierfür wird das Programm TreeNet herangezogen, welches für das Auswerten von kleinen Datensätzen sowie das Aufdecken von Mustern in den Datensätzen besonders gut geeignet ist.

Ergebnisse dieser Kurzzeitdaten zeigen, dass sich alle vier Tierarten, die durch Langzeitstudien als sozial beschrieben sind, sozial verhalten. Sie weisen deutlich ähnliche Resultate zu Langzeitstudien auf. Hierdurch wird die Anwendbarkeit der analytischen Herangehensweise bestätigt. Des Weiteren wurden sehr ähnliche Muster des Sozialverhaltens sowie die Fähigkeit zur Individualerkennung auch bei den beiden als nicht sozial beschriebenen Bärenarten gefunden. Diese Ergebnisse unterstützen die Annahme der Existenz sehr ähnlicher Sozialstrukturen bei Affen-, Wal- und Bärenarten. Die Resultate sollten das Überdenken von Bärenmanagement-Strategien weltweit mit Nachdruck anregen.

Durch die Einführung eines neuen Ansatzes zur Analyse von Verhaltensdaten, welche bisher als nicht hinreichend analysierbar galten, können viele neue Möglichkeiten und Perspektiven zur Herangehensweise an die Auswertung von Verhaltens- und weiterreichenden Daten möglich gemacht werden. Daten, welche soziale Verhaltensweisen bei Tieren untersuchen, könnten für viele Arten und weltweit erhoben werden, ebenso dort, wo Langzeitstudien nicht mehr anwendbar sind, was auf viele bedrohte Tierarten zutrifft. Ebenso können bereits existierende Kurzzeitdatensätze rückwirkend auf bestimmte Muster überprüft werden.

Globale Kooperationen und Datenaustausch spielen für zukünftige Forschung und das Weiterkommen des Wildtiermanagements eine wichtige Rolle. Aufgrund dieser Tatsache werden alle Daten, auf denen diese Arbeit basiert, global und online als Metadaten (NBII) zur Verfügung gestellt.

1 Introduction

1.1 Social Structure - Why it Matters

Under what circumstances is it important for animal species to have a social structure; how do social structure and individual perception relate to each other, and why does it matter in the first place? Why and especially when does evolution select for social structure in a certain species, and how does this species increase its survival due to being social? These are crucial questions for real-world wildlife management applications which behavior research attempts to address and answer.

So far these questions have only been answered for few species. There are still many gaps to fill due to the believe that long-term data is crucial to reach conclusive results (INSLEY *et al.* 2003). Thus, the main problem occurring across most behavior studies is the actual global availability of long-term data. This 'culture' might well pre-clude us from new investigations and finding knowledge, or an improved management. In this thesis, a new approach using opportunistic marginal behavior data, as achievable in the wild for most situations and across most species, is pursued. Such an approach can help to bring the knowledge of animal behavior research a step forward and make short-term behavior data usable. In the following, questions on sociality, dominance hierarchy and the ability of individual perception in six higher mammal species are investigated.

Described already since the 19th century (DARWIN 1858), behavior evolved out of the evolutionary approach: The ability to survive and to pass on genes is the main goal in individual's survival. While competing to access the best resources available (survival of the fittest), such as food, mates and habitat, individuals within one population have to interact. Individual interaction is among the most survival-efficient way to optimize resources. When animals congregate over a certain time of the year or all year round, they tend to develop a well-evolved social structure (group living: VAN LAWICK-GOODALL 1973; MCGREW *et al.* 1996; MANN *et al.* 2000; ALCOCK 2001; WILLIAMS *et al.* 2002; STOINSKI *et al.* 2003); (congregations: PARRISH and HAMNER 1997; MANN *et al.* 2000). Sophisticated interactions between animals, and therefore behavior traits, play a crucial role for individual and kinship survival (CLEMMONS and BUCHHOLZ 1997; GADAGKAR 1997; STOEN *et al.* 2005).

What is 'social'? How must an individual behave to be 'social'? When does a 'social structure' exist in a population? These concepts are not that easy to define consistently and often there is no clearcut definition. New attempts to discuss and explain this 'dilemma' are carried out. In the following, a short overview on relevant definitions and their interpretation is given:

“Sociality to me is the study of choices in social relations.

It explores the motivations to take actions, examines what choices are available (perceived or real) in relations, and studies the consequences of such choices.

Therefore, central to sociology is the analysis of both, action and structure: choice behaviors in the context of structural opportunities and constraints”

(LIN 2001).

Lin (2001) describes actors being motivated by instrumental or expressive needs to engage other actors in order to access these other actors' resources for the purpose of gaining better outcomes. Conclusively, it is reasonable to assume that choice actions lead to social structure. Therefore, the dominance status of an individual maintains a central role in sociality. The concept of dominance can be understood as: one or both of the interacting animals express dominant behavior towards each other. The dominance receiving individual either indicates subordinate behavior to prevent collision, or avoids the dominant acting animal. Definitions and the concept of dominance are wide-ranging. Drews (1993) summarizes this fact:

“The concept of dominance has contributed greatly to our understanding of social structure in animals. Over the past three decades, however, a variety of concepts and definitions of dominance have been introduced, leading to an ongoing debate about the usefulness and meaning of the concept. Criticisms aimed at one definition of dominance do not necessarily apply to other definitions. Existing definitions can be structural or functional, refer to roles or to agonistic behavior, regard dominance as a property of individuals or as an attribute of dyadic encounters, concentrate on aggression or on the lack of it, and be based either on theoretical constructs or on observable behavior.”

Looking at congregations where sociality and dominance occur, in the literature the well-known term 'societies' stands out. A society is a number of individuals united together by mutual consent, in order to deliberate, determine, and act jointly for some common purpose. Again, we find reproductive success described as the main interest in building societies:

“How can one account for intra- and inter-specific variability in partitioning of reproduction? This is one of the most intriguing problems in the study of social behavior, and understanding the factors underlying this variability is one of the keys to understanding the properties of complex animal societies” (KELLER and REEVE 1994).

Keller and Reeve (1994) describe reproductive success and the apportionment of breeding and upbringing among individuals being the key feature to define cooperative animal societies. The opinion that in the evolution of animal societies, selection has promoted efficiency through division of labor, is widely shared by other researchers (SENDOVA-FRANKS and FRANKS 1999; ANDERSON and FRANKS 2001). This is especially true for group hunting insects and mammals, as wolves (*Canis lupus*) and lions (*Panthera leo*) for instance.

The evolution of cooperation can occur in several ways, such as repeated interactions with the same individuals (TRIVERS 1971; AXELROD 1984) or through haplodiploidy and increased relatedness between cooperating individuals (BOURKE and FRANKS 1995). Either way, the results are cooperative, functional and adaptive assemblages. Unfortunately, however, there are few unambiguous ways to measure and rigorously compare the degree of behavioral coordination in different animal societies (ANDERSON and FRANKS 2001). The same is the case for showing the ability to individual perception in species. A very basic definition of individual recognition is given by Insley *et al.* (2003):

“differential treatment of an individual by other individuals based on individually distinctive cues”.

The existence of societies is widely described and widespread across vertebrate and even invertebrate species. It ranges from insects, which provide a bewildering variety of forms, ergonomic organization, and social complexity (CHAUVIN 1968; BOURKE and FRANKS 1995; GADAGKAR 1997; BOURKE 1999; ANDERSON and MCSHEA 2001) over birds (PARRISH and HAMNER 1997) continues with large mammals such as proboscidea (elephants), primates and cetaceans (dolphins, porpoises and whales) (CHAUVIN 1968; SMUTS *et al.* 1987; MCGREW *et al.* 1996; GADAGKAR 1997; MANN *et al.* 2000).

Conclusively, all attempts to explain the evolution and existence of sociality, dominance and societies, rely on the evolutionary concept described inherently as selfish individual actions, focusing primarily on the above described resources: food, mates and habitat (PARRISH and HAMNER 1997; ALCOCK 2001). Understanding how environmental variation affects social structure is a major concern in conservation management and its study will help to implement more effective management plans (KOMDEUR and DEERENBERG 1997). Surprisingly, the traditional wildlife and game research is often lacking detailed knowledge on sociality as well as animal societies. De Waal and Tyack (2003) make clear that more attention should be paid to social complexity in carnivores and for an improved management. In times of intense environmental change, vaster knowledge of sociality is required to effectively manage species of which a complex social structure can be assumed.

1.2 Social Structure and Dominance Hierarchy in Higher Mammals

1.2.1 Overview

For some large mammals, the occurrence of very sophisticated behavior interactions and networks is convincingly described through long-term data studies (KREBS and DAVIES 1987; ALCOCK 2001). It is especially well studied in primates (VAN LAWICK-GOODALL 1973; SMUTS *et al.* 1987; MCGREW *et al.* 1996) and cetaceans (BROWN *et al.* 1995; MANN *et al.* 2000; BRUNO *et al.* 2004).

So far, most research on social structures was implemented due to animals being either approachable in the wild or due to the interest in species which have a genetic closeness to humans, mainly monkey and ape species (VAN LAWICK-GOODALL 1973; WILLIAMS *et al.* 2002; STOINSKI *et al.* 2003). Findings from such studies were summarized and introduced to the public by Smuts *et al.* (1987) in 'Primate Societies' and by Mc Grew *et al.* (1996) in 'Great Ape Societies' for instance. Recently, with the advent of sophisticated research equipment, surprisingly detailed social patterns as described in primates were found in cetacean species published as 'Cetacean Societies' by Mann *et al.* (2000). Many other marine mammals such as pinnipeds have recently been found showing pattern of sociality and individual recognition (INSLEY *et al.* 2003).

In many higher order species there is a widely acknowledged lack of information on social structure, mainly due to the inaccessibility of long-term data (INSLEY *et al.* 2003). It seems reasonable to assume possible social structures for many more mammalian species which have not yet been subjected to broad behavioral research.

This lack of quantitative and detailed behavior information on animal species poses problems to professional management practice. Management implications for animals with a dominance hierarchy and with the ability of individual perception are very different than for species lacking these social traits. For example, European researchers found recently a correlation between kinship and female home range overlap in Scandinavian brown bears (*Ursus arctos*) (STOEN *et al.* 2005) as well as infanticide caused through new intruding males (SWENSON *et al.* 1997; BELLEMAIN *et al.* 2006). On the other hand, Canadian and American researchers have not found kinship patterns and focused infanticide through new intruding males (MCLELLAN and HOVEY 2001; MILLER *et al.* 2003; MC LELLAN 2005).

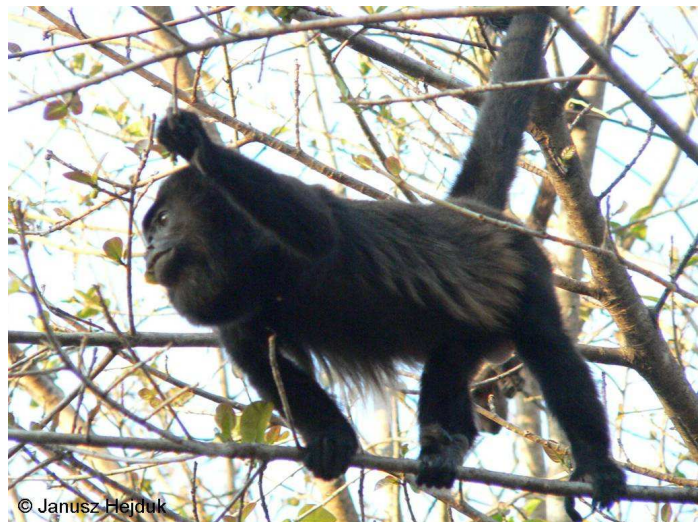
Further, in polar bears, virtually no social structure or ability of individual perception has been described so far either. For polar bears only few studies exist that deal with social topics. Indeed these studies suggest, but don't directly show, that a high sociality could exist (STIRLING 1974; LATOUR 1980; WATERMAN and ROTH 2002; OVSYANIKOV 2005). Better investigated are the social and kinship relations in the third North American bear species, the black bear (*Ursus americanus*). For instance Terry De Bruyn (1999) spent intimate field time with three generations of moms and cubs and Benjamin Kilham (2002) and Steven Stringham (2002) raised orphaned black bear cubs. Their studies provided a strong baseline for the social behavior traits observable in bears. It can already be concluded that bears seem to interact socially far more than ever expected (KILHAM and GRAY 2002; STENHOUSE *et al.* 2005).

In this study, correlations of dominance such as proximity, vocalizations, approach retreat, displacement, as well as overt indicators of dominance including fighting, are examined. This is done to determine whether or not a dominance hierarchy is maintained in all investigated species (howling monkeys, humpback whales, brown bears polar bears, spotted seals, and muskoxen). A justification for using these species is given in the following.

1.2.2 Howling Monkeys (*Alouatta palliata*)

Table 1.1 Howling monkey classification (ITIS 2008)

Kingdom	<i>Animalia</i>
Phylum	<i>Chordata</i>
Subphylum	<i>Vertebrata</i>
Class	<i>Mammalia</i>
Subclass	<i>Theria</i>
Infraclass	<i>Eutheria</i>
Order	<i>Primates</i>
Family	<i>Cebidae</i>
Subfamily	<i>Alouattinae</i>
Genus	<i>Alouatta</i>
Species	<i>Alouatta palliata</i>



Picture 1 Howling monkey

Howling monkeys constitute the largest new world monkey species and are found throughout South and Middle America (KINZEY 1986). These arboreal folivore monkeys have been studied for decades (MILTON 1980; GLANDER 1992) and are, as most other primate species, widely described as social animals. Mantled howling monkeys are, as most primates, engaged in numerous activities such as grooming and playing that confirm their social structure. Howlers

form consistently large, stable social groups composed of several adult males and several adult females. The persistence of these strong male-male and male-female partner preferences in mantled howlers helps to explain the stability of relatively large multimale-multifemale groups observed across populations (DIAS and LUNA 2006; BEZANSON *et al.* 2007). Males are usually dominant over females. Both, male and female juveniles can leave their natal troops to join a new group. Upon joining a new group, a new dominance rank is attained (GLANDER 1992).

Howlers are well known to maintain their social structures through dominance hierarchies. A dominance hierarchy in howlers is defined as a “*social ranking within a group, having an influence in social integration and peaceful coexistence in the group*” by De Waal (1987). Dominance is important for howling monkey survival (GLANDER 1992).

Dominance rank confers certain advantages and assures access to resources such as food and mates. Subordinate individuals usually give way to others, often even conceding useful resources to others without a fight. A males' position in a dominance hierarchy is important for non-seasonal breeders, such as howling monkeys, because alpha males sire all, or almost all, of the infants in the group (PAUL 1997). Therefore sperm competition is also affected by dominance (DUNBAR and COWLISHAW 1992; STRIER 2003). Dominance hierarchies are often reinforced by aggression, are dynamic, and may change over time (JURMAIN *et al.* 2004).

Different types of social structures exist across animal species. Fission-fusion structured social systems were so far thought to be restricted to primates as ateles (spider monkeys) and pan (chimpanzees) (MCFARLAND SYMINGTON 1990; FEDIGAN and JACK 2001). Nevertheless, Dias and Luna (2006) as well as Bezanson *et al.* (2007) describe the existence of fission-fusion structure in mantled howling monkeys. Flexible grouping patterns do occur.

Although all subadult individuals are described to leave their natal groups, and thus kinship has not believed to play any crucial role in hierarchy structures and social associations, kinship still is a major determinant of individual association preference in howler males (DIAS and LUNA 2006).

In the Ometepe howling monkey population, Benzanson *et al.* (2007) found different subgroups. They conducted research for partner preferences and patterns of spatial association. Their data indicate that Ometepe howler groups are fragmented into subgroups of 1-20, averaging five to six individuals. Subgroup size and membership reflect individual patterns of social affiliation and social tolerance.

1.2.3 Humpback Whales (*Megaptera novaeangliae*)

Table 1.2 Humpback whale classification (ITIS 2008)

Kingdom	<i>Animalia</i>
Phylum	<i>Chordata</i>
Subphylum	<i>Vertebrata</i>
Class	<i>Mammalia</i>
Subclass	<i>Theria</i>
Infraclass	<i>Eutheria</i>
Order	<i>Cetacea</i>
Suborder	<i>Mysticeti</i>
Family	<i>Balaenopteridae</i>
Genus	<i>Megaptera</i>
Species	<i>Megaptera novaeangliae</i>



Picture 2 Humpback whale

The life-cycle of the humpback whale shows marked seasonal contrast in geographic distribution and behavior. The humpback whale inhabits all oceans being distributed cosmopolitan. The species breeding grounds are located in low latitude areas in winter. They migrate to their feeding grounds in high latitude waters in summer (CHAPMAN 1974). This baleen whale species is described as only feeding throughout summer, occasionally starting during migration. Humpback whales are generalized feeders, being highly mobile and opportunistic. They feed upon plankton as well as large fish swarms (READ *et al.* 2008). Global information on the specie's distribution and available online data is presented in the Ocean Biogeographic Information System (OBIS) (READ *et al.* 2008). Humpback whales are long-lived, slow breeding animals. A reversed sexual dimorphism is described with females being slightly larger than males (CLAPHAM 1996; LALIME 2005). For further species and ecological background information see Lalime (2005), Vang (2002); and Baker *et al.* (1986) for population structure in the North Pacific.

Humpback whales are found in dense aggregations on shallow banks during their breeding season in the tropics. There is no direct evidence of territoriality. Seasonal returns to the same feeding and breeding grounds of most humpbacks are registered (WEINRICH 1998; KURLANSKY 2000).

Observations of migratory movement by marked individuals suggest that humpback whales form relatively discrete subpopulations for periods of time. These subpopulations are not separated by obvious geographic barriers, thus why they form is not completely understood.

Altogether, the social status of cetaceans is well developed and described as showing striking convergence to primates (MARINO 2002). Especially toothed whales have complex family structures and groups which they live and hunt with through their whole life. Strong and longterm associations exist between transient individuals in Orcas for example (BAIRD and WHITEHEAD 2000). The baleen species are thought of being less social where the Humpback whale is believed to be an exception (VALSECCHI *et al.* 2002). Many social displays ranging from underwater bubble net feeding and vocalisations to above surface activities and displays as breaching, flipper- and tail-slapping, are described in humpbacks (SILBER 1986; LALIME 2005).

During migration humpback whales can be observed mostly travelling in small groups of 2 to 4 animals and rarely appears to travel alone. In summer feeding regions they are described to hunt together in groups. During winter they form groups up to 20 individuals with one single female as core of the group, surrounded by escorting males (CLAPHAM *et al.* 1992). In winter breeding grounds, aggressive behavior between males is observed regularly (SILBER 1986; SPITZ *et al.* 2002).

Still discussed is the mating system in humpback whales due to a lack of information and understanding. It is believed to be a mixture of leks and a male-dominance polygyny as it is similar and at the same time sufficiently different to both of these mating systems. Therefore, Clapham (1996) proposes the mating system term 'floating-lek' for humpbacks.

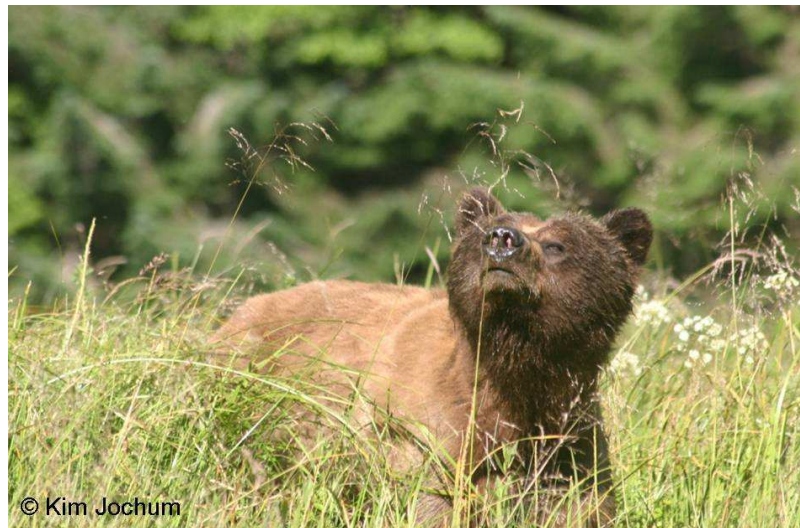
The social system in humpback whales has not yet been differentiated clearly either. Kin relation seems not to play a role in group formations (VALSECCHI *et al.* 2002). Over the last 10 years the term 'fission-fusion' system is used more regularly. Clapham (CLAPHAM 1996) already states the small group characteristic in humpbacks depending on the absence of predation, the patchy mobile nature of most prey, the absence of territoriality and the minimal importance of kinship in groupings at the summer feeding grounds. Valsecchi (2002) describes the fission-fusion nature in humpback whale societies being characterized by small, unstable groups existing during feeding as well as during breeding seasons. The social fission-fusion structure in humpback whales is very similar to the one regularly described in spider monkeys, chimpanzees and humans (MARINO 2002).

Due to the importance of communication in social animals, vocal communication abilities play a key role. Most marine mammals, especially humpback whales, are highly vocal. Significant differences in humpback songs are described between isolated ocean basins. Only small differences occur within an oceanic population showing small annual changes in song organization (WINN *et al.* 1981). Playback experiments carried out by Tyack (1983) support the conclusion that the songs and social sounds of humpback whales mediate the responses of approach or avoidance that humpback whales make to singing whales or large groups in which aggressive behavior is occurring. These so called 'social songs', mainly uttered during breeding season, are believed to function in male social ordering, (SILBER 1986; DARLING and BÉRUBÉ 2001), also named dominance hierarchy. The establishment of a temporary social dominance in groups of males is suspected by Silber (SILBER 1986).

1.2.4 Brown Bears (*Ursus arctos*)

Table 1.3 Brown bear classification (ITIS 2008)

Kingdom	<i>Animalia</i>
Phylum	<i>Chordata</i>
Subphylum	<i>Vertebrata</i>
Class	<i>Mammalia</i>
Subclass	<i>Theria</i>
Infraclass	<i>Eutheria</i>
Order	<i>Carnivora</i>
Suborder	<i>Caniformia</i>
Family	<i>Ursidae</i>
Genus	<i>Ursus</i>
Species	<i>Ursus arctos</i>



Picture 3 Brown bear

Brown bears occupy a variety of habitats, from desert edges to high mountain forests and ice fields (DEWEY and BALLENGER 2002). They are distributed throughout North America and Eurasia, occurring widely across western Canada and Alaska. In the US, brown bears are considerably declining (BROWN 1993). This omnivorous bear species is highly opportunistic, consuming virtually anything, however preferences and seasonal needs exist. Their preferred food sources are salmon (*Oncorhynchus spec.*), berries (*Vaccinium spec.*), vertebrates, foliage and roots depending on seasonal availability and accessibility (BROWN 1993; RUSSEL and ENNS 2004). For detailed habitat and ecological descriptions of brown bears see Brown (1993) and Clark *et al.* (1999); also Graeber (2006) for spatial distributions.

Especially in American research the description of social characteristics of brown bears is rare. The following statements are usually made throughout the bear literature: Bears are solitary (EGBERT and STOKES 1976; MCLELLAN and HOVEY 2001; STOEN *et al.* 2005) and they are feared predators (SNYDER 2003; ETLING 2004). Also, similar beliefs towards brown bears in Europe are still high (BREITENMOSER 1998; RØSKAFT *et al.* 2003).

However, bears may sometimes gather in large numbers at major food sources, and they interact showing complex ways of interaction. Under these conditions, dominance hierarchies are formed and maintained with aggressive actions. Highest-ranking individuals are large adult males but the most aggressive bears are usually females with young. Least aggressive and lowest-ranking are usually subadults. The only social bonds stated to be formed are between females and their offspring (DEWEY and BALLENGER 2002; GENDE and QUINN 2004).

Over the last ten years, social traits are increasingly found and described in brown bears because of improved data due to the forthcoming GPS transmitting technique and genetic analysis throughout wildlife populations. Brown bears maintain home ranges which greatly overlap across conspecifics of both sexes, but are non-territorial (MACE and WALLER 1997; MCLELLAN and HOVEY 2001; DAHLE and SWENSON 2003; BELLEMAIN *et al.* 2006). Females are described to mate promiscuously, showing an overall mating system of males mating with multiple females and females mating with multiple males (MC LELLAN 2005; BELLEMAIN *et al.* 2006).

Recently, European researchers found somewhat unexpected social relations in the Scandinavian brown bear. They described a correlation between kinship and female home range overlap (STOEN *et al.* 2005) as well as infanticide caused by new intruding males (SWENSON *et al.* 1997; BELLEMAIN *et al.* 2006). For Canada on the other hand, none of these kinship patterns as well as no infanticide caused by new intruding males is described in the peer-reviewed literature so far (MCLELLAN and HOVEY 2001; MC LELLAN 2005).

Nevertheless, Canadian researchers (e.g. STENHOUSE *et al.* 2005) suggest that grizzly bears can spend a considerable amount of time interacting with conspecifics. They state further that *“behavioral interactions between grizzly bears are more complicated than we understand”*.

Currently, only very few long-term studies on free-ranging bears exist, or are freely available. These either focus on single families (DEBRUYN 1999) or cubs from one litter (STRINGHAM 2002; RUSSEL and ENNS 2003; 2004). Population-oriented bear behavior research is still rare to find and just starts to be conducted (SWENSON *et al.* 1997; GENDE and QUINN 2004; FISCHBACH and

REYNOLDS 2005; STOEN *et al.* 2005). Stoen *et al.* (2005) states that the lack of long-term studies in solitary species might explain variation in findings concerning relatedness and proximity.

Due to the fact that bears are hard to access, the lacking public availability of data, such as telemetry, for a public assessment has harmed a wider review, analysis and eventually progress on this issue though (HUETTMANN 2005).

Concerning movement patterns and possible territoriality in brown bears, seasonal changes are found with generally male territories being larger than female territories. Nagy and Haroldson (1990) suggest that male brown bears, which have very large breeding-season ranges, reduce their movements after the breeding season in order to maximize nutritional intake. Further Swenson *et al.* (1997) describes that expansive movements of male brown bears create the lead wave in population expansions. This could explain the more vulnerable status of adult male bears to hunting and other human-caused mortality factors (AMSTRUP, DURNER *et al.* 2001).

1.2.5 Polar Bears (*Ursus maritimus*)

Table 1.4 Polar bear classification (ITIS 2008)

Kingdom	<i>Animalia</i>
Phylum	<i>Chordata</i>
Subphylum	<i>Vertebrata</i>
Class	<i>Mammalia</i>
Subclass	<i>Theria</i>
Infraclass	<i>Eutheria</i>
Order	<i>Carnivora</i>
Suborder	<i>Caniformia</i>
Family	<i>Ursidae</i>
Genus	<i>Ursus</i>
Species	<i>Ursus maritimus</i>



Picture 4 Polar bear

Polar bears are distributed across the circumpolar Arctic. Officially, they are split in 19 populations (IUCN/SSC 1998). Polar bears are omnivores, but they feed in the wild throughout their range predominantly on ringed seals (*Phoca hispida*) and to a lesser degree on bearded seals (*Erignathus barbatus*) (STIRLING and ARCHIBALD 1977; SMITH 1980). Seals are the only accessible and approachable prey for polar bears that can saturate polar bears energy intake needs. They have high energetic demands due to living in the high Arctic on the sea ice,

especially females to still be capable to reproduce. In particular in southern populations, where seals are unavailable during open water season, they represent a high caloric return per unit of energy during fasting (STIRLING *et al.* 1999; AMSTRUP *et al.* 2000). Global information on the specie's distribution and available online data is available from the Ocean Biogeographic Information System (OBIS) (READ *et al.* 2008)

Polar bears are at the top of the Arctic food chain and gained the status of the representative indicator species for human-induced global warming over the last years (GOUGH and WOLFE 2001; LUNN and STIRLING 2001).

Adaptive management discussions and expert statements on the polar bears' future are, so far, widely based on population estimates through mark-capture-recapture and bear movement patterns (AMSTRUP *et al.* 2000; AMSTRUP, McDONALD *et al.* 2001; PARKS *et al.* 2006). This determines the research agenda and limits current knowledge. For instance, telemetry studies can only be conducted on females.

Worldwide, a major lack of knowledge on polar bear behavior exists (PAETKAU *et al.* 1995; WATERMAN and ROTH 2002). Most behavior research that has been conducted on the world's polar bear populations, so far, focuses on the impact of tourism on polar bears (ECKHARDT 2000; WATERMAN and ROTH 2002; DYCK and BAYDACK 2003; DALEY 2007). Only few initial studies were carried out dealing with additional behavior focuses; two earlier Canadian studies (STIRLING 1974; LATOUR 1980) and one recently published Russian study (OVSYANIKOV 2005).

The first published approach to describe basic behavior patterns in polar bears was probably carried out by Stirling (1974). He describes that 'meetings' between unrelated polar bear individuals would be uncommon. The polar bears sense of vision appears to be poor but their sense of smell is acute. They constantly gain information of their surroundings through licking air supporting their sense of smell (OVSYANIKOV 2005). Therefore, most potential encounters of bears can be avoided. Stirling further observed adult bears and family groups passing each other very closely without any overt sign of aggressive behavior or fast movement. Adult females with cubs were observed to pass other family groups or adult males with a distance of up to 150m and adult males passing adult males were found up to 30m close with the described low reaction response. Stirling (1974) states that the simple visible effect of relative size is probably sufficient enough to determine dominance when bears are clearly visible to each other. Adult females as well as adult males have always been observed being dominant over subadults, e.g. displacing them from feeding sites. Adult males are not necessarily dominant over females with cubs (STIRLING 1974).

Nikita Ovsyanikov mainly studies polar bears in coastal congregations during fall when waiting for the ice to form. He observed behaviors in polar bears which disagree already with the conventional view of polar bears being solitary predator. In the absence of food, many individuals gather in a relatively small area. They permanently meet, and therefore have to regulate their social relations steadily (OVSYANIKOV 2005). The congregations of polar bears during the ice free period on Hudson Bay are suggested to have the meaning of a socialisation period using this non-competitive time in their annual cycle to assess position in the hierarchy structure of the population (LATOUR 1980). During the limited hunting and mating season just a minimal amount of time is spent on social interactions and behavior displays (STIRLING 1974; LATOUR 1980).

1.2.6 Spotted Seals (*Phoca largha*)

Table 1.5 Spotted seal classification (ITIS 2008)

Kingdom	<i>Animalia</i>
Phylum	<i>Chordata</i>
Subphylum	<i>Vertebrata</i>
Class	<i>Mammalia</i>
Subclass	<i>Theria</i>
Infraclass	<i>Eutheria</i>
Order	<i>Carnivora</i>
Suborder	<i>Caniformia</i>
Family	<i>Phocidae</i>
Genus	<i>Phoca</i>
Species	<i>Phoca largha</i>



© Lloyd Lowry / Kathy Frost (Alaska Department of Fish and Game)

Picture 5 Spotted seal

Areas inhabited by spotted seals are found along the continental shelves of the North Pacific Ocean, Bering Sea and on the ice flows of the Beaufort, Chukchi, and Okhotsk Seas. They migrate as far south as the northern parts of the Huanghai, and the western Sea of Japan (SHAUGHNESSY and FAY 1977; LOWRY *et al.* 1994). Similar to polar bears, spotted seals are also strongly associated with sea ice. During summer they gather around the remaining ice packs and on land when no ice is available (SHAUGHNESSY and FAY 1977). Spotted seals are sociable ice-breeding animals and can form large groups (LOWRY 1984). For further ecological background information see (LOWRY 1984; LOWRY *et al.* 1994; READ *et al.* 2008). Global information on the specie's distribution and available online data can be accessed at the Ocean Biogeographic Information System (OBIS) (READ *et al.* 2008)

Research on spotted seals with a population oriented focus has rarely been conducted so far (LOWRY *et al.* 1998). In phocids (seals), in contrast to otariids (fur seals and sea lions), generally neither stable aquatic territories nor harems where females aggregate are developed. This is the case due to their high level of mobility and due to living in a boundary-less, three-dimensional medium with unstable sea ice conditions (BARTHOLOMEW 1970; STIRLING 1975). *Phoca largha* is one of the rare pinniped species described as living in a monogamy mating system (BURNS *et al.* 1972; BURNS 1978).

Individual recognition is found to be widespread in pinniped species, at least between mothers and offspring. Otarrid pinnipeds congregate for pupping and are therefore believed to have better mother offspring recognition abilities developed than ice-breeding phocids (INSLEY *et al.* 2003). But even less common adoption has been observed in spotted seals, compared to otarrid species, predicting well developed offspring recognition abilities (BURNS *et al.* 1972). Further it is suggested that permanent vocal auditory imprinting occurs, demonstrating the potential in pinniped species to complex interactions over long periods of time (INSLEY *et al.* 2003).

Male-male recognition is reported to exist in elephant seals (*Mirounga grey*) and other otariid pinnipeds. The ability of male-male recognition is believed to play a crucial role in dominance relationships. Most ice-breeding phocids engage in complex underwater vocal and visual displays. These are believed to act as advertisement of individual fitness for females (CLEATOR *et al.* 1989; ROGERS *et al.* 1996).

Altogether, individual recognition in pinnipeds has not been thoroughly tested in any sensory modality apart from the acoustic mode. Visual, olfactory and spatial cues used in recognition are believed to play a crucial role (INSLEY *et al.* 2003).

1.2.7 Muskoxen (*Ovibos moschatus*)

Table 1.6 Muskox classification (ITIS 2008)

Kingdom	<i>Animalia</i>
Phylum	<i>Chordata</i>
Subphylum	<i>Vertebrata</i>
Class	<i>Mammalia</i>
Subclass	<i>Theria</i>
Infraclass	<i>Eutheria</i>
Order	<i>Artiodactyla</i>
Family	<i>Bovidae</i>
Subfamily	<i>Caprinae</i>
Genus	<i>Ovibos</i>
Species	<i>Ovibos moschatus</i>



Picture 6 Muskox

Muskoxen are nonterritorial ungulates (FORCHHAMMER and BOOMSMA 1998). They choose moist meadows and snow bed vegetation for summer grazing and wind-exposed, dry dwarf shrub heath vegetation in winter. *Graminoids* dominate their winter diet. Willows (*salix spp*) are the main component of their summer diet. Females tend to retain fat reserves through the winter to draw upon during the post-calving period of lactation. Alternate year breeding is a common occurrence, and calves are normally not weaned before the end of their first winter. Mean calf mortality is relatively low since predation is rare and the removal by hunters approaches the annual increment (THING *et al.* 1987). Ecological background information on Muskoxen is provided in detail by Spencer and Lensink (1970), Thing *et al.* (1987) Lent (1988), Schaefer and Messier (1995) and Forchhammer and Boomsma (1998).

Detailed knowledge on muskoxen behavior is mainly based on older studies (REINHARDT and FLOOD 1983) revealing general information on free ranging adult muskoxen (GRAY 1973; SMITH 1976; SAELZLE 1979). The existence of a majority of mixed groups, less only-male groups, and few only-female groups is described (GRAY 1973).

Muskoxen are found to be social and are encountered in relatively stable harem groups implicating males defending females against non-group males as well as courtship behavior during rutting. Frequent splitting and fusion of groups is observed as well (GRAY 1973; LENT 1988). The existence of a dominance hierarchy within groups is stated due to observed dominance fights and contests, especially between males (LENT 1988). Gray (1973) describes a linear dominance hierarchy in male muskoxen and similar dominance behaviors displayed by females in only-female groups.

A mother does not isolate her calf from the group; it becomes a member of the group with birth. Mothers and infants maintain close and frequent contact but also social contact with other group members such as social play occurs frequently.

In dominant interaction displays, adult males always win over females and most often subadult males win over adult females as well. Up to a five step cascades of exhibiting dominance behavior towards a less dominant individual are observed, concluding to muskoxen having the ability to differentiate between individuals. Never dominant behavior was exhibited towards an individual that displayed dominance behavior before through the cascade (GRAY 1973).

Same principals are observed in subadult muskoxen by Reinhardt and Flood (1983). They describe the dominance rank order in juvenile muskoxen as a principally linear structure with animals of high rank dominating all individuals of lower rank. These dominance relationships were found to be stable through at least 6 months of observations. Although female juveniles were in general heavier than male juveniles, males were dominant over females. Dominance rank was not found to depend on aggressiveness but to hold a high dominance rank ensured undisturbed food selection.

An impressive, and requiring sophisticated social activity, is the so called defence formation of muskoxen. When approached by a predator, the adult animals build a circle with their tails towards the inside of the circle and their heads facing the predator. Calves are protected by being inside the circle; adult animals are protected from behind at the same time. This group protection feature is not observed in any other social group living animal (LENT 1988) and might be seen as an evidence for high social structure.

1.3 Review of Using Opportunistic and Marginal Data

In behavior sciences, marginal opportunistic data is basically declared as not usable. Even when having access to relatively large opportunistic data sets in social behavior studies, they are thought of not being applicable for any relevant quantitative conclusions and without the ability to differentiate between individuals. It became a tradition that only larger amounts of field hours can present reliable findings, and thus, represents worthy science to be published in high-quality international peer-reviewed journals (STACEY and KOENIG 1990; WELLS 1991; WHITEN *et al.* 1999). Why for example is it worth, and especially required, to spend 151 man years (WHITEN *et al.* 1999) observing chimpanzees to conclude on social structure? Here, this view is

challenged for various reasons. This traditional approach leaves science, even in the twenty-first century, with a huge lack of wildlife behavior information across species, particularly relevant for management in large mammals (CLEMMONS and BUCHHOLZ 1997; GADAGKAR 1997). Secondly, unique and important but opportunistic sightings get ignored for the sake of the general picture, e.g. when just interpreting linear regressions in a complex cloud of points. And lastly, many species these days require urgent and immediate management actions. Still, many behaviorists across the world are teaching and using traditional statistics (parametric statistical methods) referring to p-values and significances as basically the only applicable behavior statistics. They are based around the goal of maximizing likelihood, parsimony, generalizations, and assumptions such as homogeneous error variances and normally distributed data sets for example. Thus, analysing these data require sufficient knowledge to state the hypothesis and know the validity of assumptions, for which we depend on large and precise data sets as mentioned above (HOCHACHKA *et al.* 2006). Alternatives have been brought forward using Bayesian and other approaches.

Here, a new approach conducting predictive modeling and a basic meta-analysis to marginal opportunistic short-term behavior data is presented. The goal is to investigate basic marginal but available behavior datasets soundly and efficiently as well as in more detail and still find overall and valid patterns. The applicability, the constraints and the limitations of this statistical approach to behavior data will be assessed and first conclusions drawn.

In some disciplines of science other than behavior research, mostly in spatial niche modeling so far, limited, biased and marginal data has been successfully applied and used already for important conclusion drawing for many years (PETERSON 2001; GRAHAM *et al.* 2004; KADMON *et al.* 2004). In disciplines such as ecology and where exact and repeatable experiments cannot be achieved, limited spatial data is frequently used for spatial distribution, biodiversity and accuracy assessments.

Further, researchers make use of limited spatial data in predicting possible habitat for endangered species (i) via presence-absence data, through the use of (ii) presence only data (BROTONS *et al.* 2004; KADMON *et al.* 2004; HIRZEL *et al.* 2006) and through (iii) only occurrence data (ENGLER *et al.* 2004).

It is crucial to achieve knowledge on species distribution and habitat availability, even if extrapolated and inferred from so-called poor learning data. Most important is 'true information' that goes into decision-making. Incomplete data is often all one can achieve when working with

endangered species and their habitats. This concept is well publicized in the disciplines of data-mining and modeling.

With applying incomplete and limited data sets more frequently, overall conclusions can be of higher importance than having 'good', perfect and comparable data, e.g. through applying the same methodology across data sets or species, instead of having a high quantity of data. Engler *et al.* (2004) show that quality, spatial distribution and locational accuracy of data appears to be more important than quantity, and that data quality prevails therefore over quantity as such.

Behavior assessments in wild animals are as important as pure habitat observation knowledge. Animal behavior and the occurrence of animals in a certain habitat are linked very closely. Behavior is intensely linked with ecology (KREBS and DAVIES 1993). They choose what habitat to seek based on resource and mate availability and especially by the social rank they occupy in the population. An animal observed in a certain habitat is not necessarily in its optimal habitat.

The focus of this thesis is on behavior research, to test the applicability of incomplete and short term data. Important to remember is that animals behave a certain way for certain reasons. According to the theory of natural selection, there is no behavior that develops by chance in evolution and survives (KREBS and DAVIES 1993; ALCOCK 2001).

The difference between our data sets and for example Kadmon *et al.* (2004) and Hirzel *et al.* (2006), is the use of marginal spatial behavior data instead of marginal spatial ecology data. The applicability of such data on behavior studies, focussing on bears eventually but comparing the validity across taxa worldwide, is validated in this study.

1.4 Data Mining in Behavior Sciences

To not go beyond the scope of this thesis, the history and different predictive modeling strategies available will not be investigated. These issues are already discussed and outlined in great detail e.g. by Guisan and Zimmermann (2000), Breimann (2001), and Onyiahialam *et al.* (2005) for methods and Graeber (2006) for bears.

1.4.1 Overview

In almost all research disciplines, statistical methods are used as main analytical tools with typical parametric statistical techniques (HOCHACHKA *et al.* 2006; CRAIG and HUETTMANN in

press). When modeling is considered for analysis, 98% of all statisticians generate data by stochastic data models (BREIMANN 2001). As just 2% of researchers apply algorithmic modeling (data-mining) as modeling data technique, still much criticism is brought forward against algorithmic data mining. Due to lack of wider experience with this data-analyse approach, some researchers still have problems with trusting the algorithmic modeling structure and its programs: Data-mining operates with a complex and unknown black-box, the estimation of precision is difficult (e.g. no p-values and significances to refer to) and 'messy data' with inaccuracies, missing data as well as outliers are believed to effect the results (LAWRENCE *et al.* 2004; PRASAD *et al.* 2006). Hirzel *et al.* (2006) states that models predicting species spatial distribution are increasingly applied to wildlife management issues, but methods to evaluate the accuracy of their predictions are few and have never been validated.

This statement can be verified as many validation tests exist, e.g. cross-validation, bootstrapping, bagging and boosting. Data mining strongly emphasizes validation of models and measuring model performance (HOCHACHKA *et al.* 2006). Cross-validation testing assesses how well one model built with one set of data (training set) can predict observations in a set of data that was not used to build the model (validation set) (HOCHACHKA *et al.* 2006). Bootstrapping brings together ideas of re-sampling and simulation-based statistical analysis. The aim is to understand bias, variance, and other measures of uncertainty through computer simulations. Bagging is a variance reduction method for model building (ELITH *et al.* 2006). The aim is to reduce the variance through building multiple models from samples of the training data. Boosting associates weights with entities in the dataset and increases the weights for those entities that are difficult to model. A sequence of models is constructed. After each model is constructed, the weights are modified to give more weight to those entities that are difficult to classify (WILLIAMS 2006). In many data mining models, assessments through bagging, boosting as well as cross-validation are included in the model output already (HOCHACHKA *et al.* 2006).

Data mining is defined as the search for patterns and hidden information in data using modern, highly automated, computer intensive methods. The terms 'search' and 'automated' are key to this definition (STEINBERG and GOLOVNYA 2004).

In general, data mining provides success in analysing data and gives information about the mechanisms producing the data. The commitment of statisticians to stochastic data modeling prevents them from entering new scientific disciplines though where data is not suitable for analysis by stochastic data models. Still, the growth of algorithmic modeling over the past fifteen years has been rapid and actually developed in fields outside statistics (BREIMANN 2001; HOCHACHKA *et al.* 2006). For example, data-mining is increasingly found in disciplines such as

ecology (GRAEBER 2006; RUTZEN 2007) and economic studies (AGGARWAL and YU 2000; BOUNSAYTHIP and RINTA-RUNSALA 2001).

But why exactly is algorithmic modeling an advanced theory and when should algorithmic modeling be applied? Ecological data and other factors affecting species and their distribution, to which animal behavior belongs, are highly complex and non-linear in nature. To interpret such data, alternative analytical techniques as classification and regression trees developed in data-mining, tend to outperform traditional modeling methodologies in regards of time, transparency and accuracy (ELITH *et al.* 2006; CRAIG and HUETTMANN in press). Algorithmic modeling can be used on both, large complex data sets as well as on marginal data sets, providing more accurate and extensive information than stochastic data modeling (BREIMANN 2001). Algorithmic models perform fast, they are non-parametric, the number of predictor variables modeled is not limited and they are effective in uncovering the underlying structure in data (BREIMANN 2001; ELITH *et al.* 2006; CRAIG and HUETTMANN in press).

Neither in the zoological, nor in the animal behavior context, many research studies can be revealed, yet, using data-mining as their main statistical approach. The only approaches found, where the terms modeling and behavior occur together, relate to social market economy research in the background of marketing strategy development (AGGARWAL and YU 2000; BOUNSAYTHIP and RINTA-RUNSALA 2001) as well as in computer modeled behavior for synthetic characters (NIEDERBERGER 2005). We therefore step into a completely new field when modeling animal behavior data with algorithmic modeling techniques

“If our goal in a field is to use data to solve problems, then we need to move away from exclusive dependence on data models and adopt a more diverse set of tools.”

