Wolf behavior at the densite and responses to simulated wolf and coyote howls near rendezvous sites

By

Sophie Czetwertynski
Biology Department
Acadia University, Wolfville, Nova Scotia
B0P 1X0

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1. General Introduction

Most large-scale wolf field studies aim to measure population parameters to establish management strategies, often in relation to one or several prey species. The majority of information available pertaining to wolf behavior, on the other hand, is derived from direct observations made on captive wolves. Both of these approaches offer specific advantages to studying particular aspects of wolf ecology. Wolves are elusive animals traveling over vast expanses of territory generally making it infeasible to conduct any type of behavioral study where visual observations are necessary. Conversely, such aspects as population trends, harvest rates, predator-prey interactions etc. are simply impossible to measure in captivity. Long-term field studies have managed to include certain behavioral aspects into the scope of the field research, however, these are never the main focus of the research due to the uncertainty of obtaining sufficient data and justifying the high cost involved in studying aspects with often limited management implications.

The Quebec Ministry of Environment and Fauna (MEF) funded a wolf research study in the Laurentide wildlife reserve and surrounding area from 1995 to March of 1998 (field research in 1998 was supported by funding from NSERC and the Imax Co.) with the dual purpose of obtaining general information on the population and measuring the potential effects of ecotourim activities on wolf behavior. What makes this study unique is the fact that the primary initiative for conducting the project was in response to potential behavioral consequences that human activity might have on wolf packs affected by ecotourism activities and the desire to identify, measure, and possibly reduce this potential disturbance. Ecotourism is a fast growing industry that prides itself on the economic value of "friendly" non-consumptive activities (Berle 1990). However, the fast growing pace at which it is expanding makes it difficult for protective legislation to keep up and has already led to many examples of long-term detrimental effects on both habitats and species (Mathieson and Wall 1982, Boo 1991). The MEF initiative of studying the effects of wolf howling activities, with the activity being in its infancy, should be an example to be followed by other government bodies where resources are directly affected and the potential impacts are not immediately obvious or easily observable.

The Laurentide reserve and surrounding area were chosen as a study site because there was already an ecotoursim company running howling excursions in the reserve and because several other wolf management issues in this area required investigation. Wolf densities in wildlife reserves are estimated from questionnaires given to moose hunters (Crête and Messier 1987), and wolf harvest is calculated using officially registered pelts from each reserve. Based on previous years of data, MEF biologists were concerned that the estimated harvest rate of 25% in the Laurentide reserve was high and might not be sustainable. Actual field data from this reserve was also desired in order to validate this method as a management tool. Additionally, the Laurentide reserve is the closest source of wolves that could potentially naturally recolonize the northeastern US (Harrison and Chapin 1997). Several conservation groups, believing that a wolf captured in Maine originated from the Laurentide reserve, were applying pressure on the MEF to reduce trapping pressure in the area in order to facilitate natural recolonization. More detailed information on population parameters was necessary to evaluate this possiblity. Finally, the MEF was also intersected in determining the number of packs exerting predation on a reintroduced caribou herd in the Grands-Jardins park adjacent to the reserve. Therefore, the Laurentide reserve was the ideal location to address these questions (Jolicoeur 1995).

Fieldwork for the project was divided so that pertinent information could be gathered on the entire wolf population of the reserve while the behavioral components of the study were concentrated on selected packs. This type of organization allowed for information to be gathered on both the population and individual levels. General population characteristics are described by Jolicoeur (1999) and several other reports describe various aspects of the Laurentide wolves (Jolicoeur et al.1998, Larivière et al. 2000, Manseau et al. in prep).

Any research conducted on free-ranging wolves is bound to attract attention due to the often polarized views held by concerned parties. This is particularly true of an area such as a wildlife reserve where wolves compete with hunters for prey and are valued as both a consumptive and non-consumptive resource. Wildlife reserves in Quebec are open to logging, hunting, fishing, trapping, as well as to many non-consumptive educational and tourist activities. Hunters therefore in many cases view the presence of wolves as a nuisance while trappers and ecotourism companies benefit from their presence.