(BREIMANN 2001)

“Linking computational software with wildlife ecology and conservation management in an interdisciplinary framework can not only be a powerful tool, but is crucial towards obtaining sustainability.” (CRAIG and HUETTMANN in press)

1.4.2 Why TreeNet

Many data-mining tools exist, each showing different specialisations: e.g. CART – decision trees, MARS – multivariate adaptive regression splines, ANNs – artificial neural networks, RandomForests – ensembles of trees with random splits, TreeNet – stochastic gradient tree boosting (STEINBERG and GOLOVNYA 2004; ELITH *et al.* 2006; PRASAD *et al.* 2006).

TreeNet, also known as MART (multiple adaptive regression trees), is among the latest advance in the theory of boosting developed by Jerome Friedmann (Salford Systems) in 1999 (FRIEDMAN 2002) and is known to be among the best performing algorithms for model predictions (ELITH *et al.* 2006; GRAEBER 2006). This program selects the best performing model by ranking the most powerful predictors (SALFORD SYSTEMS 2003).

TreeNet naturally supports both, classification and regression problems. It is characterized by high speed, predictive accuracy and most important for this study, robust results even when working with 'dirty' data (SALFORD SYSTEMS 2003; CRAIG and HUETTMANN in press). Regression models in TreeNet are used to model a continuous outcome. Applied predictors can be a mix of continuous and categorical variables without requiring any preparation. Most traditional classification models are developed for binary response problems predicting a 0/1 or Yes/No response (SALFORD SYSTEMS 2003). However, more than two categories and continuous responses can be modelled as well.

How TreeNet works

First, a residual and initial guess need to be defined. The residual depends on the loss or likelihood function used; the initial guess is the mean for regression trees. The model is built with multiple runs, ranging from hundreds to thousands. During model building, a sample from the training data is taken (validation data) and a fixed-size small regression tree that predicts the current residuals is grown. Following, this one single tree grown gets combined with previous grown trees using addition (boosting) and shrinking (bagging, averaging). The evaluation of models across different tree amounts grown is important to validate results (bootstrapping). Performing the evaluation on a separate test set is auxiliary to find the optimal model (cross-validation) (HASTIE *et al.* 2001; STEINBERG 2005).

TreeNet models are a sum of factors that become progressively more accurate as the expansion continues. The expansion is written as:

$$F (X) = F_0 + \beta_1 T_1 (X) + \beta_2 T_2 (X) + \dots + \beta_M T_M (X)$$

F represents the dependent variable, related to one or more other variables X. F₀ is the offset (intercept), β_M are constants (coefficients) and T_M are small trees. Each weighed sum of terms is obtained from the appropriate terminal node of a small tree (SALFORD SYSTEMS 2003).

New innovations compared to earlier data-mining tools speed up processing and allow additional safeguards against overfitting. Small tree sizes determine the order of interaction and

shrinkage forces and thus the learning process slows down to allow more obscure features to be exploited. The repeated use of the data (subsampling) prevents overfitting through working only with a portion of the original data at each step. New methods of 'patient learning' are applied and testing is accomplished via cross-validation (SALFORD SYSTEMS 2003; STEINBERG 2005).

The main advance of TreeNet is the capability to work with very small samples, as little as 60 events, without losing its robustness and predictive accuracy (SALFORD SYSTEMS 2003). Thus this algorithmic data mining tool - TreeNet - is a very powerful tool.

"When TreeNet doesn't find anything one can be rather sure that there is no signal in the data"
(cited after CRAIG and HUETTMANN in press).

1.5 Meta-analysis – Overview

Meta-analyses combine the results of several studies. Each addresses a set of related research hypotheses but might use different datasets or methods. Traditionally, such studies were difficult to summarize, but with the advent of many new research projects and publications, approaches that can combine studies towards a coherent result are still on the rise. Statistically, this is achieved for instance with Mixed Models (HEDGES 1992). Meta-analysis allow similar evaluations, but in a less quantitative and more summarizing framework. They are very useful and powerful in complex ecological questions, and it is not unusual to see them applied to 1000s of projects. Hedges (1992) describes Meta-analysis as *'the analysis of the results of statistical analyses for the purpose of drawing general conclusions'*. The idea of a Meta-analysis is to analyze the results from a group of studies that perform a more precise data analysis. The attempt is to overcome the problem of reduced statistical power in studies (no p-values and no significances), especially with small sample sizes.

The statistical concept of Meta-analysis is fairly old already, reaching back to the 17th century where it was applied in astronomy. It took long for this concept to be applied to other disciplines. Although Karl Pearson first implemented Meta-analyses in the medical field in 1904, the term 'Meta-analysis' itself was first introduced by Gene Glass in 1976 (EGGER *et al.* 2002).

Today, Meta-analysis are widely used in medical research and epidemiology (ANANTH *et al.* 1997; PHAROAH *et al.* 1998; MAURIZIO and MASSIMO 2000), social sciences (HITSMAN *et al.*

2003) and are starting to be more and more implemented in ecology and climate change studies even (WORM and MEYERS 2003; WORM *et al.* 2005).

As well as algorithmic modeling, Meta-analyses highlight the practical importance of the effect size instead of the statistical significance of individual studies. Thus, again the strength of the results is not fully comparable to parametric statistical techniques.

Although the achievements of Meta-analysis in some fields, as the clinical trial research field, are impressive, not all journal editors consider well-constructed systematic reviews and Meta-analyses as original research (EGGER *et al.* 2002).

1.6 Overall Logic for Approach

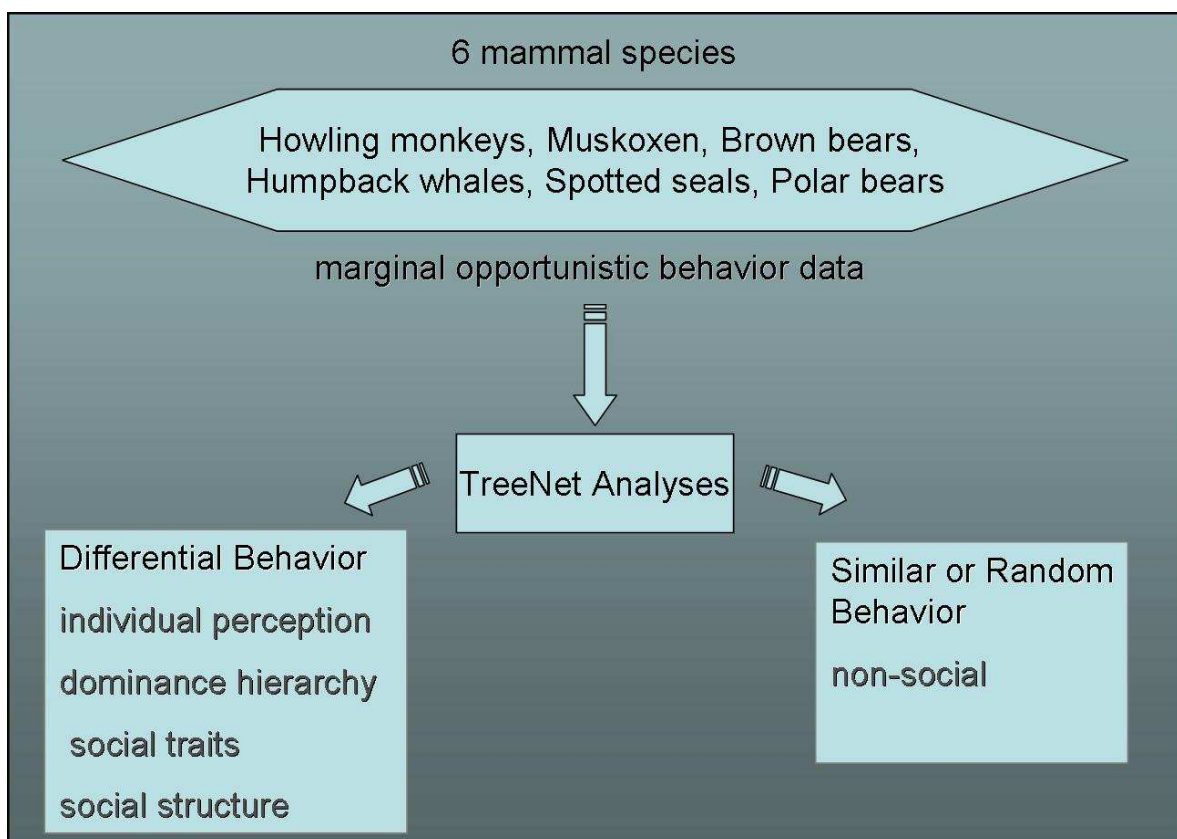


Figure 1.1 Overview of analysis approach and flow of logic

Marginal opportunistic behavior data was collected for 6 mammal species analysed with algorithmic modeling with the use of the program 'TreeNet'. When similar or randomly expressed behaviors are displayed in animals, it suggests that they do not choose and adopt their behaviors to other individuals, and thus are non-social.

When animals display differential behavior they show selective behavior and express social traits. Social traits follow social structure; social structure follows a dominance hierarchy when animals interact closely. Individual perception abilities have immense advantages for individual survival. The term 'opportunistic' implicates dealing with a less structured research design. We compare three methods: very opportunistic, opportunistic and well structured. All of these methods are marginal, working with small to very small sample sizes.

1.7 Justification of Approach

Animals being described as NON-SOCIAL species, e.g. bears (BELLEMAIN *et al.* 2006), should not show ANY social traits in their behavior. Thus, NOT A SINGLE social interaction should exist and be recognized in any data collection – short-term, long-term and opportunistic. Basically, data size or research design should not be a limitation here because if small social evidence is found, this already will suffice for showing animals are social and result into a follow-up, if not revision, of their status regarding sociality.

This approach is compared across mammal species that are known to be social (howling monkeys, humpback whales, spotted seals, muskoxen), with other mammal species described as non-social (brown bears), or are virtually not described (North American polar bears). Latest statistics are applied as a powerful detection method to search for 'signals' of sociality in animals within such data as one can believe that this presents a new angle and progress regarding scientific knowledge, which is crucial for their survival when doing science-based management. Further, the experience will be informative for future studies regardless.

The following expectations and hypothesis are considered the core of this thesis:

(1) To test the applicability of the proposed approach, the approach is applied to species which are known to be social through long-term studies. Thus, one can compare them with so-called non-social species. The expectation is that then one would obtain different results.

(2) When animals are social, they will show a distinct decision-making for interacting with any other individuals they encounter.

(3) Thus, animals that are social should show distinct patterns and differentiated behavior between individuals. The result graphs should show noisy, varying patterns in curves and surfaces across age classes and body sizes. Behavior metrics such as 'Distances between

social individuals' should not be centered around central means and should not be equally distributed, but vary by each individual instead.

(4) When animals are non-social, they will not show a distinct decision-making for interacting with any other individual.

(5) Bears are widely described in America as non-social, and therefore all bear data points should be centered around the mean or distributed randomly (= flat surfaces and curves in distance histograms and interaction diagrams) when using metrics x (e.g. indistinct behavior towards any individual). They would respond similar to individuals of the same body size and age class, and thus be indifferent.

(6) If evidence is found that this is not the case, one shows that they act strategically, and thus, that they differentiate between either body size, age class, sex or even individuals, and probably do this because of social structure; the previous topics being the requirement for being social.

(7) Only small data sets and opportunistic designs are on hand. Thus, one could miss events; fine. However, one should not find anything different than flat curves or congregations of data points around the central means (=no evidence that animals make distinctive decisions). Even with incomplete data one should get these patterns certainly.

(8) To further address a potential critique that the proposed method would not allow to draw such conclusions, three different types of sophisticated approved behavior methods, ranging from very basic to well structured, are applied and results can be validated.

(9) To even further address the methodological critique many species well-known to be social and worldwide are investigated. Through this approach, basic repeats and controls from established, approved and studied cases are given.

In this thesis, 'algorithmic modeling' and 'short term behavior data' get combined for the first time. Both terms have widely been ignored for a long time regarding their usability on drawing valid conclusions. It is clear that there is a high demand to introduce new promising approaches to behavior data, especially to species where we lack long-term data due to their inaccessibility in the wild, by scientific administration and culture. Sociality, dominance hierarchies and individual perception are crucial factors influencing management concepts and their implementation for all animal species. To start the process advancing, assessing the usability of marginal behavior data is the main goal of this study.

2 Methods

Different amounts of data, ranging from 12 to 50 contact hours across species and methods were collected. Three different methods analysing behavior are applied across six species. The requirement for data collection was that two ‘separate’ individuals of the observed species had to be in sight. Animals being subadults or older and therefore being independently responsible for their own survival count as ‘separate’ individuals. The exact amount of data collected depended on the accessibility of observation periods during a data collection timeframe of one month. Only one species, Muskoxen, was observed in captivity, and data was collected over four months.

Through comparison of the three different methodologies applied, it is assessed (i) where the limits and boundaries of applying marginal opportunistic behavior data are, and (ii) from what amount of data and from which method most specific and valid conclusions can be drawn. Considering what type of observations are possible to conduct on free-ranging mammal species, the following methodology setup was chosen:

Table 2.1 Overview behavior sampling methods

Thesis method	1 st Method:	2 nd Method:	3 rd Method:
Sampling method	instantaneous scan sampling & continuous event sampling	instantaneous event sampling	instantaneous event sampling
Species	Howling monkeys Humpback whales Brown bears Polar bears	Muskoxen	Spotted seals
BSI (body size index) available	yes	yes	no
structure-degree of method	well structured	basic	very basic

The first method is probably the most precise and structured one. In this methodological setup different and well founded behavior sampling approaches (ALTMANN 1974) are combined. The second method is less structured only sampling when events occur. The third method doesn’t collect data on single individuals and focuses on animal groups and clusters in the wild.

Age and sex determination is not always possible in the field; its determinability varies widely across species. Therefore the Body Size Index (BSI) was implemented (Appendix 8.1). This index is important for the comparability of results within one species as well as across mammal species. BSI sizes are defined as ranging from 1 to 10; the larger the individual, the higher its

BSI. Following BSI sizes and their connection to sex and age class are verified for all species except humpback whales and spotted seals. In humpback whales no validation of BSI sizes and sex could be achieved; in spotted seals no BSI sizes were collected. BSI sizes 1 to 3 describe infants, 4 juveniles, 5 and 6 subadults, 7 adult females or young adult males, 8 to 10 refer to adult males. The BSI sizes 1 and 10 were never applied to any species because individuals fitting this description were not encountered or reliably identified. For most species, infants (yearling cubs, calves) are always travelling with their mother; they strongly depend on her. Juveniles (first year cubs, calves) still depend on their mother but are observed to investigate closer surroundings on their own. Subadult individuals are not with their mothers anymore; they are independent and are usually not fertile yet. Adult females can have infants (yearling cubs, calves) or juveniles (first year cubs, calves) with them. All subadult and adult individuals count as independent animals and are included in the data collection.

In two species - howling monkeys and muskoxen - the BSI and the age class of the animal could always be set in relation accurately; in another species - humpback whales – this was never the case. For all other species, BSI and age as well as sex class are put in relation but could not always be determined due to observation conditions in the wild. Precise definitions for all species are outlined in Appendix 8.1.

The first observation-method (s. Table 2.1) is well structured and applied to four, free-ranging mammal species (Howling Monkey, Humpback whale, Brown Bear and Polar Bear). Two robust sampling methods were applied (Altmann 1974; Geissmann 2002): The non-invasive instantaneous scan sampling methodology was used at ten minute intervals estimating spatial proximities between all individuals. Between instantaneous scans, the continuous event sampling methodology was applied to record interactions. Interactions were classified in categories and subcategories (e.g. category: play; subcategory: playfight). These definitions are species-dependent and therefore explained in more detail in Appendix 8.3.

The second method in this thesis is more opportunistic and only applied on captive muskoxen. Behavior data was collected only with the instantaneous event sampling method, collecting interactions and spatial proximities at the time the event took place. In this method distances are only recorded when an event took place and not in an instantaneous scan pattern, what presents a major difference to the first described method. The same interaction classification scheme is applied as described and applied in the first observation-method (s. Appendix 8.3).

The third observation-method in this thesis used is again more general and was only applied on free-ranging spotted seals. Behavior data and interactions were recorded with the

instantaneous event sampling method, as done in the captive muskoxen population. The major difference to sampling the muskoxen population is that no individuals were assigned. The only related parameters known are 'group size', proximity to each other, and the 'number of animals interacting' at the time the event took place. Like in muskoxen, distances were recorded in combination with occurring interactions and not in a regular instantaneous scan pattern.

Across all sampling and observation methods, date, time, observation location, weather, and individual identification code (if possible) were recorded. During scan time for the first observation-method and during event time for the second and third observation-method the following data was collected: BSI sizes (except for seals), age and sex (if possible), proximities between all individuals in sight, behavior of all individuals, location parameters of all individuals (except seals and muskoxen) and comments concerning anything that could have influenced the animals behavior at that time. When an event (interaction) occurred, the following data was collected throughout all methods: categorisation of interactions occurring between individuals, age and sex of interacting animals (if possible), BSI sizes of interacting animals, detailed description of interaction, duration of interaction, location of interaction (except seals and muskoxen) and remarks how independent factors could have influenced the animal's behavior at the time.

Observed interactions were classified by body sizes (BSI), and, when possible, transformed to gender information. Interactions can be either neutral, which implies that both individuals did not change their state of mind and usually not their behavior because of being close to another individual (= no impact), or positive for one individual and negative for the other one in a dominance situation (= impact on behavior). In this case, one individual is dominant over the other. For detailed definition see Appendix 8.1.

Another comparable more objective measure, the 'personal space zone' (PSZ), was introduced to optimize behavior and interaction categorisation as well as to support the uncovering of differentiated spatial behavior schemes. The PSZ is defined as the distance individuals must keep from a particular individual in order for it to not change its behavior due to the presence of the other individual(s) (see Appendix 8.1 and 8.3).

Data was collected from 2 to 8 individuals at a time. Except in spotted seals no individual data was recorded and larger aggregations of up to 50 individuals were observed. Consistency of the methodologies is provided by having one principle data collector for each species as well as each thesis-method, and following compatible protocols. Data on the first robust observation-method (howling monkeys, humpback whales, brown bears and polar bears) was collected by

Kim Jochum. All data considering the second and third more opportunistic observation-methods (musko xen and spotted seals) was collected by Falk Huettmann.

2.1 Field work

2.1.1 Howling Monkeys

Study site

This study was conducted in a secondary growth tropical dry forest on Ometepe Island located in Lake Nicaragua (11° 40' N and 85° 50' W), southern Nicaragua (BEZANSON *et al.* 2007; POPP *et al.* 2007). Ometepe Island is a large volcanic island (256km²) (Garber and Jelinek 2005). The study site is located in the southern part of the island at the bottom of Maderas Vulcano next to San Ramon and is surrounded by cattle pastures and agricultural fields. This tropical dry forest is situated on sea level and experiences two distinct seasons: wet (March through October) and dry (November through February) (GARBER *et al.* 1999).

Data collection setup

Mantled Howling Monkey observations took place during dry season, between December 27th 2005 and January 8th 2006. Three to five hours of data was collected each morning between 6am and 12pm. The total data set consisted of 30 contact hours in the field including 860 proximity measurements and a total of 127 interactions observed among individual howling monkeys.

The study animals were tracked each day around sunrise by listening to their vocalizations. In the evenings, right before sunset, we located the animals at their resting sites again to allow an easier next morning recovery. Howling monkeys rarely move during darkness spending the night mainly in one tree. The group size was difficult to determine as howlers at Ometepe live in subgroups (BEZANSON *et al.* 2007). We observed subgroup sizes which changed over the course of the study, ranging from four to eight animals at a time. Observations were conducted being fairly close to the animals, most of the time standing right under the tree they stayed in. Since researchers have been collecting behavior data on this population for decades, the observed population is completely habituated to humans neglecting a bias through the presence of observers. The estimate of individuals observed during the whole data collection lies between 30 to 40 different individuals. The BSI sizes in howling monkeys always describe the defined age and sex class due to the close observation possibility. To describe the location between animal pairs it was distinguished between 'sitting on the same tree' or 'sitting on different trees'. No special equipment was used for observations ('naked eye') (JOCHUM and HUETTMANN 2006).

For howling monkeys, the PSZ was defined at 5 metres. Howling monkeys generally start to interact with other individuals being that close; sometimes in a neutral, sometimes in a dominant manner.

2.1.2 Humpback Whales

Study site

The humpback whale study site includes the closer surrounding of Rivers Inlet, Strait of Georgia, British Columbia, Canada. The area ranges from Cape Calvert in the west to Brunswick in the east, north to Fish Egg Inlet and south into Goose Bay (51°23' N to 51°37' N and 127°33' W to 127°55' W).

Data collection setup

The Humpback whale data was collected during the 2nd and the 19th of July 2006. The dataset altogether consisted of 50 data hours, 582 proximity measurements and 48 interactions. Two to seven hours were collected each day from morning to the afternoon and twice in the evening before sunset.

Dawsons Inlet and Rivers Inlet were checked for whale activity every day. When there were no humpback whales found in this range, Goose Bay or Fish Egg Inlet was investigated. Whales were detected by driving a speedboat and looking for spouts observable above the water surface. When spouts were sighted, the animals were slowly approached up to a maximum closeness of 100m for photo identification and BSI size determination. To observe more individuals at a time, larger distances were kept to the animals after having determined the required parameters. The estimate of individuals observed over the whole data collection period lies between 20 to 30 individuals. BSI sizes are not applicable to age and sex classes in humpback whales. Only above surface observations were conducted. Location differences collected for humpback whales distinguished between being 'close to shore' and being 'offshore'. When an individual had a distance of 100 metres or less to the shore it was defined as being 'close to shore', all further distances were classified as 'being offshore'. Special equipment used was a speed boat for whale observations, a camera for photo identification pictures (Canon, Rebel 300mm), a camcorder (Sony, DCR-DVD105) for video taping and a compass (Recta DP2) for triangulation of locations.

In humpback whales the PSZ was defined to be 500m. The use of the PSZ optimizes behavior and interaction categorisation as well as supports the uncovering of differentiated behavior schemes. See Appendix 8.1 and 8.3 for operational definitions.

2.1.3 Brown Bears

Study site

The Brown Bear study site is situated in the Chilkoot River State Recreation Area at Chilkoot River located about 10 km northeast of Haines, southeastern Alaska (59° 19' N and 135° 33' W). Observations took place from 2 observation spots. The salmon weir belonging to the Fish & Game Department in Haines, Alaska represented one observation spot. During salmon run season, July through September, the weir is positioned about 1 kilometer upriver, between the estuary and Chilkoot Lake (CRUPI 2003). The observable range of the river from this observation location is about 1 kilometer, 300m upriver and 700m downriver. The view to both sides is restricted through curves in the river flow and vegetation. The second observation spot is the Chilkoot River Bridge. From here, the open spaced estuary area and about 500 metres upriver are observable, overlapping about 200 metres with the downstream observation area from the weir observation spot (CRUPI 2003).

Data collection setup

The observations on Brown Bears were carried out between the 7th and the 30th of August 2006. The observable bear activities were constricted to a few hours around sunrise and a few hours around sunset due to no, or very few, bears being at the river during the day. This bear absence over the day is believed to be caused by human activities such as fishing. Data was collected in the morning hours from 4.30am to 9am and during the evening between 6pm and 10.30pm. Altogether 40 hours of data are collected, including 680 proximity measurements and 94 classified interactions. About 15 to 20 individuals are the estimate of animals observed during the whole data collection. BSI sizes in brown bears are well distinguishable and to a very high degree associated with the age but less to the gender of the individuals. BSI sizes of 5 and 6 indicate subadults, BSI 7 usually refers to an adult female (s. Appendix 8.1). For bear species, numerous locations were defined throughout the whole study area. For brown bears 85 locations exist. Special equipment that was used included a camcorder (Sony, DCR-DVD105) and binoculars (Leica Trinovid10x32 BN).

The PSZ for brown bears was defined to be 50 metres. See Appendix 8.1 and 8.3 for operational definitions.

2.1.4 Polar Bears

Study Site

The Western Hudson Bay polar bear population congregates around Churchill, Manitoba, Canada during fall. It is not completely clear why these congregations of hundreds of animals

happen each year as apparently this is not traditional bear behavior (LATOURE 1981). It is widely believed that congregations occur due to ice freezing patterns of the Hudson Bay (GOUGH and WOLFE 2001; LUNN and STIRLING 2001) in order for bears to get onto the ice to hunt as soon as possible. Less dense concentrations still occur in natural and wilderness conditions. On the entire Hudson Bay, the ice begins to form earliest around Cape Churchill enforced trough current streams, wind and the closeness of Churchill River (ROUSE *et al.* 1995). The Churchill Wildlife Management Area (CWMA) is located 30-35km east of Churchill (58°450' N to 58°480' N, and 93°380' W to 93°500' W) on the south-western coast of Hudson Bay. The habitat in the Churchill area can be described as a gradual transition from the boreal forest ecotone to the tundra ecotone (ROUSE *et al.* 1995) and is characterised by gravel spits, foreshore flats, post-glacial beach ridges, shallow lakes and ponds surrounded by willows (*Salix* spp.) (RITCHIE 1962; CLARK *et al.* 1997; DYCK and BAYDACK 2003). The habitat around Churchill describes an intersection between the boreal forest ecosystem and the tundra (ROUSE *et al.* 1995). The so called 'bear season' lasts 6 to 8 weeks in October and November (LUNN and STIRLING 2001). We conducted observations on this population in the CWMA nearly exclusively from Gordon Point tower with an observable range of about 5 km², ranging from The Great White Bear Camp, to Gordon Point, to The Tundra Buggy camp. Only few observations (2 days) were conducted from the Tundra vehicles driving through the CWMA approaching sighted bears for eco-tourism reasons. The observable range from these vehicles ranged between 1 to 2 kilometers.

Data collection setup

Polar Bear observations were conducted from the 15th to the 27th of October 2006. Field work was accomplished in cooperation with Kim Daley (private researcher), Churchill, Manitoba, Canada and the Churchill Northern Studies Centre (CNSC). The estimated number of polar bears observed is about 50 to 80 individuals. BSI sizes were distinguishable and are to a very high degree associated with age and to a high degree with the sex of the individuals. BSI sizes 5 and 6 are usually subadults, BSI 7 represents an adult female or a young adult male, BSI sizes 8 and 9 indicate adult males. For polar bears, 86 locations were defined throughout the whole study area. Special equipment was used to record data; two spotting scopes (one for long distances: Pentax PF-80ED (60x-20x) (D=80mmP), focal length 8mm-24mm and a smaller one mainly used for focal animal observations: LEOPOLD Wind River (15x-45x), Wilderness Optics), one camcorder (Sony, DCR-DVD105), binoculars (Leica Trinovid10x32 BN) and one four-wheeler ('Bronko') to reach the observation tower located in the CWMA.

The PSZ in Polar bears was defined to be 100m. Starting at a 100m distance, individuals change their behavior due to the presence of other individual(s). See Appendix 8.1 and 8.3 for operational definitions.

2.1.5 Spotted Seals

Study Site

This specific study area is located in the western Sea of Okhotsk, Russian Far East, and represents one of the last wilderness areas and untouched watersheds in the Northern Pacific. Seals were observed in the Verengy River at the Vostochnaya Reserve, eastern Sakhalin Island (approximately 50° 47' N and 143° 34' E). A seabird colony ('bazaar') was nearby but did not affect seals. Seals were attracted to the estuary by a high number of migrating salmon. Orcas (*Orcinus orca*) visiting the study area were observed occasionally (READ *et al.* 2008). Sightings were carried out from a coastal, about 20m high hill via binoculars (9*42) in a distance of about 200m from the animals (HUETTMANN 2006). Vegetation around the study site is mainly determined by coastal shrubs such as willows (*salix spec*) and alders (*alnus spec*).

Data collection setup

In 9 sessions during 4 days, from August 28th through August 31st 2006, 20 hours of data were collected from which 12 contact hours could be used for data analysis. Between 8 and 24 animals were constantly in sight. The number of all seals in view was noted at the beginning of each session. For a subset of seals the occurrence and the time of the occurrence of clustering and social behavior was noted. The time, when a change in number in seal groups occurred, was noted as well. The estimated number of individuals observed for the whole data collection period, were about 100 individuals. No BSI sizes are collected on the seal population. Also specific location data could not get collected for the animals in the marine habitat; distances were visually estimated. Binoculars (9*42) were used for field work observations (HUETTMANN 2006).

The PSZ for spotted seals was defined to be 10m. See Appendix 8.1 and 8.3 for operational definitions.

2.1.6 Muskoxen

Study Site

The data collection was carried out during spring 2007 with the herd of muskoxen at the Robert G. White Large Animal Research Station (LARS) in Fairbanks, Alaska (64° 49' N to 147° 52' W). They are maintained for research and educational purposes (ROSA *et al.* 2007). This herd, belonging to the Institute of Arctic Biology, was founded in 1980 from a population on Nunivak Island, Alaska, which was originally populated with animals translocated from Greenland (BARBOZA *et al.* 2003). Muskoxen were extirpated from Alaska by the late 1800s and were reintroduced in 1930 by using 34 animals brought from Greenland (Bell 1931; Klein 1988). This

herd has ranged from the original 16 animals to a high of 85 animals in the mid-1990s. The herd at LARS is currently maintained at approximately 40 animals (ROSA *et al.* 2007). Animals were prepared with individual markers and tags for ID. A specific list of all animals was provided (JACOB and HUETTMANN 2007).

Data collection setup

Observations were conducted from February 2007 till May 2007 with observation periods of 1 and 2 hours. Data was collected on the basis of 15 observation days. The observer looked down at the animals at all times and had an overview of the complete enclosure throughout observations. These data used for the analysis consist of 16 hours and 13 min. Animals were prepared, colour and number marked by Sandy Garbowski, Aerin Jacob and Bill Hauer. Important to notice is that data was recorded in an artificial release to supplemental feeding setup. Less feeding buckets than animals existed to facilitate a situation of artificial competition, enforcing dominance behaviors. Therefore a relatively high amount of interactions was recorded over a short period of time. The Muskoxen group size in the enclosure ranged from 5 (just bulls), to a second group of 12 (just adult females) up to a group of 21 (adult females with calves) individuals.

Altogether, 27 adult and subadult individuals, 22 females and 5 males, were observed as well as 8 calves. BSI sizes applied are based on the age, size and the weight of the individuals (s. Appendix 8.1). Location differences within the cage and among cages were not assessed. Similar holds for the different enclosure sizes. Other than field notepads, no special equipment was used for data collection (JACOB and HUETTMANN 2007).

To optimize behavior and interaction categorisation as well as to support the uncovering of differentiated behavior schemes, the PSZ of captive muskoxen was defined to be 1m. This very short personal space zone is justified due to the 'release to supplemental feeding' setup where animals have to interact on the feeding buckets. See Appendix 8.1 and 8.3 for operational definitions.

2.2 Statistic Programs

For statistical investigations, methods were applied that have not been used in behavior research so far. This was required due to the specific nature and amount of the data. Data mining approaches through the use of algorithmic modeling (TreeNet) are conducted in order to investigate the data via multi-tree regression boosting and bagging models. S-PLUS was applied providing specific histograms to describe distance relations and diagrams displaying

interactions between individuals of one species. Meta-analysis (WORM and MEYERS 2003; WORM *et al.* 2005) are applied for comparison within and across species, as well as for management applications.

2.2.1 Modeling with TreeNet

2.2.1.1 Model Setup across Species

One multiple regression model was run for each species. Regression models are used to model a continuous outcome. They have the advantage that predictors used can be a mix of continuous and categorical variables (SALFORD SYSTEMS 2003), as is the case for our predictors (s. Appendix 8.5). Categorical variables are non-parametric (for details see SALFORD SYSTEMS 2001; 2003; STEINBERG and GOLOVNYA 2004; STEINBERG 2005).

The 'distance between individuals' embodied the target size with a varying number of predictors across species that ranged from six to eight. Five parameters were used the same across all species (except in spotted seals): 'day', 'time' in hours, the 'BSI', 'neutral interactions' and the 'dominant interactions'. Individual species predictors were always assigned to a location. The location feature is helpful to distinguish between choosing certain habitats and resources, and therefore looking for preferences and dominant status of individuals in each species. For many species, a selective and specific behavior is strongly influenced through the closeness of other individuals and their dominance hierarchy structure (Schneider 1984). Further, the grown number of trees varied by species and was chosen depending on the model output. The program TreeNet itself defines the optimum number of trees grown (s. Appendix 8.6, mean and squared absolute error).

The output for each species is presented as the gains, the mean absolute error, the mean squared error, the one variable dependence of the three most important target depending parameters to the target size, and the variable importance table (s. Appendix 8.5). The gains chart is used to judge the overall performance of a regression model for a given data set. The gains are presented in percent, and are not directly comparable to p-values, but substitute p-values in algorithmic models (Salford Systems 2003).

2.2.1.2 TreeNet model for Howling Monkeys

The howling monkey data set encloses the most BSI sizes, ranging from BSI 2 to BSI 8. The one additional species-dependent predictor describes the state of the distance measured individuals as sitting on the same tree or on different trees (s. Appendix 8.5). The optimum number of trees grown in the model is 200.

2.2.1.3 TreeNet Model for Humpback Whales

Only one location-specific predictor was applied in humpback whales, 'close to shore', describing an animal as being in a 100m range to shore or closer, or being 'offshore', when animals are further offshore than 100m (s. Appendix 8.5). BSI sizes range from BSI 4 to BSI 8. In the humpback whale model, 1000 trees are grown due to the best predictability; the mean error is the smallest possible in the 1000 tree model run.

2.2.1.4 TreeNet Model for Brown Bears

For bear species, multiple locations are defined through the whole study area. Altogether, 85 locations are defined in the brown bears population chosen through animals observed at varying locations. For the analysis, they are combined in two ways: in one approach it is defined as being either 'close to the weir' when the location is in a 30m range off the weir, or 'off weir' when bears are further away from the weir than 30m. The second approach is the bear being either 'downstream' or 'upstream', taking the weir as borderline (s. Appendix 8.5). In brown bears a 200 tree model was applied to reach the highest predictability.

2.2.1.5 TreeNet Model for Polar Bears

For polar bears, 86 locations were defined, chosen by observations of the animals (see brown bears). For the analysis, the location numbers are split into three different predictor categories: one is 'in the willow area' or 'in the coastal area' where less to no willows are present. The second is 'close to the sea shoreline' (up to about 200m) or 'inland'. The third location predictor is 'close to a tundra vehicle camp' (up to about 100m) or 'further away from a tundra vehicle camp' (s. Appendix 8.1 and 8.5). In polar bears a 200 tree model was applied for best predictability.

2.2.1.6 TreeNet Model for Spotted Seals

In spotted seals, predictor parameters vary from all the other species as this data is the most basic one and we are not able to compare across BSI sizes. The comparable parameters 'number of interacting animals', 'number of all animals in the observed group', 'time' in hours, the 'start time' of the observation period, the 'end time' of the observation period, the occurring 'neutral interactions' that took place during data collection and the occurring 'dominant interactions', are formed (s. Appendix 8.5). The optimum number of trees grown in the spotted seal model is 196. The mean error is the smallest possible in the 196 tree model run.

2.2.1.7 TreeNet Model for Muskoxen

The muskoxen data set was split in a female and a male component to make different behavior patterns apparent. As the muskoxen population is captive, this is the only population in this study where the sex and the age of each individual are known. No location-specific parameters

were collected. The only additional predictor formed in these data sets is the 'month' in which the observations took place (s. Appendix 8.5). This is the only species in which observations were conducted over more than one month (four months). The female muskoxen model is built of 921 trees to obtain the best predictability possible. The male muskoxen model was run with 200 trees.

2.2.2 Prediction Accuracy of the TreeNet Model

Although model outputs give a certain percentage of accuracy, it is difficult to compare this percentage factor with p-values and significances. As the approaches are totally different, the comparability is not fully achievable, but the strength of a certain model is found and assures applicability.

One way of achieving strength in testing is to apply cross-validation. In modeling, cross-validation is used to test the strength of the results achieved within a certain model setup. For each species, all predictors applied in each regression model were run in a classification model again including the earlier target parameter 'distance' as one further predictor and the new target parameter 'cross-validation' (STONE 1973). The target parameter 'cross-validation' tells TreeNet to build two data sets out of one data set via splitting the distance data set into two similar sized data sets. These partial data sets differ in their distance combinations. For example one sub-sample includes all distances up to 1000m distances and the second sub-sample set includes all distances between individuals over 1000m. The results of both sub-data sets were then compared and set in relation.

To test the prediction accuracy, classification models were run, the testing with the v-fold-cross-validation was set to ten and balanced class weights are used. 'Balanced' implies to upweight small classes to the equal size of the largest target class. Classification accuracy is based on how often a model classifies a record correctly or incorrectly. This model type is chosen when data should be simply tagged as 'yes' or 'no', different to the regression model applied in the regression TreeNet model run (SALFORD SYSTEMS 2003).

The predictive accuracy of the classification model is presented in a ROC (AUC) diagram. Classification trees have a ROC, continuous trees have gains showing model accuracies. The ROC represents the area under the ROC curve. In machine learning, the ROC is probably the most common model criterion used representing a measure for the overall model performance tied closely to the ability of the model to correctly rank records from most likely to not likely to be '1' or '0' (SALFORD SYSTEMS 2003).

2.2.3 Distance Histograms

We show the frequency distributions in the distance histograms with great detail to test evidences for animals being selective. All data input took place in Excel sheets. These are saved as Text files (txt) and are subsequently imported into S-Plus 8.0. For the description of distances between different individuals of one species, we focus on the BSI sizes and set the distance in relation to the BSI sizes. Histograms were only created when a minimum of 20 samples per BSI combination exist. The mean is displayed in each histogram. Due to the lack of BSI size determination in spotted seals, no histograms were build.

In Appendix 8.7 two exemplary distance histograms for patterns are shown, and as one would expect them to look like for non-social species: Distances between two individuals are either congregated around the mean (=always the same behavior) or randomly dispersed (=invariant behavior). These histograms will not be tested against the result-histograms in detail and quantitatively due to obvious differences. It is felt that visual assessments will show the differences convincingly and across species.

2.2.4 Interaction Diagrams

To display interactions that occurred in each species between different BSI sizes, S-Plus 8.0 was used. Data input took place in S-Plus manually. Results for all BSI sizes in each species are presented in one diagram. One diagram exists for neutral interactions and one shows dominant interactions. In seals, only neutral interactions are observed. In the polar bear data interactions with humans (tundra vehicles) are presented additionally as they appeared to occur regularly.

2.2.5 Meta-analysis

A Meta-analysis is applied to each species. They present a basic overview across statements made by researchers across the world and disciplines concerning the existence or negation of individual recognition and social structure in these 6 species. It is important to notice that these introduced papers present only a short but representative extract of references available. The focus is on covering the wide-ranging field of varying statements made across countries and institutions, if possible.

Meta-analysis are applied across different fields, focussing onto ecological questions with world-wide impacts (WORM *et al.* 2006) for example. Here we compare total amounts in percent of social statements or non social descriptions made through literature for each species.

3 Results

3.1 Preface

Five statistical analyses were applied and compared across the six studied species. In order to provide for a coherent picture and assessment scheme in the text, each species will be dealt with separately according to the methods mentioned above. First, data investigations via TreeNet modeling will be presented. Cross-validation via classification models will be applied across the regression TreeNet models' results to provide a strength-measure of the relationships between the target size and predictors. Then, distance histograms between different BSI combinations will be presented, focussing on specific BSI combinations that stand out in the regression TreeNet model results. Interaction diagrams, presenting all dominant interactions of all BSI combinations in one diagram and all neutral interactions of all BSI combinations in a second diagram, will be compiled. Finally, Meta-analyses will be presented to bring forward a generalizable result for the obtained social interactive knowledge in each species.

3.1.1 Preface to Modeling with TreeNet

For each species, one model with the optimum number of trees grown was generated. The same model approach was applied to all species in order to investigate the collected data consistently. In each model, the proximity (distance) represents the target size. Due to the missing BSI classification in spotted seals two different diagrams were generated: one diagram displaying the distance in relation to the number of interacting animals, a second diagram showing the relation of distance to all animals being part of the observed group (group size) while interactions occur.

In the following results, then the strongest dependent predictors will be pointed out and described in more detail is the connection as such between the BSI sizes and proximities. This is important in order to explore dominance hierarchy structures and individual perception abilities.

3.1.2 Preface to Prediction Accuracy of the TreeNet Model

In order to verify model strength, a cross-validation test was applied to each model run. The distance parameter in each data set was split in 2 samples, presenting comparable sample sizes. These two generated test data sets were assessed through a classification model run testing how findings match.

3.1.3 Preface to Distance Histograms

In each species, all distance histograms for which a minimum amount of 20 sample points existed, were generated for all possible BSI combinations. The minimum of 20 data points for distance histograms was set after investigating the data. It was focused on taking a closer look at the distance histograms of the specific BSI combinations that were standing out in the TreeNet results. First will show the 'frequency histogram of the largest distance' with over 20 data points existing, and second the 'frequency histogram of closest distance' with over 20 data points predicted by TreeNet. This concept demonstrates the relation between algorithmic modeling and traditional statistics; it tests the applicability of 'behavior modeling'. The reason for showing the frequency distributions in great detail is to provide the evidence for animals being selective.

The mean distance will be presented in each histogram as a blue vertical line. Means are included to give a better overview; they do not have a specific biological meaning. All other distance histograms will be presented in Appendix 8.6. No distance histograms for spotted seals were generated due to the BSI category impossible to determination.

3.1.4 Preface to Interaction Diagrams

For all species, two interaction diagrams will be presented; one displaying all dominant and one displaying all neutral interactions that occurred during the entire observation time between all BSI combinations. For spotted seals, only neutral interactions were observed. Therefore, only one interaction diagrams is generated displaying the relationship between numbers of neutral interactions and group size (number of individuals in group during interactions).

3.1.5 Preface to Meta-analysis

Meta-analysis will focus on relevant, best available scientific literature references providing general statements on social aspects and dominance hierarchies of the studied mammal species. The free online accessibility of articles is rare and not achieved yet. All references fitting the topic are presented, but still some could have well been missed. However, this analysis should allow for a representative picture.

Total numbers of statements undermining the occurrence of sociality and numbers of statements describing non-sociality, were compared for each species. Results will be presented in percentages.

3.2 Howling Monkeys

3.2.1 Modeling with TreeNet

In order to detect pattern existing in the howling monkey behavior data, 6 different predictors as displayed in Table 3.1 were tested in a model.

Table 3.1 Variable importance of the 200-tree howling monkey model

Predictor	Score (%)
On same tree	100.00
Body size index (BSI)	58.29
Day	29.16
Time (h)	29.01
Dominant interactions	5.58
Neutral interactions	5.41

The proximity in howling monkeys depended mainly on the spatial distribution parameter: monkeys sitting on the same tree or on different trees (100%). To a high degree, the proximity depended on the BSI sizes of the animals observed (58.29%). The day animals were observed played also a role in closeness of individuals (29.16%) (Table 3.1).

Algorithmic models do not present the power of a model run via p-values. Instead, gains of model runs are given in percent for its predictive ability. The gains of the howling monkey data had an approximate value of 75 % (Figure 3.1). This result allows for satisfactory model accuracy (SALFORD SYSTEMS 2003).

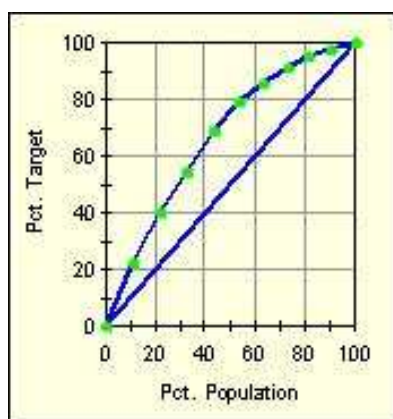


Figure 3.1 Gains of the howling monkey model

The gains chart was used to judge the overall performance of a regression model on a given data set. Pct. Target stands for the simple cumulate of the % Target in Bin; Pct. Population stands for the simple cumulate of the % Population (Salford Systems 2003). Bins are subsamples of the whole data set generated for the v-fold-cross-validation applied automatically in the regression TreeNet model run.

If the relation between the target parameter (distance) and the predictors was distributed randomly (= similar to the predictors not having any influence on the target size), the blue straight line would represent the result graph (Figure 3.1). In this case, the model would not have found relevant depending relations in the data, and the distances between individuals would count as randomly dispersed in relation to the predictor parameters. Considering the results expected in our study looking for the existence or absence of social structure, gains of 50% would display the absence of social actions and interaction, thus confirming the absence of a social structure. Animals would not be selective.

This is not the case in the howling monkey data. A social structure was found and further amplified by the following statistical approaches.

A high partial dependence of BSI combinations in Figure 3.2 amplifies that these BSI sizes stayed further apart from each other than all other BSI combinations, having a lower partial dependence. The y-axis is just a relative index, and therefore has no real units. It represents a rank of the event occurring. A partial dependence of 4 was the furthest observed distance between two individuals (40m for the howling monkey data), the lowest minus four (0m, correlating with body contact). This means that some individuals in the howling monkey group keep a notably further distance to each other than others, thus they do not behave similar. Distinct differences in distances between individuals are kept.