The MEF Laurentide wolf project was to be a cooperative effort and included various contributors such as the Mikin ecotourism company, the SEPAQ (Société d'Etablissements de Plen Air du Québec), and the Quebec Provincial Trappers Association (FTGQ). The main goal to be achieved by these parties was to gain information on this population in order to develop a strategy to manage the population to the benefit of both wolves and humans. This included management of the harvest as well as the determination of the possible effects of ecotourism and possible alternatives to reduce the disturbance while pursuing the activity.

This study concentrates on the behavioral component of the study and is divided into two chapters. The first deals with wolf behavior at the densite at both the pack and individual levels. The second chapter addresses the potential behavioral effects of wolf-howling excursions. Extensive fieldwork also led to the development of a more humane trapping method which is described in a technical paper.

In spring, wolves tend to return to traditional denning sites used over many years and their movements during this period are somewhat restricted due to the presence of pups (Murie 1944, Joslin 1967). This is a crucial period since most deaths in wolves occur during the first six months of life (Van Ballenberghe and Mech 1975), a time when the pups are entirely dependant upon adult members of the pack for food (Murrie 1944; Mech 1970, Fentress and Ryon 1982). There are limited data on precise movements of individual wolves, the division of labor and specific roles that individual wolves take on during this time (Mech 1999). Although several studies have quantitatively described densite behavior (Harrington and Mech 1982, Ballard et al. 1991), the differentiation between age class and the plasticity of this behavior over several years are unknown. This study examines the densite behavior of one particular pack over three years to determine the importance of age and social structure of packs in affecting behaviors of individual wolves by comparing behaviors of specific individual wolves over time.

As mentioned above, wolf-howling excursions are not only a growing activity, but also an important tool for educating the public with regard to such a controversial species. In the wolves' vocal repertoire, howling is the only sound that can be heard over long enough distances to serve in both inter- and intra-pack communication (Joslin 1967; Harrington and Mech 1978). Manseau et al. (in prep) found an effect on the long-term attendance patterns of pack members, but observed no short term effect, in response to simulated alien wolf howls based on data obtained from the Laurentide project (coyote howls were not found to affect the attendance pattern of wolves). In this study, immediate responses after both simulated wolf and coyote howls are compared. Both response rate and immediate changes in behavior and movement are described in order to justify assumptions made on the potential information transferred via these vocalizations. Based on these observations, ecotourism companies may better be able to structure their activities to both increase the odds of eliciting a response while, at the same time, being more aware of the behavioral effects, reducing potential negative impacts.

The capturing of animals is usually an essential part of most field-based projects and the increasing interest of the general public in research has put much focus on the treatment and welfare of studied animals (Gilbert 1991). This in turn puts biologists under scrutiny to minimize any injuries that might be incurred by the affected species. Over four years of wolf captures, modifications to Soft Catch #3 leg-hold traps (Lemieux 1999) resulted in a significant reduction in trap-related injuries. These modifications are described in a technical paper at the end of the thesis.

The extensive behavioral data collected throughout this study on the behavior of all individual wolves within packs is unprecedented. It is also an important contribution to the limited information on wolf behavior in forested habitats. The following papers will hopefully spur advancements and further discussion in the field of behavioral ecology.

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2. Den site attendance characteristics at the pack and individual levels

S. Czetwertynski[a], P. McLeod[a]

[a] Acadia University, Psychology Department, Wolfville, Nova Scotia. B0P 1X0.

Current address of corresponding author:

Sophie Czetwertynski
5797 Ave de la Terrasse
Rawdon, PQ
J0K 1S0

2.1 Abstract

A wolf (*Canis lupus*) pack den site in Quebec, with all individual members collared, was monitored during three consecutive years. Alpha individuals, prey availability and sex of auxiliaries remained constant throughout the study and pack structure differed only in the age structure and number of female subordinates. General pack behavior was found to vary over the three years suggesting that environmental circumstances alone cannot account for the behavioral changes observed. Observations on individual wolf behavior revealed greater variability between years than among similarly ranked individuals within a particular year. Additionally, the same two wolves maintained their alpha status during the three years but their behavioral patterns were significantly different between years. These results suggest that even though rank plays a role in determining general behavioral characteristics, pack structure plays an important role and affects den site behavior of all individual wolves. Results suggest that wolves' movements are coordinated in such a way as to maximize hunting experience. These results may be characteristic of a population dependent on moose as their primary prey and therefore requiring the coordination of several pack members to secure food.

2.2 Introduction

Wolves (*Canis lupus*) are social canids living in packs generally composed of nuclear families with a single breeding pair (Murrie 1944; Mech 1970) since non-alpha individuals may forgo breeding and remain with the pack for varying durations of time before dispersing (Fritz and Mech 1981; Ballard et al. 1983; Messier 1985; Mech 1987; Gese and Mech 1991; Boyd et al. 1995). When pups are born in the spring, wolf activity is centered around the den site for one-to-several months until the pups are strong enough to be moved to temporary rendezvous sites (Murie 1944, Joslin 1967). Throughout this period, pups are entirely dependent on older members of the pack for food (Murrie 1944; Mech 1970, Fentress and Ryon 1982; Mech et al. 1999).

Research into the role of individual pack members in providing food for pups in both captive and wild situations have found that generally both adults and yearlings feed pups, yearlings are fed by adults, and adults are not fed by yearlings (Mech et al. 1999, Fentress and Ryon 1982). While the behavior of the alpha male is usually related to hunting forays to feed his offspring, that of the alpha female is divided between the care of pups and hunting (Mech 1999). The relative attention that is given to these two mutually exclusive activities is thought to be dependent upon prey availability, the social structure of pack, and the age of pups (Ballard et al 1991). While several studies conducted in the wild suggest that non-reproducing individuals may intercept food from pups (Harrington and Mech 1982, Ballard et al. 1991), Mech et al. (1999) found that auxiliaries were found to help feed pups more than they competed for food. These observations suggest that the behavior of non-reproducing wolves is more variable than that of adults, and perhaps, more directly related to immediate environmental factors. For example, Harrington et al. (1983) found a positive correlation between number of auxiliaries and pup survival at 7-8 months in an area of high prey density while the relationship was absent or negative in an area of low prey density.

The evolution of cooperative group hunting in wolves suggests the need for behavioral plasticity and thus the opportunity for the development of individual variability in behavior (Sullivan 1979). In fact, Nunamiut Alaskan Inuit have observed that individual wolves play differential roles in hunting and killing prey. Similar observations have been made on the individual variability of wolves' hunting behavior in enclosures (Fox 1972; Fox and Andrews 1973; Sullivan 1979). Variability in individual behavior and dominance relationships have been observed in pups at eight weeks of age and these were shown to persist into maturity (Fox 1972). Therefore, it is important that observations on wolf behavior should be made at both the pack and individual levels before drawing conclusions referring to general wolf behavior.

In addition to individual variability, wolf behavior at den sites is thought to be influenced by various factors including latitude, age of pups, food resources, and sex and age composition of the pack (Ballard et al. 1991, Mech and Merrill 1998, Potvin et al. 2000). Due to the difficulty of obtaining accurate data on such an illusive animal, most behavioral studies on wolves base their conclusions on combined observations from different wolves and packs (Joslin 1967; Kolenosky and Johnson 1967; Mech and Merrill 1998). Two studies offer quantitative data on the attendance of individual wolves at the den site, however, conclusions were based on observations of a subset of pack members during a single season (Harrington and Mech 1982, Ballard et al 1991). Mech (1999) described the dominance relationship between pack members through visual observation over many years, but was usually unable to recognize individual wolves from one season to the next.

Although all these studies offer insight into general patterns that may exist in the population studied and also demonstrate the presence of behavioral variability, they are not able to tease apart the relative importance of individual, social and environmental factors that might influence these behavioral modifications. Similarly, more information is needed on the behavior of individual wolves from different areas before we can determine which, if any, behavioral characteristics can be generalized across different populations and various ecological circumstances.