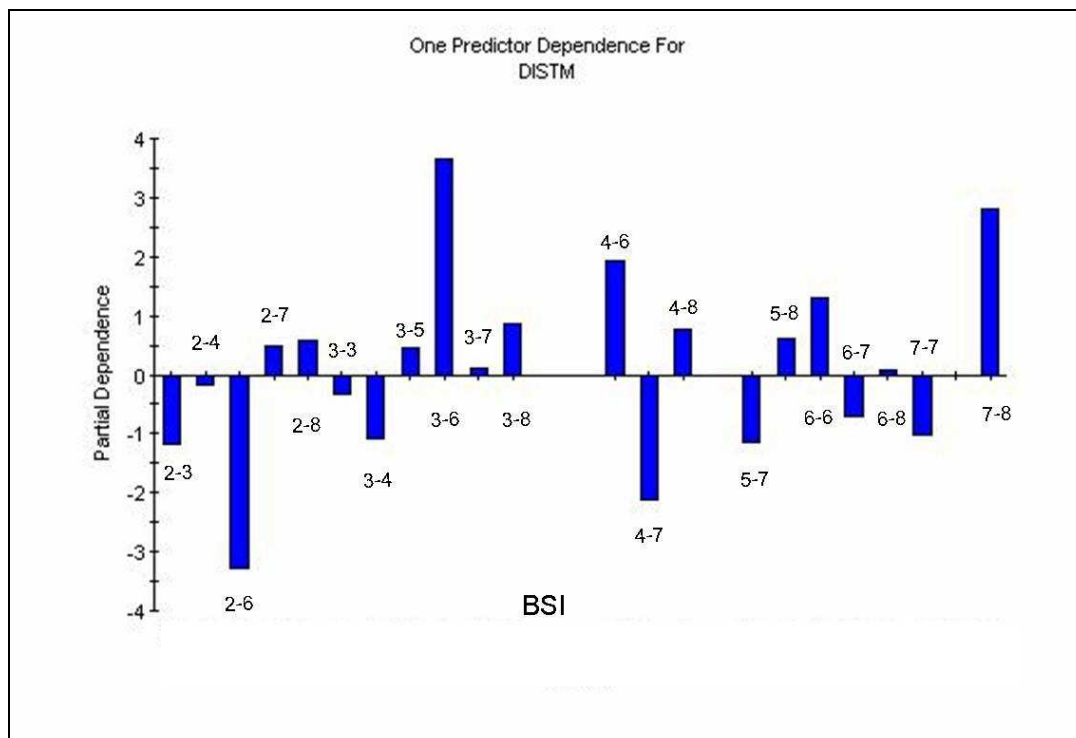


Figure 3.2 One predictor dependence (2) for howling monkeys; importance ranking 58.29%

On average, juvenile individuals kept a large distance from subadult individuals (BSI sizes 3-6 and BSI sizes 4-6). Also, adult males stayed in relatively distant positions from each other (BSI sizes 8-8). The juvenile-subadult distance data relies mainly on few data points (BSI 3-6 twelve occasions, BSI 4-6 thirty-four occasions). Thus for the BSI combination 3-6, a reduced interpretive value is assessed although the shown amplitude represents the best available data we have to date. Due to less than 20 data points existing, the BSI combination 3-6 was not presented in the distance histograms.

Infants and subadults (BSI 2-6) stayed very close to each other. Juveniles and adult females also stay close to each other (BSI 4-7). Juveniles (BSI 3-4), smaller subadults and adult females (BSI 5-7) as well as adult females among each other (BSI 7-7) keep a close average distance.

These findings showed that irregular distance patterns occurring across howling monkey body sizes also varied distinctly between certain age-class combinations and not only across age. For example all distance patterns between adult males (BSI 8) were considerably different to the pattern showing between adult males and subadults (BSI 6). Individuals of a certain age did not behave in a stereotype way towards all other age classes, rather individuals of a certain age were able to actively choose how to behave towards individuals they were interacting with.

3.2.2 Prediction Accuracy of the TreeNet Model

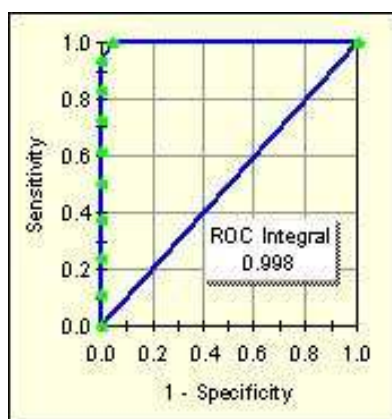


Figure 3.3 ROC curve of the howling monkey model

Table 3.2 Prediction success of the 200-tree howling monkey model

Actual Class	Total Cases	Percent Correct
1	510	99.80
2	342	98.25

The predictive accuracy of the classification model is presented in a ROC diagram (Receiver operating characteristics). The ROC is the area under the ROC curve and the most common model criterion to describe the ability of a model to correctly rank records from most likely (1) to not likely (0). The ROC curve compares the two predictor classes (1 and 2, s. Table 3.2)

validating the categories chosen for the classification model. These two classes were created via splitting the distances kept between animals in two sub-samples: one existing of all distances within a certain distance range (e.g. up to 1000m) and the other category existing of all distances above that certain distance range (e.g. above 1000m). To reach comparable sample size (342 and 510) the data splitting distance was chosen to be 10m for the howling monkey data.

Figure 3.3 shows the accuracy of the classification model being 0.998. An accuracy of 1 would be a statistical complete fit, an accuracy of zero means no fit. Thus, a good predictability of the model existed. One should keep in mind that such fits are based on the quality and structure of the empirical data used. No complete fit is real. Ecological and behavior data is never collected completely and always includes mistakes and is biased to some amount.

3.2.3 Distance Histograms

Twelve distance diagrams were built with the howling monkey data. The histograms not presented in the results, are to be found in Appendix 8.6.

Frequency histogram of largest distance proximities

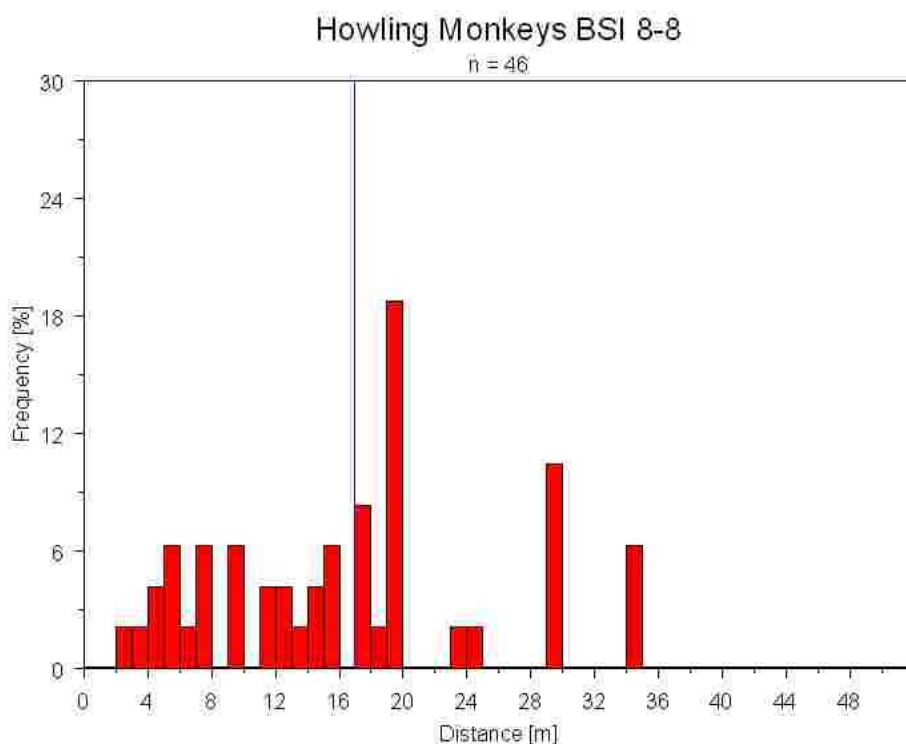


Figure 3.4 Distance histogram for the interacting BSI sizes 8 vs. 8 in howling monkeys; the vertical blue line represents the mean

Adult males are never observed closer than 2m from each other. The mean distance they kept is 17m (Figure 3.4) and the highest deflection is located around 20m. Important to notice is that there was no constant pattern as it would be expected in social species that make conscious and strategic decisions towards individuals. Differences between same BSI sizes show a 'noisy structure' with one main peak at 20m, which further supported the notion that howling monkeys show distinct social responses to other individuals; thus, they were able to differentiate other individuals and adjust their behavior accordingly.

Frequency histogram of closest distance proximities

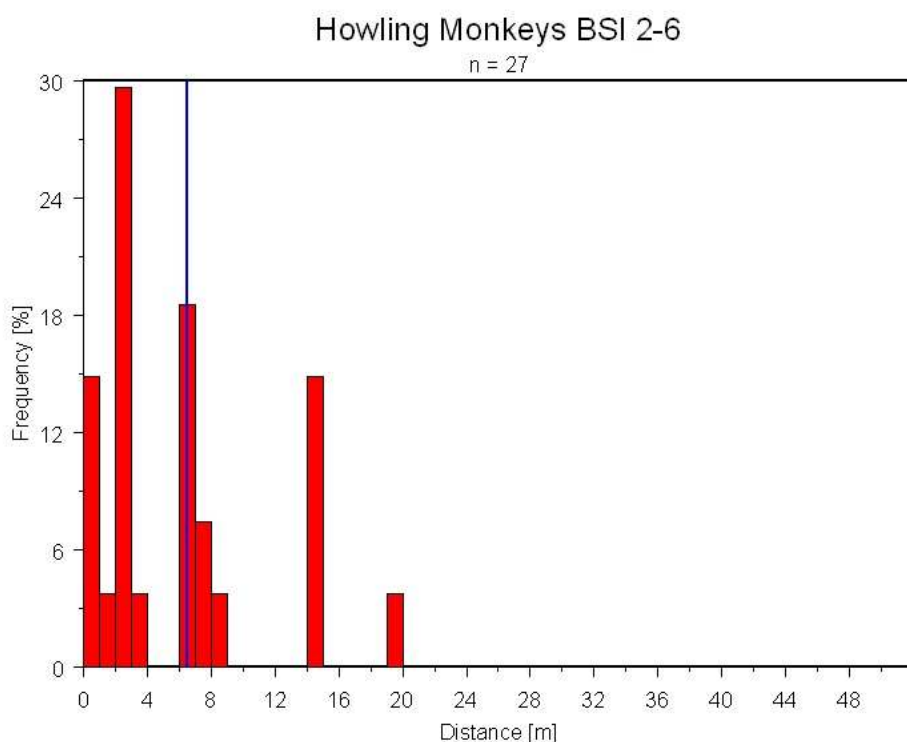


Figure 3.5 Distance histogram for the interacting BSI sizes 2 vs. 6 in howling monkeys; the vertical blue line represents the mean

Infants were not only close to their mothers, they were also close to subadults. The pattern showed three separate peaks with a mean distance of 6.5m, indicating the existence of social relations between very young howlers and individuals others than their mother. The mothers tolerated some subadults being close to their offspring, but for others they do (Figure 3.5).

All distance histograms of the howling monkey data show similar choosing patterns and varying distances across BSI sizes.

3.2.4 Interaction Diagrams

Detailed descriptions of observed interactions and their classification are presented in Appendix 8.3.

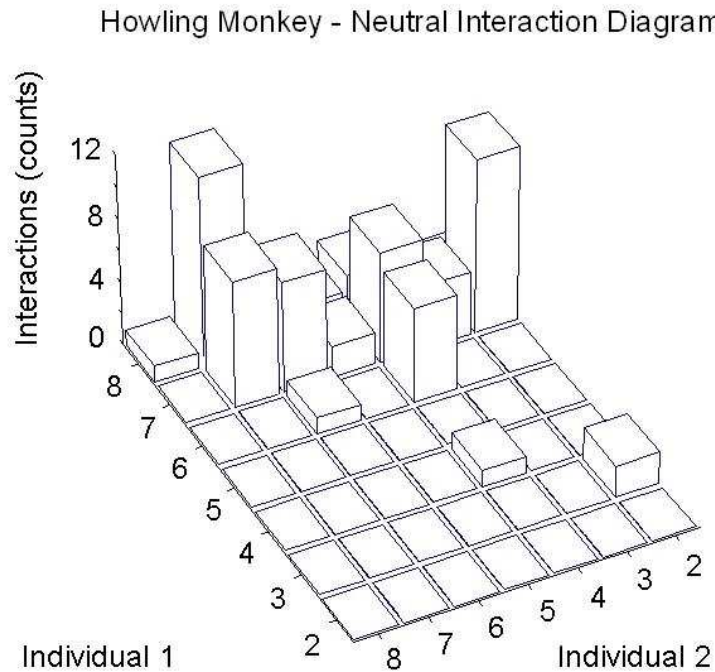


Figure 3.6 Neutral interactions in howling monkeys across BSI sizes; numbers on x- and y-axis represent BSI sizes (for detailed definition s. Appendix 8.1)

In most neutral interactions between howling monkeys, adult females (BSI 7) were involved. The highest counts of interactions occurred between adult females and adult males (12 interactions) as well as between adult females and infants (11 interactions). Adult females further interacted very frequently with other adult females. No flat similar interaction surface existed; no uniform behavior scheme was displayed in howling monkeys. Not all individuals and body sizes interacted with each other and different amounts of interactions occurred across BSI sizes. These findings state the existence of actively choosing behavior, and therefore confirm the existence of a social structure.

Howling Monkey - Dominant Interaction Diagram

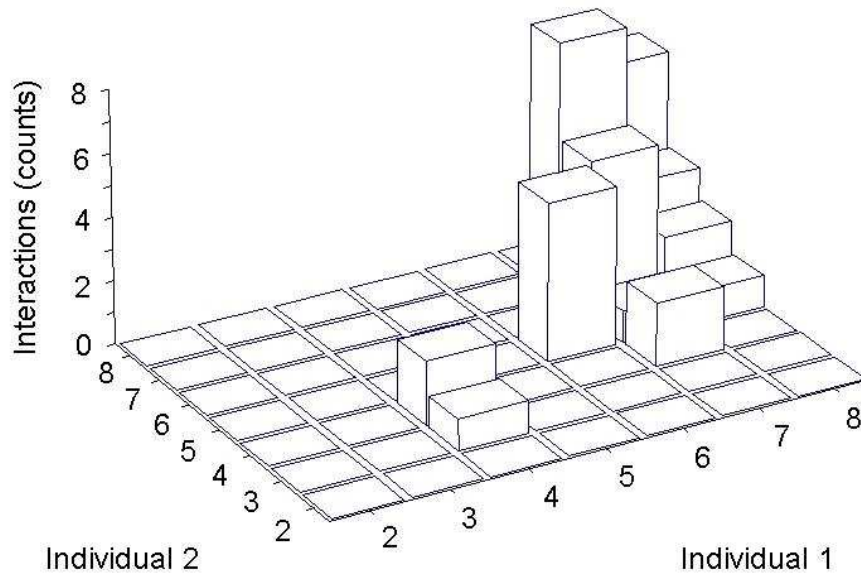


Figure 3.7 Dominant interactions in howling monkeys across BSI sizes; Individual 1 is dominant over Individual 2; numbers on x- and y-axis represent BSI sizes (for detailed definitions see Appendix 8.1)

Not only neutral interactions also dominant actions are performed most frequently by adult females, followed closely by adult males. In dominant howling monkey interactions the animal with the higher BSI always seemed to dominate. Only in adult individuals (BSI 7 and 8) and in juveniles (BSI 4) dominant interactions between animals of the same BSI took place. This shows the existence of a dominance hierarchy and suggests the existence of a linear hierarchy across body sizes.

3.2.5 Meta-analysis

Overall, statements showed the existence of all social features expected (Table 3.3). Howling monkeys are described as being social throughout literature with 95.8% of the studies reviewed being in agreement. All state the existence of social traits, the existence of individual recognition and only one early study concludes that dominance hierarchy in howling monkeys is not existent. For howling monkeys 8 of 8 major references on social issues state the existence of

Table 3.3 Meta-analysis of howling monkeys (*Alouatta Palliata*)

Publication type	Author / Year / Title	Country institution	Research population	Study length	Social aspects	Dominance hierarchy	Individual recognition	Remarks
Journal paper	Young 1983 "An example of 'apparent' dominance-submission behavior between adult male howler monkeys (<i>Alouatta palliata</i>)"	USA	Panama - Barro Colorado Island	6 month	yes	no	yes	no evidence for hierarchy among males within a troop
Journal paper	Crockett and Pope 1988 "Inferring patterns of aggression from red howler monkey injuries"	USA	Venezuela - Llanos	6 years, 30 month	yes	yes	n/a	
Journal paper	Glander 1992 "Dispersal patterns in Costa Rica mantled howling monkeys"	USA	Costa Rica - Hacienda La Pacifica	20 years	yes	yes	yes	
Journal paper	Clarke et al. 1998 „Infant-nonmother interactions of free-ranging mated howlers (<i>Alouatta palliata</i>) in Costa Rica"	USA	Costa Rica - Hacienda La Pacifica	22 month	yes	yes	yes	variability in social group size
Journal paper	Zucker 1998 "Agonistic and affiliative relationships of adult female howlers (<i>Alouatta palliata</i>) in Costa Rica over a 4-year period"	USA	Costa Rica - Hacienda La Pacifica	4 years, 955h	yes	yes – different opinions on structures exist	yes	social relationships in groups are dynamic
Journal paper	Dias & Luna 2006 "Seasonal changes in male associative behavior and subgrouping of <i>Alouatta palliata</i> on an island"	Spain / Mexico	Mexico – Agaltepec Island	1 year, 1935 scans	yes	yes	yes	fission-fusion social structure
Journal paper	Bezanson et al. 2007 "Pattern of subgrouping and spatial affiliation in a community of male howling monkeys (<i>Alouatta palliata</i>)"	USA	Costa Rica – Ometepe Island	2 years, 255h	yes	yes	yes	large stable groups fragmented into subgroups
German M.Sc. thesis (this study)	Jochum 2008 "Benefits of using marginal opportunistic wildlife behavior data"	Germany / USA	Costa Rica – Ometepe Island	2 weeks	yes	yes	yes	fission-fusion social structure
Final Scores					8 / 8 – 100%	7 / 8 – 87.5%	7 / 7 – 100%	= 95.8% social

social traits, 7 of 8 the existence of a dominance hierarchy and 7 of 7 their ability to individual perception.

Overall, a statistically ‘noisy’ pattern occurred between all BSI sizes. No consistent and standardized patterns occurred in any age class, as one would expect to find if animals would have a regular social response. Noisy pattern, as found here, were predicted and expected for a social species with a well structured dominance hierarchy. This sets a baseline pattern for a species with a known social structure.

3.3 Humpback Whales

3.3.1 Modeling with TreeNet

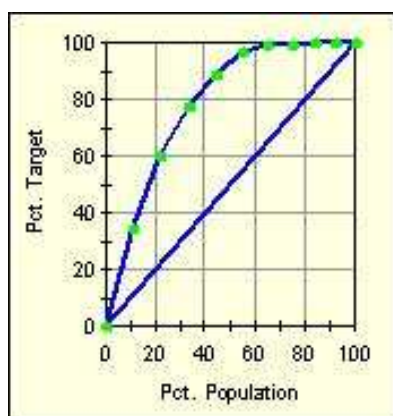
In humpback whales six parameters are brought in relation to proximity, and applied in the model (Table 3.4) in order to search for underlying patterns in the data.

Table 3.4 Variable importance of the 999-tree humpback whale model

Predictor	Score (%)
Body size index (BSI)	100.00
Time (h)	51.71
Being close to shore	46.38
Day	43.58
Dominant interactions	22.64
Neutral interactions	19.54

The BSI was the most dependant predictor influencing the distance kept between individuals of different sizes (100%). Time played an important role as a predictor as well, showing dependence to the morning and evening hours (51.71%). The spatial parameter, the ‘closeness of individuals to the shoreline’, influenced the distances kept between individuals of different BSI sizes too (46.38%). Also the predictor ‘day’ had an effect on distances kept between individuals. Conclusively, these results show that body size was playing a crucial role for distances kept between individuals. They further kept different distances to each other in the morning than in the evenings. Therefore, it appears that the time budget of a humpback whale is split in different behaviors displayed in the morning and in the evening (e.g. feeding, travelling). The spatial predictor had an influence as well (46.38%). Interactions play the least important role. This

implicated that the distances animals kept from each other depended only to a minor extent on occurring interactions.



The gains of the humpback whale data have an approximate value of 90 % (Figure 3.8), allowing for a rather good model prediction.

Figure 3.8 Gains of the humpback whale model

The y-axis is a relative index, and has no real units. A partial dependence of 3000m was the furthest observed distance between two individuals (8000m in the humpback whale data), the lowest minus 1000 (here 1m) showing different distances kept between different BSI combinations and thus dependant behavior displays.

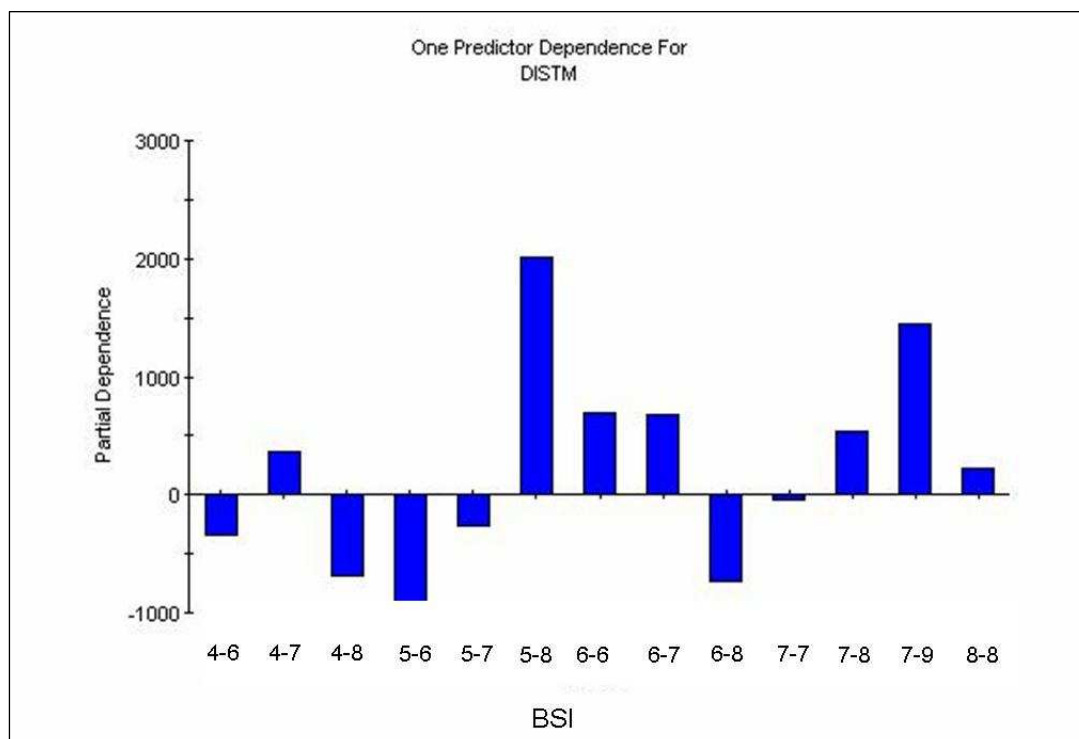


Figure 3.9 One predictor dependence (1) for humpback whales; importance ranking 100%

The BSI sizes 5 and 8 stay apart from each other above average, as well as the BSI sizes 7 and 9. Less than 20 data points were collected for both of these BSI combinations. Therefore, they

have a reduced interpretive value but represent the best available data. These BSI combinations are not presented in distance histograms. The next largest distances kept between BSI sizes were found for the combination 6-6.

Relative closeness between individuals was found in the similar BSI sizes 5 and 6 and the BSI combination 6-8. Thus a preference of animals with close BSI sizes, to keep a further distance from each other, existed. These patterns reveal selective behavior across body sizes, and thus a social trait in humpback whale populations.

3.3.2 Prediction Accuracy of the TreeNet Model

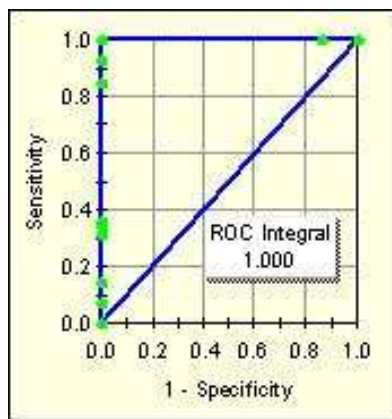


Figure 3.10 ROC curve of the humpback whale model

Table 3.5 Prediction success of the 999-tree humpback whale model

Actual Class	Total Cases	Percent Correct
1	226	100.00
2	241	100.00

For humpback whales distance categorisation, the cross-validation predictor split the data into sub-samples at 500m resulting into comparable sample sizes of 226 and 241 data points (Table 3.5). This approach was applied to test the accuracy of the regression model.

Figure 3.10 shows the accuracy of the humpback whale classification model. A 100% match of model distance categories is described. Both partial data-sets predicted exactly the same dependencies. This exact match showed that the model can explain all the data but the real ecological meaning is somewhat unclear. A complete predictability is usually never achievable in ecology and behavior biology, and likely somewhat of an artefact. However, the trend that sociality exist remains clear.

3.3.3 Distance Histograms

Nine distance histograms for humpback whales were generated with a minimum of 20 samples. The histograms not presented here can be found in Appendix 8.6.

Frequency histogram of largest distance proximities

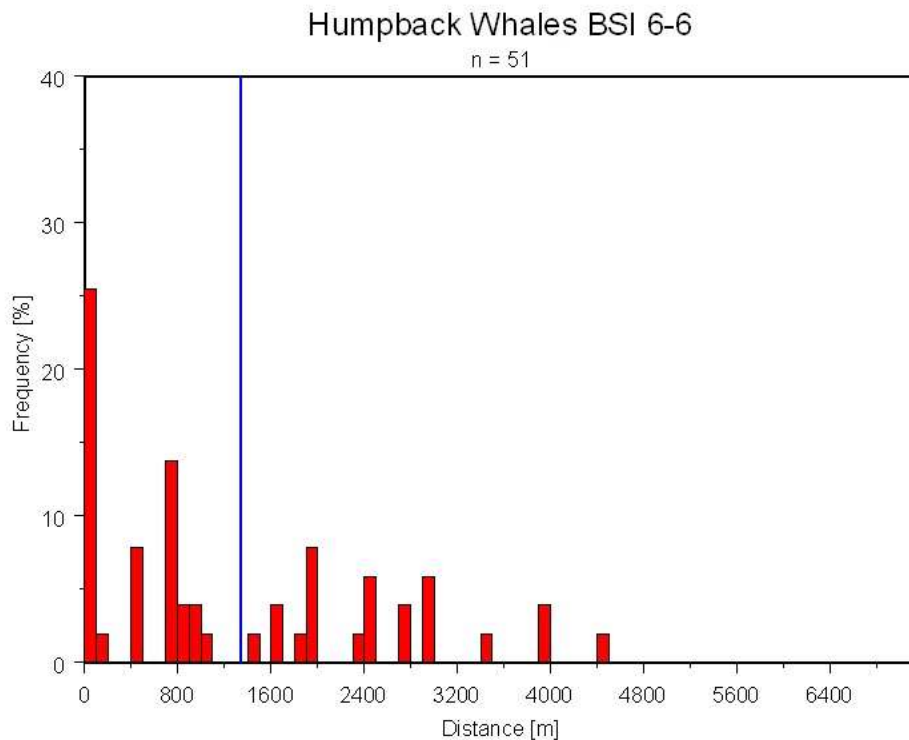


Figure 3.11 Distance histogram for the interacting BSI sizes 6 vs. 6 in humpback whales; the vertical blue line represents the mean

For humpback whales, the furthest distance from each other maintained animals of similar size (BSI size 6-6). They were observed to keep a distance between 1m and 4500m and had a mean distance of 1400m. There was no constant pattern; their distances were spread across the whole distance range. Still, the closer they were to each other, the more data points existed (Figure 3.11). This patchy irregular pattern states the existence of actively choosing behavior and thus social traits existing in humpbacks, here in the BSI size 6.

Frequency histogram of closest distance proximities

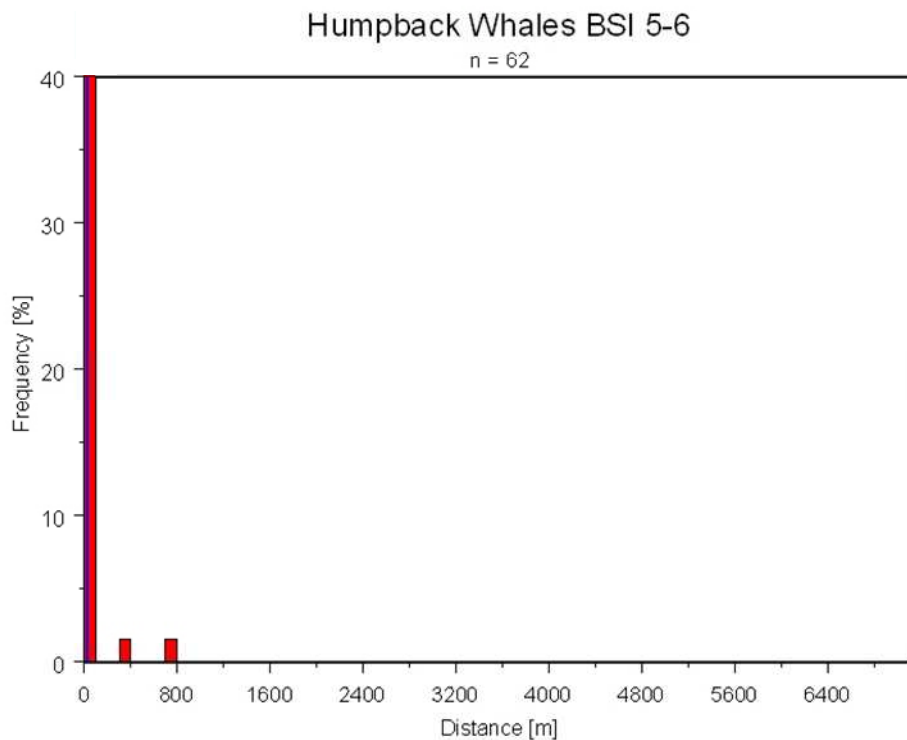


Figure 3.12 Distance histogram for the interacting BSI sizes 5 vs. 6 in humpback whales; the vertical blue line represents the mean; the first interval (0m-100m) is cut off, ranging normally up to 88%

Humpback whale individuals of the BSI sizes 5 and 6 tended to stay close. They preferred to stay within a very close range of less than 100m. The furthest distance observed was 800m (Figure 3.12). A strong association pattern revealed showing social bonding under a distance of 100m. Bonding, representing a social trait, occurred only between certain individuals of the population although they had the same BSI size as other not bonding individuals. This result indicates the existence of selective behavior based on recognition in humpback whales. Judged by these major distance peaks and distinguished behaviors, a social relationship and selective behavior actions are expected.

3.3.4 Interaction Diagrams

Detailed descriptions of observed interactions and their classifications are presented in Appendix 8.3.

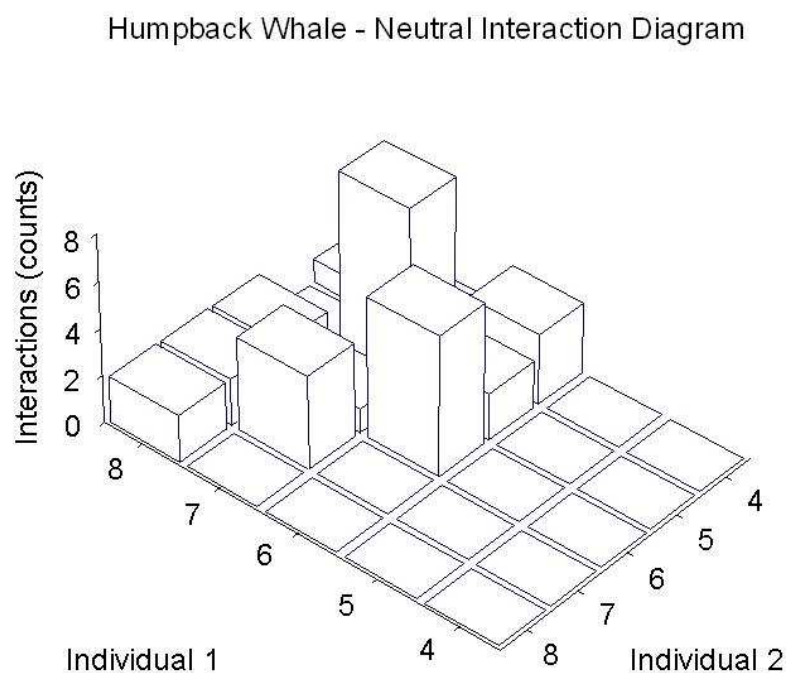


Figure 3.13 Neutral interactions in humpback whales across BSI sizes; numbers on x- and y-axis represent BSI sizes (for detailed definitions Appendix 8.1)

Larger humpback whale individuals interacted more often in a neutral manner than smaller ones. Most commonly, the BSI sizes 5 and 7 followed by the BSI combinations 6-6 and 7-7 interacted neutrally (Figure 3.13). The BSI size 8 interacted with most different BSI sizes in a non-dominant way. Differentiated interactions occurred in humpback whales in a similar manner as in howling monkeys and thus are in support of the existence of a social structure.

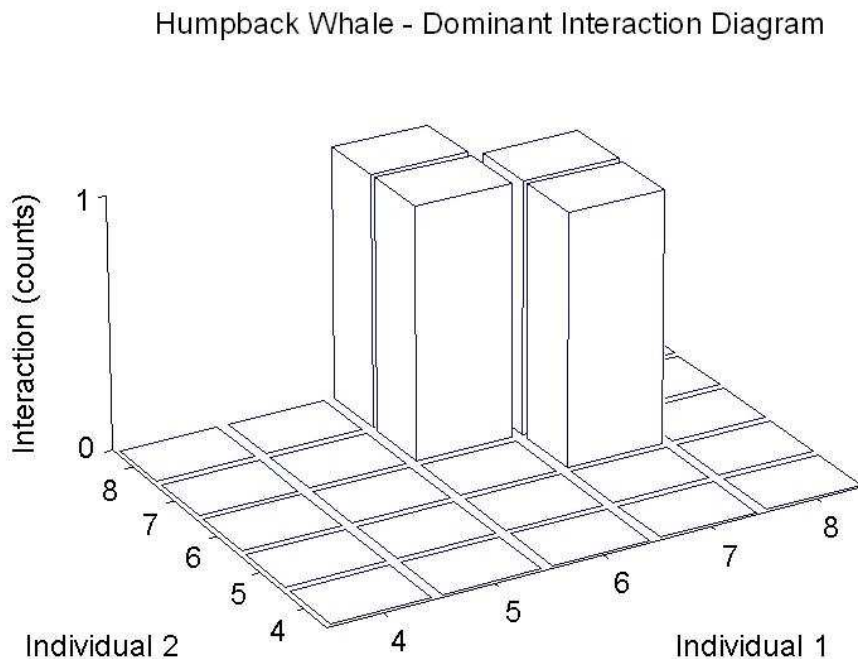


Figure 3.14 Dominant interactions in humpback whales across BSI sizes; Individual 1 is dominant over Individual 2; numbers on x- and y-axis represent BSI sizes (for detailed definition s. Appendix 8.1)

Dominant interactions in humpback whales were only performed by individuals of the BSI size 6 and larger and are rarely observed. Thereby, individuals with a BSI size 6 were dominant over those with BSI sizes 7 and 8. Humpbacks with a BSI size 7 were only observed to act dominant over the BSI sizes of 6 and 7. No dominant interactions occurred between the BSI size 7 and 8 (Figure 3.14). This indicates that animals with BSI 6 were the most dominant ones, although it should be kept in mind that the sample size was very small for humpback whales. Overall, these differentiated patterns were in favour of the existence of a dominance hierarchy.

3.3.5 Meta-analysis

In humpback whales, all references consulted conclude to humpback whales being highly social. The score is 100% for social aspects, for the existence of dominance hierarchies as well as for individual recognition abilities.

Table 3.6 Meta-analysis of humpback whales (*Megaptera novaeangliae*)

Publication type	Author / Year / Title or Affiliation	Country institution	Research population	Study length	Social aspects	Dominance hierarchy	Individual recognition	Remarks
Journal paper	Tyack and Whitehead 1983 "Male competition in large groups of wintering humpback whales"	USA	USA - Hawaii	n/a	yes	yes	n/a	males compete for access to females
Journal paper	Silber 1986 "the relationship of social vocalisations to surface behavior and aggression in the Hawaiian humpback whale (<i>Megaptera novaeangliae</i>)"	USA	USA - Hawaii	2 years, 8 month	yes	yes	yes	males compete aggressively for access to females
Journal paper	Clapham 1996 "The social reproductive biology of humpback whales: An ecological perspective"	USA	worldwide-review	n/a	yes	yes	n/a	small unstable groups are characteristic
Journal paper	Marino 2002 "Convergence of complex abilities in cetaceans and primates"	USA	worldwide-review	n/a	yes	yes	yes	fission-fusion social structure exhibited
Journal paper	Spitz et al. 2002 "The relation of body size of male humpback whales to their social roles on the Hawaiian winter grounds"	USA	USA - Hawaii	3 years, 11 month	yes	yes	yes	existence of short-term dominance hierarchies
Journal paper	Valsecchi et al. 2002 „ Social structure in migrating humpback whales (<i>Megaptera novaeangliae</i>)"	Australia	USA - Hawaii	1 year, 2 seasons	yes	yes	yes	fission-fusion nature in societies
German M.Sc. thesis (this study)	Jochum 2008 "Benefits of using marginal opportunistic wildlife behavior data"	Germany / USA	Canada – Pacific Coast	2 weeks	yes	yes	yes	Germany /USA
Final Scores					7 / 7 – 100%	7 / 7 – 100%	5 / 5 – 100%	= 100% social

3.4 Brown Bears

3.4.1 Modeling with TreeNet

In order to search for patterns in the brown bear behavior data via data-mining, 7 predictors are tested in the model (Table 3.7).

Table 3.7 Variable importance of the 199-tree brown bears model

Predictor	Score (%)
Body size index (BSI)	100.00
Day	92.76
Being up river from weir	82.38
Time (h)	69.36
Being close to weir	54.83
Neutral interactions	41.72
Dominant interactions	15.45

The highest scoring distance influencing predictor was the BSI (100%), stating a high impact of animal's body size on their spatial distribution. The predictor 'day' played a fairly important role as well (92.76%), implying changes in distances kept between individuals through the observation month. The proximities maintained between individuals was dependent on the spatial parameter 'being upriver from the weir' (82.38%) in relation to 'being downriver from the weir'. The salmon weir represented a borderline for this definition. This shows that habitat had an influence on individual distribution. Again, the interactions occurring are the least important predictors.

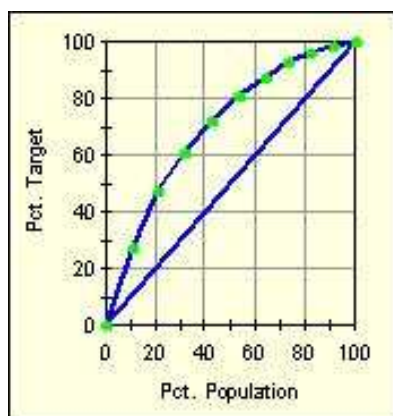


Figure 3.15 Gains of the brown bear model

The gains of the brown bear data have an approximate value of 80 % (Figure 3.15) allowing a fairly good prediction accuracy.

In Figure 3.16 the partial dependence of 120 displays the furthest observed distance between two individuals (2200m for the brown bear data), the lowest distance between individuals was displayed at minus 60 (0m for brown bears). The y-axis is just a relative index, and thus has no real units.

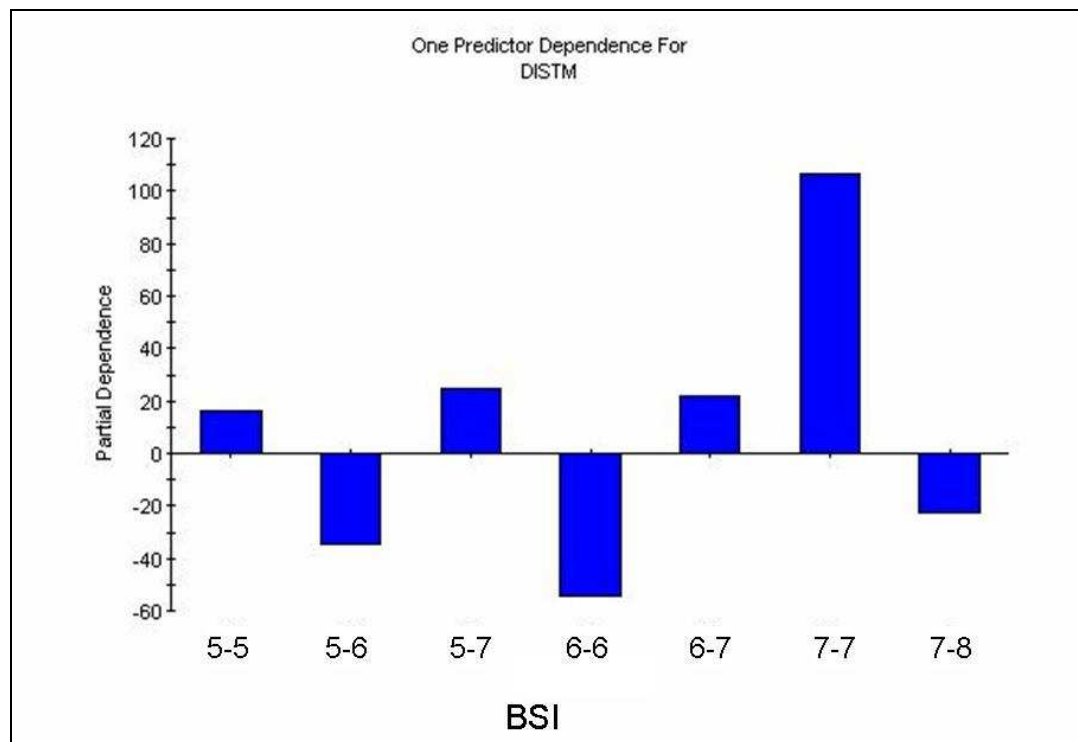


Figure 3.16 One predictor dependence (1) for brown bears; importance ranking 100%

Adult males were observed rarely during early morning hours and during data collection only once (BSI 7-8). Adult females (BSI 7-7) kept the furthest distance from each other. Small subadults and adult females (BSI sizes 5-7) stayed second furthest apart, closely followed by larger subadults and adult females (BSI sizes 6-7). Adult females showed furthest distances to all age classes. Larger subadults of the same BSI (6-6) had a short mean distance from each other as do smaller and larger subadults (BSI 5-6). Less than 20 data points existed for the BSI combinations 5-5- and 7-8. They are not presented in distance histograms.

3.4.2 Prediction Accuracy of the TreeNet Model

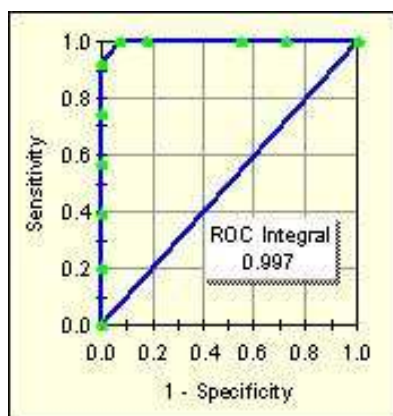


Figure 3.17 ROC curve of the brown bear model

Table 3.8 Prediction success of the 199-tree brown bear model

Actual Class	Total Cases	Percent Correct
1	177	100.00
2	214	99.53

The distance categorisation for the prediction accuracy in brown bears was split at 100m into sample sizes of 177 and 214 data points (Table 3.8).

The predictive success of the brown bear classification model was 0.997 (Figure 3.17), presenting a good model and fitting most of the data.

3.4.3 Distance Histograms

For the brown bear data, five histograms were generated with a minimum of 20 samples. For histograms not presented here see Appendix 8.6.

Frequency histogram of largest distance proximities

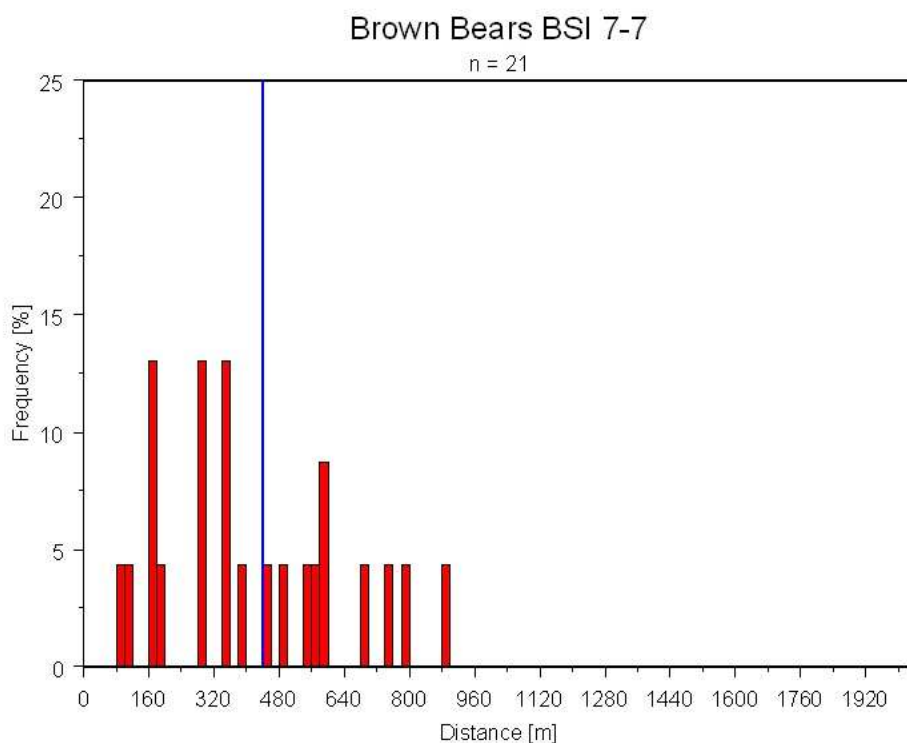


Figure 3.18 Distance histogram for the interacting BSI sizes 7 vs. 7 in brown bears; the vertical blue line represents the mean

The furthest mean distance kept between brown bears existed between adult females (Figure 3.18). They were never found to be closer to each other than 80m. The mean distance between them was displayed at 440m stating their tendency to stay apart. As not many adult females with cubs of the year or first year cubs were observed, this may have influenced the far distance kept to a certain degree. Nevertheless, a distinct pattern was obvious. Data points were dispersed irregularly in the results, describing selective behaviors between individuals of BSI sizes 7.

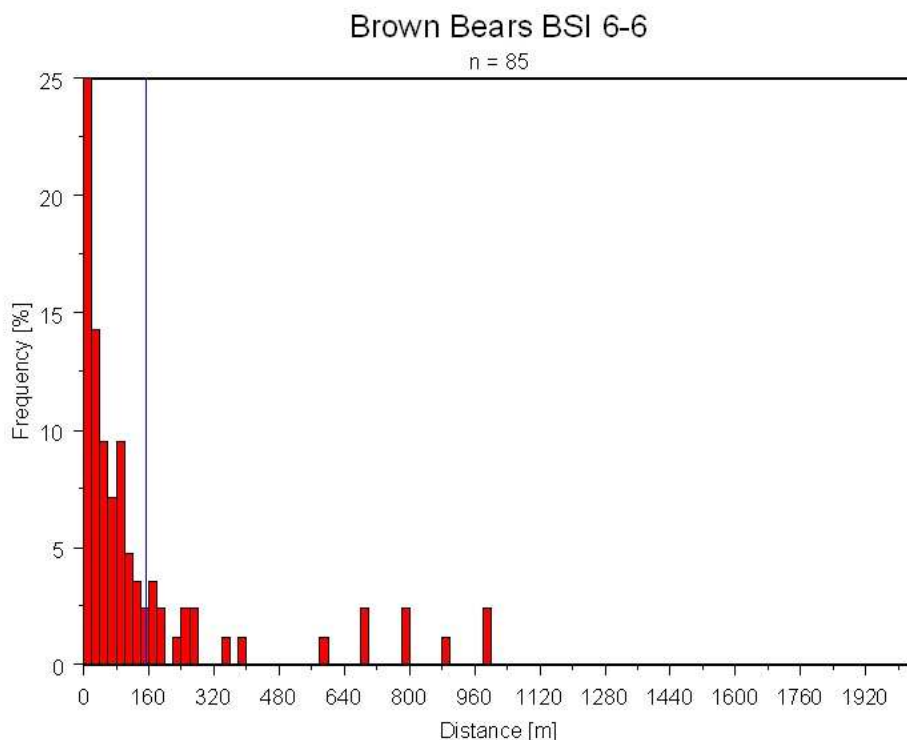
Frequency histogram of closest distance proximities

Figure 3.19 Distance histogram for the interacting BSI sizes 6 vs. 6 in brown bears; the vertical blue line represents the mean

Subadult individuals of the same age (BSI 6-6) kept close proximities to each other. Most data was recorded in close distances but observations showing a larger distance up to 1000m existed (Figure 3.19). The mean distance-average was 160m. The biological meaning of this distinct varying pattern once more supports the existence of a social structure and predicts brown bear's ability to individual perception.

3.4.4 Interaction Diagrams

Detailed descriptions of observed interactions and their classifications are presented in Appendix 8.3.

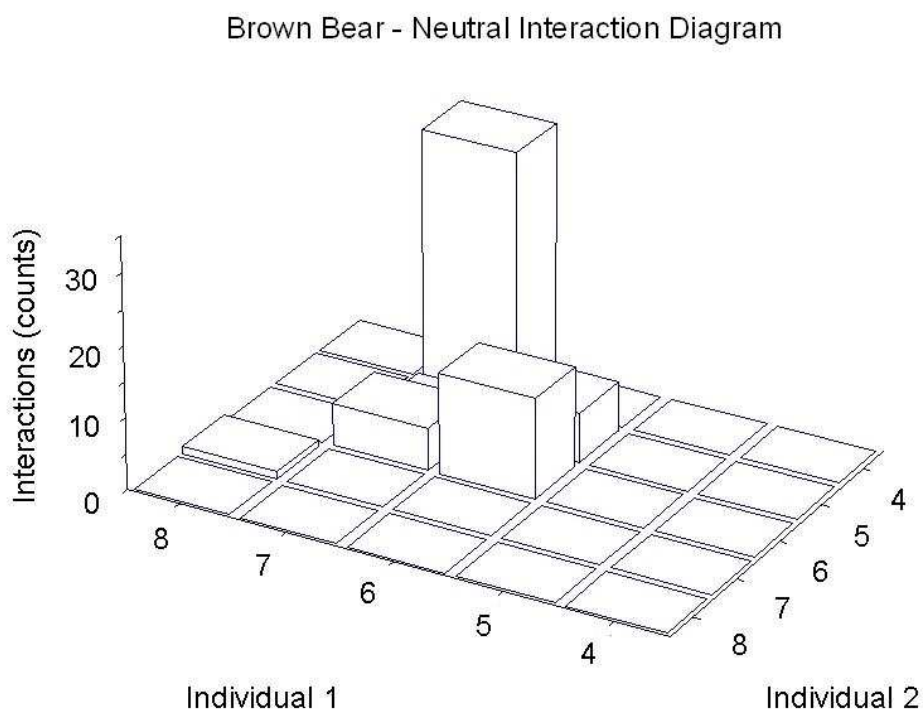


Figure 3.20 Neutral interactions in brown bears across BSI sizes; numbers on x- and y-axis represent BSI sizes (for detailed definition s. Appendix 8.1)

Most neutral interactions were performed by adult females (BSI 7) interacting with their juvenile cubs (BSI 4) (main data from one female with second year cub). On occasion, they were also observed interacting with subadults in a neutral manner. Subadults interacted with each other frequently and without exhibiting relevant dominance behavior (Figure 3.20). An adult male interacting with an adult female was observed only on one occasion during early morning. Altogether, a differentiated interaction scheme occurs what strongly suggests the existence of a social structure in brown bears.

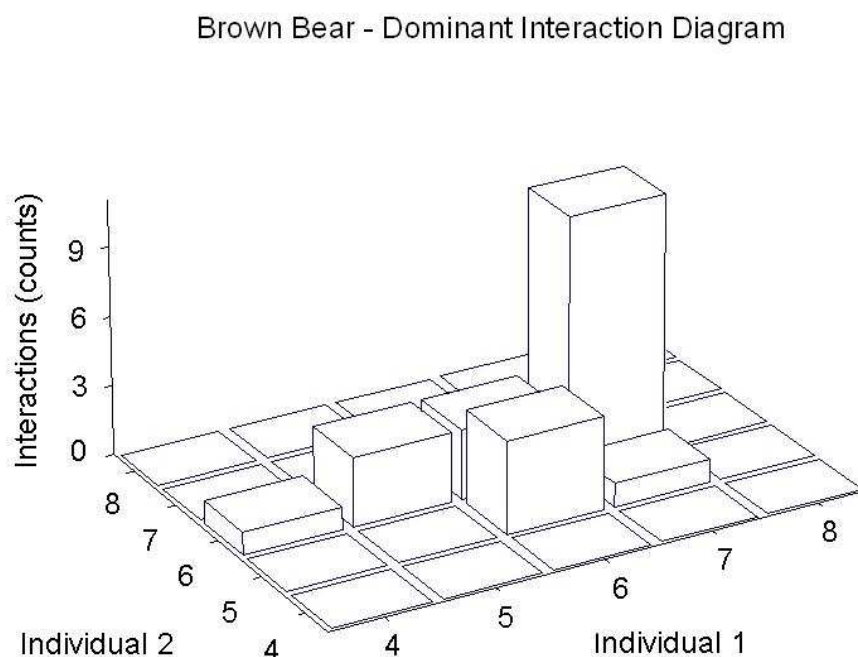


Figure 3.21 Dominant interactions in brown bears across BSI sizes; Individual 1 is dominant over Individual 2; numbers on x- and y-axis represent BSI sizes (for detailed definition s. Appendix 8.1)

Adult females interacted most often in a dominant fashion, and were dominating all subadult individuals. Subadults of the BSI 6 were more often dominant over subadults of the BSI 5 than the other way around; although both dominance relations existed (Figure 3.21). The only occasion, where the juvenile was dominant over the subadult, occurred when the adult female was close by. Differentiated dominance relations were clearly observed, and thus provide strong evidence for the existence of a dominance hierarchy.

3.4.5 Meta-analysis

Brown bears are quite well studied animals for most aspect. Dominance hierarchies such as shown here are increasingly described and social structure starts to get noticed. Clear evidence is forming strongly on this topic. However, the majority of policies, managers and many researchers still state that brown bears are solitary non-social species (MILLER *et al.* 2003; BELLEMAIN *et al.* 2006). This is particularly true for the North American continent. The meta-analysis of published literature concluded to 79.4% in favour of sociality (Table 3.9).

Table 3.9 Meta-analysis of brown bears (*Ursus arctos*)

Publication type	Author / Year / Title	Country institution	Research population	Study length	Social aspects	Dominance hierarchy	Individual recognition	Remarks	
Journal papers	Egbert and Stokes 1976 "The Social Behaviour of Brown Bears on an Alaskan Salmon Stream."	USA	USA - Alaska - Mc Neil River	2 years	n/a	yes	no	typically solitary; social affiliations restricted to family groups; simple social system	
Journal papers	Gende and Quinn 2004 "Relative importance of prey density & social dominance in determining energy intake by bears feeding on Pacific Salmon"	USA	USA - Alaska - NE Chichagof Island	2 years	yes	yes	n/a	reproductive advantage of social dominance	
Journal papers	Støen et al. 2005 "Kin-related spatial structure in brown bears <i>Ursus arctos</i> ."	Europe - Scandinavia	Norwegian, Sweden	18 years	yes	n/a	n/a	spatial social structure, social organization	
Journal papers (Ursus)	Mc Lellan 2005 "Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival"	Canada	Canada - British Columbia	25 years	n/a	yes	yes - males recognize females	removing dominant males is the right management strategy as it will always reduce infanticide	
Journal papers	Smith et al. 2005 "Alaskan brown bears, humans, and habituation"	USA - Alaska (USGS)	USA - Alaska	104 years, 515 incidents	yes - social interactions exist	yes	n/a	understanding of social bear interactions will help to better manage human activities and reduce bear-human conflicts	
Journal papers (Ursus)	Stenhouse et al. 2005 "Grizzly bear associations along the eastern slopes of Alberta"	Canada - Alberta	Canada - west- central Alberta	5 years	yes	yes	yes	human activity that affects grizzly bear associations could disrupt social behavior and reproduction	
Journal papers	Bellemain et al. 2006 "Mating strategies in relation to sexually selected infanticide in a non-social carnivore: the brown bear"	Europe - Scandinavia	Norwegian, Sweden	2 years	no - non-social species	n/a	yes - adult males	mating partner recognition through males performing sexually selected infanticide	
German M.Sc. thesis (this study)	Jochum 2008 "Benefits of using marginal opportunistic wildlife behavior data"	Germany / USA	USA – Alaska, Chilkoot River	4 weeks	yes	yes	yes		
Final Scores						5 / 6 – 83.3%	6 / 8 – 75%	4 / 5 – 80%	= 79.4% social

3.5 Polar Bears

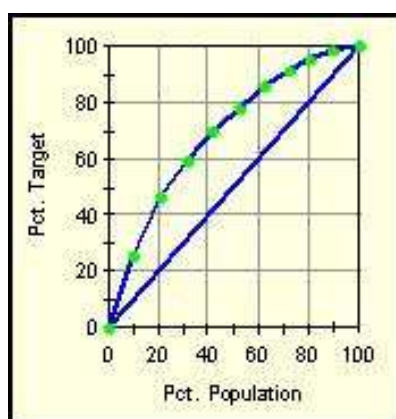
3.5.1 Modeling with TreeNet

Eight predictors are tested in the polar bear model run in order to reveal underlying pattern in the data. The predictor 'dominant interactions' had no influence on the distances between individuals and is therefore not listed in Table 3.10.

Table 3.10 Variable importance of the 200-tree polar bear model

Predictor	Score (%)
In the willow area	100.00
Body size index (BSI)	39.76
Close to a buggy camp	28.95
Time (h)	18.54
Day	12.19
Close to the sea	11.78
Neutral interactions	4.63

The spatial distribution 'being in the willow area' or in the more open habitat was the most dependent predictor to determine proximities between polar bears (100%). The BSI influenced the distances between individuals to 39.76%. As in the other three species just described, spatial distributions as well as body sizes of individuals differed greatly across distances kept. The 'closeness to a tundra vehicle camp' affected the proximity between polar bears as well (28.95%). These results show the existence of a highly variable system.



The gains of the polar bear data have an approximate value of 75 % (Figure 3.22). This result allows for still satisfying model accuracy.

Figure 3.22 Gains of the polar bear model

The y-axis presents a relative index, and has no real units. The partial dependence of 800 displayed the furthest observed distance between two individuals (6500m in the polar bear data), the lowest was minus 400 (0m in polar bears) (Figure3.23).

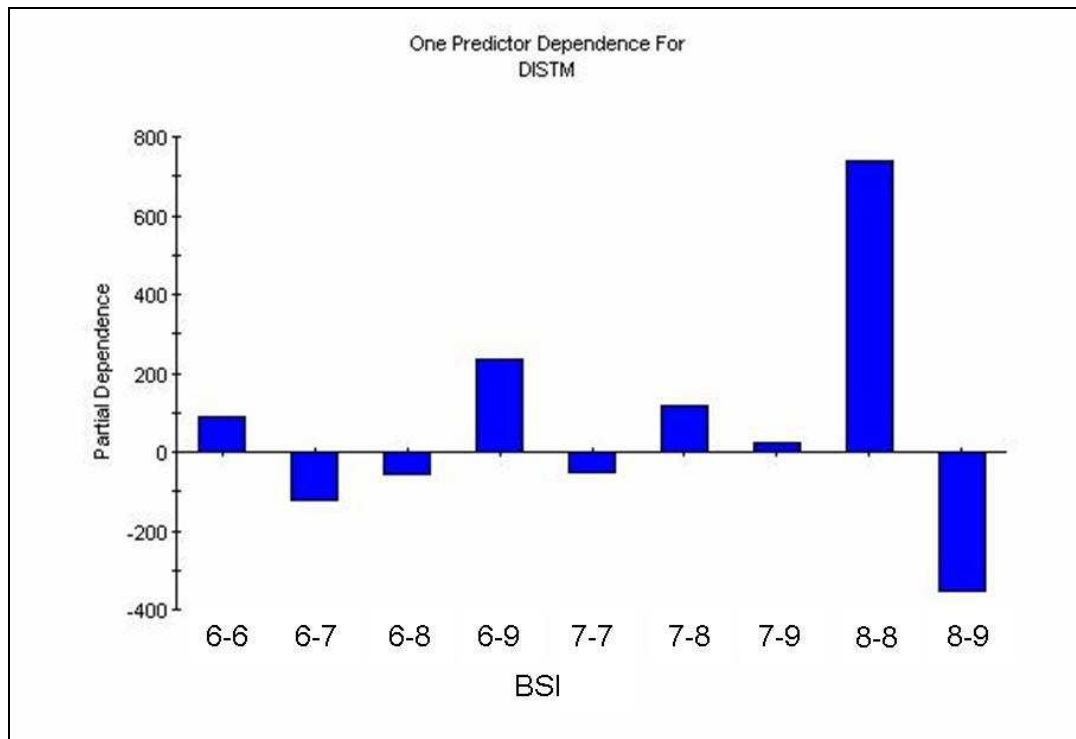


Figure 3.23 One predictor dependence (2) for polar bears; importance ranking 39.76%

Less than 20 samples exist for same-sized adult males (BSI 8-8) as well as between same-sized subadults (BSI 6-6). Therefore, both have a reduced interpretive value but represent the best available data we have. They are not presented in the distance histograms. The high interpretive value data describes that large adult males and subadults (BSI 6-9) kept the furthest distances from each other. The second furthest distance kept was found between adult females (or small adult males) and normal sized adult males (BSI 7-8). Adult males of different sizes (BSI 8-9) were observed to have the closest mean distance to each other. Subadult individuals and regular-sized females (or small adult males) (BSI 6-7) kept relatively close proximities. Noticeable differences occurred across BSI sizes indicating the existence of a social structure.

3.5.2 Prediction Accuracy of the TreeNet Model

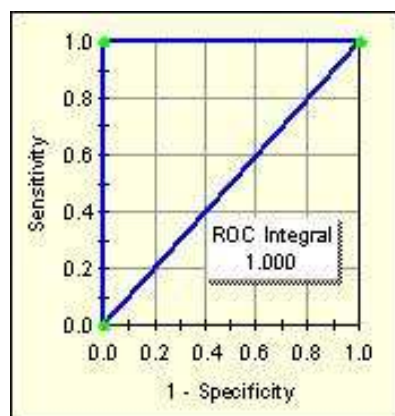


Figure 3.24 ROC curve of the polar bear model

Table 3.11 Prediction success of the 200-tree polar bear model

Actual Class	Total Cases	Percent Correct
1	421	100.00
2	353	100.00

The distance categorisation for the prediction accuracy in polar bears is split at 2000m into sample sizes of 421 and 353 data points (Table 3.11).

A 100% predictive success of model distance categories is described in Figure 3.24. The exact match shows that the model can explain all the data.

3.5.3 Distance Histograms

Seven histograms are generated with a minimum of 20 samples for polar bears. The histograms not presented here are to be found in Appendix 8.6.

Frequency histogram of largest distance proximities

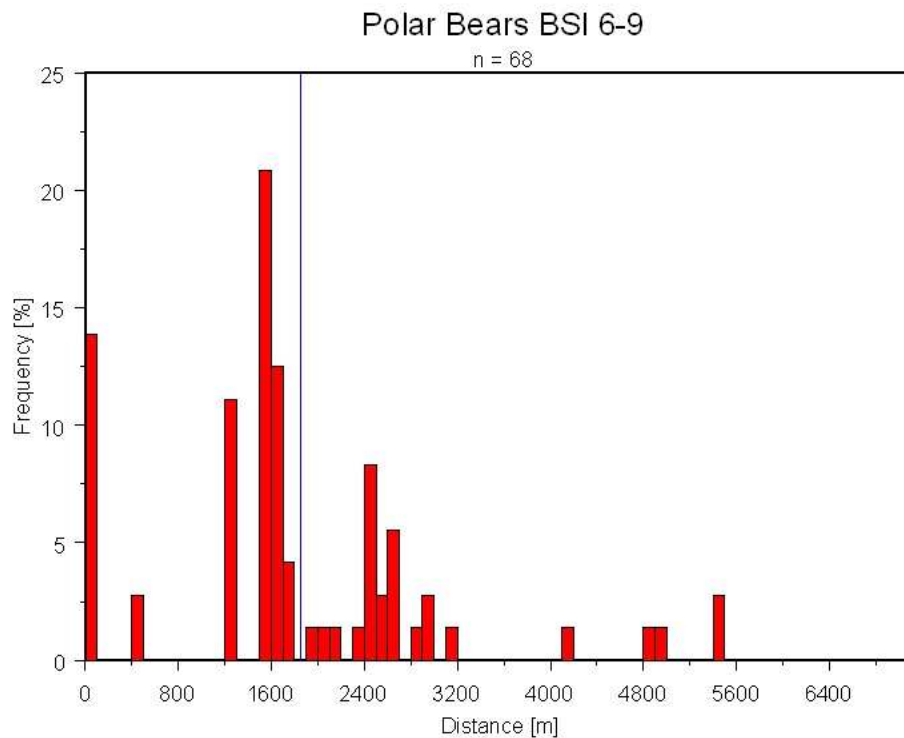


Figure 3.25 Distance histogram for the interacting BSI sizes 6 vs. 9 in polar bears; the vertical blue line represents the mean

In polar bears, large distances were found between subadult individuals and large adult males (BSI 6-9) by TreeNet. They were either observed close to each other (0-100m) or as keeping a rather far distance (>1200m). The most regular observed distances were around 1600m with a mean distance of 1850m. A pattern of three distance clusters - close, medium and far – was recognizable (Figure 3.25). A distinct distance pattern occurred. Large adult males keep differentiated distances to similar body-sized subadult individuals. This strongly indicates social recognition and strategic decision-making.

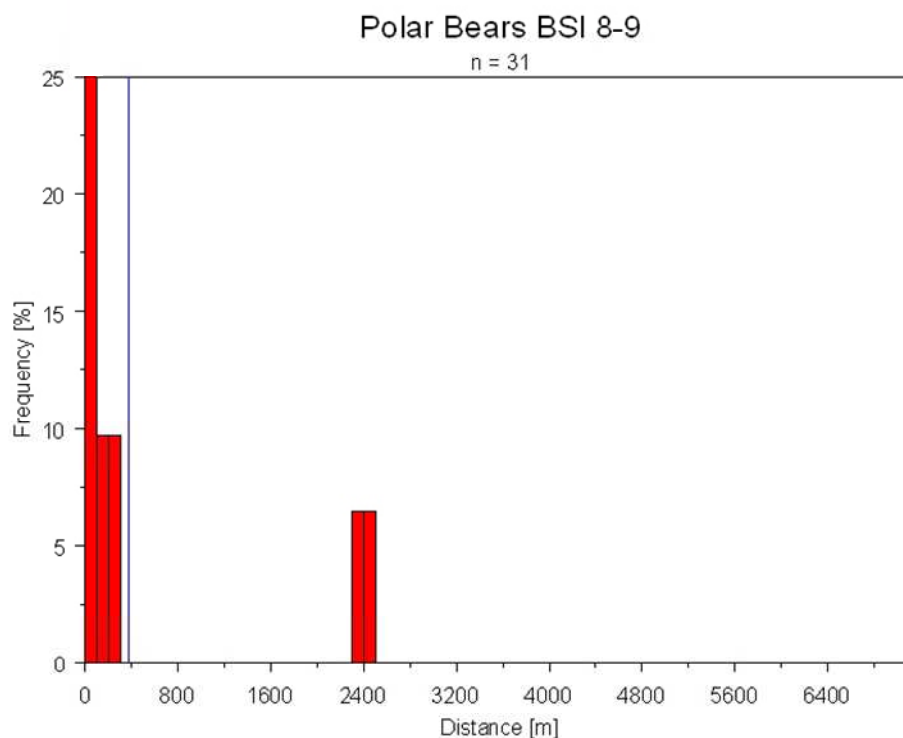
Frequency histogram of closest distance proximities

Figure 3.26 Distance histogram for the interacting BSI sizes 8 vs. 9 in polar bears; the vertical blue line represents the mean; the first interval (0m-100m) is cut off on the y-axis, ranging up to 64%

Adult males of different body sizes (BSI 8-9) were often observed to either stay very close to each other, or to keep far distances (2300m-2500m) (Figure 3.26). The mean distance was located around 400m due to the majority of the observations being within 100m distances. The biological meaning of such a pattern demonstrates the ability of polar bears to differentiate between individuals. Although animals have a uniform body size occurrence, they seemed to choose whom to be close to, and seemed to actively decide whom to avoid.

3.5.4 Interaction Diagrams

Detailed descriptions of observed interactions and their classification are presented in Appendix 8.3.

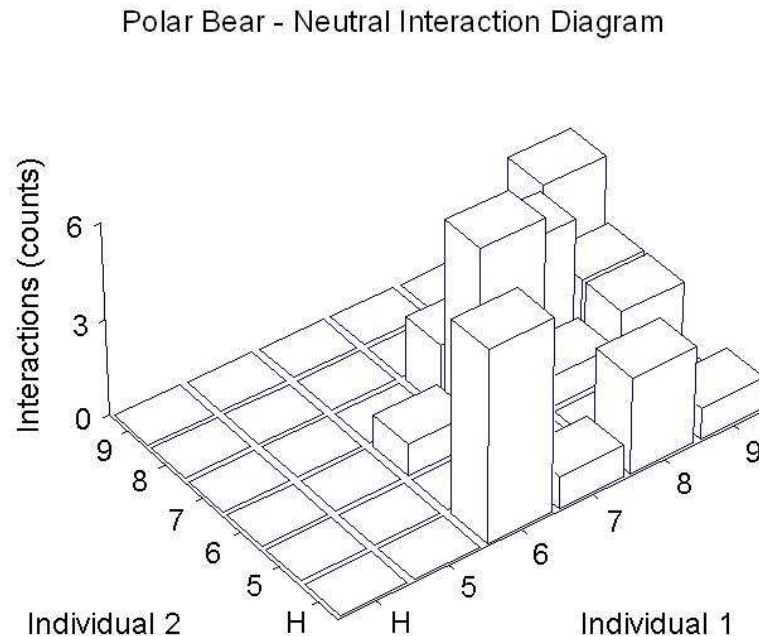


Figure 3.27 Neutral interactions in polar bears across BSI sizes; H stands for ‘human’ (in form of tundra vehicles); ; numbers on x- and y-axis represent BSI sizes (for detailed definition s. Appendix 8.1)

Neutral interactions in polar bears occurred across many BSI sizes with an overall variant pattern existing. Most frequently, neutral interactions were observed in adult females (or young adult males) and subadults (BSI sizes 6-7), humans with subadults (BSI sizes H-6) and in adult males interacting with adult males (BSI sizes 8-9). Also regularly neutral interactions between large adult males (BSI 9) and adult females as well as subadults occurred. Bears of all age sizes interacted with humans in a neutral fashion: Neutral interactions of humans with bears were defined as a bear approaching a tundra vehicle, or the tundra vehicle approaching the bear without any recognizable behavior change exhibited by the bear. In Figure 3.27 and 3.28, H stands for ‘human’ considering ecotourism-influence (s. Appendix 8.1). No regulations on approaching-distances to the bears exist thus far. Interactions with the tundra vehicles were additionally recorded only because they were recognized frequently

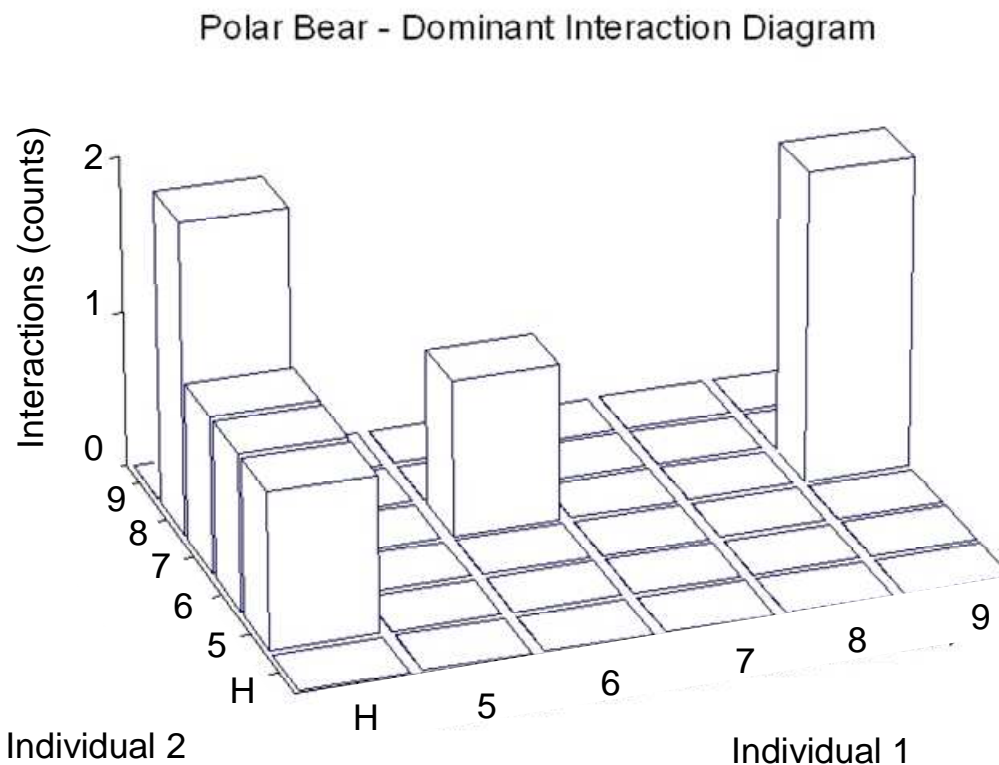


Figure 3.28 Dominant interactions in polar bears across BSI sizes; Individual 1 is dominant over Individual 2; numbers on x- and y-axis represent BSI sizes (for detailed definition s. Appendix 8.1)

Dominant interactions were rarely observed in polar bears. Most dominant interactions were caused by humans (5 dominance displacements caused by humans verses 3 caused by bears). Human enforced displacement implies the tundra vehicle approaching the bear or chasing the bear off by tundra vehicle due to noise or movement (ECKHARDT 2000; DYCK and BAYDACK 2003). Large adult males were dominant over adult females (or young adult males) and a subadult interacted dominant towards a BSI 7 individual once. It is remarkable how rarely dominance encounters took place (Figure 3.28). Such a behavior pattern, although individuals are very close to each other, would not be found in a non-social species congregating. Especially for polar bears, these congregations exhibit an uncommonly experienced closeness when compared to their live on the remote ice. Such a pattern can probably not be explained in another way but by social structure and individual perception abilities in polar bears.

3.5.5 Meta-analysis

Only a few research papers exist on free-ranging polar bear behavior research thus far. Nevertheless, all references consulted conclude that polar bears are highly social. Based on 3

Table 3.12 Meta-analysis of polar bears (*Ursus arctos*)

Publication type	Author / Year / Title	Country institution	Research population	Study length	Social aspects	Dominance hierarchy	Individual recognition	Remarks
Journal paper	Stirling 1974 "Midsummer observations"	Canada	Canada – Northern Beaufort Sea	9 days	yes	yes	yes	meetings between unrelated bears are avoided
Master thesis	Latour 1980 "Social Behavior of polar bears (<i>Ursus maritimus</i> PHIPPS) concentrated on land during the ice-free season of Hudson Bay"	Canada	Canada – Western Hudson Bay	2 years, 3 month	yes	yes	yes	
Expedition briefing	Waterman and Roth 2002 "The social complexities of an asocial species: play in adult polar bears (<i>Ursus maritimus</i>)"	USA	Canada – Western Hudson Bay	2 years, few month	yes	yes	yes	highly social
Report	Miller et al. 2006 "Demographics and Behavior of Polar bears feeding on Bowhead whale carcasses at Barter and Cross Islands, Alaska"	USA - US Fish & Wildlife Service	USA – Southern Beaufort Sea	2 years, few month	n/a	n/a	n/a	surprisingly few aggressive interactions; behavior category 'interacting'; relatively solitary animals
Journal paper	Ovsyanikov 2005 „Behavior of Polar Bear in coastal congregations"	Russia	Russia – Wrangle Island	many years, few month	yes	yes	yes	high social
Reports	USGS – US Geological Survey	USA	USA & Canada	n/a	n/a	n/a	n/a	'proposed threatened' since 2007, US Endangered Species List
Reports	PBSG (Polar bear specialist group IUCN/SSC)		world wide	n/a	n/a	n/a	n/a	listed as vulnerable, assessed in 2006
German M.Sc. thesis (this study)	Jochum 2008 "Benefits of using marginal opportunistic wildlife behavior data"	Germany / USA	Canada – Western Hudson Bay	4 weeks	yes	yes	yes	few dominating and no aggressive interactions
Final Scores					5 / 5 – 100%	5 / 5 – 100%	5 / 5 – 100%	= 100% social

papers reviewed, the score is 100% for social aspects, for the existence of dominance hierarchies as well as for individual recognition abilities.

Noteworthy here is that when a statement on sociality is given, the existence of social traits is clearly stated.

3.6 Spotted Seals

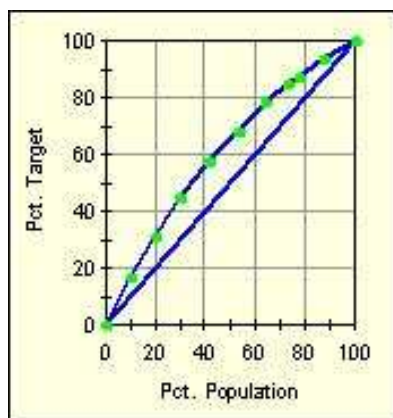
3.6.1 Modeling with TreeNet

In order to detect pattern existing in the spotted seal behavior data through data mining, 9 predictors were applied to the spotted seal model. It was found that ‘start time of the observations’, ‘day’, ‘duration of the observation time’ and ‘dominant interactions’ had no relevant influence. All distance-dependent predictors are listed in Table 3.13.

Table 3.13 Variable importance of the 196-tree spotted seal model

Predictor	Score (%)
Interacting animals	100.00
All animals in group	74.60
Neutral interactions	24.61
Time (h)	13.56
End time of observation period	6.15

The main influencing predictor to spotted seal proximity was the ‘number of interacting animals’ (100%). The ‘group size’, being present at observation time, influences the distance between individuals to 74.60%. ‘Neutral interactions’ occurring affected the seal-proximity to a fairly small amount (24.61%). The importance of animals interacting, first, and of the animals being present in the group, second, reveals the high importance of the amount of animal present at interaction time. The time of the day, daily differences and interactions occurring played a less important role.



The gains of the spotted seal data have an approximate value of 65 % (Figure 3.29). This result allows for less satisfactory model accuracy and a lower but existing predictability.

Figure 3.29 Gains of the spotted seal model

The y-axis is just a relative index, and thus has no real units. In Figure 3.30 the partial dependence of 1.5 was the furthest observed distance between all individuals in a group (8m in the spotted seal data), the lowest distance was minus 1 (0m for spotted seals).

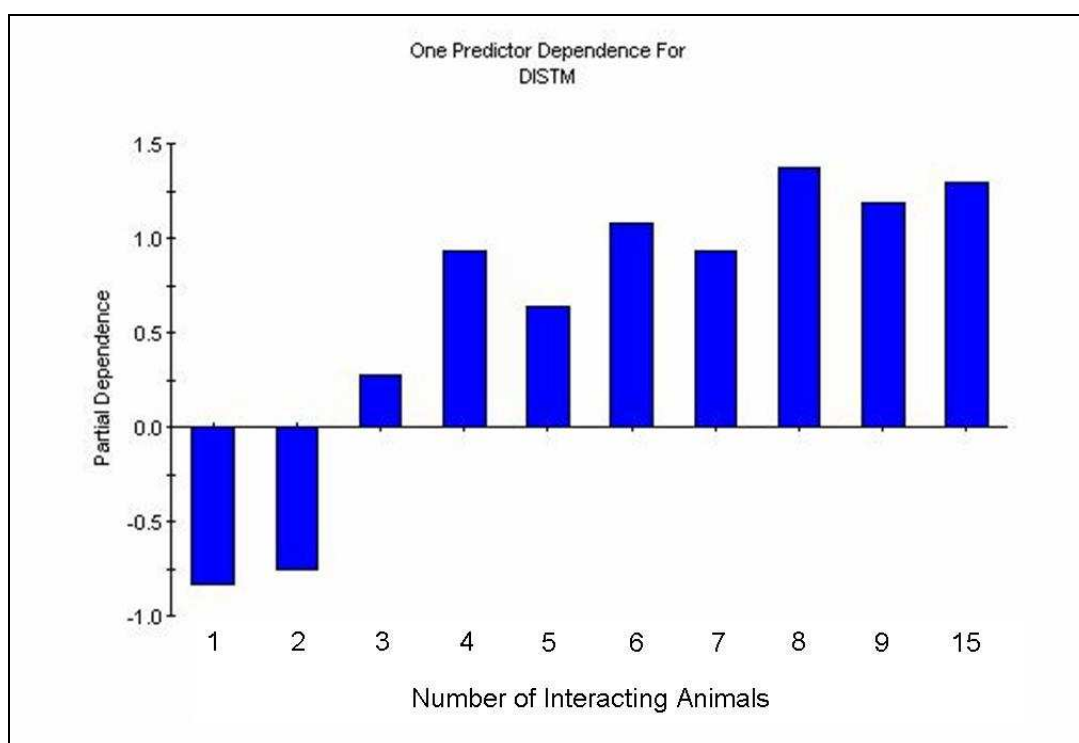


Figure 3.30 One predictor dependence (1) for spotted seals; importance ranking 100%

The increasing distance between the interacting animals in the group (y-axis) correlated with the increasing amount of individuals present (x-axis). When one or two individuals of a group interacted, they were observed to stay close (Figure 3.30). The more individuals, the further was the space they inhabited. The group spread on the other side stayed about the same when more than 8 individuals were present. Within a group, a maximum spacing in distance units of

8m was observed. Animals that stayed very close to each other and showed social contact made the existence of social behavior traits and social interactions obvious.

In Figure 3.31 the partial dependence of 1.0 shows the furthest observed distance between a group of individuals (8m in the spotted seal data), the lowest distance was minus 0.4 (0m for spotted seals).

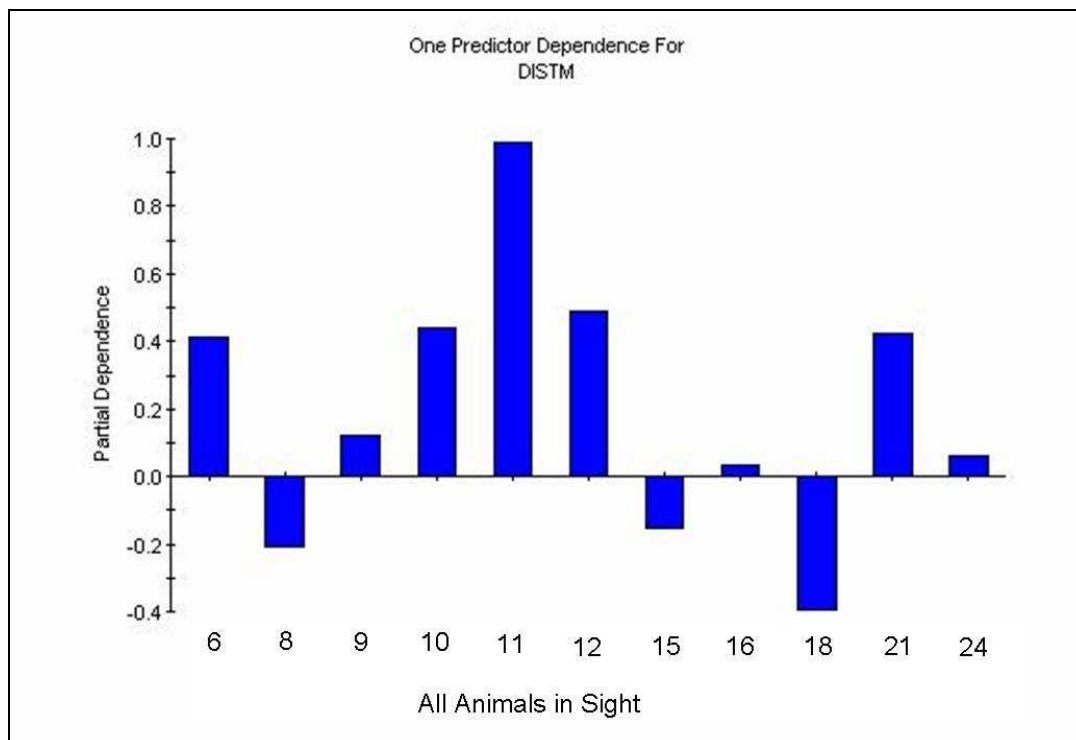


Figure 3.31 One predictor dependence (2) for spotted seals; importance ranking 74.60%

The outcome was different when looking at all individuals that were present at the time interactions between any numbers of animals took place (Figure 3.31). In a medium group size (10-12 individuals) the group-spread was relatively large, as well as when very few (6) or many (21) individuals were maintaining a group. All intermediate group sizes stayed closer together. This structure shows a distinctly variant pattern with three peaks describing closer social interactions occurring between medium sized group sizes.

3.6.2 Prediction Accuracy of the TreeNet Model

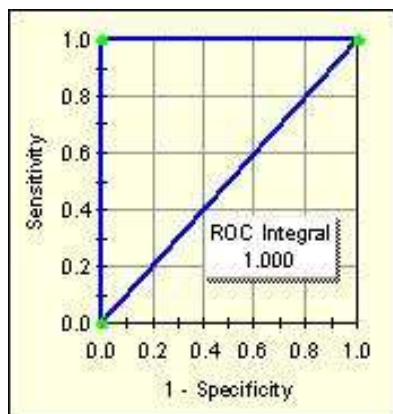


Figure 3.32 ROC curve of the spotted seal model

Table 3.14 Prediction success of the 196-tree spotted seal model

Actual Class	Total Cases	Percent Correct
1	67	100.00
2	124	100.00

The distance categorisation for the prediction accuracy in spotted seals took place at 3m. The data was split into comparable sample sizes of 67 and 124 data points (Table 3.14).

Figure 3.32 shows the accuracy of the classification model being 1, describing a 100% overlay of both model distance categories. The model can explain all the data.

3.6.3 Interaction Diagrams

Detailed descriptions of observed interactions and their classification are presented in Appendix 8.3.

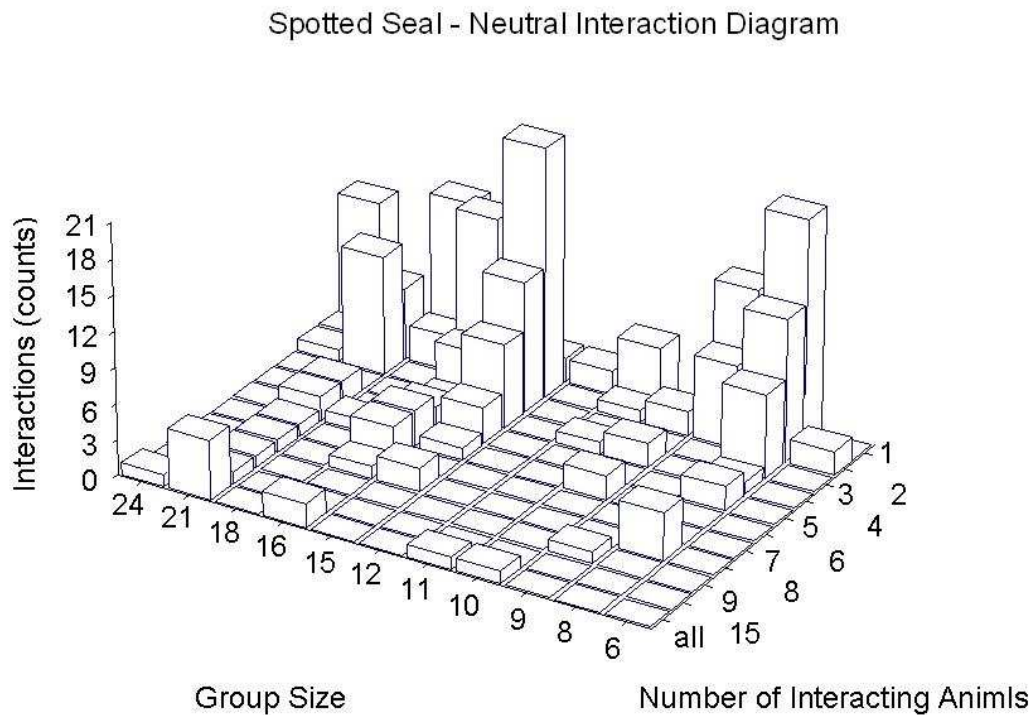


Figure 3.33 Neutral interactions in spotted seals across BSI sizes

Altogether, interactions in spotted seals occurred regularly between few specific animals (1-3 individuals) independent of the whole group size. Most of these interactions again were observed in intermediate group sizes (8 and 9 individuals and 15 to 18 individuals). Few neutral interactions occurred in medium sized group sizes (10-12 individuals) (Figure 3.33). This pattern states that intermediate group sizes (8 and 9 individuals and 15 to 18 individuals) seem to be the best group sizes for animals to interact. A variant pattern was present through group sizes and states the existence of social interactions; selective behavior occurred. No individual-based dominant interactions were observed in spotted seals. Dominant interactions probably take place under the water surface and were therefore not recorded.