The present study examines the den site behavior of a pack in the Laurentide reserve, Quebec. It is unique because it follows the attendance pattern of all pack members simultaneously 24 hours a day over three consecutive years with knowledge of the life histories of all pack members. Alpha individuals, prey availability and sex of auxiliaries (all non-alpha individuals were females) remained constant throughout the study; pack structure differed only in the age structure and number of female subordinates (the pack was composed of 6,8 and 7 wolves from 1995 to 1998). We will therefore compare general pack behavioral characteristics at the densite. Because we are comparing the same pack under similar ecological conditions, we expect that the general attendance pattern will remain constant across years. We will then go one step further and examine individual wolf behavior both within years for similarly ranked individuals and among years for wolves present over several seasons. By determining where variation is greater, we should get an indication of the flexibility of individual behavior and to what extent it might be affected by individual rank and pack structure. This will allow us to determine whether generalizations can be made about behavior at both the pack and individual levels based on surrounding conditions and to what extent individual "personalities" contribute to this variation. We will also comment on the potential 'roles' that wolves of various social status might play during the denning period.

2.3 Study Area

The territory of the Malbaie pack was entirely located within the borders of the Laurentide wildlife reserve (7 934 km^2), located approximately 80 km north of Quebec city, Canada. The reserve is characterized by one of the highest snowfalls in the province (400 to 700 cm) and is surrounded mostly by agricultural and public land. The Malbaie pack's home range (1 092 km^2) was located in the center of the reserve where the altitude is highest (approximately 800 meters) and the vegetation was almost entirely coniferous forest (*Picea mariana* and *Abies balsamea*). Logging activities were very prominent in the reserve and distorted the original makeup of the landscape leaving only islands of vegetation in recently cut areas. A more detailed description of the study area is available in Jolicoeur (1999).

Adult moose were the primary prey for the Malbaie pack during spring and summer (Tremblay et al. in prep). Moose density in the center of the reserve was low and ranged from 0.8 to 1.0 moose/10km^2 (St-Onge et al. 1995; Frenette 1990). Wolves were classified as furbearing and big game animals in the province of Quebec and could be legally trapped with no bag limit for four months out of the year and big game hunters could take one in season. Wolf trapping was permitted in the reserve, although trappers voluntarily reduced harvest pressure on the wolves during the study. The Laurentide reserve was divided into 111 exclusive trapping territories leased out to trappers on nine-year renewable leases.

2.4 Methods

As many wolves as possible from the Malbaie pack were captured in the summer using modified leg-hold traps with rubberized jaws (Lemieux 1996, 1999; Technical Paper, this Thesis). Regular aerial surveys were performed over the winter to determine the exact number of wolves in each pack. Remaining uncollared wolves were then captured in the winter using net-guns and tranquilizer darts (5 mg Telazol/ kg body weight) shot from a helicopter. Pups collared over the summer were recaptured in winter to adjust their collars. Wolves were eartagged with numbered yellow rototags and fitted with radio-collars manufactured by either Lotek (Newmarket, Ontario), Wildlife Materials (Carbondale, Illinois), or Telonics (Mesa, Arizona). Wolves were sexed and characterized by a series of morphometric measurements. Status within the pack was determined by size, age (tooth ware) and behavior (Van Ballenberghe and Mech 1975).

Monitoring stations were constructed between 0.5 and 1.0 km from den sites. Close enough to ensure accurate information while minimizing disturbance to the natural behavior of the pack. Three element directional antennas (Lotek) were connected to receivers (Lotek SRX 400 and Suretrack STR 1000) programmed with the collar frequencies of all pack members. A dummy collar was placed in the direction of the den and a dummy frequency was programmed to ensure the proper calibration of the equipment. In 1996, strip-chart recorders scanned frequencies every 30 minutes, therefore wolves and dummy frequencies were each scanned for 3.75 minutes every half hour. In 1997 these were replaced by electronic versions consisting of receivers connected to specifically designed decoders (Geneq Inc.) which transformed the intermittent "presence" signal to a constant one which could be recorded by voltage data-loggers (OWL). The information was downloaded daily onto a laptop computer (IBM Thinkpad). All the equipment was powered by a 12-volt battery charged by solar panels. Data were collected every 30 minutes per wolf in 1996 and every 10 minutes per wolf in 1997 and 1998.