3.6.4 Meta-analysis

Behavior data in spotted seals can be difficult to collect in free-ranging populations due to their mainly pagophilic life (LOWRY *et al.* 1998). Research existing and consulted in this study thus concludes that spotted seals are social animals. The existence of social aspects, the existence of dominance hierarchies as well as individual recognition, is confirmed in all studies reviewed (100%) (Table 3.16).

Table 3.15 Meta-analysis of Spotted Seals (*Phoca Largha*)

Publication type	Author / Year / Title or Affiliation	Country institution	Research population	Study length	Social aspects	Dominance hierarchy	Individual recognition	Remarks
Journal paper	Beier and Wartzok 1979 "mating behaviour of captive spotted seals (<i>Phoca largha</i>)"	USA	captive, USA	5 years	yes	yes	yes	great number of behavioral events leading to copulation
Journal paper	Sullivan 1981 "Aquatic Displays and Interactions in Harbor Seals, <i>Phoca vitulina</i> , with Comments on Mating Systems"	USA	Scotty Point on Abalone Beach, USA	2 years, 837h	yes	yes	yes	monogamy only described for <i>Phoca largha</i> and ice-breeding grey seals
Review - Marine Fisheries	Rugh et al. 1997 "Spotted Seals, <i>Phoca largha</i> , in Alaska"	USA	Bering sea, USA/Russia	2 years	yes	yes	yes	seasonal monogamous, travelling in triads (mother, cub and male)
Journal paper	Lowry et al. 1998 "Movement and behavior of satellite tagged spotted seals (<i>Phoca largha</i>) in the Bering Sea"	USA	Bering sea, USA/Russia	3 years, 1746 days tracked	yes	n/a	n/a	little understanding of movements and behavior of seals
Journal paper	Insley 2003 "A review of social recognition in pinnipeds"	USA	across the world	n/a	yes	yes	yes	Mother-cub & long-term recognition exists
German M.Sc. thesis (this study)	Jochum 2008 "Benefits of using marginal opportunistic wildlife behavior data"	Germany / USA	Vostochnaya Reserve, eastern Sakhalin Island	4 days	yes	yes	yes	
Final Scores					6 / 6 – 100%	5 / 5 – 100%	5 / 5 – 100%	= 100% social

3.7 Muskoxen

3.7.1 Modeling with TreeNet

3.7.1.1 Female Muskoxen

In order to detect pattern in the female muskoxen behavior data, 6 predictors were tested in the model (Table 3.15).

Table 3.16 Variable importance of the 921-tree female muskoxen model

Predictor	Score (%)
Day	100.00
Body size index (BSI)	97.28
Neutral interactions	81.93
Time (h)	65.66
Dominant interactions	57.96
Month	33.19

The day the observations were conducted played a crucial role in proximity-dependence for muskoxen females (100%). The BSI influenced the distance between female muskoxen to 97.28% and the 'neutral interactions' to 81.91%. All predictors tested had a relative high influence on the proximity in female muskoxen.

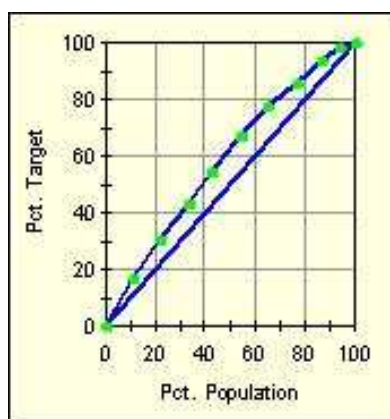


Figure 3.34 Gains of the female muskoxen model

The gains of the female muskoxen data had an approximate value of 60 % (Figure 3.34). These results indicate low but existing model accuracy on the spacing on individuals.

The partial dependence of 0.6 was the furthest observed distance between two individuals (8m in the female muskoxen data), the lowest was displayed minus 0.8 (0m for female muskoxen).

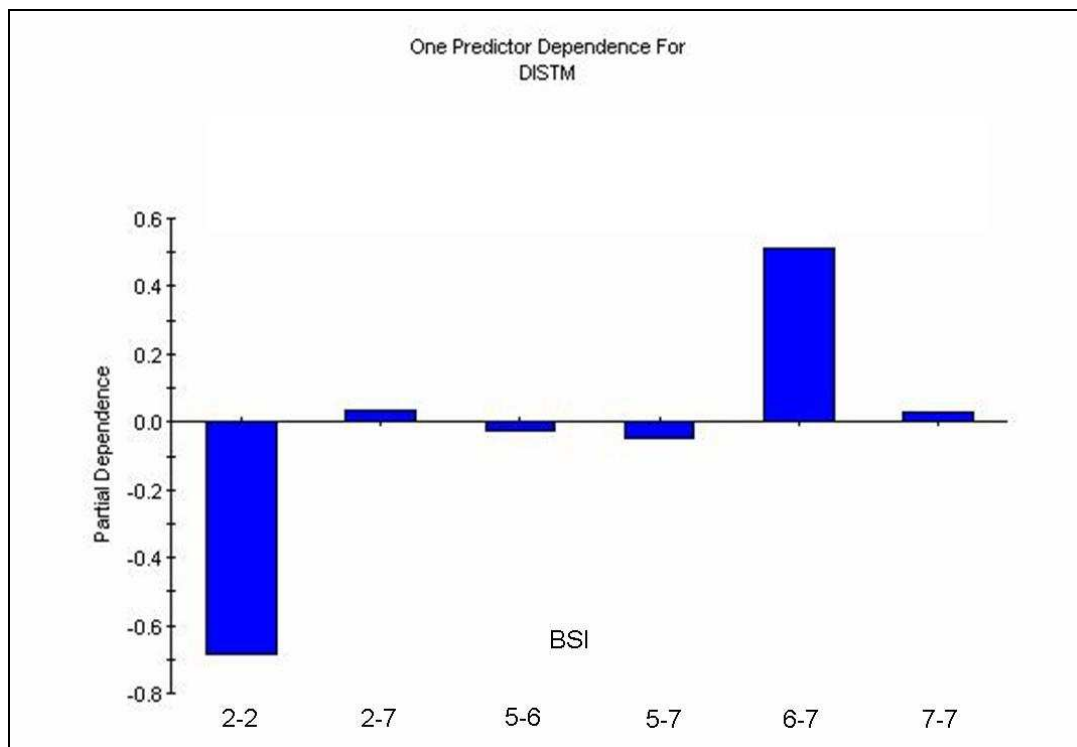


Figure 3.35 One predictor dependence (2) for female muskoxen; importance ranking 97.28%

TreeNet showed the furthest distance occurring between larger subadults and adult females (BSI 6-7). Since only one female had the BSI of 6 and one the BSI of 5 and further less than 20 data points exist, these peaks have a reduced interpretive value but still represent the best available data we have. They are not presented in the distance histograms. The only BSI combinations with over 20 data points are 7-7 and 7-2. Adult females and juveniles (BSI 2-7) as well as adult females from each other (BSI 7-7) stayed fairly close (Figure 3.35). These results indicate the existence of an irregular pattern which suggests individually differentiated behavior patterns across individual females.

3.7.1.2 Male Muskoxen

The same six parameters as tested in the female muskoxen data were run in the male muskoxen model. No variable importance ranking was found for the male muskoxen model although runs from 200 to 1000 trees were tested. This can be due to either no existing dependencies in the male muskoxen data or due to a minimum needed sample size to analyse by TreeNet. It is known that usually with 60 data points, one can receive reasonable results (SALFORD SYSTEMS 2003; STEINBERG and GOLOVNYA 2004). The male muskoxen data set only consists of 24 data points; in comparison the female muskoxen data set holds 231 data points. This puts more value on the female muskoxen findings.

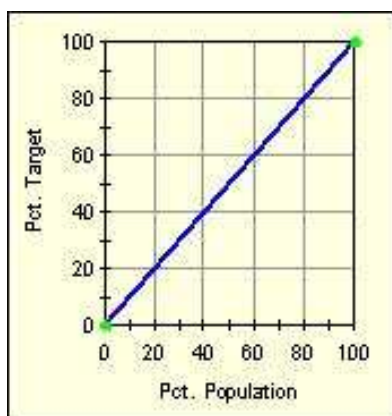


Figure 3.36 Gains of the male muskoxen model

The gains of the male muskoxen data had an approximate value of 50 %, what is equivalent to a random distribution (Figure 3.36). No model accuracy is predicted. This indicates that no factor could be found explaining male behavior metrics.

The furthest observed distance between two individuals was 6m for the male muskoxen data; the lowest observed distance was 0m for male muskoxen. During observations they stayed fairly close to each other predicting social contact and interactions happening.

No graphs were built by TreeNet in the 200-tree model for male muskoxen; no partial dependence and no variable importance were located. Out of the 200 trees, only one tree was found as being optimal (s. Appendix 8.6).

3.7.2 Prediction Accuracy of the TreeNet Model

3.7.2.1 Female Muskoxen

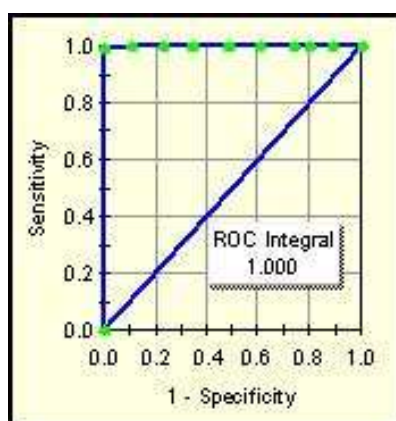


Figure 3.37 ROC curve of the female muskoxen model

Table 3.17 Prediction success of the 921-tree female muskoxen model

Actual Class	Total Cases	Percent Correct
1	152	99.34
2	79	100.00

The distance categorisation for the prediction accuracy in female muskoxen was split at 1m bearing the sample sizes of 152 and 79 data points (Table 3.17).

Figure 3.37 shows the accuracy of the female muskoxen classification model being 1, describing a 100% agreement of both model distance categories. This exact match shows that the model can explain all the data.

3.7.2.2 Male Muskoxen

The cross-validation model was run with a 200 tree as well as up to 1000 tree model setups. No output was presented in any of the male Muskoxen categorical models independent of tree numbers grown.

3.7.3 Distance Histograms

3.7.3.1 Female Muskoxen

Two histograms with a minimum of 20 samples are generated with the female muskoxen data. The histogram not presented here are located in Appendix 8.6.

Frequency histogram of largest distance proximities

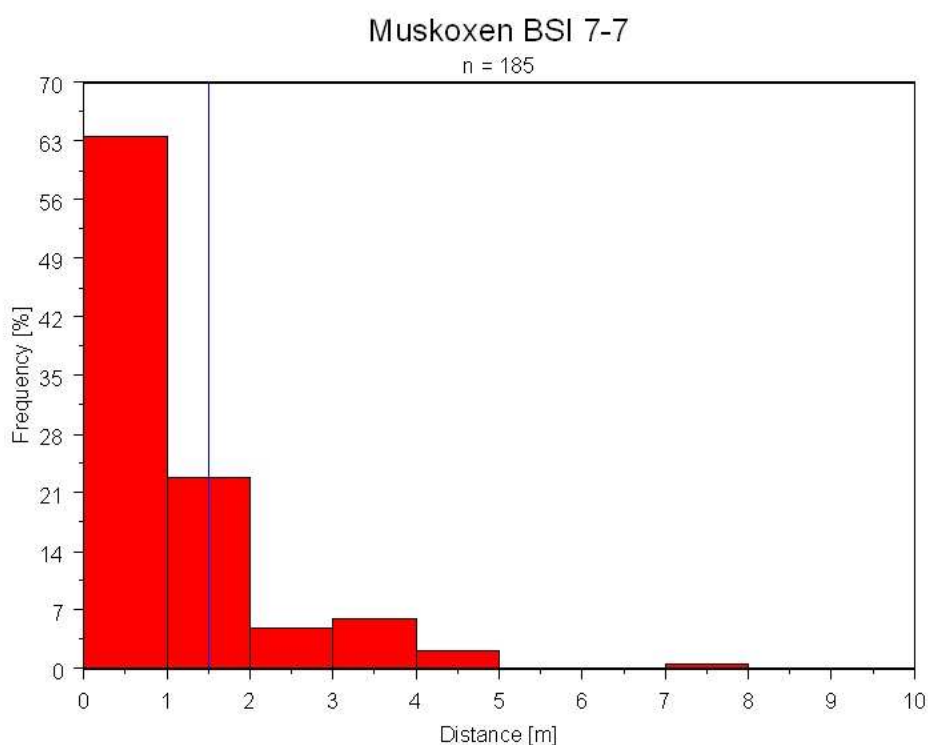


Figure 3.38 Distance histogram for the interacting BSI sizes 7 vs. 7 in female muskoxen; the vertical blue line represents the mean

Close distances were kept between individuals. TreeNet shows the distances as being 'relatively far apart' (Figure 3.35) due to the distance for a neutral response in TreeNet being defined at 1m (point of origin being 1).

Female adult muskoxen stayed close together and were not observed to be separated further than 8m from each other (Figure 3.46). Their mean distance was 1.5m; about their body size. This reveals a close social context between adult females of the group. Through their closeness they indicate social relations and structure. Not enough data points exist for male muskoxen to generate any distance histograms.

3.7.4 Interaction Diagrams

Detailed descriptions of observed interactions and their classification are in Appendix 8.3.

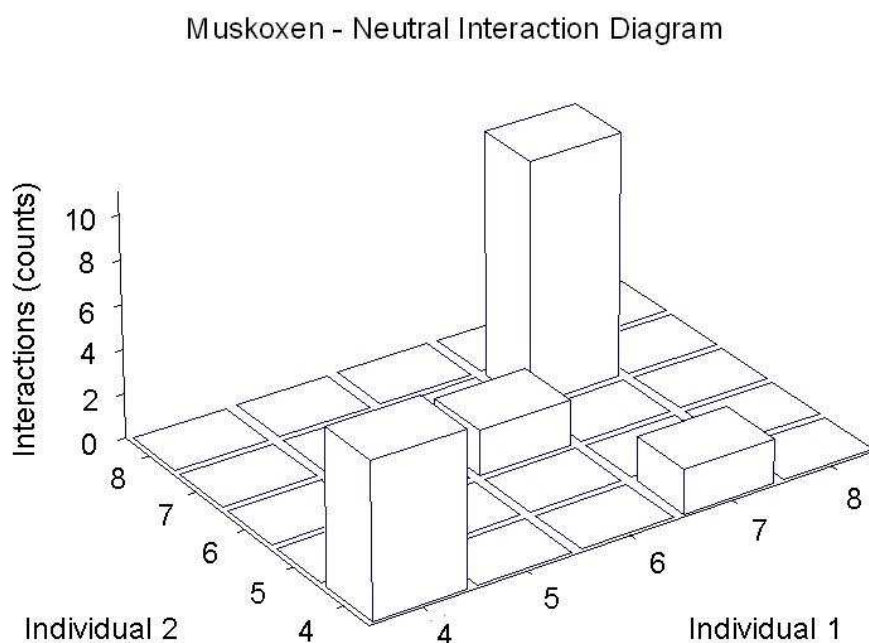


Figure 3.39 Neutral interactions in muskoxen across BSI sizes; numbers on x- and y-axis represent BSI sizes (for detailed definition s. Appendix 8.1)

Except for adult females with their calves, only identical BSI sizes were observed to interact neutral. Most neutral interacting animals were adult females. This can be due to a far higher amount of data collected for adult females than any other age class. Further, adult females

could be the most dominant individuals in the absence of males. The irregular interaction pattern described a high variance through body sizes displaying interactions what indicates the existence of a social structure related to sex and body size. (Figure 3.39)

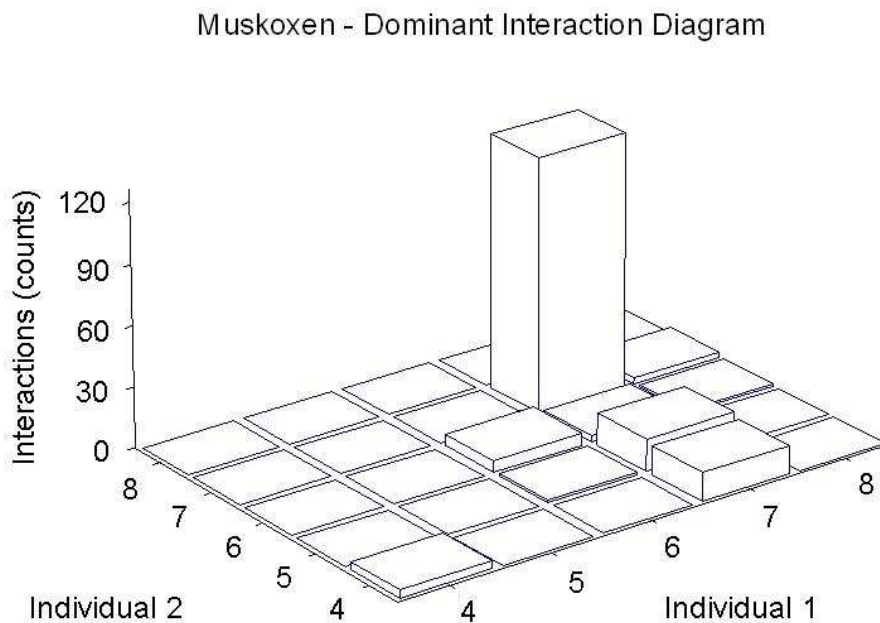


Figure 3.40 Dominant interactions in muskoxen across BSI sizes; Individual 1 is dominant over Individual 2; numbers on x- and y-axis represent BSI sizes (for detailed definition s. Appendix 8.1)

Many dominant interactions occurred in captive muskoxen (up to 120 counts for the BSI 7-7). Thus, most dominant animals were adult females. The high occurrence of dominance displays was probably stipulated by the 'release to supplementing feeding' setup. Few dominant interactions were also observed between calves. Adult males were dominant over females and subadults, indicating the existence of a classical dominance hierarchy with either males being the most dominant individuals which were never observed to lose a dominant interaction, or adult females, as they had a high potential to exhibit aggression at least when competing for food with other group members, especially in the absence of males.

3.7.5 Meta-analysis

In Muskoxen, all references reviewed concluded to the muskoxen being highly social. Social aspects, the existence of a dominance hierarchy as well as individual recognition abilities score 100% across studies (Table 3.18).

Table 3.18 Meta-analysis of Muskoxen (*Ovibos moschatus*)

Publication type	Author / Year / Title or Affiliation	Country institution	Research population	Study length	Social aspects	Dominance hierarchy	Individual recognition	Remarks
Journal paper	Spencer and Lensink 1970 "The Muskox of Nunivak Island, Alaska"	USA	USA	22 years, 32 report review	yes	yes	n/a	fission-fusion group structure; changing group sizes during seasons
Thesis	Gray 1973 "Social organization and behaviour of muskoxen (<i>Ovibos moschatus</i>) on Bathrust Island, N.W.T."	Canada	Canada	2 years	yes	yes	n/a	
Thesis	Smith 1976 "Reproductive behavior and related social organization of the muskox on Nunivak Island"	USA	USA	n/a	yes	yes	n/a	
Thesis	Saelzle 1979 "Das Verhalten des Moschusoxen (<i>Ovibos moschatus</i>)"	Germany	n/a	n/a	yes	yes	n/a	
Journal paper	Reinhardt and Flood 1983 "Behavioural assessment in muskox calves"	Canada	Canada	9 days, 27h	yes	yes	yes	detailed descriptions of displayed behaviors
Book	Lent 1988 "Ovibos moschatus"	USA	world-wide	n/a	yes	yes	yes	
Book	Feldhamer et al. 2003 "Wild Mammals of North America – Biology, Management and Conservation"	North America	North America	n/a	yes	yes	n/a	
German M.Sc. thesis (this study)	Jochum 2008 "Benefits of using marginal opportunistic wildlife behavior data"	Germany / USA	Robert G. White LARS in Fairbanks, Alaska	3 month, 15 observation days	yes	yes	yes	
Final Scores					8 / 8 – 100%	8 / 8 – 100%	3 / 3 – 100%	= 100% social

4 Discussion

4.1 Social Structures in studied Species

4.1.1 Howling Monkeys

Our results described a particular group status of male howlers. The male-male histogram showed a different pattern than all other histograms in howling monkeys. As soon as BSI dyads included an adult male, body contact did not occur (Figure 3.4, s. Appendix 8.6). Adult males kept the furthest distance from other adult males compared to all other BSI size classes. Younger adult males are believed to lead and protect a howling monkey group. Older animals maintain a less dominant status (GLANDER 1980; JONES 1980; YOUNG 1983). Since it was not differentiated between older and younger adult males in this study, no statement is made on this issue. Our results identified an adult male howler leading the group. Adult males are always dominant over all other individuals, independent of the BSI (Figure 3.7).

Adult females were the most interacting animals in the Ometepe howler group; in the neutral as well as in dominant interactions (Figure 3.6, Figure 3.7). They seemed to have a high social rank in the group winning all dominant interactions with other BSI sizes except males. Adult females with infants were of notable interest. All BSI sizes were observed trying to sit close to adult females with infants. This fact has also been described by Clark *et al.* (1998) and Zucker and Clarke (1998). Even when risking the consequences of being chased away by the adult female, subadults and other adult females tried to get close to the infant repetitive. The closeness of subadults to infants can be explained through the subadult's interest in new born animals. Subadult females are believed to practice care-taking skills (CLARKE *et al.* 1998).

Adult females were often observed to maintain body contact to other adult females while resting. On the other hand, these same females generally stayed distant to different adult females when resting (Figure 8.13). Zucker and Clarke (1998) describe similar findings.

Young howlers of different size, juveniles and subadults, stay in distance from each other (Figure 3.5). They preferably interacted and especially played with similar BSI sizes (s. Appendix 8.3).

Overall, diverse patterns occurred between all BSI size distance histograms. No consistent patterns occurred in any age class. Exactly such patterns are predicted and expected for a social species with a well-structured individual-based dominance hierarchy. Anthropologists

have not agreed yet in defining the overall structure of existing social networks in howling monkeys. But all recent studies confirm that the howling monkey truly is a social species with a sophisticated social structure built upon dominance hierarchy (CLARKE *et al.* 1998; ZUCKER and CLARKE 1998; DIAS and LUNA 2006; BEZANSON *et al.* 2007).

These findings show virtually identical results than the long-term studies for howling monkeys. The approach of applying and modeling marginal opportunistic behavior data presents matching results for the howling monkey case.

4.1.2 Humpback Whales

The accuracy assessment of the modeled humpback whale data with 90% was the highest through all TreeNet models in this study. But still, assessing the humpback whale social system in this Pacific subpopulation was a bigger challenge since an inconsistent age-size correlation in humpback whales poses difficulties when concluding from BSI sizes to age classes of the individuals.

Humpback whales have been well described as social animals living in social fission-fusion systems (CLAPHAM 1996; MARINO 2002; VALSECCHI *et al.* 2002) with aggressive behavior displayed by adult males competing for females, especially during the breeding season (SILBER 1986; CLAPHAM *et al.* 1992; SPITZ *et al.* 2002). It is not clear yet whether a preference in subadults or adult individuals traveling together exists (SPITZ *et al.* 2002). From results, age-dependant conclusions could not be drawn. Rather the general species structure could be described. Mainly dyads of humpbacks were observed travelling and feeding together. These observations are in agreement with Valsecchi *et al.* (2002). They found that humpback whales do not travel together in larger groups, mainly in dyads. In our data, the maximum number of individuals observed at one location was 4 individuals. They maintain short time associations. Commonly described are male-female pairs travelling together during migration (CLAPHAM 1996; VALSECCHI *et al.* 2002).

Generally, BSI dyads 6-6 and 6-7 kept the largest distances from each other. 25% of the BSI dyad 6-6 travelled fairly close together; other data points that showed far distances between individuals existed (Figure 3.11). The BSI dyad 6-7 stayed mainly far apart from each other, showing a different pattern than all other BSI distance histograms. This pattern could be due to adult females staying apart. Adult females were rarely observed to travel together (SPITZ *et al.* 2002). Definitely it showed selective behavior taking place across BSI sizes. No random patterns occurred. Therefore our data imply the existence of a social structure.

The closeness of the BSI dyad 5-6 can be explained through adult females travelling with their calves or through subadult individuals travelling together (Figure 3.12), also found by Spitz *et al.* (2002). They show a large percentage of male and female animals in dyads being juveniles and subadults. Further, they describe males to be generally smaller than females. The BSI dyad occurrence 6-8 can be interpreted as an adult male escorting a large adult female (Figure 8.22). A bias may have occurred in the BSI determination of the humpback whale data due to the main observations only including two individuals travelling together at a time. Only on one day, three to five animals were observed travelling and feeding together.

Interactions occurred between all BSI sizes, mainly in a neutral manner between BSI sizes 7 and 5. This may relate to mothers-calve interactions. Dominant interactions occur rarely, but when they do, they occur between BSI sizes 6, 7 and 8, conclusively only between subadults or adults (Figure 3.14). In general, patterns are varying and selective throughout all humpback whale results. Social behaviors were found and a dominance hierarchy and individual perception can be assumed to exist as well.

Drawing definite conclusions from short-term behavior observations when not being able to conclude to the approximate age class of individuals is not achievable. Not having a relative measure to compare, as the BSI in this study, reveals a big disadvantage. What can be concluded from the marginal opportunistic data though is the existence of a rank due to varying behavior patterns displayed across BSI sizes. Valsecchi (2002) notes that diffuse groups could maintain some form of social organization without the need of traveling in tight-knit units. Indeed, some level of social organization appears to persist during migration. Further, she suggests that existing long-term studies in the breeding as well as in the feeding grounds show short-lived social bonds being typical for humpback whales. Humpback whales are showing as a social species in our short-term data as well, implying the applicability of our methods for the second case in this study, humpback whales.

Thus our method and statistical modeling approach is able to show basic social patterns in animal species. We should be able to find an answer to the social status for the following four mammal species as well.

4.1.3 Brown Bears

During salmon season coastal bears focus on gaining fat reserves to survive the winter season. Thus observations took place under conditions of food competition. Except of one adult female with a second year cub, who seemed to be the most dominant individual at the river that season, adult females were rarely observed together at the river. They stayed far apart from

each other (Figure 3.18). A mother with two cubs of the year was observed only once during early morning hours while no other adult female was around. Such observations show other adult females being around but avoiding the river site when other individuals are around. Thus active spatial decisions were made by adult females and adult males. Only once in the early morning, an adult male was observed. Therefore only one data-point of an adult male existed (Figure 3.16).

Adult females and subadults were sometimes observed close to each other without showing any relevant displacement behavior. But most commonly, subadults were chase off by adult females when approaching or subadults gave way before. Both of these behaviors were observed between the same individuals on different days. It is unclear why on some days the adult female committed to a open jaw fight with this one subadult (BSI 6) and a few days later they were observed feeding on one salmon together. The dominant adult female seemed to have a different, somewhat changing, relationship to this subadult than to others. Stenhouse *et al.* (2005) describes from data for an interior mountain population that adult females meet with subadult females relatively often during berry season. Berries (such as huckleberries, *Vaccinium spec.*; especially blueberries, *V. myrtillus*) are the main nutritional food resource for the forest living brown bear populations. The reason why these congregations happen still remains unclear. Kin-ship is not known for the research population but this behavior indicated varying expressions of behavior between same BSI classes.

Subadults were observed to stay closer to each other than to other age classes. One pair of subadults regularly travelled together and most of the time they stayed closer than 50m from each other (Figure 3.19; Figure 8.30), showing high awareness. These subadults were categorized as siblings (BSI 5 and 6). The fact of siblings staying together after weaning and having a separate position and function when staying together is well described by Russel and Enns (2004) for brown bears as well as by Stringham (2002) for black bears. Other subadults never travelled together. Conclusively, a difference between subadult's closeness exists.

Across all BSI sizes, some individuals always kept long distances from each other, or they were exclusively observed at the river when no other individuals were present. From observations of where an individual approached the river from, one could frequently conclude to the individual animal. Brown bears showed individually preferred travel and habitat use, except of areas with very high salmon densities. These places were visited by several individuals frequently. These patterns strongly indicate the existence of a dominance hierarchy in the population and the animal's ability to individual perception.

Neutral interactions (Figure 3.20) were observed most frequently between the dominant mother and her second year cub. This is also due to a high observation rate of these two individuals. Subadults interacted neutrally with each other, as well as adult females with subadults of both BSI sizes (5 and 6). Most dominant interactions occurred between adult females and larger subadults with the adult females always being dominant over subadults, and hence adult females were dominant over subadults. Dominance hierarchies existed among subadults with dominance relations seemingly being independent of BSI size (Figure 3.21).

Our findings show that grizzly bears spent a considerable amount of time interacting with conspecifics even during the main feeding season.

These results from marginal opportunistic data show varying patterns and thus are similar to the results of well known social species (howling monkeys and humpback whales). Therefore the existence of social traits, a social structure and a dominance hierarchy in brown bears is suggested. Further, brown bears at Chilkoot River, and likely elsewhere, seem to have the ability to individual perception.

4.1.4 Polar Bears

Subadults and large adult males keep relatively far distances from each other (Figure 3.25) and no aggressive behavior was displayed between subadults and large adult males (Figure 3.28) although a few very close (less than 100m) data points exist. Adult males did not seem to mind certain subadult individuals being close by, but they did seem to mind other individuals of the same BSI being close. These patterns show a selective behavior, proposing social traits and a dominance hierarchy to be present in adult male polar bears. Subadult individuals tolerated by adult males might have an advantage in dominance rank compared to other subadults.

Adult males and young adult males or adult females (BSI 7) were rarely observed in close distance (Figure 8.40). However, if they came close, no aggressive behavior was displayed. Whenever adult males passed a certain threshold distance (app. 800m) to adult females with cubs, females started displaying signs of nervousness, what could be noticed as increased head-ups, standing on hind legs and smelling gestures (as stated by LATOUR 1980). When adult males approached further, females with cubs moved off and gave way, keeping a larger distance.

Close distances between adult males of different sizes (Figure 3.26), and far distances between adult males of the same size (Figure 3.23) were observed. For these occasions relatively few data points exist in our data. Latour (1981) describes male groupings as the most common

aggregations in polar bears. Data collection for this thesis was conducted during an early period of congregating at the Hudson Bay, thus one could have missed the main male congregation forming (LATOURE 1981; ECKHARDT 2000; DYCK and BAYDACK 2003).

Largely varying distances existed between subadults and adult females or young adult males (BSI 7). They kept a mean distance of 2400m, showing a trend of staying separated. Only few observations of relative closeness were made, even within 100m distances. During these approaches only once aggressive behavior was displayed (figure 3.28).

Polar bears seem to recognize each other far earlier than one is able to observe. Thus, our findings represent underestimates re. the sophistication of interactions. The mechanisms of individual recognition remain unresolved but would deserve more attention. Very close approaches of individuals leading to standing side by side, walking around each other, showing open mouth displays or playfight was only observed in individuals of close BSI sizes (s. Appendix 8.4). Overall, aggressive behavior in polar bears was rare to find during fall congregations what presents a strong hint for sociality in a species (KREBS and DAVIES 1993; ALCOCK 2001). Neutral interactions were observed between all observed BSI sizes, showing that polar bears interact regularly.

Polar bear distance histograms show inevitable similar 3 peak patterns as presented throughout the howling monkey histograms. This may indicate the existence of similar social structures in howling monkeys and polar bears. Although howling monkeys are group living throughout the year and polar bears are not, similar structures could exist during the group living time period. This 3 peak pattern similarity is obvious and warrants further investigations (s. Appendix 8.6).

Across all BSI sizes varying patterns are found. Therefore one can conclude that polar bears are a social species; a species maintaining a social structure and a dominance hierarchy. Individual perception exists, even on large spatial scales, and likely maintained over years. This finding has not been described in more detail for North American bears, and has several larger implications that will be addressed in following sections of this discussion.

4.1.5 Spotted Seals

Our data shows varying behavior depending on the group size as well as on the number of individuals interacting. Many individuals stay close to each other, maximal 8m for dyads in a group are recorded (Figure 3.30), indicating social bonding. Depending on their life cycle period, spotted seals are described to generally live in groups (LOWRY 1984; RUGH *et al.* 1997; LOWRY *et al.* 1998).

Distances kept between individuals across different group sizes varied strongly. In intermediate group sizes (8 and 9, and 15 to 18), animals stayed fairly close to each other (Figure 3.31) and interacted regularly (Figure 3.30). In medium and smaller group sizes on the other hand, distances kept were relatively larger, and less interactions occurred. Intermediate group sizes seem to be the best achievable group sizes for spotted seals and / or seem to have some sort of social advantage compared to medium and smaller sized groups, as animals spent more time interacting. They might feel more secure due to spending less time watching out for predators for example.

No dominant interactions were observed in spotted seals. Dominant interactions probably take place underneath the water surface and were therefore not recorded. The fact of collecting short-term data further limited the interpretation of the data set since interactions taking place could have been missed. Nevertheless conclusions can be drawn from the data obtained and behavior displays observed.

Spotted seals showed the basic social traits throughout our data, although no body sizes and no sexes were recorded. Our data suggest the existence of all verified social aspects including individual recognition. We virtually come to the same conclusions as long-term studies (BEIER and WARTZOK 1979; SULLIVAN 1981; INSLEY *et al.* 2003). Our approach of opportunistic marginal data works, and confirms the overall social status of spotted seals. Therefore our methods applied and our conclusions drawn from the bear species results should be valid.

4.1.6 Muskoxen

Our data reveals no output for male muskoxen probably due to a too low amount of data points (less than 3 hours; s. page 95).

Female muskoxen interacted regularly in a neutral form (Figure 3.39) with certain other adult females but behaved aggressive towards other adult females at the same time (Figure 3.40). Dominance interactions were often displayed by adult females; subadults were involved less often (Figure 3.40). Differentiated behavior patterns were observed. Such selective behavior confirmed the existence of social structure and a dominance hierarchy, as it was described by Lent (1988), Spencer and Lensink (1970) and Gray (GRAY 1973).

The distance histograms built show varying distances between adult females as well as adult females and calves (Figure 3.38 and Figure 8.49). Distance differences vary remarkably less than in free-ranging mammal species. This can be explained by the enclosure situation and by the 'release to supplemented feeding' setup during muskoxen data collection. The small

differences between distances in captive animals should be of greater importance compared to small differences found in free-ranging species' distances. Characteristically, agonistic activities are said to be related to feeding (REINHARDT and FLOOD 1983). Muskoxen, forced to feed simultaneously from one feeding resource, show a high degree of competition. The same setup and the same results are shown in our data, especially focussing on the female-dominant interactions occurring during the release to supplementing feeding (Figure 3.40).

Altogether, although results for muskoxen are fairly limited, we propose that a social structure and a dominance hierarchy exist. Due to decision making and differing behaviors displayed towards different individuals, the existence of social recognition is suggested as well. Again, and as stated in all other taxa, the method of collecting marginal opportunistic behavior data shows similar social tendencies as long-term studies do (GRAY 1973; SMITH 1976; SAELZLE 1979; LENT 1988).

4.2 Use of Opportunistic and Marginal Datasets for Evidence and in Behavior Studies

The term 'opportunistic' implicates having no structured research design. We compared three methods, very opportunistic, opportunistic and well structured. All of these methods are marginal, working with small to very small sample sizes.

The reason for showing the frequency distributions in such detail is to provide clear evidence for animals being selective. In this study, social patterns were found across all 6 species. All distance histograms showed noisy varying patterns indicating selective behavior. All interaction diagrams led to the same conclusions.

When collecting short-term data, certain events are likely to be missed. But what will never happen is that one is observing behavior traits which do not exist. Therefore, one can draw conclusions from our results, to the amount as what was observed. In this case, the existence of a social structure was investigated, and it was shown without relevant doubt.

4.3 Modeling with TreeNet

Applying the concept of data-mining via algorithmic modeling to behavior data appeared to be helpful and quantifies patterns. Results with the accuracy of up to 90% were given and provide

a generalizable pattern. Received were indicative results for the short-term behavior data leading to conclusions comparable to the ones derived from long-term data. Limits of the approach were highlighted in only one case: In male muskoxen the gains showed an accuracy of 50%, which is conform to randomness. This result may depend on either the method and / or the extremely limited amount of data collected (sample size of 24).

Different data collection methods seemed to change the accuracy of the models. Strong differences in outputs across methods occurred. When the behavior method is well-structured (1st Method, s. Table 2.1) as the case for howling monkeys, humpback whales, brown bears and polar bears, an accuracy of 75% to 90% was reached. The less structured methods (2nd and 3rd method), as the case for the muskoxen and spotted seal data, resulted in an accuracy of 50% to 65%. In all opportunistic behavior methods general signals were recognizable, but in the well-structured opportunistic behavior method results revealed higher reliabilities.

Further, the amount of data can influence the model output. With the well structured method, a minimum amount of 30 data hours and a maximum of 50 data hours were used. The less structured methods used over 10h of data for spotted seals and female muskoxen but only 2 hours and 45min of data for the male muskoxen model (the only model not delivering any relevant results). One can conclude that a minimum amount of data, with at least more than three data hours, is necessary to obtain a relevant model output. A minimum of 10 data hours (which would include a minimum of 60 data points with a 10 min scan time frame as applied in the well-structured method) would be advisable. TreeNet has been described to deliver usable results with 60 data points by Salford Systems (2003).

Conclusively, the coherence between the method setup and the amount of data hours used is not completely clear. Still we can conclude that with the well-structured method as well as with an amount of 30 data hours used, good model accuracies (75% and higher) can be reached. These numbers can be perceived as absolute minimum-standards for studies inferring on basic social traits through animal populations. However, even if one would double these requirements, major conclusions can be drawn from data material which can be collected easily, cheaply and world-wide on various animal species. In addition, this opens analysis for short data sets that traditionally might have been perceived as 'unusable' so far, e.g. in regards to the research design and data amount.

Testing of the prediction accuracy of TreeNet models via cross-validation (data splitting in different distance-intervals) further confirms the applicability of algorithmic modeling to behavior data. The output of the classification TreeNet models shows high overlap for all species,

ranging from 98% to 100%. Thus the accuracy of the predictive regression models is stated as well as the applicability and reliability of the program TreeNet when used to model marginal opportunistic behavior data in a quantitative fashion.

4.4 Meta-analysis

In this thesis the most important, relevant papers discussing social issues across all investigated species were presented. This approach was helpful to find overall pattern, tendencies, and the amount of studies published giving statements on social structure in these species (WORM and MEYERS 2003; WORM *et al.* 2005; WORM *et al.* 2006). No complete set of studies was presented, but a representative subset to reveal sociality across all 6 researched species.

A positive match in the comparison of our short term-data results with long-term data, which exist mainly for the four species described as being social, was achieved in the applied Meta-analysis. Brown bears have only been described as social by 79% of the studies (Table 3.9). In addition to our findings, this amount is surprisingly high, considering brown bears being managed as a non-social species. Throughout the other species, only howling monkeys do not reach 100% in the literature review (Table 3.3). The reason is one fairly old study denying the existence of dominance hierarchies in howler groups. All other four researched species are described as being social, which includes the maintenance of a dominance hierarchy as well as their ability to perceive individuals. Very surprising were these results for polar bears, also still managed as non-social predators. Only few (5) references existed giving a social statements on polar bears (Table 3.12). But they were all in agreement with our empirical data.

The availability of online behavior data is still very rare, and basically not to be found. Our data is already partially, and will be completely, put online and fully available for open access in a NBII Metadata data base (HUETTMANN 2006; JOCHUM and HUETTMANN 2006; JACOB and HUETTMANN 2007).

4.5 Meaning and Context of Key Findings

Nine expectations and hypothesis were introduced at the beginning of the study: (1) General applicability of the methods is stated. The well-structured method reveals higher accuracies of the model runs than the less structured methods (s. Table 2.1). Results between long-term studies and our short-term results complement each other, as expected.

Results for all species tested did not appear to be dependant on the species being described as 'social' and 'non-social' through long-term studies. Not a single distance histogram showed comparability to histogram results one would expect in non-social species (Appendix 8.7). The exact opposite was the case: Matching results were found indicating the researched species, including bears, being social. (2) Distinct decision-making was found to take place across all species, not only in the species described as social. (3) All animals of the investigated species were found to show differentiated selective behavior across individuals. The resulting graphs showed noisy, varying patterns in curves and surfaces across age classes and body sizes.

Distances between social individuals were not centred around the means. Thus, sophisticated sociality is concluded for all species researched (4, 5, and 6). Not a single result graph confirmed the hypothetical pattern of non-sociality existing in any species. Flat curves, flat surfaces and data points centred around the mean or dispersed randomly were never found. Animals always responded to individuals selectively; likely in a strategic fashion.

Bears were shown to be able to differentiate between individuals, and to do this because of an underlying social structure and its mechanisms. (7) Although using incomplete marginal short-term behavior data, we did not find any signs for non-sociality across all species. (8) The different methodological approaches help to verify and validate results. (9) Working with many mammal species world-wide, would strengthen further the validity of our methodological approach.

Patterns across all species included in this thesis showed diverse and individually driven behavior patterns, no matter if a species was described as social (howling monkeys, humpback whales, spotted seals and muskoxen) or a species described as non-social (brown bears and polar bears). Individuals seemed to purposely choose what distance to keep to other individuals, independent of the size and age class of the other individuals. Important to notice is that such actively chosen selective behaviors remained, even when looking at animals of the same body size and age classes. Conclusively, the reason for the latter selective behaviors occurring, were strongly pointing towards individual perception abilities and long-term social

memories. Differentiated behavior occurred between all individuals in these populations, independent of body size and age. It can be concluded that at least a basic social structure exists in all these six species.

Following a short summary across the use of all statistical approaches is presented: Distance histograms allowed for a closer look into distances kept between BSI sizes; interaction diagrams helped to get an overview of interactions displayed. Overall, BSI sizes had an influence in all model runs across species, ranked as most dependant predictor twice and as 2nd important predictor three times. The only other first ranked parameters across model runs were spatial parameters. These results implement the high importance, dependence and correlation of spatial parameters (habitat) and behaviors in animals as such, and also between spatial parameters, behaviors and the social status of the animals in the group (BSI).

4.6 Strength and Weaknesses of Approach

Table 4.1 Conclusions possible and not possible to draw from short-term behavior modeling

Conclusions from short-term data	YES - can be concluded	NO – can not be concluded
without BSI	all observed social interactions and behaviors	missed social interactions are likely to exist
	existence of social patterns and partial descriptions of social traits existing	definitely not all existing social traits will be recorded
	existence of social structure	specific social structure type
with BSI	differences in behaviors displayed across body sizes and age classes	more detailed social pattern and social structure type

Received results show good and transparent directions in regards to short-term behavior data delivering same statements than long-term data can. It seems that one can draw some general conclusions. These results definitely show that algorithmic modeling can reveal underlying patterns even in behavior data and that this issue opens up a completely new field and also challenges behavior research and scientists further.

Through research of short-term behavior data, an overall general pattern can well be revealed. Still, the results stay general. One will probably not be able to reach as conclusive results as long-term studies can when it comes to specific and more advanced research questions.

4.7 Individual Perception in Bears

Many researchers use the term 'social' in recent brown bear publications and describe social structures such as dominance hierarchies, socially selected infanticide (SSI) and home range overlap. Home range overlap in females is even linked with kin-ship (MC LELLAN 2005; STØEN *et al.* 2005; BELLEMAIN *et al.* 2006). How can officials neglect such findings and still treat brown bears as a solitary non-social species? So far, no obvious management implementations are known to us that truly consider such findings on bear sociology, even though suggested so for a long time by established scientists (SWENSON *et al.* 1997; STENHOUSE *et al.* 2005).

For polar bears, no social system is described although Latour (1981) already recognized the flexibility of polar bears' social system. They undergo annual changes in behavior: from active hunting, essentially solitary individuals to social congregations of non-hunting individuals. During polar bear gatherings in certain areas close to shore, they are in a non-competitive life situation, not competing for any resources as food and mates. Why should they gather in the first place? When being solitary, they should not be interested in concentrations. All these statements were made by Latour (1980) and (1981) already but were not really followed up any further. All statements made on polar bear sociality so far are rather conservative: *"Under non-competitive conditions a population of solitary carnivores can reallocate their total active time towards more social behavior"* (LATOURE 1981).

Ovsyanicov (2005) proclaims for Russia the existence of advanced social relations, the complexity of communication processes, a good memory and advanced deductive capabilities in polar bears. Polar bears owe these capabilities to life in a uniform, fast changing habitat. The landscape constantly changes, so do mark disposition, weather and possible hunting places.

These findings are not quantitative in the classic sense, but completely in agreement with bears being social animals. Thus, the existence of social behavior traits, the existence of a dominance hierarchy and the existence of a social system leading to the conclusion that bears are social species, are support.

5 Overall Conclusions and Study Suggestions

Despite its current and active discrimination, so far, marginal opportunistic data collection can be very effective and powerful. It leads to similar results than what is achieved from more time investing and expensive long-term research. It was shown that even so called 'poor data' are useful to address crucial questions for management and beyond. Methods were provided to do so convincingly.

If we open our mind for new analytical approaches and open up more research fields for data mining tools, we can derive different views on data, its applicability and usage. Further, we advise to make more behavior data available online, even data that is considered 'poor' or 'useless'. Thus, data can be analysed in a bigger linked picture and can easily reveal so far unknown facts to provide progress in research and science. We should extend our knowledge about sociality, as broad as it may be for monkeys and apes, to other animal species, including bears, in order to help develop effective measures for their management and conservation. Other potential species for such approaches are ravens, albatross, ducks, cranes, squid, sharks and ants for instance.

From our experience we want to state 4 key pieces of advice for further studies: (i) mine existing poor data for their validity, (ii) make such data publicly available, (iii) revise or describe social systems in species and (iv) apply the use of marginal opportunistic data to other fields in behavior research.

Future studies do not necessarily have to demand more detailed data, or a full research design study. Instead, it seems plausible to stay within the framework of using widely existing marginal opportunistic data and to improve a reliable analysis of such data. More data of this kind should be made accessible through online data-bases.

To answer research questions trustworthy and enhance wildlife management, marginal opportunistic data holds major potentials. We could easily gain a vaster knowledge from data that we already today possess and use.

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8 Appendices

8.1 Appendix: General Definitions

Body Size Index (BSI): the BSI is the relative body size of an individual belonging to a certain species. 'Relative' implicates the size is set in relation to the body sizes of the whole species size range. An adult male howling monkey has a different real size than an adult male polar bear, but set in relation to the female, subadult, juvenile and infant body size, their body sizes are comparable within the same species. The BSI is defined as ranging from 1 to 10. Body sizes of 1 and 10 were not observed in any of the researched species.

BSI categorisation for each species:

- Howling Monkeys: 2 infants, 3-4 juveniles, 5-6 subadults, 7 adult females, 8 adult males.
- Humpback Whales: 4 juveniles, 5 subadults, 6-9 subadults or adults
- Brown bears: 2-3 first year cubs, 4 yearling cub, 5-6 subadults, 7 adult females or young adult males, 8-9 adult males
- Polar bears: 2-3 first year cubs, 4 yearling cub, 5-6 subadults, 7 adult females or young adult males, 8-9 adult males
- Spotted Seals: no categorisation
- Muskoxen: 2-4 calves, 5-6 subadults, 7 adult females, 8-9 adult males

'personal space zone' (PSZ): is defined as the distance individuals of a species must keep from a particular individual in order for it to not change its behaviour due to the presence of the other individual(s). There are certain individuals who are allowed to cross this invisible line, others who are not. The PSZ for polar bears is defined as less than 100m, for brown bears less than 50m, in humpback whales as less than 500m and in howling monkeys less than 5m. The PSZ for spotted seals is defined at 10m, for muskoxen as close as 1m.

A **separate individual** is defined as an animal being old enough to live on its own and no longer depends on mother care.

A **group** is here defined as animals of one species coming, staying and traveling together for a certain period of time.

An individual 1 is defined as being **dominant** over another individual 2 when (1) individual 2, encountered by individual 1, moves off by backing up, walking away or running away, or (2) the presence of individual 1 caused an approaching animal (individual 2) to alter its direction of movement (LATOIR 1981).

Classification of interactions: can be 'neutral' or one individual can be dominant over the other one. ('positive-negative'). '**Neutral**' is an interaction when both interactors behave friendly and generate no aggressiveness again each other. They are not presenting any dominant behavior. When an interaction is '**positive-negative**', at least one of the two interacting animals expresses dominant behavior towards the other. The second individual either indicates subordinate behavior to prevent collision or avoid the dominant acting animal.

A **tundra vehicle camp** consists of four rebuild tundra vehicles; one kitchen wagon, one dining wagon and two sleeping wagons. Overnight stays are rented during bear season by the tundra vehicle companies. Altogether, two camps exist (GREAT WHITE BEAR TOURS; THE TUNDRA BUGGY ADVENTURE). The predictor 'close to tundra vehicle camp' in the polar bear model tests on human impact on polar bear behavior. Two tundra vehicle companies maintain altogether 18 permits to drive through the CWMA. Tundra vehicles vary in sizes putting up to 40 people in one tundra vehicle.

8.2 Appendix: Observed Activities

Following activities were recorded across species:

Table 8.1 Observed activities across species

Activity	Definition	HMs	HWs	BBs	PBs	MKs	SSs
sitting		X		X	X		
feeding		X		X on salmon	X	X	X on fish
walking		X		X	X	X	
standing		X		X	X	X	
hanging		X					
looking		X		X	X		
laying		X		X	X	X	
reaching	mainly for leaves & branches	X					
vocalising		X				X	
traveling	moving forward; recorded by spouting & visible fin		X				
traveling slow			X				
lunge feeding / breaching	moving forward slowly		X				X
jumping	forehead, back (dorsal fin facing water surface) or spin jump		X				X
side flip			X				
spy hopping			X				X
flipper waving/fluke splash	laying on one body side; one flipper & often half fluke shown		X				X
belly sunbathing							X
diving							X
walking slow	often head low, scanning ground for food or look around & meandering/walking slow around, seem not to have a destination			X	X	X	
swimming	often head low, scanning ground for food or look around & meandering/walking slow around, seem not to have a destination			X	X		X
grazing				X			
fishing				X			
runing	to actually catch an alive fish			X	X	X	
playing				X	X	X	
rolling					X		
head low					X	X	
smelling					X	X	
standing up	head up, nose highest point				X		
standing up on vehicle					X		
bagging					X		
nursing					X		
swimming					X		
grazing					X	X	

8.3 Appendix: Interaction Categories

8.3.1 General Interaction Definitions

Altogether following species varying behaviour categories and subcategories were defined:

Except of one, all interactions classified in this study take place between two 'separate' individuals. Five interaction categories are defined, split into twenty five subcategories.

To the interaction category '**approach retreat**' belong all interactions based on two individuals being in a certain range of each other, and of their knowledge of the other individual being around. This certain range is species dependent.

'Travelling together' occurs when individuals do not mind another separate individual entering their 'personal space zone'. They do not show any signs of nervousness and of feeling uncomfortable. Further they do not indicate any different behaviour than before and travel the same direction. They stay close walking or swimming around. (HM, HW, BB, PB, SS, MK)

The interaction subcategory '**Approach**' occurs when the 'personal space zones' of two separate individuals overlap for a certain amount of time. One individual is moving into the 'personal space zone' of another. An 'approach' can be 'neutral' or one individual can be dominant over the other one ('positive-negative'). When their interaction is neutral, they accept each other being close but do not walk on together. They separate again for travelling. (HM, HW, BB, PB, SS, MK)

The subcategory '**chase off**' describes a certain reaction after one individual comes close to the PSZ of another. One individual gets chased away by the other; both individuals start running for a few seconds, one chasing, the other one taking off. Therefore this category is always positive for one and negative for the other. (HM, HW, BB, MK)

The interaction subcategory '**distance displacement**' combines long and short distance displacements, though the distance between two individuals to each other is during the whole interaction larger than their PSZ. One individual changes locations due to another individual moving in. Mostly these types of interactions happen slowly and are not observable often as the animals smell each other over a longer distance than one is able to observe them. (HM, HW, BB, PB)

When animals do not recognize by smell which animal is approaching them, as happening often when the wind blows from the other direction the animal is approaching, an interaction named '**check**' occurs. When hearing an approach before smelling, they stand up on their hind legs, ears turned up front, nose up high in the air (being the highest body part) and look into the direction the approaching animal is suspected to come from. A founded '*check*' is followed by either an 'approach' or a displacement, e.g. 'chase'. (BB)

The subcategory '**Fish stealing**' is rarely to observed as it happens just occasionally. Here, one individual is approaching another and steals the fish another recently caught or found. They separate most often through running off or one chasing the other one away. (BB)

'**Grooming**' is defined as skin and fur care implemented by another individual of the same species. (HM)

The interaction category '**Play**' includes any interaction between two individuals spending time in close contact playing with each other. Interactions can be neutral or positive for one and negative for the other one. In all 'play' subcategories the crossing of the PSZ and often body contact occurs.

'**Basic play**' includes all play interactions except the ones defined separately in the other play categories. It is not specified more precisely. (HM, SS)

'**Backlash**' pictures two individuals taking turns in chasing each other. The animals stop shortly before touching the chased individual. When they catch up with one another the one who chased before becomes the one who is being chased and the other way around. (HM) (BB)

'**Playbite**' is when two individuals bite each other carefully so they don't hurt the other one playing with. Preferred places to bite are ears and arms. (BB)

'**Playfight**' includes all playful fighting behaviours between two individuals. Body contact always occurs. The aim is not to put force on the other individual but to play with him and develop fighting skills (REF). The duration may be up to an hour. (HM, PB)

The subcategory '**spin jump**' is described as a playful behavior. The animal jumps lateral out of the water spinning his body at the same time around his own body axis, landing sideways on the water surface with generating a big splash. (HW)

A '**forehead jump**' is a horizontal jump with the dorsal side of the animal facing the sky. At the emergence onto the water surface the body is hunched down and therefore is not as noisy and far to hear as 'back jump' and 'spin jump' behaviour. (HW)

'**Patting**' is touching of another bear with the front paws while standing on hind legs. It might be an invitation to join play. (BB)

In the interaction category '**fight**' all interactions including aggressive behaviors one individual exposes towards another are combined. All 'fight' subcategories end positive for one and negative for the other individual, they have always a more and a less dominant interactor. In all 'fight' subcategories the crossing of the personal space zone and often body contact occurs.

'**Jump on**' occurs when an individual jumps on another one repeatedly. Often the one being jumped on vocalises and tries to get away. (HM)

The subcategory '**grabbing**' is defined as a fight carried out with hands. Both individuals try to grab one another. (HM)

'**Threat**' occurs when two individuals get closer to each other than 10m, standing opposite, facing each other. This position may take up to a few minutes without any movement of the animals or they walk into a direction a few slow steps simultaneously to keep the few metres of distance. This may go along with vocalisations as e.g. deep grunts in bears. (BB, MK)

'**Aggressive behavior**' is defined as animals showing aggressive behavior without having body contact to another individual. They display signs of aggression trying to prevent a fight by demonstrating their strength and letting others know that it is not worth it to start a fight.

During the display of '**fluke waving**' only the tail and the fluke are visible. Other body parts of the animal remain under the water surface. The fluke is brought up into the air, followed by fast slapping onto the water surface for about 6-12 times in a row without neither getting the fluke under the water surface nor another body part above the water

surface. This perspective is not completely established yet; there is space for further interpretation. It was mainly observed in aggregated animals. (HW)

The subcategory '**proximity**' occurs when one individual reacts aggressive to a second or third individual because of its closeness. (PB, MK)

'**Communication**' includes all communicative behaviours occurring between more than 2 individuals.

The only subcategory is '**group movement**'. All individuals of one 'group' react to a behaviour displayed by one individual through behaving in an according way. (HM, HW, SS, MK)

8.3.2 Species Categorisation

Table 8.2 Howling monkey behavior categorisation

Category	Subcategory	Distance	Species Dependant Definition
Approach Retreat (AR)	travelling together	< 5m	
	approach	< 5m	e.g. dominant 'positive-negative' 'approach': when an individual is leaving a preferred resting space due to a higher ranked individual showing up
	chase off	< 10m	The 'chase off' distance is twice the PSZ
	distance displacement	> 10m	
	grooming	body contact	
Play	backlash	< 5m	
	playfight	body contact	includes wrestle, grab, push and pull
	basic play	< 5m	
Fight	jump on	body contact	
	grabbing	body contact	
Communi- cation	group movement	all	same reaction pattern of whole group to behaviour of 1 animal out of the group

Table 8.3 Humpback whale behavior categorisation

Category	Subcategory	Distance	Species Dependant Definition
Approach Retreat (AR)	travelling together	< 100m	always neutral
	approach	< 500m	
	chase off	< 500m	
	distance displacement	> 500m	
Play	forehead jump	all	
	spin jump	all	
Aggressive Behavior	fluke waving	all	
Communi- cation	group movement	all	important for feeding success e.g. 'lunge feeding', they work together

Table 8.4 Brown bear behavior categorisation

Category	Subcategory	Distance	Species Dependant Definition
Approach Retreat (AR)	travelling together	< 50m	includes not to back up; always neutral
	approach	< 50m	
	chase off	< 50m	
	check	> 50m	
	fish stealing	< 5m	
	distance displacement	> 100m	
Play	playbite	body contact	
	backlash	all	appears like false charging
	patting	body contact	
Fight	threat	< 10m	mouths wide open, lower lip hanging down, nose, highest point of the body, ears lowered and ear tips turned backwards

Table 8.5 Polar bear behavior categorisation

Category	Subcategory	Behavior	Distance	Species Dependant Definition
Approach Retreat (AR)	travelling together		< 100m	includes not to back up; always neutral
	approach		< 100m	always interaction between two bears (only species where human interactions are collected as well ('approach by human', 'approach by bear'))
		approach by human	< 100m	approach of bear by 'human' (e.g. tundra vehicle, helicopter)
		approach by bear	< 100m	approach of 'human' by bear (e.g. tundra vehicle, helicopter); always neutral
		distance displacement		> 100m
Play	playfight		body contact	running onto each other (false charge) alternating, paws on paws or on other body part of the playmate while standing on hind legs, both showing open mouth display
Aggressive Behavior	proximity		< 10m	

Table 8.6 Spotted seal behavior categorisation

Category	Subcategory	Behavior	Distance	Species Dependant Definition	
Approach Retreat (AR)	travelling together	swim together	<10m	travelling together; moving forward and staying close at the same time	
		dive together	<10m	animals disappear together from the water surface; diving	
		swim synchronized	<10m	identical swimming movement of animals	
		swim parallel	<10m	swimming parallel to each other on water surface	
	approach	approach	<10m	swimming towards each other	
			snout to snout	body contact	snout contact between animals
			in line	<10m	swimming in a line, following each other
Play	basic play	fluke splash	<5m	use of fluke to splash water	
		body breach	<10m	jumping out of the water with landing dorsal or ventral on the water surface; includes also half body breach	
Communi- cation	group movement	cluster	<10m	animals concentrated within a specified distance	
		look at each other	all	heads are out of the water and individuals are looking at each other	
		heads up synchronized	<10m	more individuals looking out of the water with an erected head simultaneously	
		body interaction	body contact	one animal responds with another animal by body contact, e.g. by flipper	
		synchronized fluke splash	<10m	coordinated fluke splash among animals	
		complete group movement	<30m	all animals moving together or respond to the behaviour implemented by one individual; e.g. diving	

Table 8.7 MuskoX behavior categorisation

Category	Subcategory	Behavior	Distance	Species Dependant Definition
Approach Retreat (AR)	travelling together	travelling together	< 5m	related animals move together
	approach	approach	< 5m	active process, ends in standing together or feeding together; always neutral
		displacement	< 5m	one animal displaces another animal from a point in space, and occupies that space
		food displacement	< 5m	one animal displaces another animal from a food source (i.e. supplemental pellets or hay)
		mounting	body contact	one animal mounts another animal
	chase off	chase off	< 5m	one animal chases another, causing the second animal to run away
		vocal	< 10m	an animal makes an aggressive or responsive noise (growl, blow or snort)
Aggressive Behavior	proximity	defence	< 1m	defending its space
		food defence	< 1m	defending food
		scare	< 5m	scaring other animal away
Fight	threat	horn push	body contact	pushing other animal away with horns
		head butt	body contact	when two animals butt heads with each other
		feeding challenge	< 10m	approaching feeding animal
		horn chase	< 10m	scare animal off with horns by lowering head
		fighting	body contact	horn clash
		push	body contact	one animal makes physical contact with another and pushes (not with horns)
		complete group movement	all	animals move as a group

8.4 Appendix: Ethograms

Table 8.8 Howling monkey category classification

Category	Subcategory	Remarks	Body Size (dom indiv)	Body size (less dom indiv)	Assessment		
					neutral	pos /neg	
Approach Retreat (AR)	travelling together		7	8	n.o.	1	
			7	7	1	1	
			7	4	1	n.o.	
			7	3	2	n.o.	
			7	2	1	n.o.	
	approach			8	8	1	n.o.
				8	7	12	1
				8	6	3	2
				8	5	2	1
				8	4	3	n.o.
				8	2	1	n.o.
				7	7	7	3
				7	6	7	2
				7 (inf)	6	n.o.	2
				7	5	2	n.o.
				7	4	6	2
				7	3	2	n.o.
				7	2	8	n.o.
				6	5	n.o.	3
				6	4	5	n.o.
	chase off			8	8	n.o.	1
				7	7	n.o.	1
				4	3	n.o.	1
	distance displacement			8	8	n.o.	4
		ni		8	3	n.o.	1
		ni		7 (inf)	7	n.o.	2
		ni		7 (inf)	6	n.o.	3
grooming			2	7	2	n.o.	
Play	backlash		3	2	1	n.o.	
	basic play		6	6	1	n.o.	
			4	4	1	n.o.	
	playfight			7	5	n.o.	1
				6	5	n.o.	1
			6	4	1	n.o.	
			3	2	1	n.o.	
Fight	grabbing		8	8	n.o.	1	
			7	7	n.o.	3	
			7 (inf)	6	n.o.	1	
			6	5	n.o.	1	
			4	4	n.o.	1	
	jump on			8	7	n.o.	1
				4	4	n.o.	1
Communi- cation	group movement	ni	changes	all	5	n.o.	

ni = not included in interaction diagrams; n.o.= not observed

Table 8.9 Humpback whale category classification

Category	Subcategory	Re- marks	Body Size (dom indiv)	Body size (less dom indiv)	Assessment		
					neutral	pos /neg	
Approach Retreat (AR)	travelling together		8	8	2	n.o.	
			8	7	2	n.o.	
			8	6	2	n.o.	
			8	4	1	n.o.	
			7	7	4	n.o.	
			7	6	1	n.o.	
			7	5	6	n.o.	
			6	6	6	n.o.	
			6	5	2	n.o.	
		6	4	2	n.o.		
	approach			7	7	n.o.	1
				7	6	n.o.	1
				6,4	8	1	1
	chase off	ni	8,6,4	7	n.o.	1	
distance displacement	ni	7,7	6	2 (?)	n.o.		
	ni	7	6,5	2 (?)	2		
Play	forehead jump		7	5	1	n.o.	
	spin jump		7	5	1	n.o.	
				7	4	1	n.o.
	back jump	n.o.					
flipper waving	n.o.						
Aggressive Behavior	fluke waving		6,4	7	n.o.	1	
Communi- cation	group movement		6	4	1	n.o.	

ni = not included in interaction diagrams; n.o.= not observed

Table 8.10 Brown bear category classification

Category	Subcategory	Remarks	Body Size (dom indiv)	Body size (less dom indiv)	Assessment		
					neutral	pos /neg	
Approach Retreat (AR)	travelling together	ni	7	4	35	n.o.	
			8	7	1	n.o.	
			7	6	1	n.o.	
			7	5	1	n.o.	
			6	6	7	n.o.	
			6	5	6	n.o.	
	approach	H		8		n.o.	1
		H		6		n.o.	3
			7,4	6		4	1
		ni	7,4	6,5		n.o.	1
			7	6		1	n.o.
			6	6		5	n.o.
		ni	6	6,5		n.o.	1
			6	5		1	2
			5	6		n.o.	2
		chase off	H		7,4		n.o.
	H			6		n.o.	1
			7,4	6		n.o.	8
			7,4	5		n.o.	1
			7	6		n.o.	1
			6	6		n.o.	2
			6	5		n.o.	1
			5	6		n.o.	1
	check			6	6	2	n.o.
				6	5	n.o.	1
	fish stealing		6	6	n.o.	1	
	distance displacement	ni	7,4	6,6		n.o.	2
ni		7,4	6		n.o.	1	
ni		7	6		n.o.	1	
Play	playbite	ni	7	4	1	n.o.	
	backlash	ni	7	4	2	n.o.	
	patting	ni	7	4	1	n.o.	
Fight	threat		7,4	6	n.o.	1	
	physical	n.o.					

ni = not included in interaction diagrams; n.o.= not observed

Table 8.11 Polar bear category classification

Category	Subcategory	Remarks	Body Size (dom indiv)	Body size (less dom indiv)	Assessment		
					neutral	pos /neg	
Approach Retreat (AR)	travelling together		9	8	3		
			9	6	1	n.o.	
			7	7	1	n.o.	
			7	6	3	n.o.	
		ni	7	5,5	1	n.o.	
		ni	7	4	1	n.o.	
		ni	7	3,3	2	n.o.	
	approach			9	8	1	n.o.
				9	7	2	1
				9	6	1	n.o.
				8	7	4	n.o.
				8	6	1	n.o.
				7	6	2	n.o.
				6	7(Fu2)	n.o.	1
	approach by bear			H	9	1	n.o.
				H	8	2	n.o.
				H	6	5	n.o.
	approach by H			H	8	1	2
				H	7	1	n.o.
				H	7(Fu2)	n.o.	1
			H	6	1	1	
			H	5	n.o.	1	
distance displacement		ni	8	7	n.o.	3	
		ni	7,6	7	n.o.	1	
Play	playfight		7	7	1	n.o.	
			7	6	1	n.o.	
			6	6	1	n.o.	
Aggressive Behavior	proximity		9	7	n.o.	1	

ni = not included in interaction diagrams; n.o.= not observed

Table 8.12 Spotted seal category classification

Category	Subcategory	Behavior	Time[h] of observation	Group Size	Number of Interacting Animals	Assessment	
						neutral	
Approach Retreat	travelling together	swim together	19-20.30	6	2	1	
			8.15-12 & 13.15-14.30	8	2	10	
					3	7	
					4	1	
					5	2	
			8-11	10	2	2	
					4	1	
					6	1	
			8-11	15	2	13	
					3	11	
					4	7	
					5	3	
					6	1	
					8	2	
			15.30-18	16	2	9	
		3			4		
				4	1		
				5	2		
				6	3		
				7	3		
				8	1		
		14-17	21	2	1		
				3	9		
				5	2		
				6	1		
				7	1		
				9	1		
		dive together	8.45-11.15 & 13.15-14.30	9	2	1	
			15.30-18	16	2	4	
			14-17	21	2	1	
					3	1	
			15	1			
	18.30-20.30	24	2	1			
	swim synchronized	8.45-11.15 & 13.15-14.30	9	2	1		
		8-11	15	2	1		
				3	1		
	swim parallel	8.15-12 & 13.15-14.30	8	2	1		
	approach	approach	8.15-12 & 13.15-14.30	8	2	1	
			8-11	10	6	1	
13.30-16			18	2	1		
14-17			21	2	3		
18.30-20.30			24	3	1		
snout to snout		8.45-11.15 & 13.15-14.30	9	2	1		
		8-11	15	2	1		
in line		14-17	21	8	1		
Play		basic play	fluke splash	19-20.30	6	2	1
				8.15-12 & 13.15-14.30	8	1	9
					2	4	

			8.45-11.15 & 13.15-14.30	9	1	3	
					2	3	
			19-20.30 & 18.30-20.30	11	1	5	
					2	1	
			8-11	15	2	5	
			15.30-18	16	1	7	
					2	1	
			13.30-16	18	1	7	
					2	1	
					6	1	
			18.30-20.30	24	1	4	
					2	3	
			body breach	8.15-12 & 13.15-14.30	8	1	3
				8.45-11.15 & 13.15-14.30	9	1	1
				19-20.30 & 18.30-20.30	11	4	1
	8-11	15	1	1			
	15.30-18	16	1	1			
Communication		cluster	14-17	21	6	1	
					4	1	
		look at each other	14-17	21	2	1	
		heads up synchronized	8-11	15	2	1	
		body interaction	8.45-11.15 & 13.15-14.30	9	2	1	
		synchronized fluke splash	13.30-16	18	2	1	
		complete group movement	8.15-12 & 13.15-14.30	8	all	4	
			8.45-11.15 & 13.15-14.30	9	all	1	
			8-11	10	all	1	
			19-20.30 & 18.30-20.30	11	all	1	
			15.30-18	16	all	2	
			14-17	21	all	5	
			18.30-20.30	24	all	1	

Table 8.13 Muskox category classification

Category	Subcategory	Behavior	Body Size (dom indiv)	Body size (less dom indiv)	Assessment	
					neutral	pos /neg
Approach Retreat (AR)	travelling together	travelling together	7	7	2	
	approach	approach	7	7	6	
			6	6	2	
			2	2	3	
		displacement	8	7		2
			7	7		14
			7	6		2
			7	5		5
			7	2		7
			2	7		2
		food displacement	7	7		77
			7	6		1
			7	5		8
			7	2		4
			6	5		1
			2	2		3
	chase off	chase off	2	2	4	
			7	7		16
			7	5		2
			7	2		3
		6	6		3	
	vocal	8		2		
	Aggressive Behaviour	proximity	defence	7	7	
			7	5		1
food defence			7	7		2
scare			7	7		1
Fight		horn push	7	7		3
		head butt	8	7		1
			8	6		1
			7	7		7
			6	6		2
		feeding challenge	7	7		2
		horn chase	7	7		1
		fighting	6	6		1
		push	7	7		2
2	2			1		
Communication	group movement	complete group movement	7	all	1	

8.5 Appendix: TreeNet Model Setup

Species	Target size	Continuous Predictors	Categorical Predictors
Howling Monkeys	distances between individuals (m)	day	BSI
		time (h)	neutral interactions
			dominant interactions
			sitting on the same tree/different trees
Humpback Whales	distances between individuals (m)	day	BSI
		time (h)	neutral interactions
			dominant interactions
			being close to shore /offshore
Brown Bears	distances between individuals (m)	day	BSI
		time (h)	neutral interactions
			dominant interactions
			close to/far from the weir
			downstream/upstream
Polar Bears	distances between individuals (m)	day	BSI
		time (h)	neutral interactions
			dominant interactions
			in the willow/coastal area
			close to/away from shoreline
			close to/away from tundra vehicle camp
Spotted Seals	distances between individuals (m)	time (h)	number of interacting animals
		start time (h)	number of all animals in the observed group
		end time (h)	dominant interactions
			neutral interactions
			dominant interactions
Muskoxen	distances between individuals (m)	day	BSI
		time (h)	neutral interactions
		month	dominant interactions

8.6 Appendix: Additional Result Figures

8.6.1 Howling Monkeys

8.6.1.1 TreeNet Output

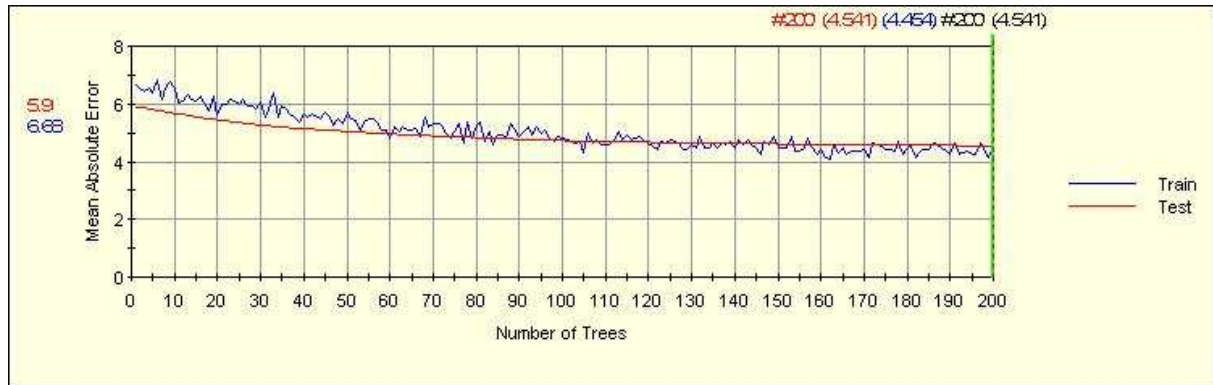


Figure 8.1 Mean absolute error in the howling monkey model

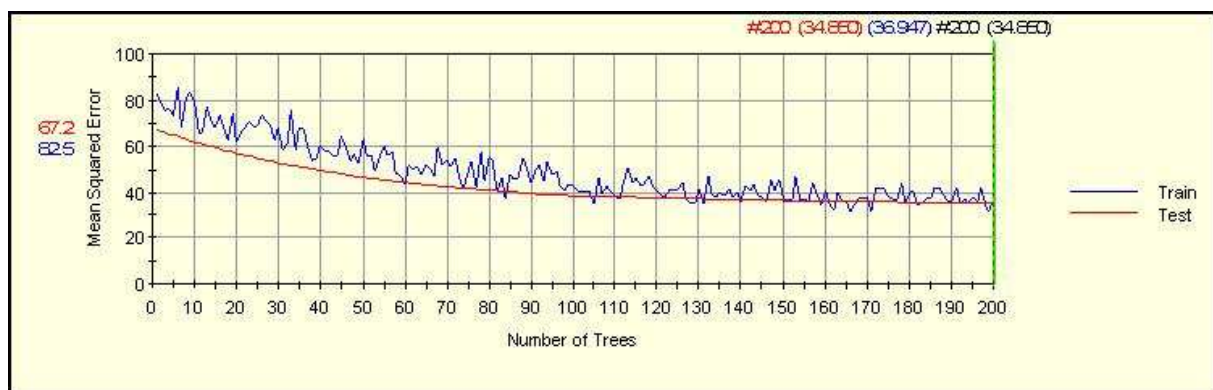


Figure 8.2 Mean squared error in the howling monkey model

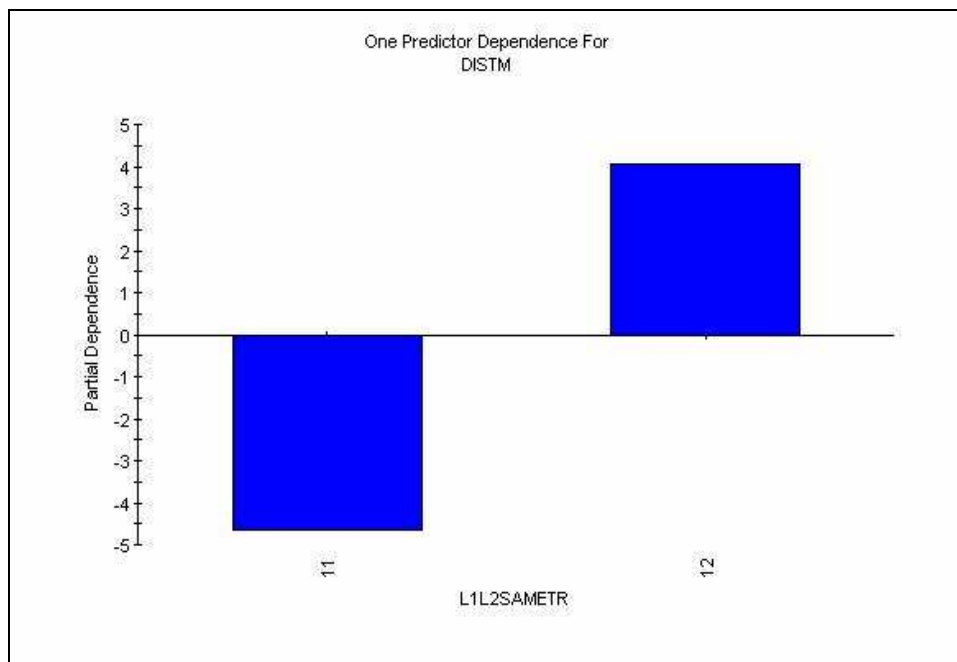


Figure 8.3 One predictor dependence (1) for howling monkeys; importance ranking 100%

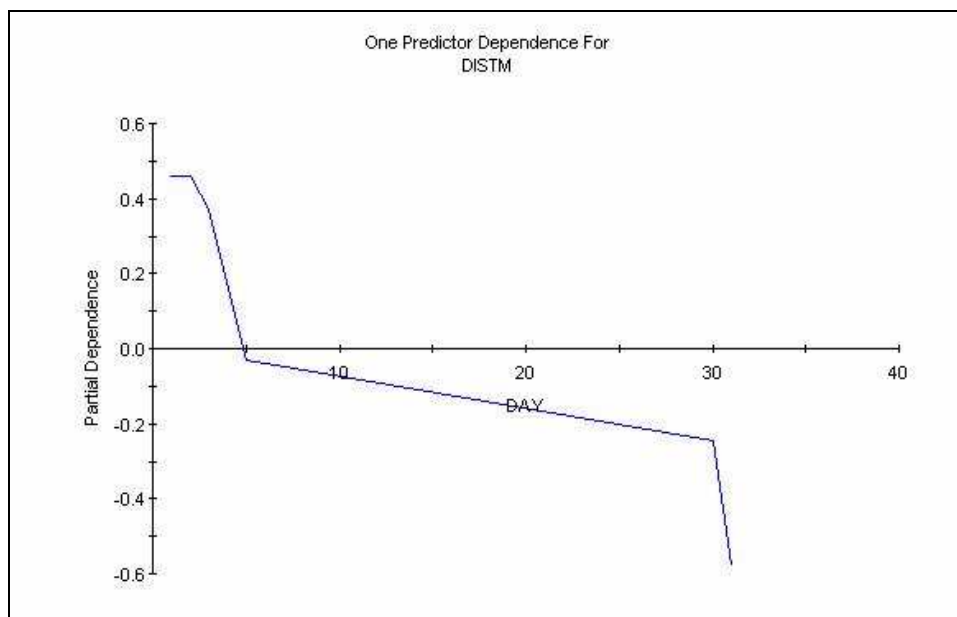


Figure 8.4 One predictor dependence (3) for howling monkeys; importance ranking 29.16%

8.6.1.2 Distance Histograms

All BSI combinations with over 20 sample points for each species are presented. The vertical blue line represents the mean.

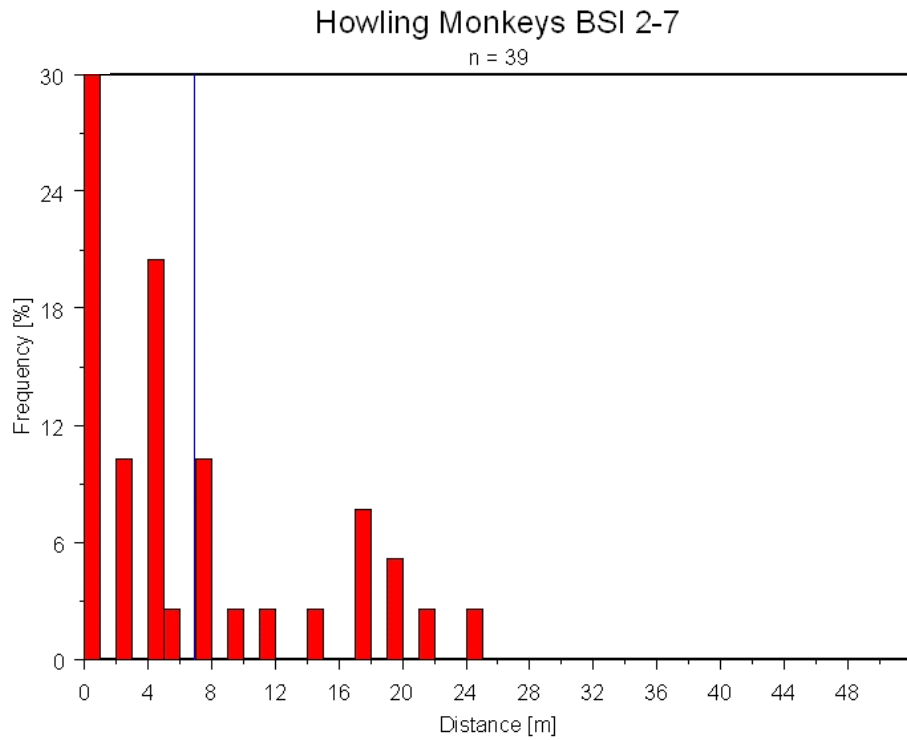


Figure 8.5 Distance histogram for the interacting BSI sizes 2 vs. 7 in howling monkeys; the first interval (0m-1m) is cut off ranging up to 37,5%

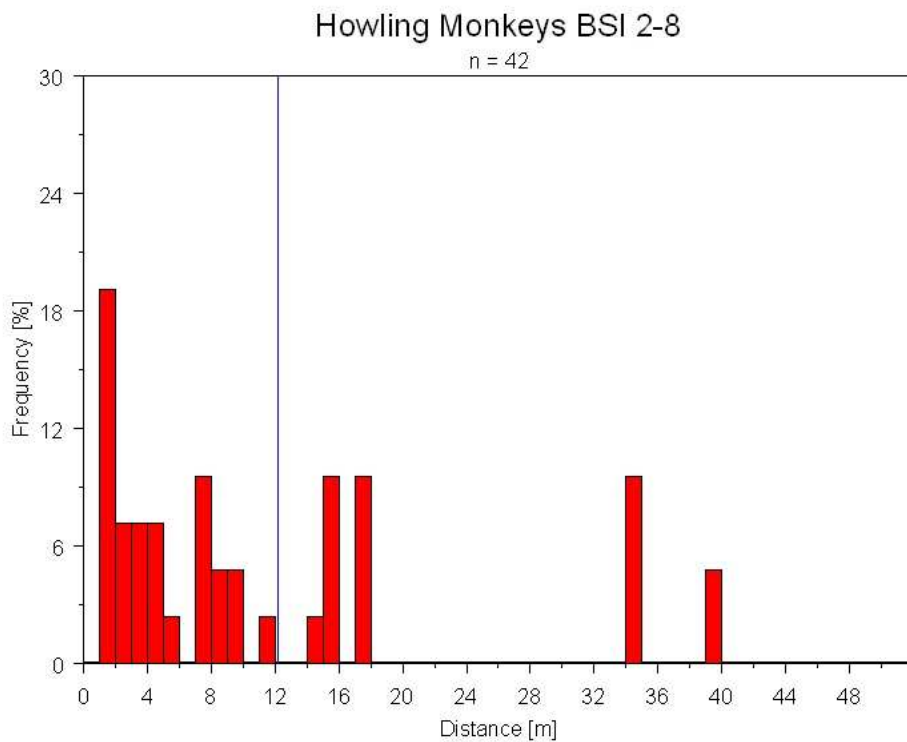


Figure 8.6 Distance histogram for the interacting BSI sizes 2 vs. 8 in howling monkeys

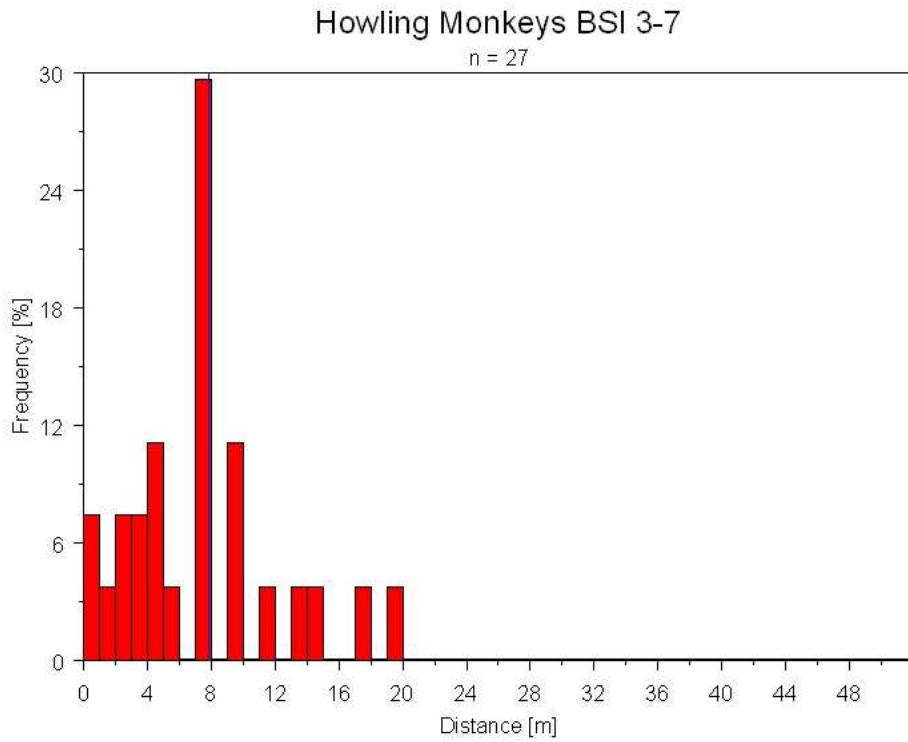


Figure 8.7 Distance histogram for the interacting BSI sizes 3 vs. 7 in howling monkeys

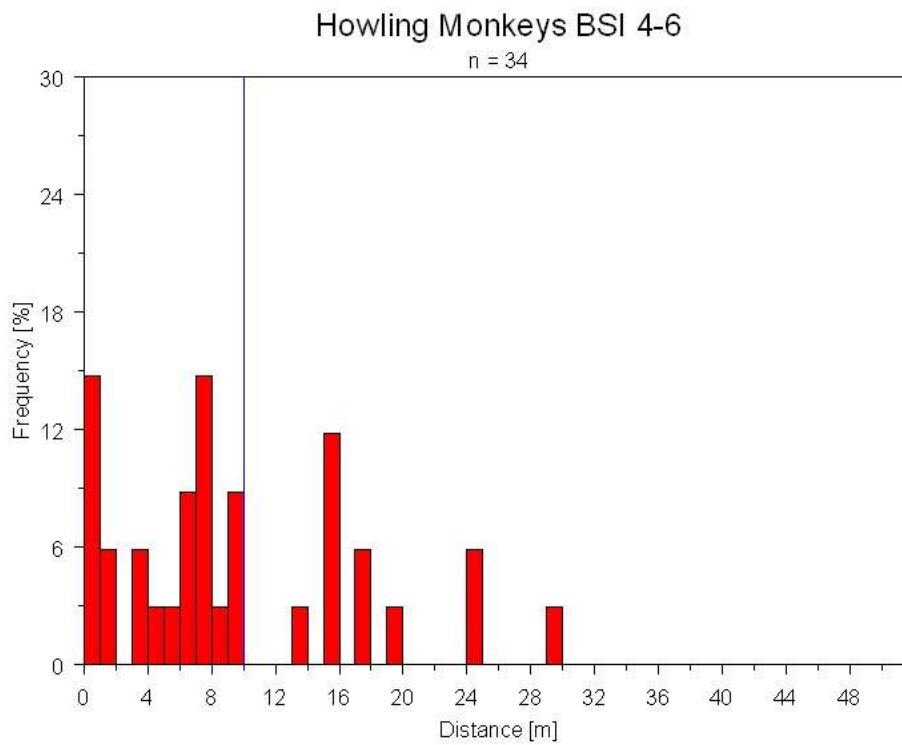


Figure 8.8 Distance histogram for the interacting BSI sizes 4 vs. 6 in howling monkeys

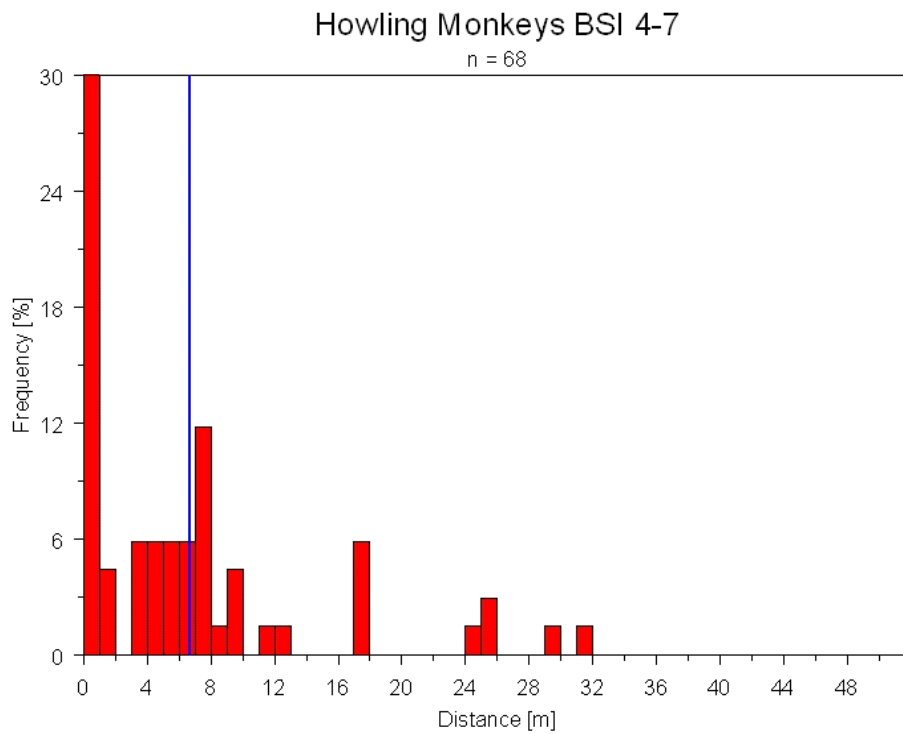


Figure 8.9 Distance histogram for the interacting BSI sizes 4 vs. 7 in howling monkeys; the first interval (0m-1m) is cut off ranging up to 38%