The Malbaie pack (Figure 1) occupied the same den site during 1996 and 1997 but moved to a site approximately 10 km away in 1998. The dens were monitored from the time it was possible to travel to the den sites to install the equipment (due to snow conditions) until the wolves left the den in 1996 and 1997. In 1998, monitoring was ceased before the pack abandoned the den site. The sites were monitored for 89, 91 and 93% of the time consecutively representing 1416, 893 and 1481 hours of observation respectively from 1996 to 1998. All wolves (including pups) that were not present the following year as yearlings succumbed to various causes of mortality. Only F421 and F552 dispersed from the pack.

Due to periodic fluctuations in signals, if attendance or absence was recorded for a period of 30 minutes or less, the data points were smoothed over to the status of the animal surrounding the break in data. If animals were present during the scan then they were considered present for the duration of time until the following scan (5 to 30 minutes depending on the pack and year). The type of sampling data obtained from the monitoring stations is often referred to as 'one-zero' sampling (Hansen 1966). Although some authors do not recommend this method (Altmann 1974); its major drawback is the overestimation of the amount of time spent at a given activity (Dunbar 1976; Tyler 1979).

In our case, the sampling interval is sufficiently small compared to the average bout length for estimates of attendance and absence to be relatively accurate (Simpson and Simpson 1977).

Three to six pups from the Malbaie pack were captured every spring from 1996 to 1998 inclusively. Although pup size and weight varies within a litter, over a given area and between years (Van Ballenberghe and Mech 1975), most wolves from a particular area tend to give birth during a similar period each year (Mech 1966; Rausch 1967; Van Ballenberghe and Mech 1975). We therefore made the assumption that the Malbaie alpha female gave birth at approximately the same date over the three years in order to compare individual behavior over several years. Based on similar average pup size during spring captures, we believe this assumption to be reasonable. Therefore, in order to control for changes in wolf behavior associated with pup development, we first limited comparisons among years to the longest period common to all 3 years of the study (the "restricted" period - 6/7 to 7/1). The Malbaie pack was monitored for 87±3% of this time period over the three years. As an added precaution and because the assumption of similar parturition dates over the three years cannot be confirmed, all inter-year comparisons were also made with all of the data from specific years in order to verify the consistency of results.

The frequency of attendance was measured by calculating the proportion of times individual wolves were present at every hour throughout the day for the entire monitoring period. The Friedman test, the nonparametric analogue of the two-way analysis of variance, was used to compare daily attendance among wolves and years (Wayne 1990).

In comparing the distribution of arrival and departure times, the exact number of events (arrivals or departures) occurring during a specified time period was used. The coordination of arrivals and departures among wolves was calculated by considering individuals as arriving or departing together if the events were within half an hour of each other. Because the sample size for arrivals and departure times was small for individual wolves, we compared the distributions of these events during the restricted period to all the data available. There were no significant differences between these two data sets for any wolves in 1996 and 1997 (chi square >0.05), so all of the events monitored were used to increase sample size. Sample sizes in 1998 were not large enough to make this comparison (less than 5 events in many blocs); nevertheless, we used the entire data set to compare behaviors among all three years.

Survival analysis, a statistical tool used to compare bout durations, was performed at both the pack and individual levels. Sequences of attendance during which there was interruption of data collection at the beginning of the interval due to technical malfunction were omitted. Right censored intervals (intervals for which the exact time the bout ends was unknown) were estimated using the non-parametric Kaplan-Meier estimator for survivor analysis (SYSTAT). P-values given are from the Mantel log-rank test.