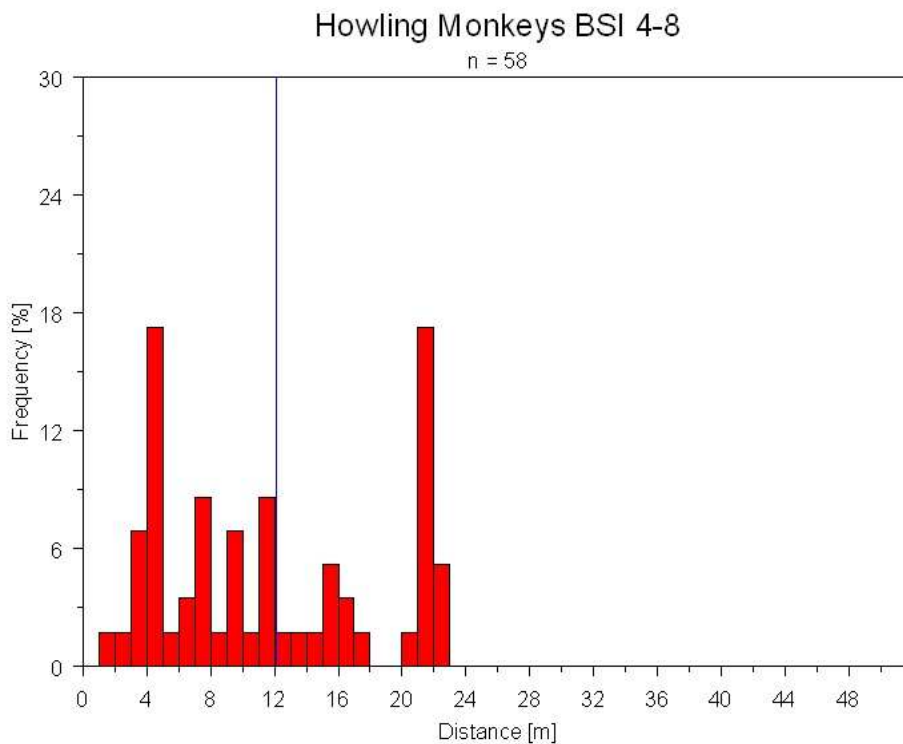


Figure 8.10 Distance histogram for the interacting BSI sizes 4 vs. 8 in howling monkeys

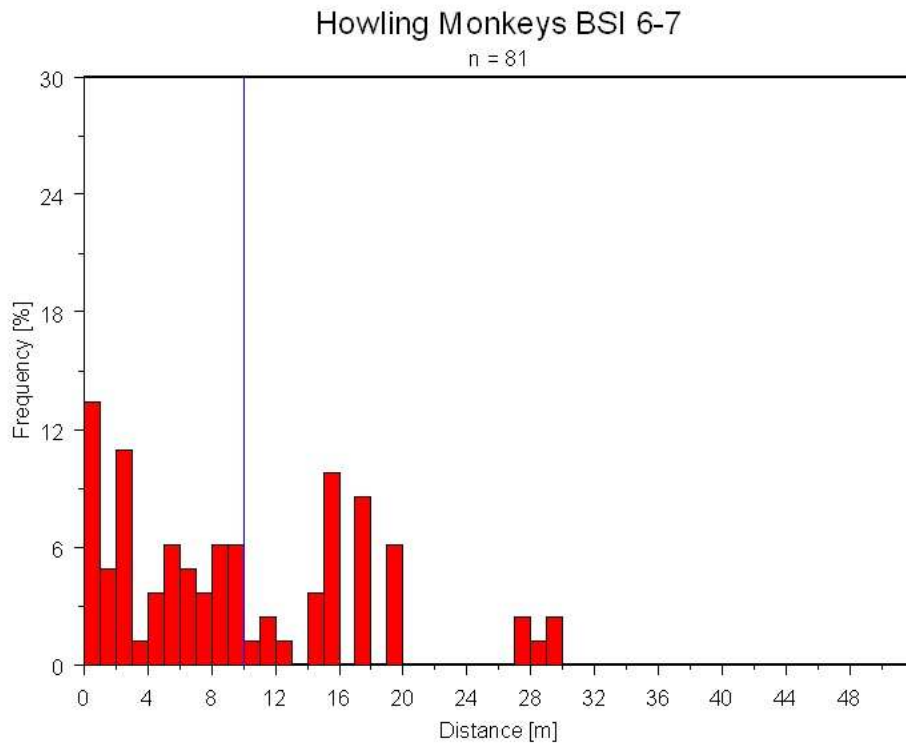


Figure 8.11 Distance histogram for the interacting BSI sizes 6 vs. 7 in howling monkeys

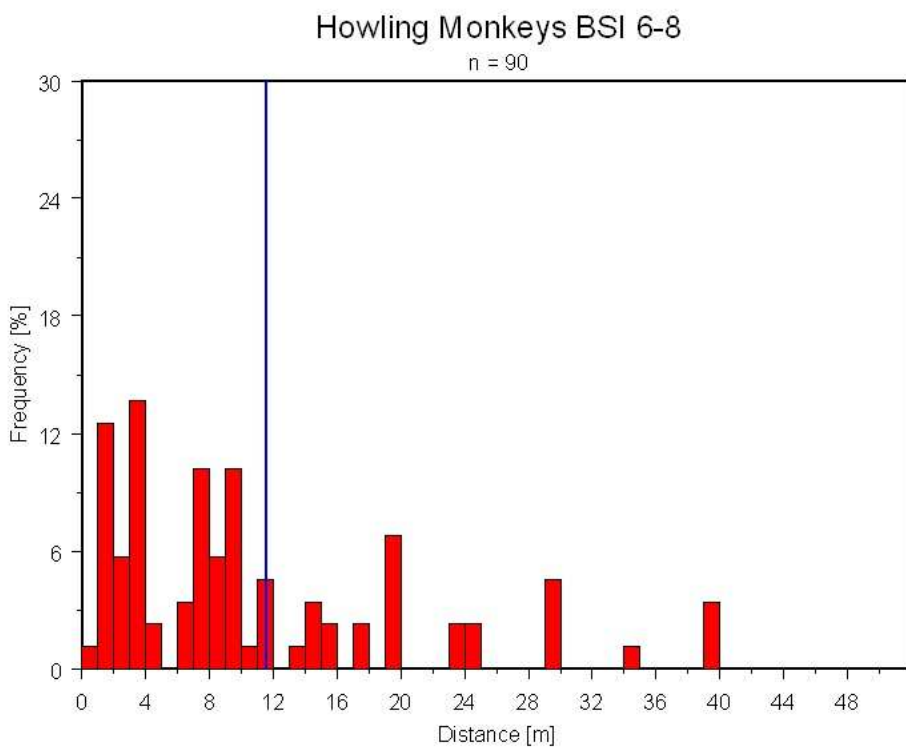


Figure 8.12 Distance histogram for the interacting BSI sizes 6 vs. 8 in howling monkeys

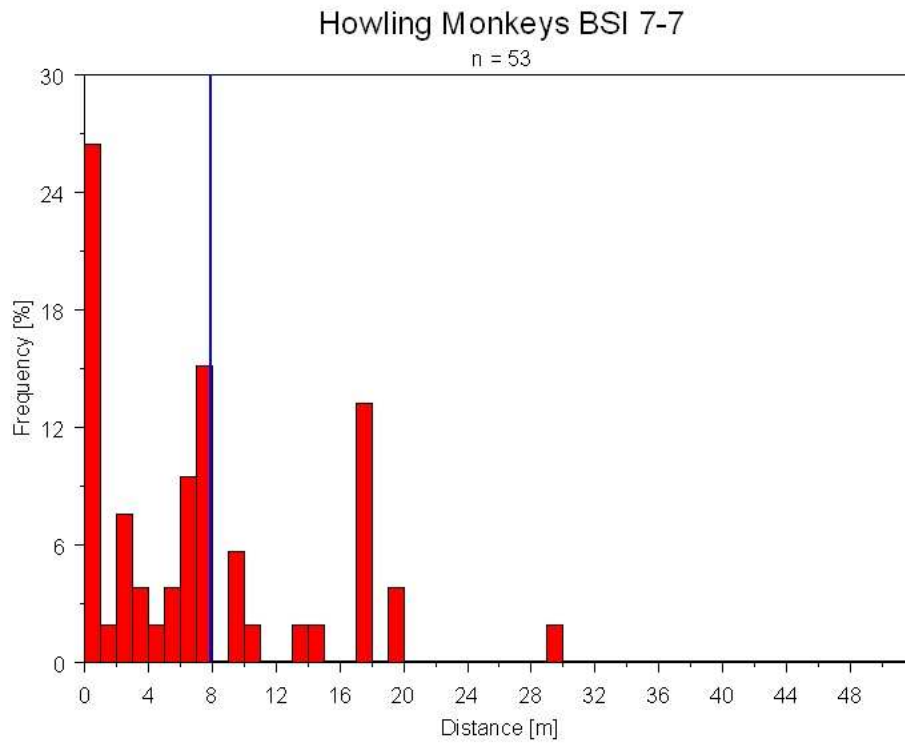


Figure 8.13 Distance histogram for the interacting BSI sizes 7 vs. 7 in howling monkeys

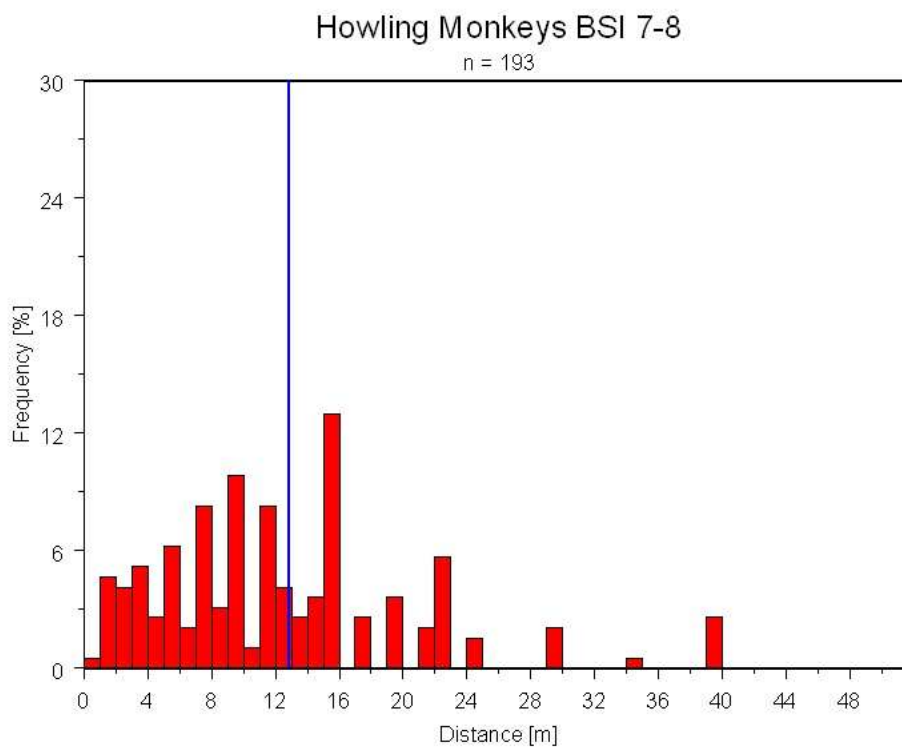


Figure 8.14 Distance histogram for the interacting BSI sizes 7 vs. 8 in howling monkeys

8.6.2 Humpback Whales

8.6.2.1 TreeNet Output

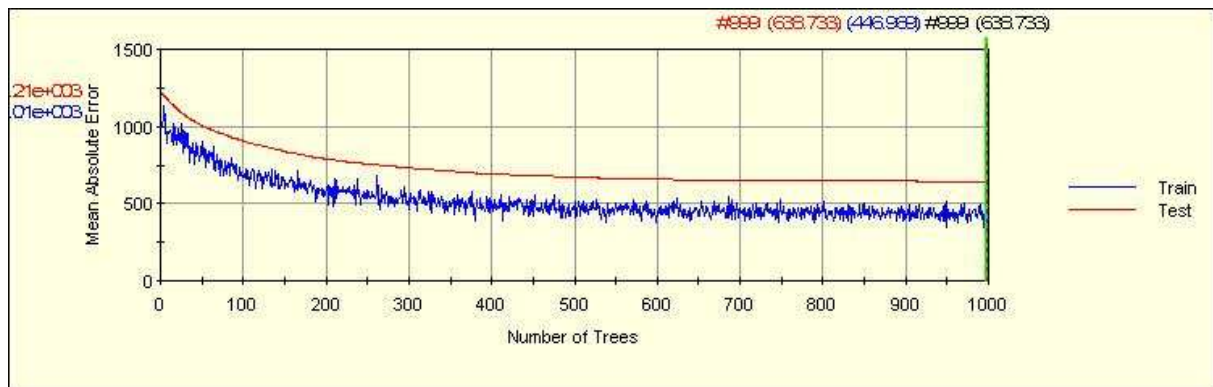


Figure 8.15 Mean absolute error in humpback whale model

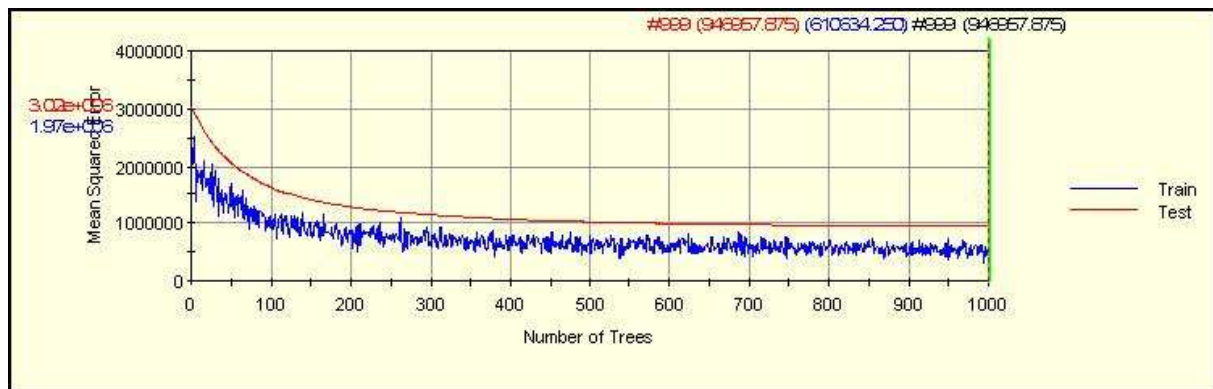


Figure 8.16 Mean squared error in the humpback whale model

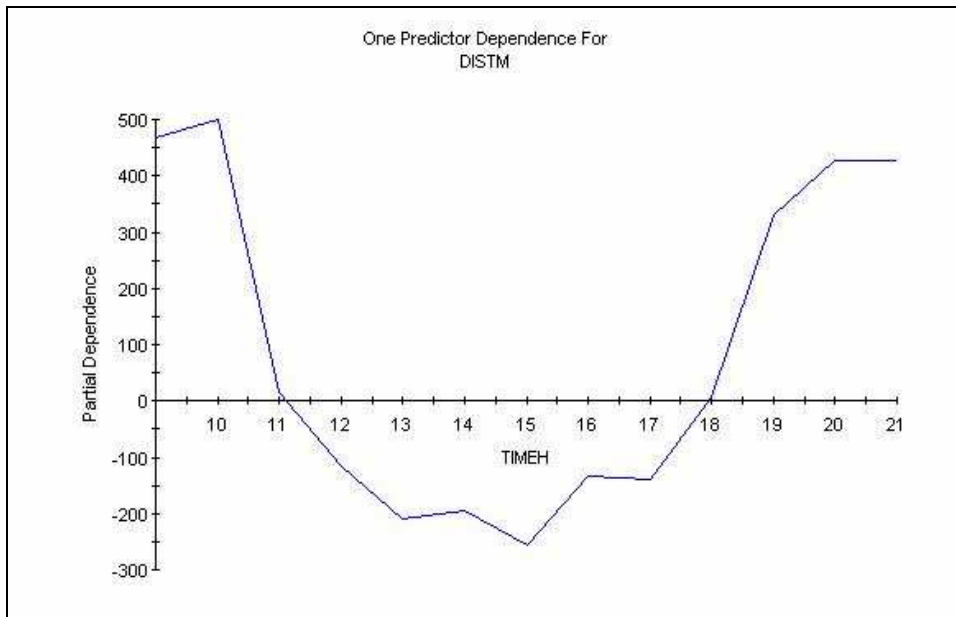


Figure 8.17 One predictor dependence (2) for humpback whales; importance ranking 51.71%

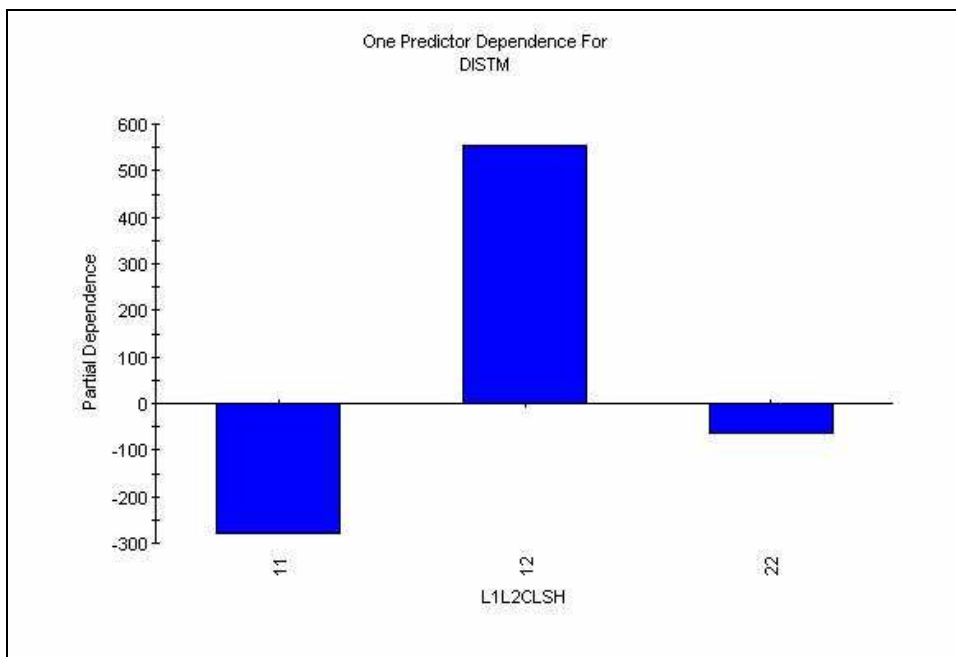


Figure 8.18 One predictor dependence (3) for humpback whales; importance ranking 46.38%

8.6.2.2 Distance Histograms

All BSI combinations with over 20 sample points for each species are presented. The vertical blue line represents the mean.

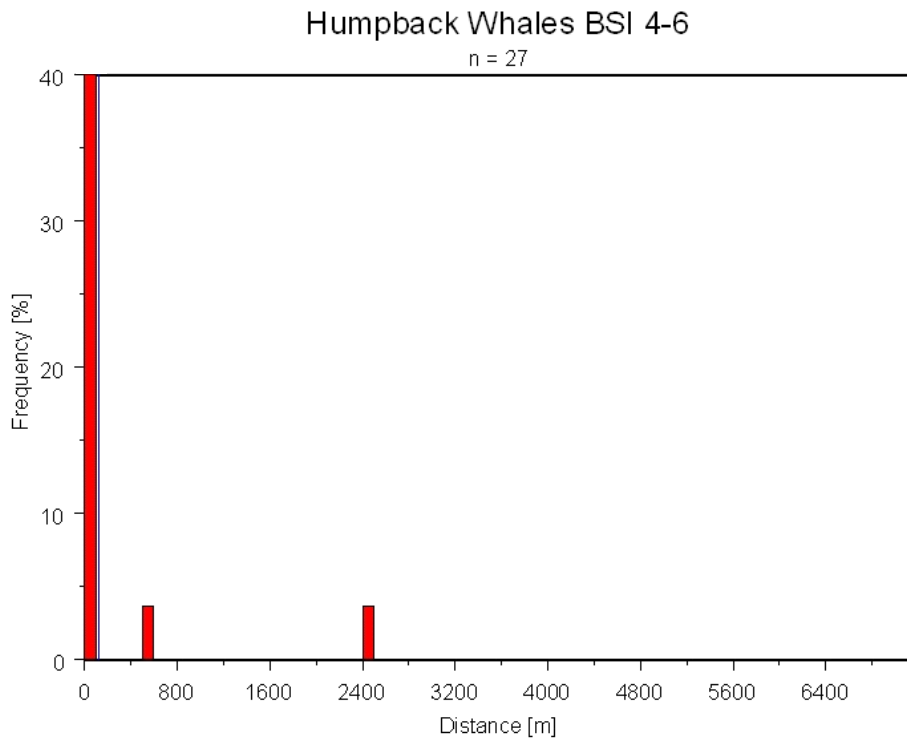


Figure 8.19 Distance histogram for the interacting BSI sizes 4 vs. 6 in humpback whales; the first interval (0m-100m) is cut off ranging up to 86%

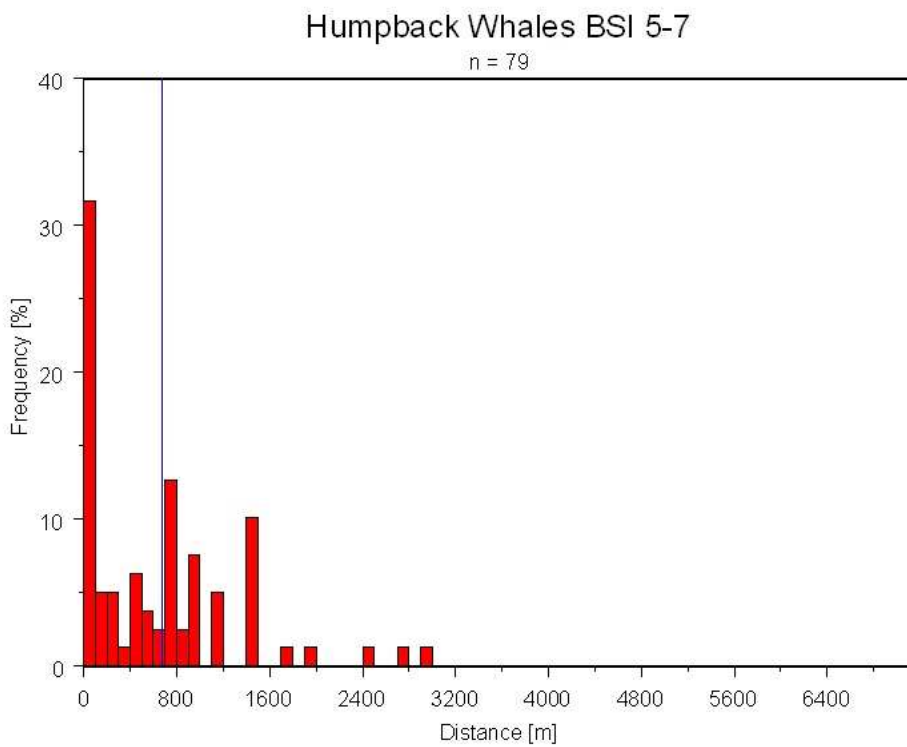


Figure 8.20 Distance histogram for the interacting BSI sizes 5 vs. 7 in humpback whales

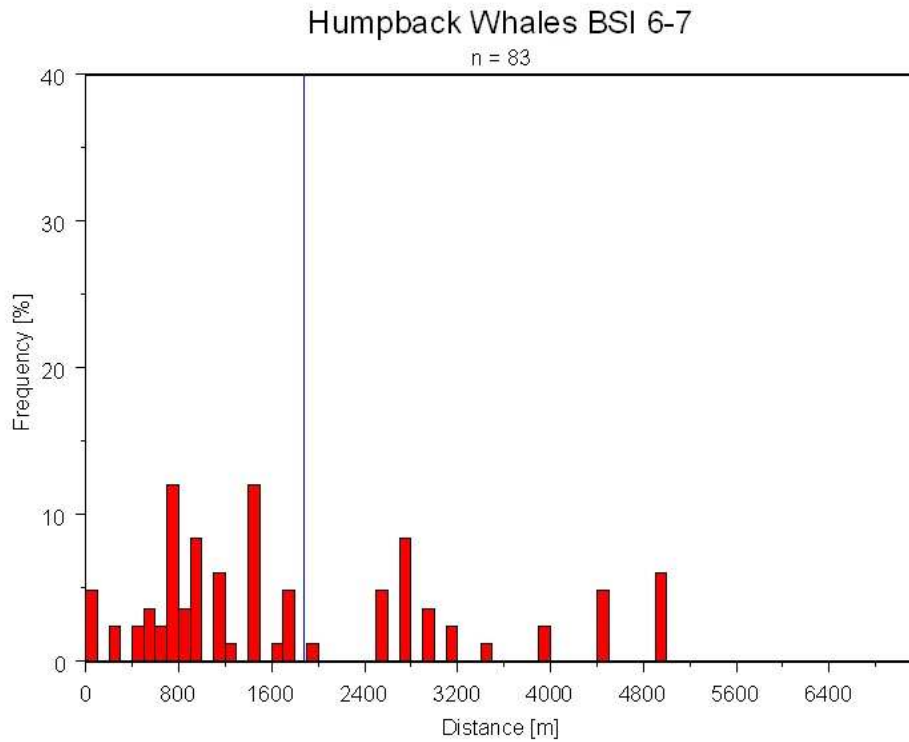


Figure 8.21 Distance histogram for the interacting BSI sizes 6 vs. 7 in humpback whales

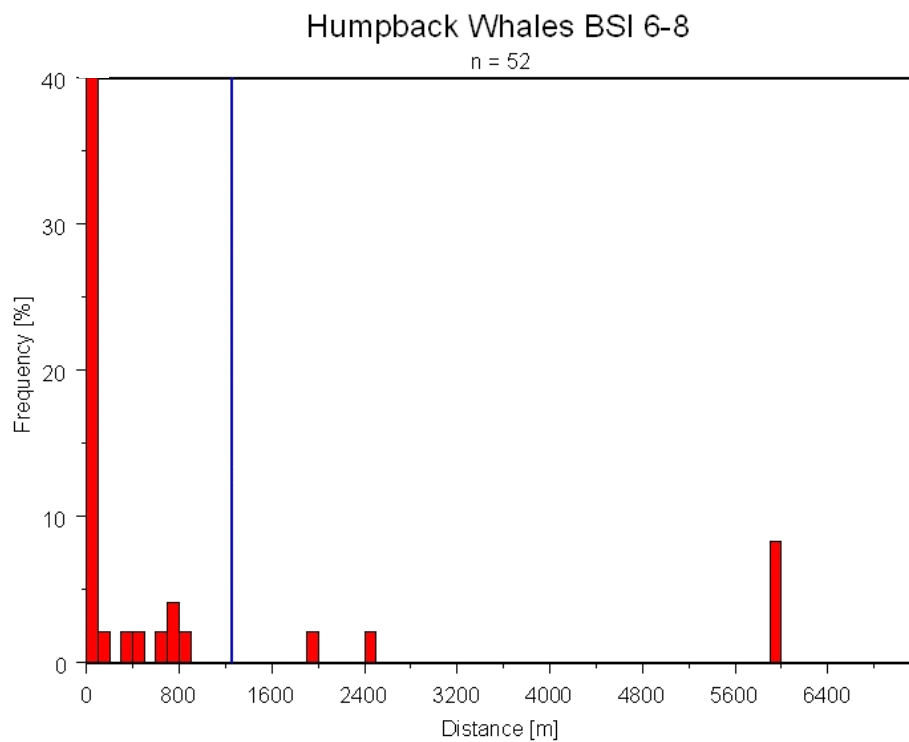


Figure 8.22 Distance histogram for the interacting BSI sizes 6 vs. 8 in humpback whales; the first interval (0m-100m) is cut off ranging up to 64%; the x-axis is cut off with one interval (8000m-8100m) exists with a frequency of 8%

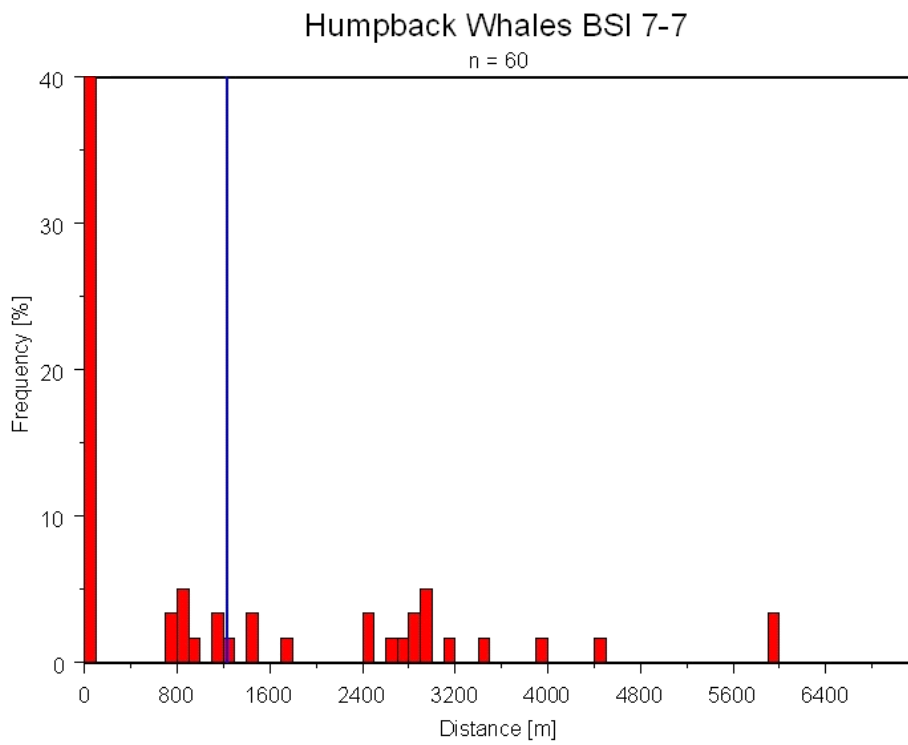


Figure 8.23 Distance histogram for the interacting BSI sizes 7 vs. 7 in humpback whales; the first interval (0m-100m) is cut off ranging up to 54%

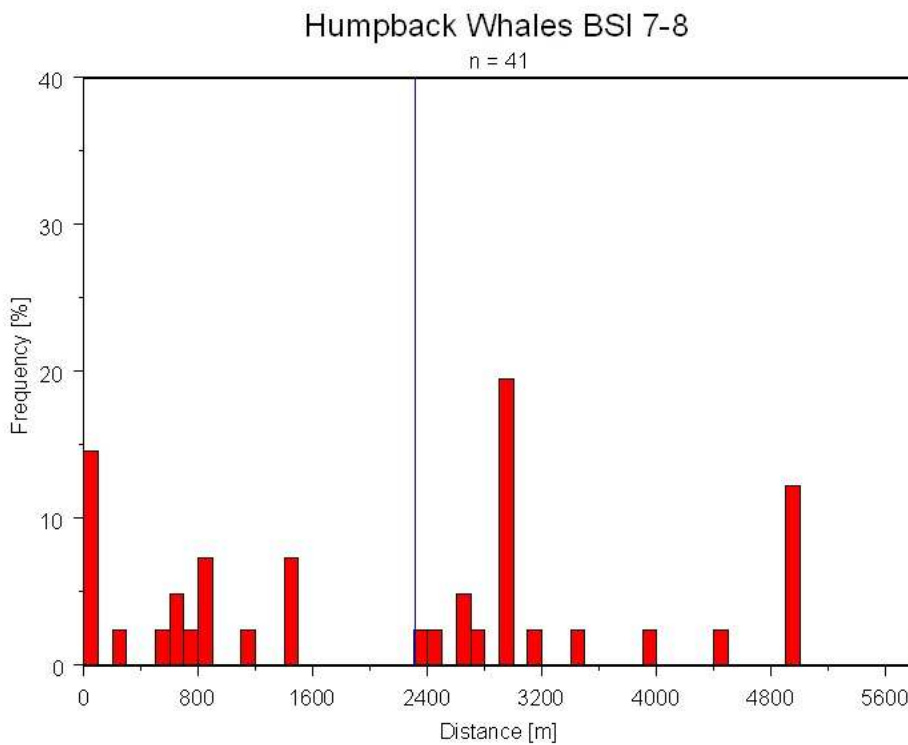


Figure 8.24 Distance histogram for the interacting BSI sizes 7 vs. 8 in humpback whales

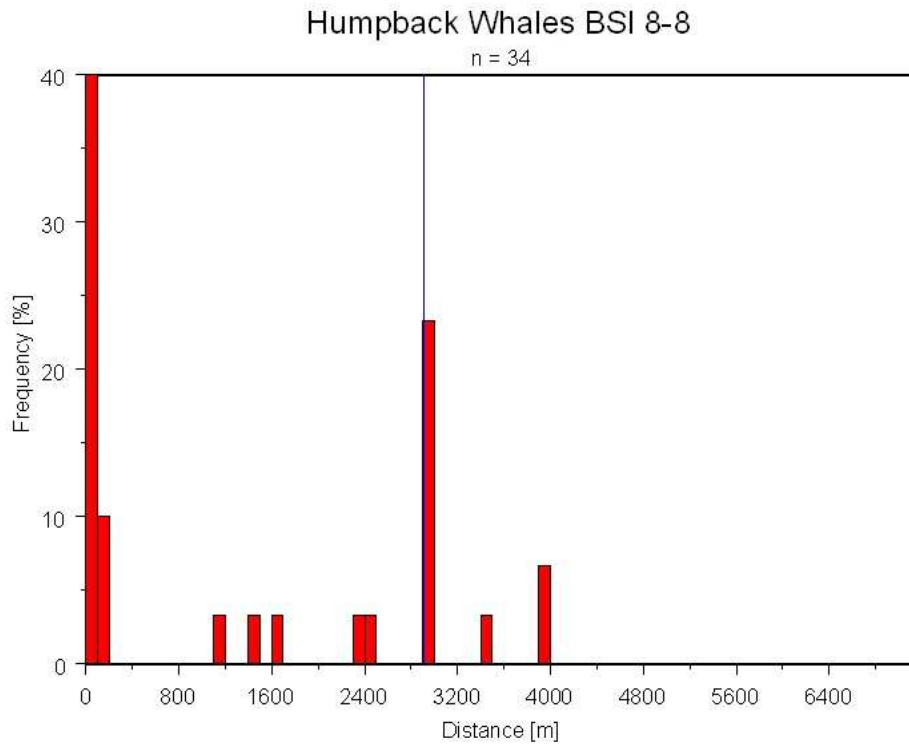


Figure 8.25 Distance histogram for the interacting BSI sizes 8 vs. 8 in humpback whales

8.6.3 Brown Bears

8.6.3.1 TreeNet Output

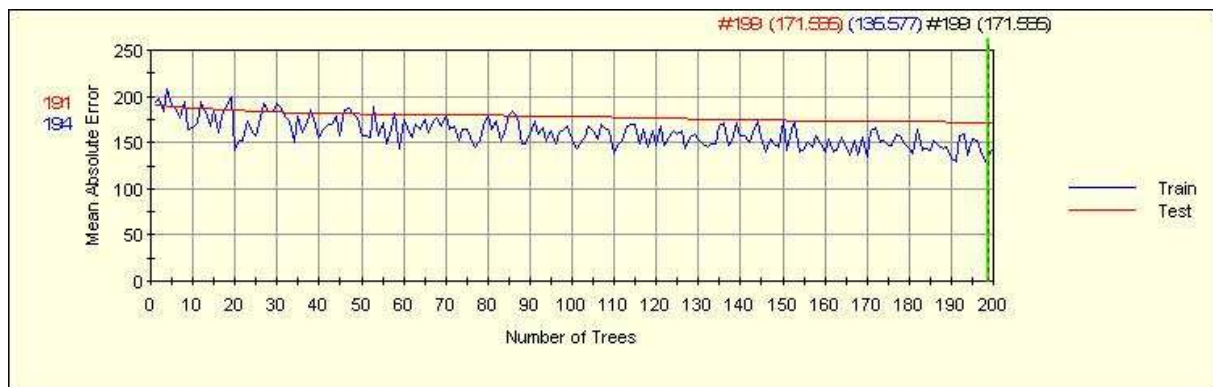


Figure 8.26 Mean absolute error in brown bear model

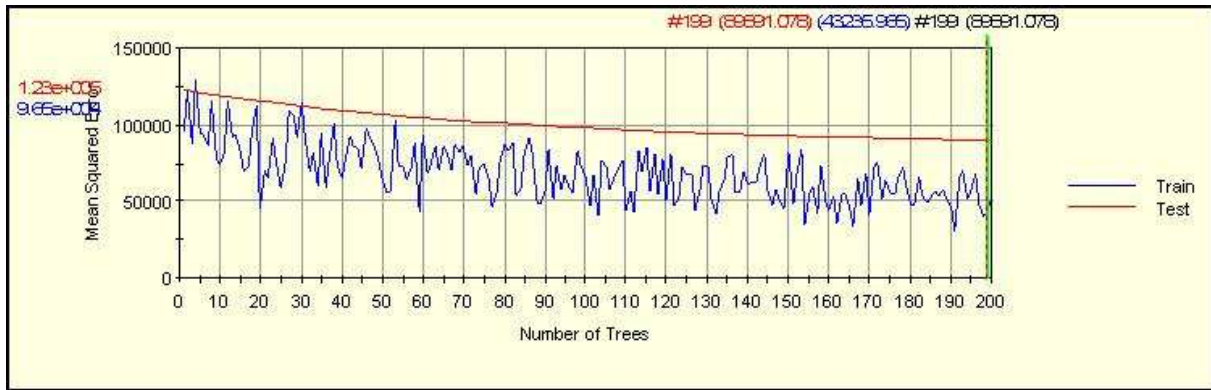


Figure 8.27 Mean squared error in the brown bear model

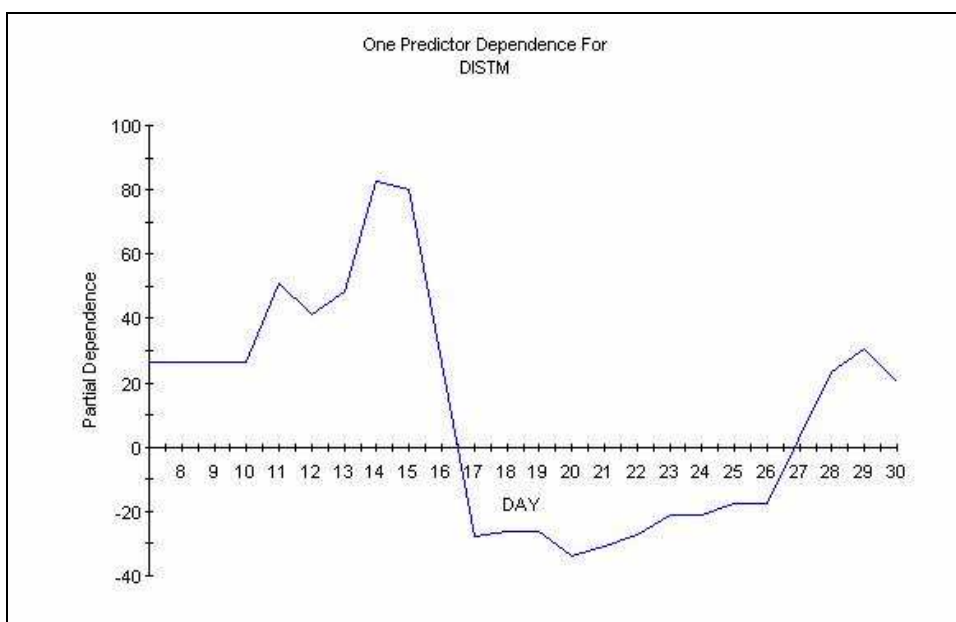


Figure 8.28 One predictor dependence (2) for brown bears; importance ranking 92.76%

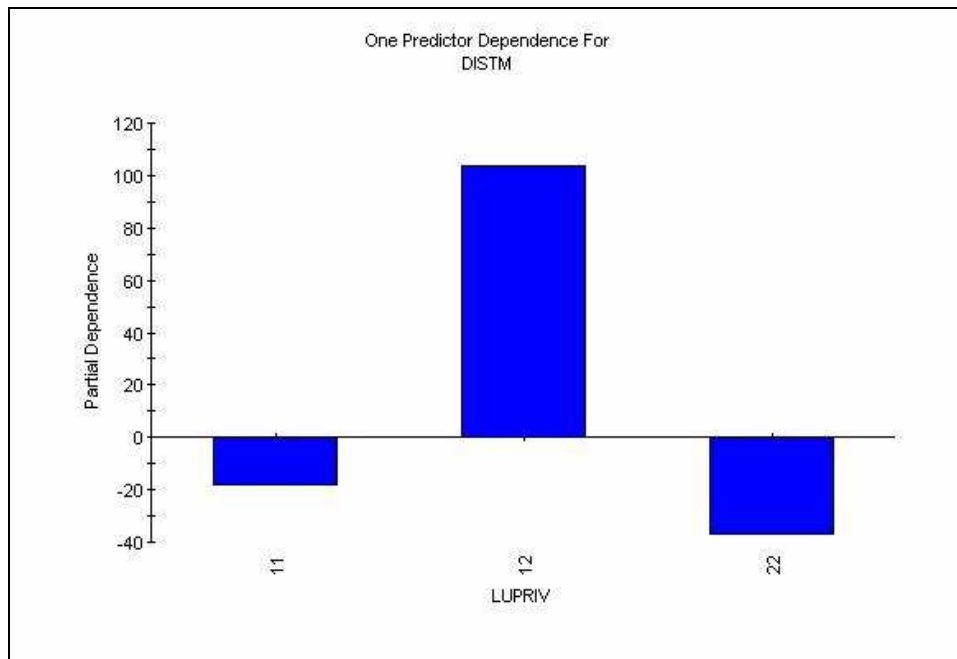


Figure 8.29 One predictor dependence (3) for brown bears; importance ranking 82.38%

8.6.3.2 Distance Histograms

All BSI combinations with over 20 sample points for each species are presented. The vertical blue line represents the mean.

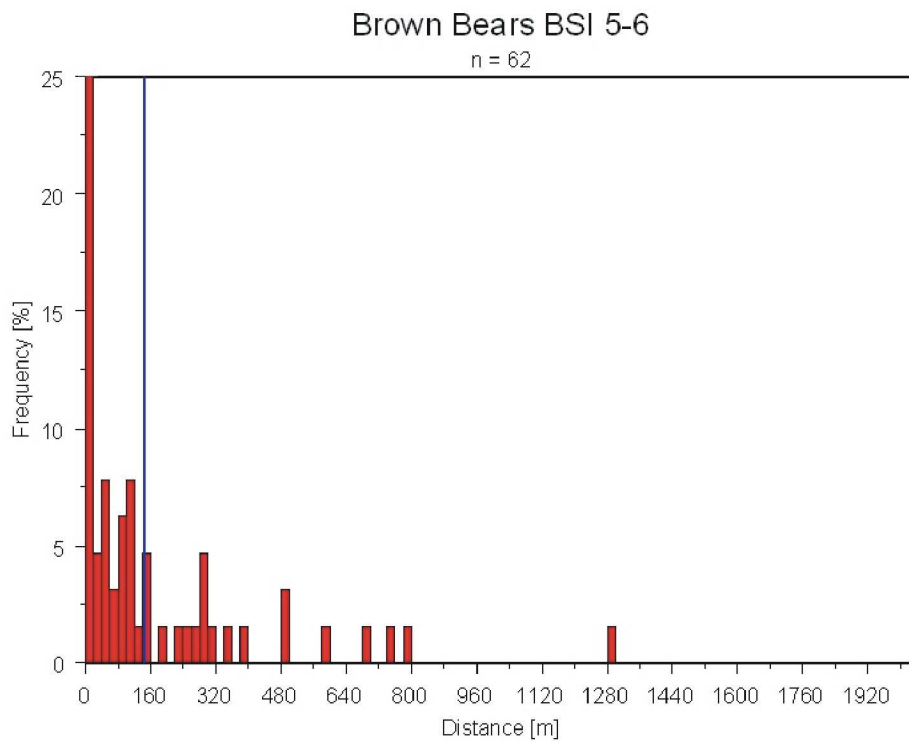


Figure 8.30 Distance histogram for the interacting BSI sizes 5 vs. 6 in brown bears; the first interval (0m-20m) is cut off ranging up to 37,5%

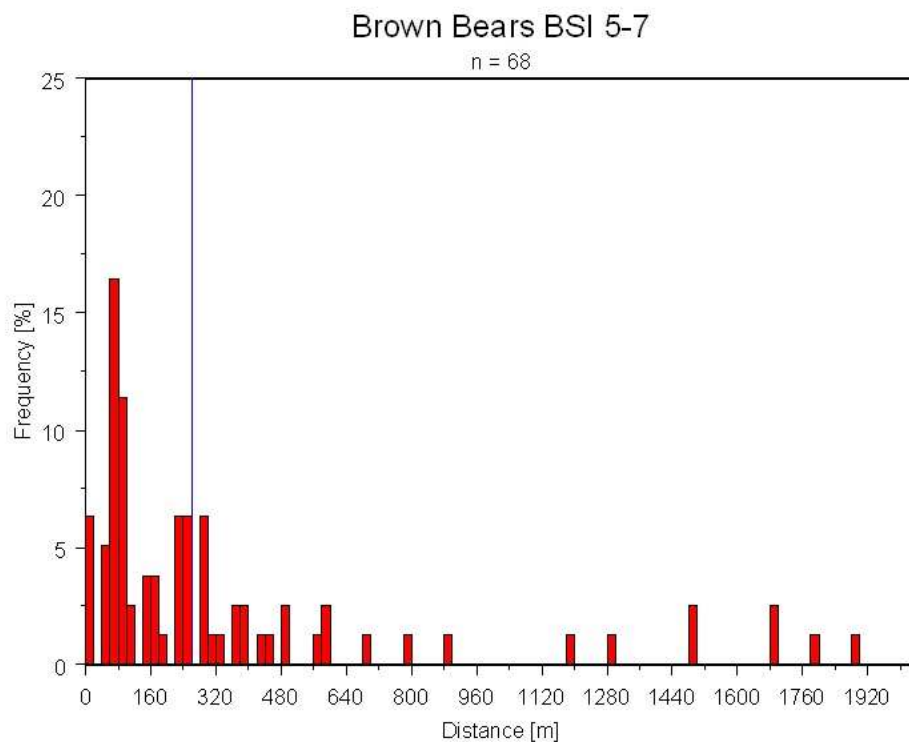


Figure 8.31 Distance histogram for the interacting BSI sizes 5 vs. 7 in brown bears

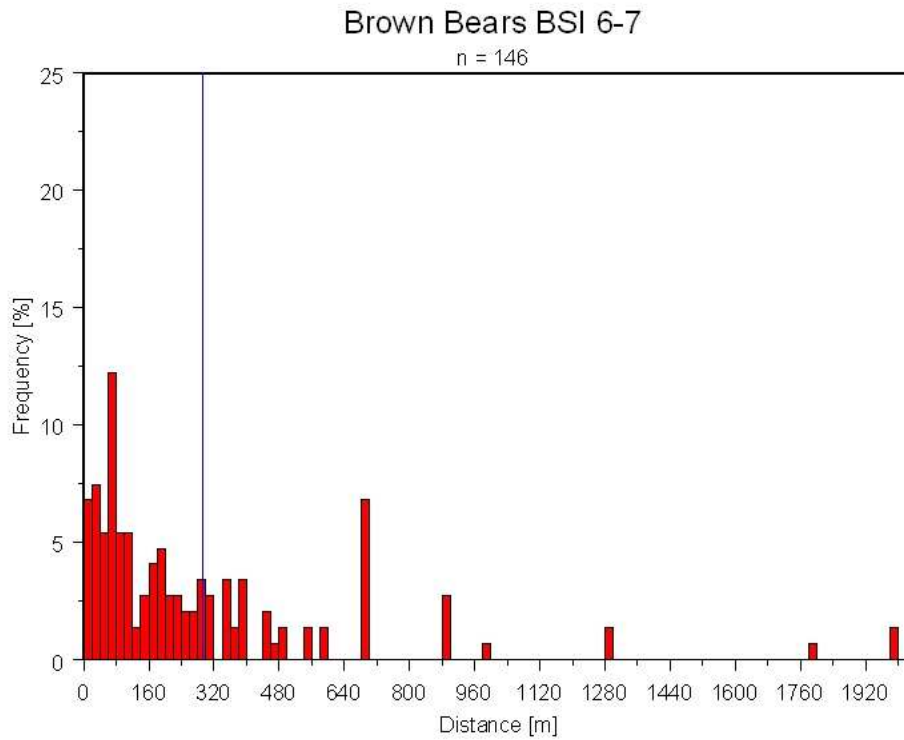


Figure 8.32 Distance histogram for the interacting BSI sizes 6 vs. 7 in brown bears

8.6.4 Polar Bears

8.6.4.1 TreeNet Output

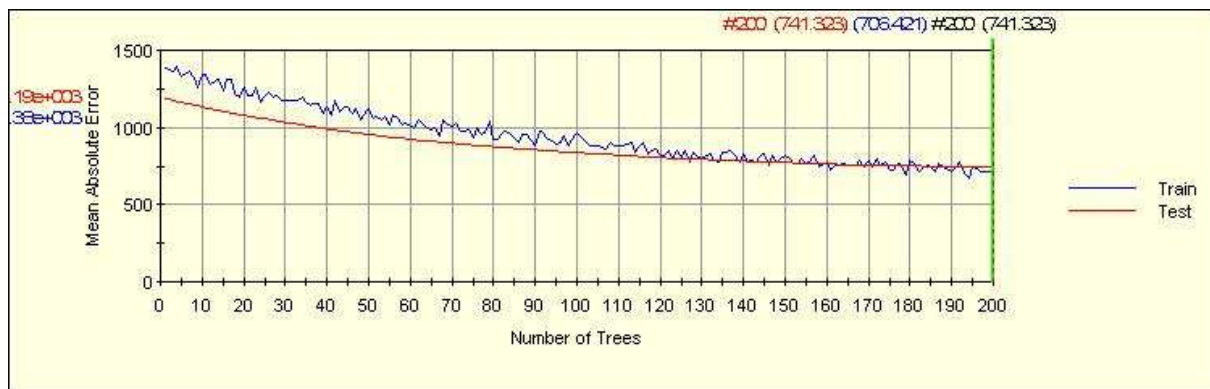


Figure 8.33 Mean absolute error in the polar bear model

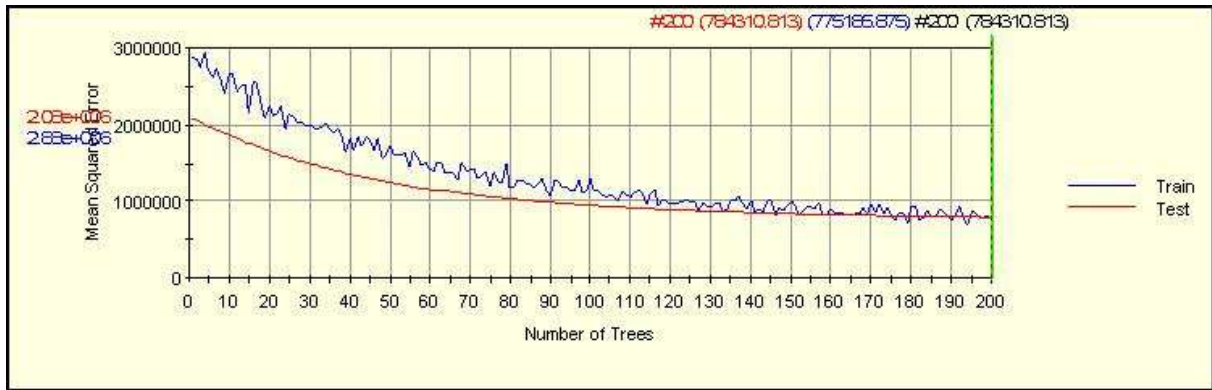


Figure 8.34 Mean squared error in the polar bear model

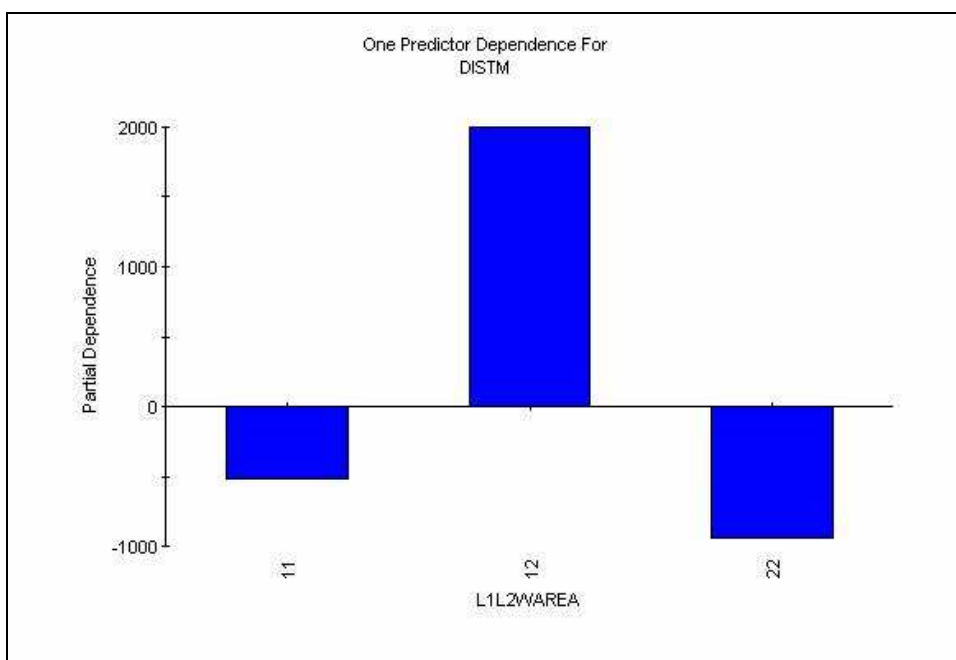


Figure 8.35 One predictor dependence (1) for polar bears; importance ranking 100%

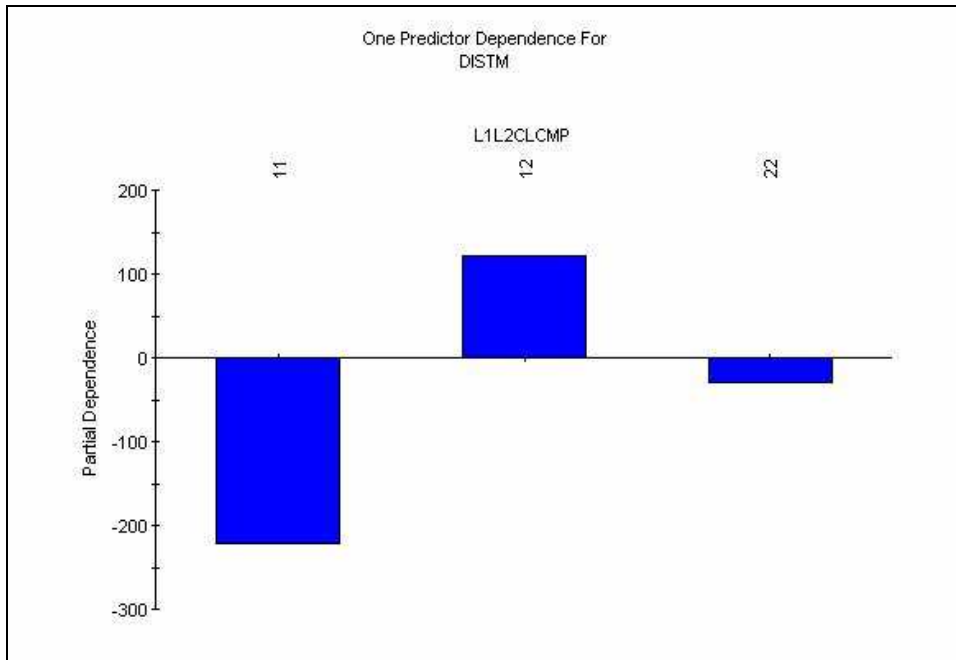


Figure 8.36 One predictor dependence (3) for polar bears; importance ranking 28.95%

8.6.4.2 Distance Histograms

All BSI combinations with over 20 sample points for each species are presented. The vertical blue line represents the mean.

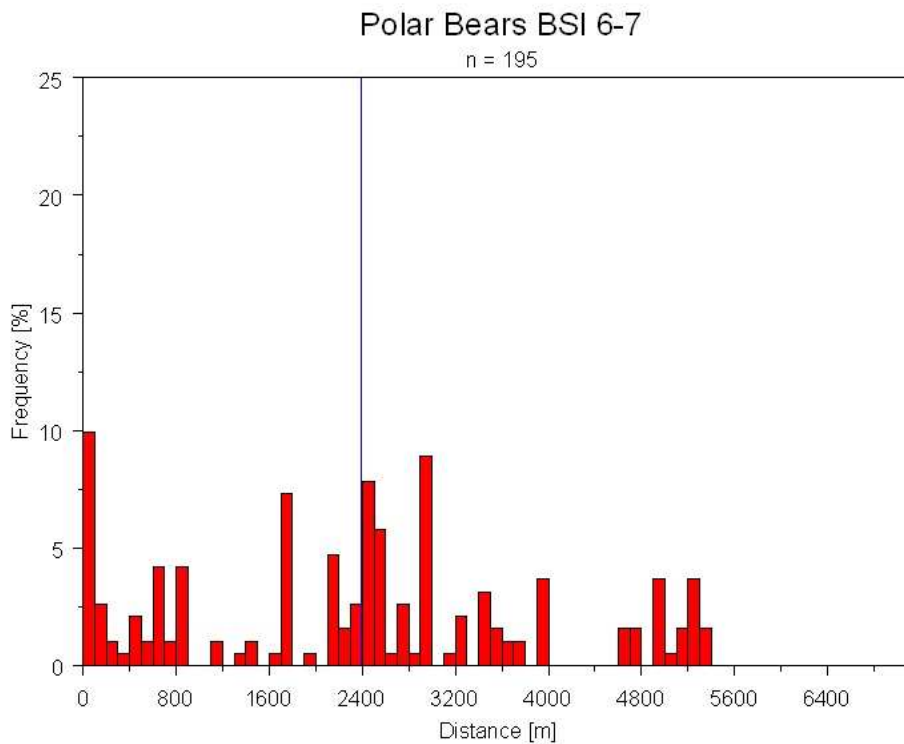


Figure 8.37 Distance histogram for the interacting BSI sizes 6 vs. 7 in polar bears

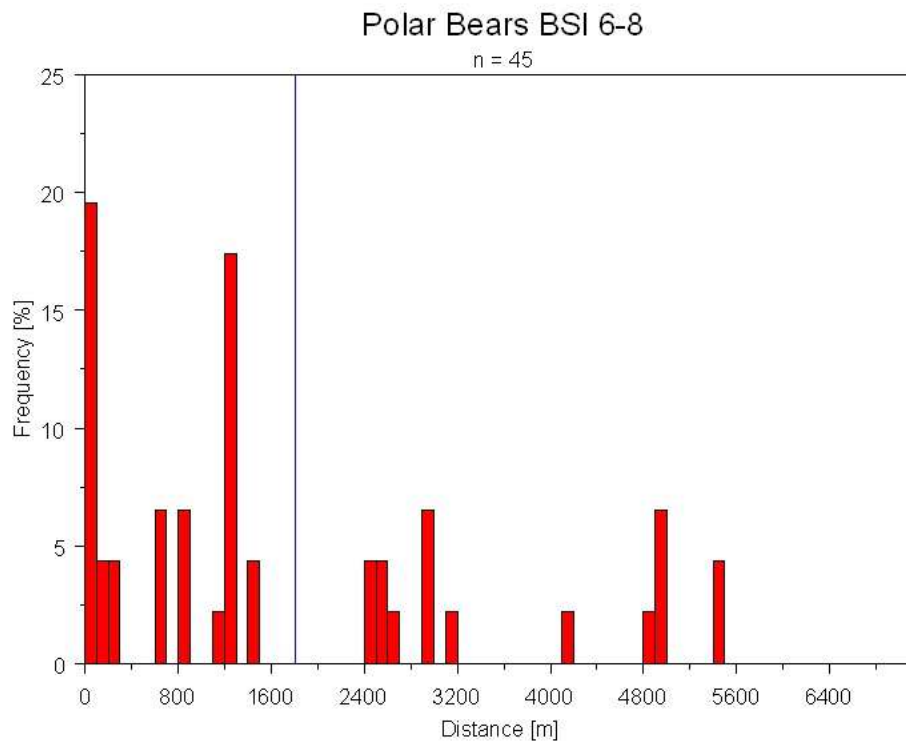


Figure 8.38 Distance histogram for the interacting BSI sizes 6 vs. 8 in polar bears

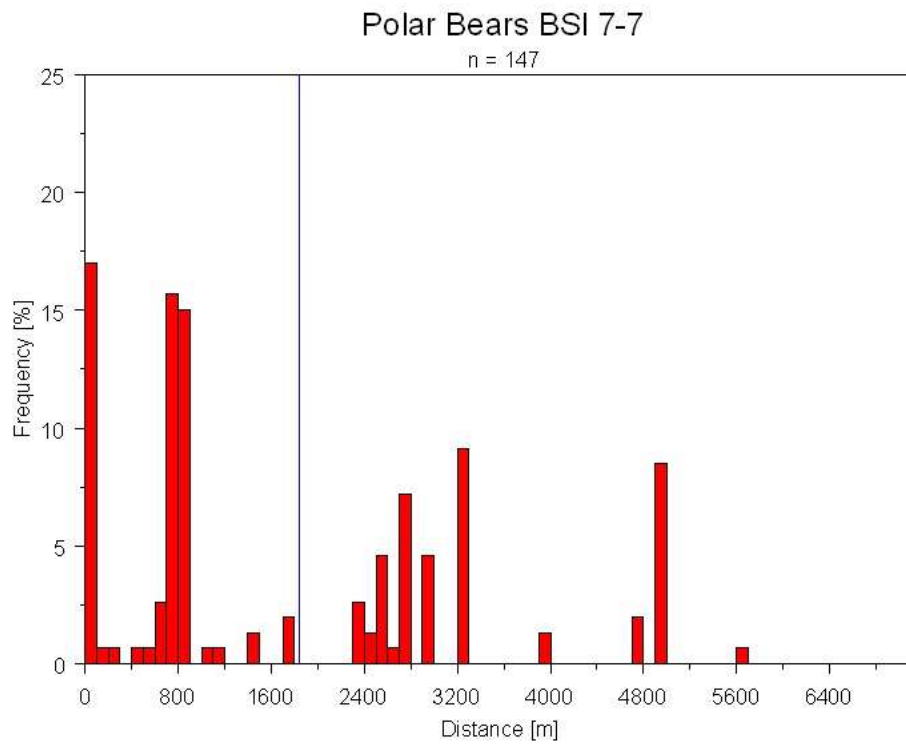


Figure 8.39 Distance histogram for the interacting BSI sizes 7 vs. 7 in polar bears

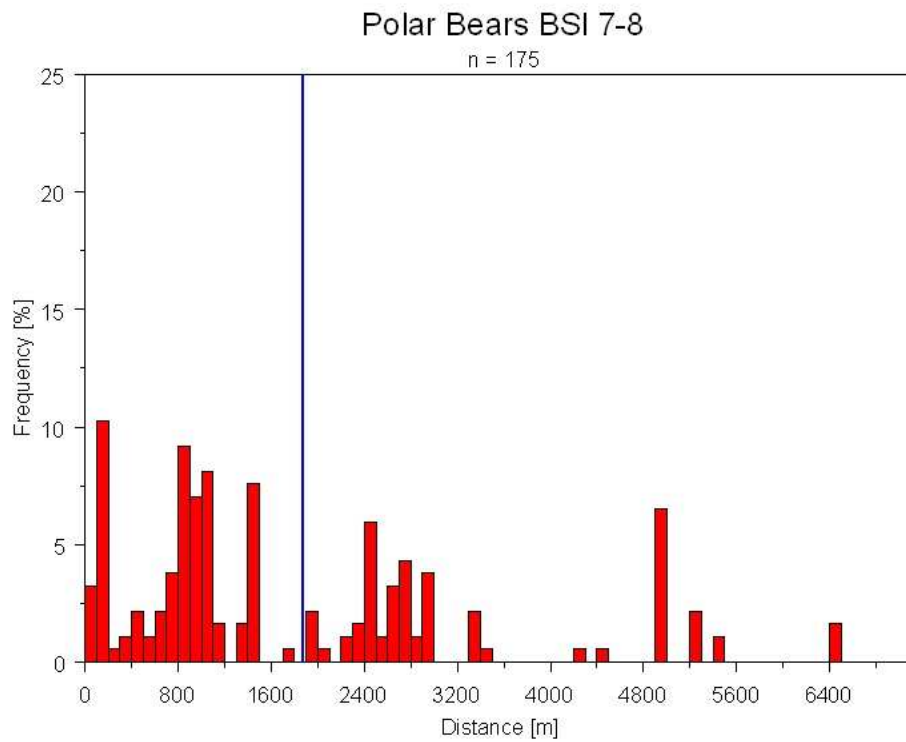


Figure 8.40 Distance histogram for the interacting BSI sizes 7 vs. 8 in polar bears

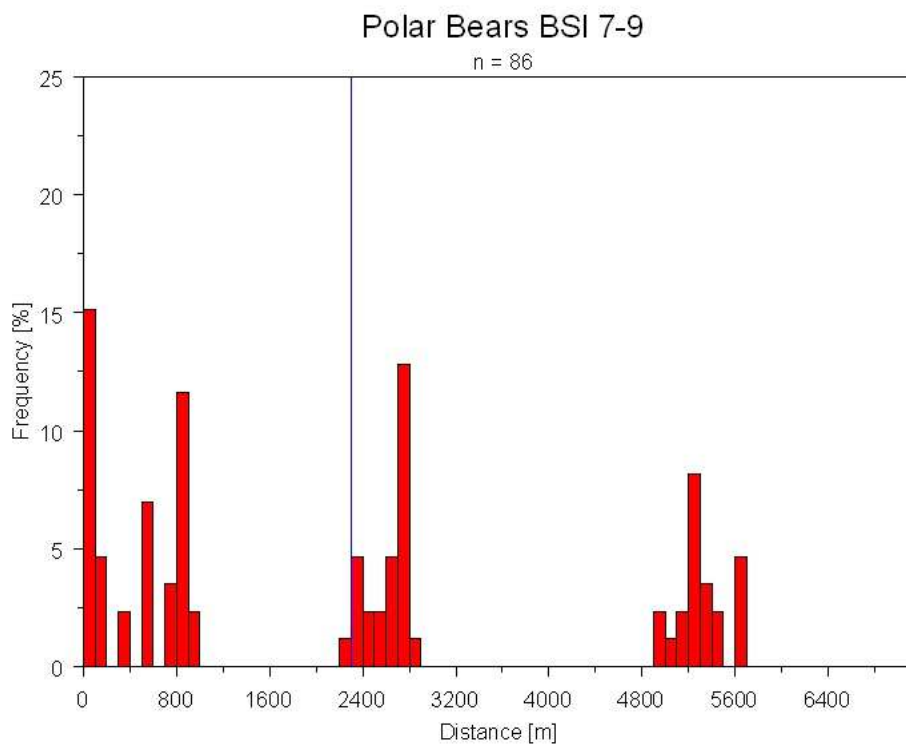


Figure 8.41 Distance histogram for the interacting BSI sizes 7 vs. 9 in polar bears

8.6.5 Spotted Seals

8.6.5.1 TreeNet Output

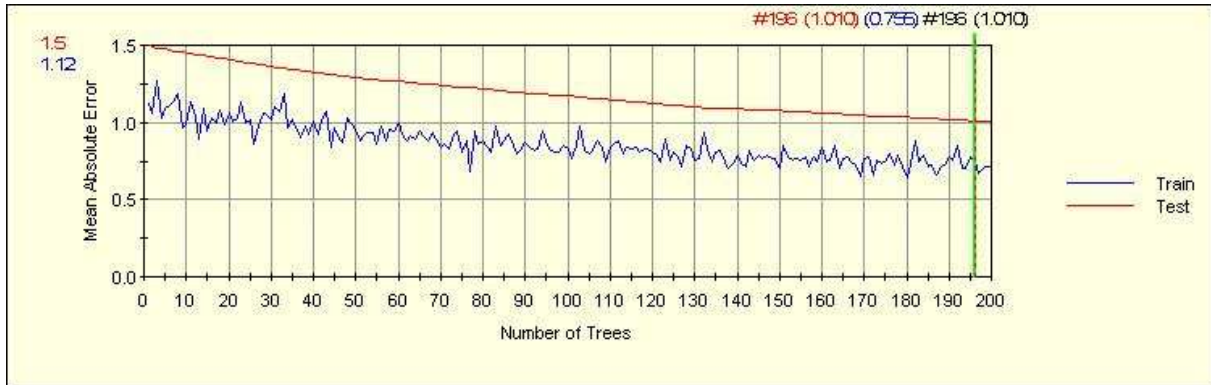


Figure 8.42 Mean absolute error in the spotted seal model

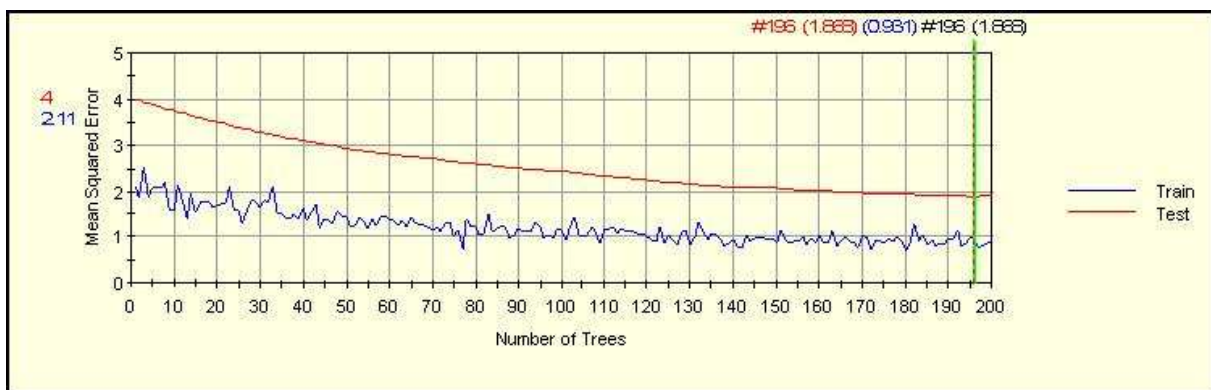


Figure 8.43 Mean squared error in the spotted seal model

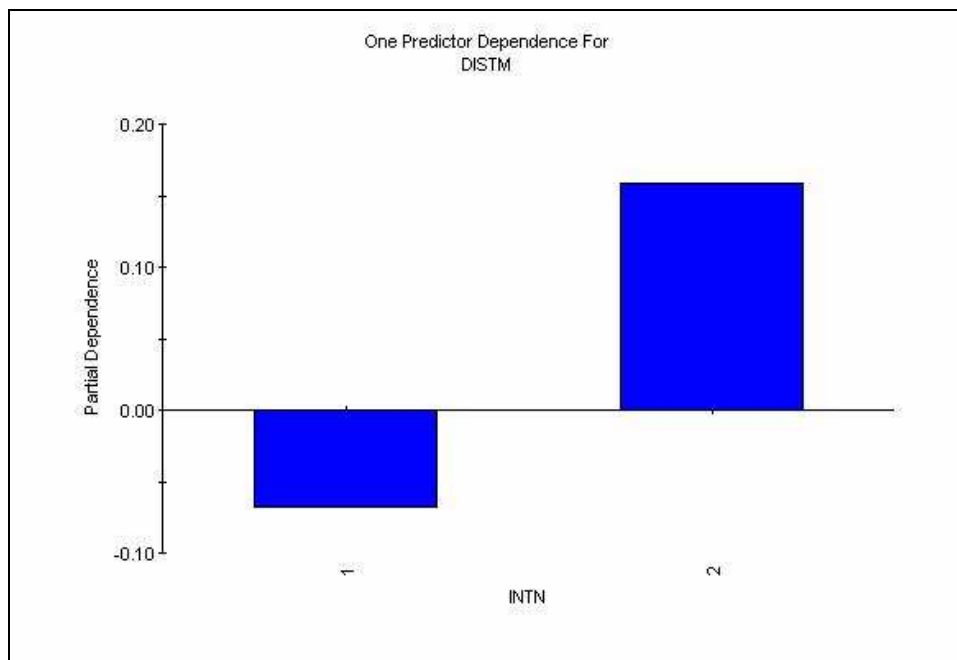


Figure 8.44 One predictor dependence (3) for spotted seals; importance ranking 24.61%

8.6.6 Muskoxen – females

8.6.6.1 TreeNet Output

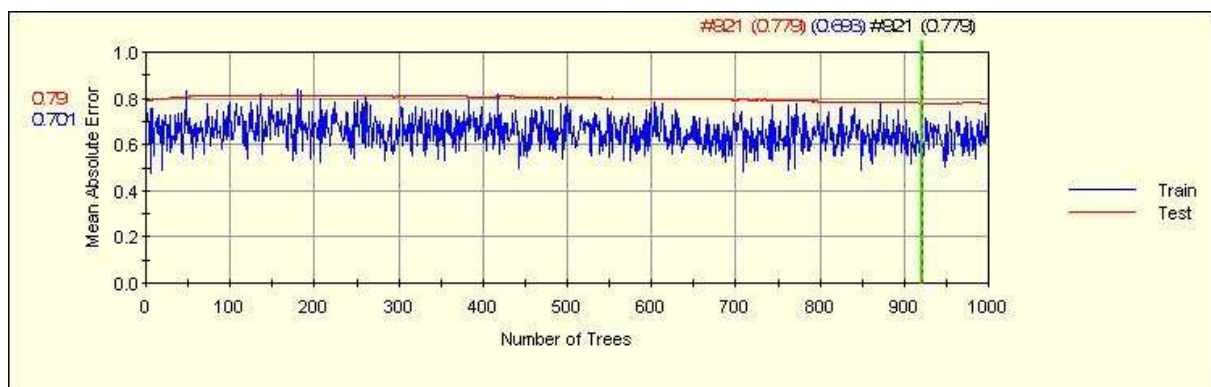


Figure 8.45 Mean absolute error in the female muskoxen model

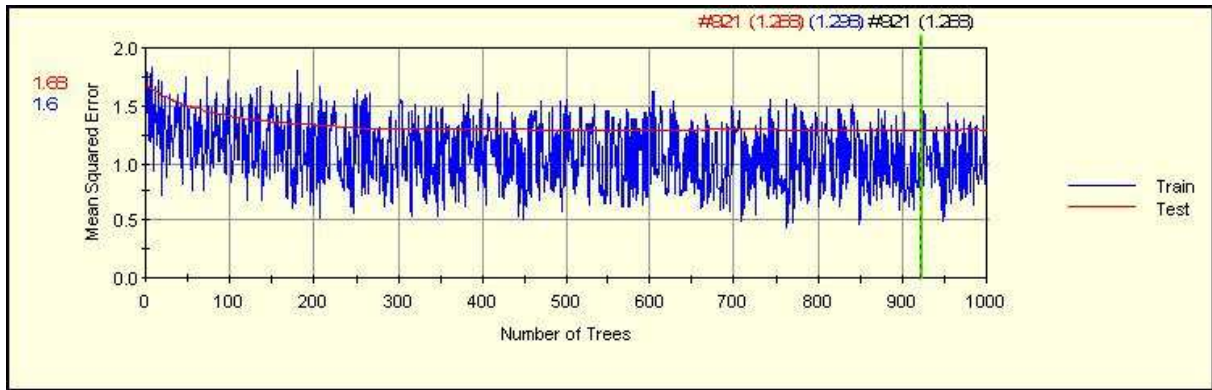


Figure 8.46 Mean squared error in the female muskoxen model

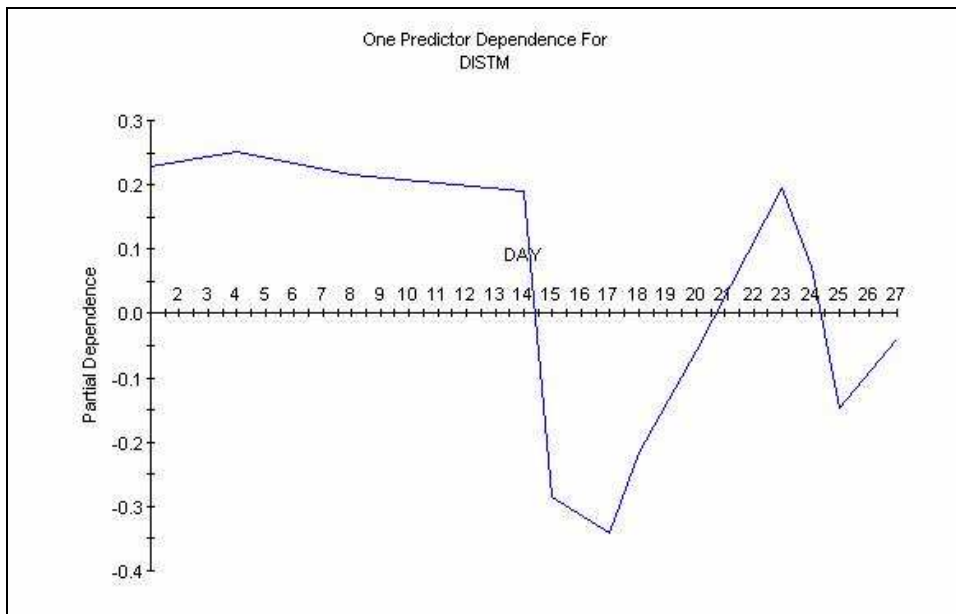


Figure 8.47 One predictor dependence (1) for female muskoxen; importance ranking 100%

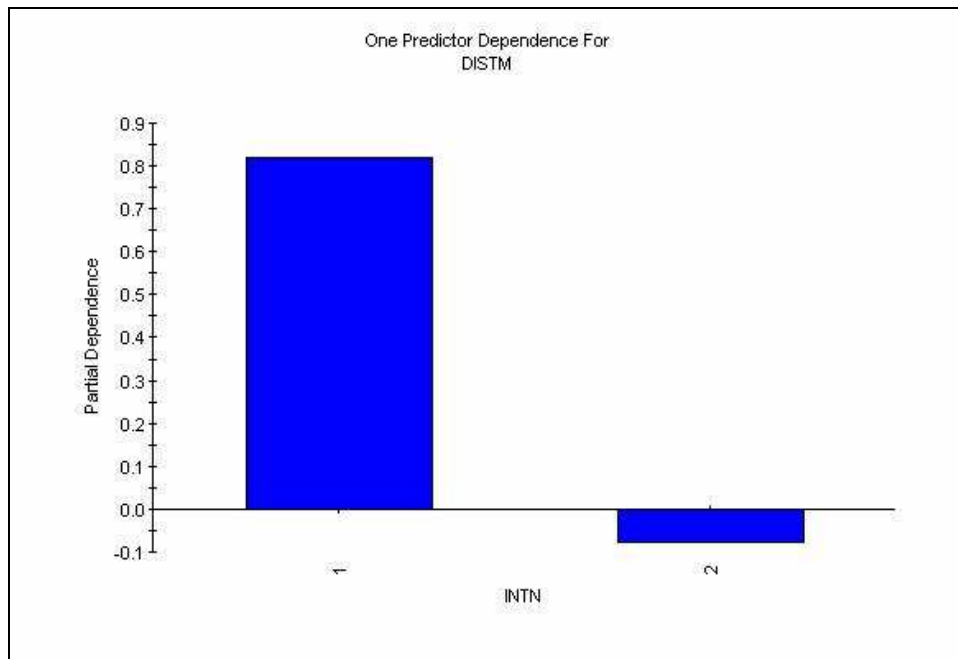


Figure 8.48 One predictor dependence (3) for female muskoxen; importance ranking 81.93%

8.6.6.2 Distance Histograms

All BSI combinations with over 20 sample points for each species are presented. The vertical blue line represents the mean.

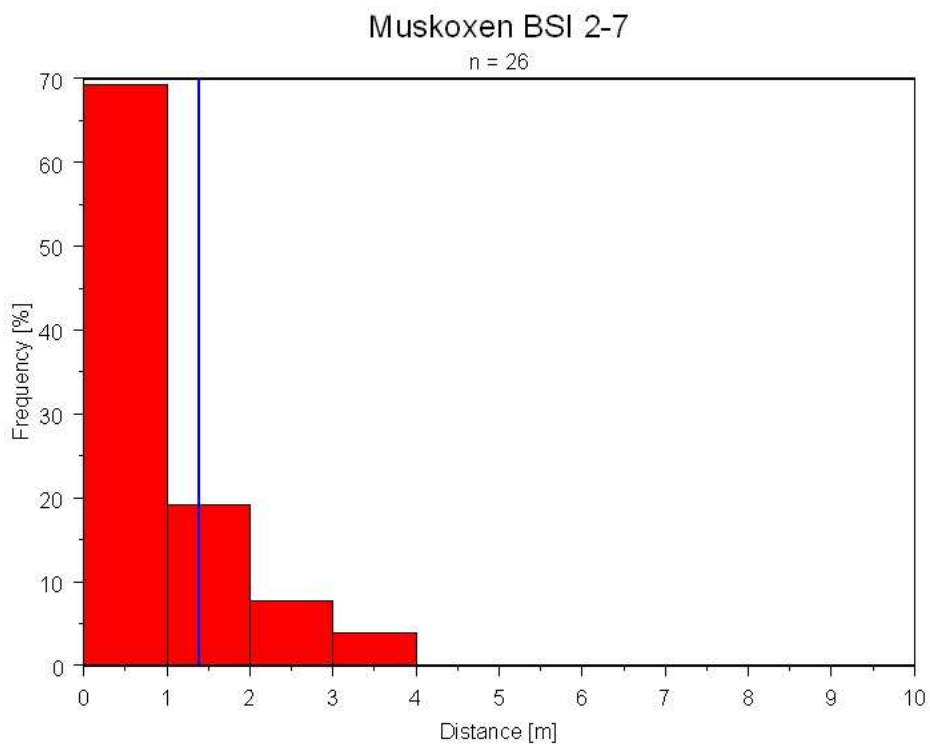


Figure 8.49 Distance histogram for the interacting BSI sizes 2 vs. 7 in female muskoxen

8.6.7 Muskoxen – males

8.6.7.1 TreeNet Output

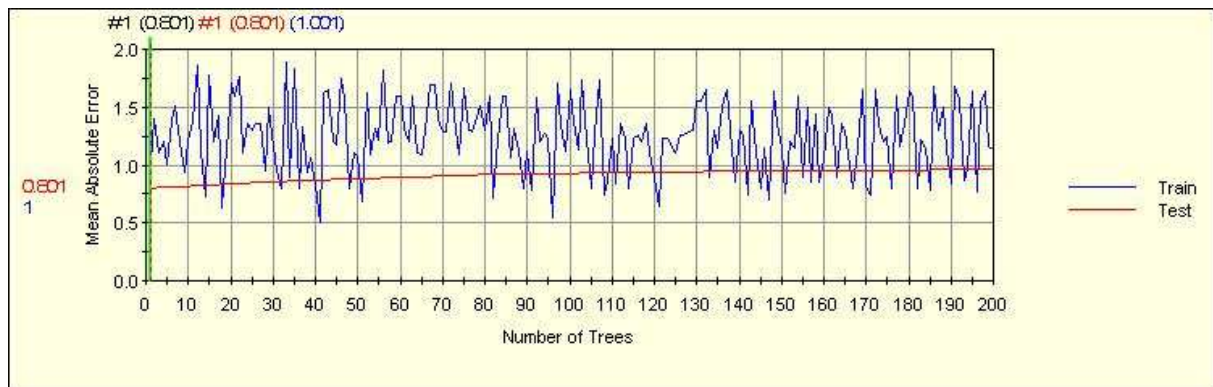


Figure 8.50 Mean absolute error in the male muskoxen model

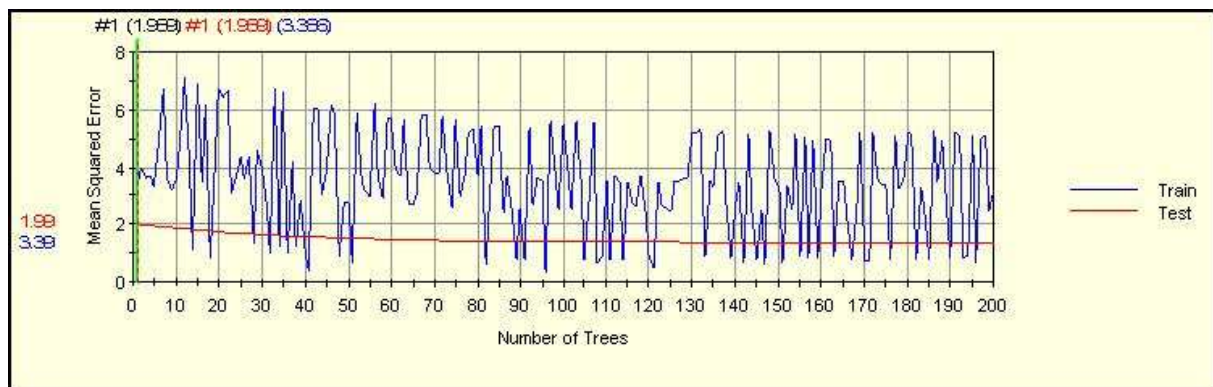


Figure 8.51 Mean squared error in the male muskoxen model

8.7 Appendix: Example Distance Histograms as expected in non-social Species

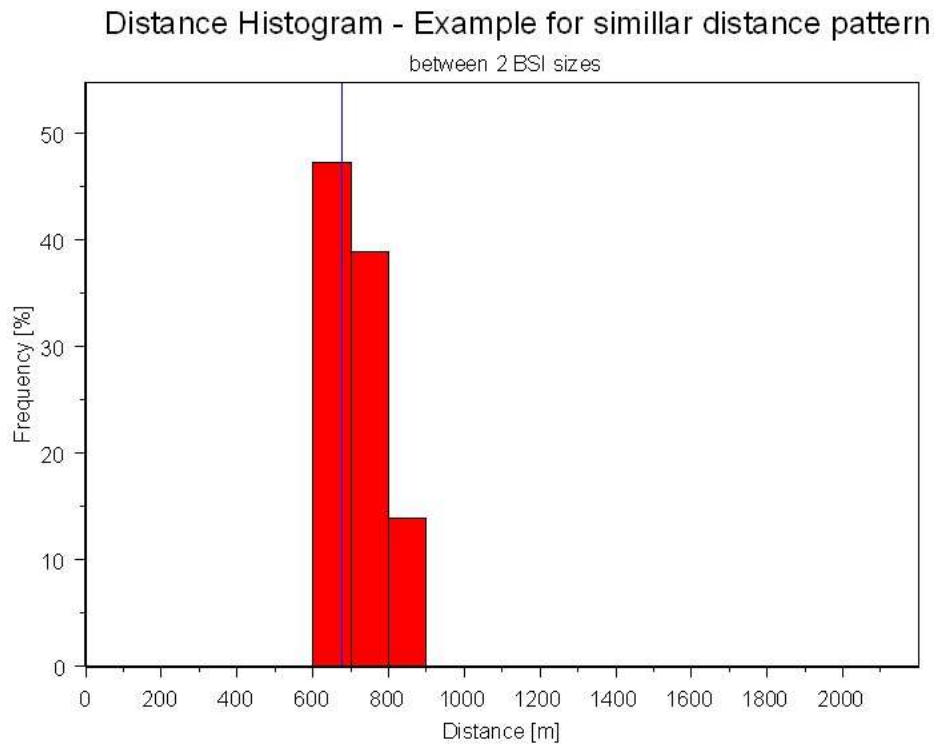


Figure 8.52 Example for expected similar distance pattern in non-social species

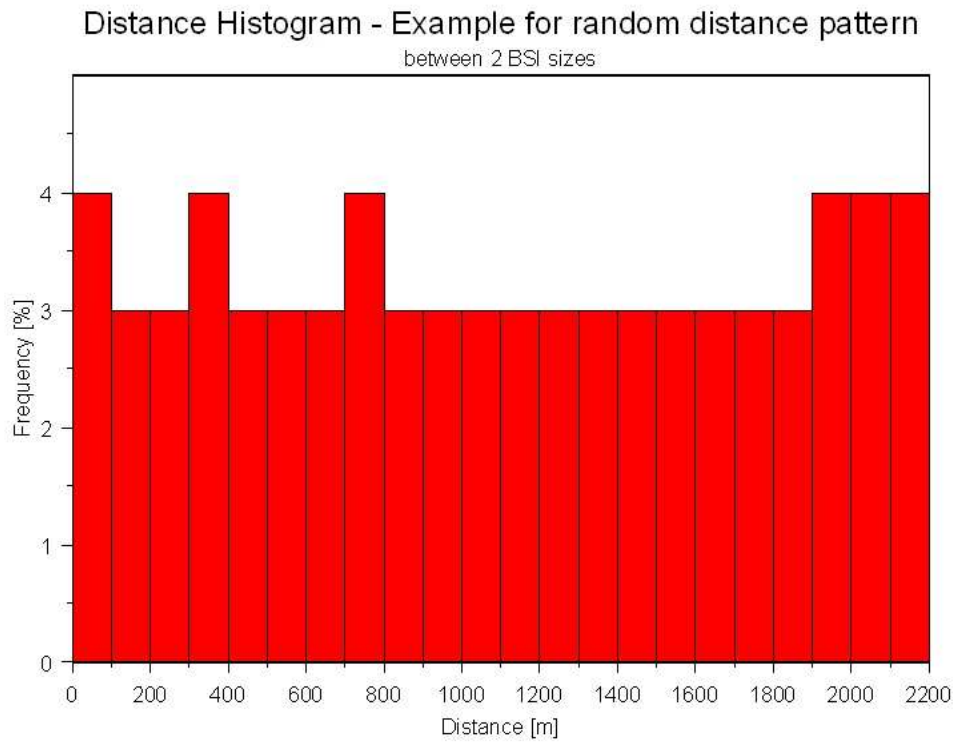


Figure 8.53 Example for expected randomly dispersed distance pattern in non-social species

8.8 Appendix: CD

The CD includes the digital form of this thesis (pdf).