Single-link cluster analysis was used to determine the relative association of arrivals and departures among the wolves and to compare these associations among years. To account for the differences in events among wolves, the data was normalized using the method described by Morgan et al. (1976) where similarity = xy/(x+y) where "xy" is the number of times individuals arrived or departed together and "x" and "y" are the individual numbers of events for each wolf (Dice 1945; Lehner 1979). Values were then multiplied by 1000 to simplify the interpretation. Therefore, if individuals always arrive together the value for similarity would be 0.5, which would then give 500 after multiplying by 1000.

Wolf associations were calculated by determining the amount of time that individuals spent together regardless of other wolves present. In order to standardize among years, only data on the half-hour was used from the 1997 and 1998 data sets. In order to determine whether certain wolves or groups of wolves were found together more often than would have been expected by chance, a chi-square analysis was performed. However, in order to account for the difference in attendance among wolves, expected frequencies were computed using the individual attendance of the wolves in question. Single-link cluster analysis was then used to determine the relative association among the wolves and to compare these associations among years. As for arrivals and departures, the data were normalized as described above.

For analyses within years, all available data for that particular year were used. In instances when daily patterns were measured over time, only days monitored for at least 70% of the time were retained for analysis and missing values were interpolated using distance-weighted least squares. Durations of bouts of attendance and absence were compared using survival analysis and the non-parametric Kaplan-Meier model (SYSTAT). Curves were compared using the Mantel-Haenszel test (SYSTAT), which attributes equal weighting to individual time periods.

The percent daily attendance of individual wolves was compiled over time, again using only those days where over 70% of the day was monitored. Breaks in the data were estimated using distance-weighted least squares, therefore all non-missing values contribute to the missing data estimates. A three-day moving average was applied to smooth out the data set and a regression analysis was performed on the values obtained to look at trends in attendance over time. A significance of alpha=0.05 was used for all of the above analyses.

2.5 Results

2.5.1 Pack behavior

In order to compare pack behavior over years, information on all wolves regardless of age or rank was combined. To account for the differences in pack size from year to year, only groups of 0 to 4 wolves were compared. Overall, the relative frequency of these group sizes was different among years (x^2, $p<0.000$) (Figure 2), with larger groups occurring less frequently when pack size was largest in 1997. In 1996, group sizes of 1-4 occurred at relatively the same frequency and approximately twice as often as no wolves present. In 1997, groups of 1 and 2 wolves are more frequent than 0 wolves as well as larger group sizes with groups of 2 wolves being most frequent. In 1998, the frequency of 0 wolves present is higher than any group size.

The frequency of different group sizes throughout the day also differed among years (Appendix I). In 1996, group sizes of 1-4 were just as likely to occur throughout the day (Friedman test statistic = 7.24, 3df, p= 0.07). In 1997, groups of 3-4 wolves were just as likely to occur throughout the day (Friedman = 0.52, 1df, p= 0.47) but were less frequent than groups of 1-2 wolves, particularly in the middle of the day. In 1998, groups of 1-3 wolves were just as likely to occur throughout the day (Friedman test statistic= 0.948, 2df, p= 0.623) and were significantly less likely to occur than 0 wolves present throughout the entire day (Friedman= 59.84, 3df, p<0.000). In 1996, the frequency of finding more than 2 wolves at the den was least likely from 22:00 to 3:59 and random throughout the rest of the day ($x^2=8.81$, 3df, $p=0.03$). In 1997, groups were more likely to occur from 22:00 to 9:59 (x^2=8.09, 3df, p=0.04) while in 1998 groups of more than two wolves were just as likely to occur at any time of day (x^2=3.78, 3df, p=0.29) (figure 3). The patterns in the data samples common to the three years were similar to those observed for the entire data sets for each individual year. Thus, there was no constant daily pattern of wolves congregating at the densite.

Arrivals and departures from the den site for all the wolves were combined and divided into the six-hour time periods (22:00-3:59, 4:00-9:59, 10:00-15:59, and 16:00-21:59) used by Mech (1998). The distribution of arrivals in the Malbaie pack among these time periods was similar over the three years (x^2 = 7.83, 6df, p=0.25; N=94, 114, 56 for 1996, 1997 and 1998) with arrivals being twice as frequent between 10:00 pm and 10:00 am as during the other half of the day (figure 4,5). On the other hand, the distribution of departures among these periods was significantly different from year to year (x^2=17.71, 6df, p=0.007; N=89, 110, 54 for 1996, 1997 and 1998). From 1996 to 1998, departures from the den increasingly differed from random between the four time periods (x^2 =7.58, 3df, p=0.06 in 1996, x^2=10.00, 3df, p=0.02 in 1997 and x^2=28.82, 2df, p<0.000 in 1998), and in 1998 wolves were three times more likely to depart between 4:00 and 10:00 am than during any other time period. The distributions during the restricted period were similar to the entire data set for all years (chi square p>0.05 for all years), lending credence to the assumption that our samples were representative of the behavior of the pack for that season. Overall, the frequency of wolves arriving alone at the den site was similar across the three years (x^2 = 0.034, 2df, p= 0.98) and represented 79.7±1.3% of the total number of arrivals recorded (N=412). Although the overall frequency of single departures is also similar across the three years (x^2 = 0.92, 2df, p= 0.63), there was approximately a 10% increase in the proportion of lone departures from 1996 to 1997 and 1998 (61.0% in 1996, 69.2% in 1997 and 70.59% in 1998). In 1996, 17% (N= 123) of departures consisted of three or more wolves leaving together, whereas in 1997 and 1998, this was only the case in 9 and 11% of recorded departures (N= 130 for 1997 and N=85 for 1998) (Appendix II).

Lengths of time that pack members spent at the den were combined for all years (Table 1). There was no significant difference in mean time of attendance among years for the Malbaie pack (Mantel chi square = 3.66, 2df, p =0.16). However, mean bout length was longest in 1998. On the other hand, mean time of absence was not equal over the 3 years (Mantel chi square = 17.249, 2df, p=0.000) and was almost twice as long in 1998 as in 1996 and 1997.

The Malbaie pack pups are left alone for an average of 14, 16 and 29% of the time during 1996, 1997 and 1998 respectively. Based on the amount of time individual wolves spent at the den and assuming random and independent attendance, the pups would be expected to be left alone 9, 6 and 13% during the three consecutive years, significantly less often than actually occured ($x^2 = 39.14$, 2df, $p<0.000$). Thus in each year, wolf attendance was clumped and the pups were left alone 1.6 to 2.7 times more than would have been expected by chance (Figure 6).

2.5.2 Behavior of individual wolves

Overall, individual wolves spent varying amounts of time at the den within a specific year and their attendance also changed between years (table 2). Within a specific year, attendance varied both within and among wolves of different age classes. In 1996, three of the four yearling females spent similar amounts of time at the den site (Friedman test statistic= 3.94, 2df, p= 0.14) while F402 spent significantly more time at the site (Friedman test statistic= 14.19, 3df, p= 0.003) (Appendix III). In 1997, the pack included three yearlings and three 2-year old female wolves. The attendance pattern was similar among the three yearlings who spent an average of 26.6±2.6% of their time at the den site (Friedman test statistic= 1.02, 2df, p= 0.60) but differed among the 2-year olds (Friedman test statistic=36.65, 2df, p<0.000) (Appendix IV). In 1998, the two-year old female F253 spent close to twice as much time at the den site as the two-year old F370 (Friedman test statistic= 24.00, 1df, p< 0.000), however, monitoring of F253 ended on June 15th which adds uncertainty since attendance decreased throughout the denning period. The attendance of yearling F180 was also higher than that of yearling F552 (Friedman test statistic= 24.00, 1df, p< 0.000). All of the above patterns held true when all the available data were used (p<0.05).

We compared attendance patterns among years of individual wolves for which there was more than one season of data and whose status within the pack remained constant, as a function of the time of day (Appendix V). For the alpha pair (M450, F381) and the handicapped wolf (F470), there were three years of data available. In 1996 and 1997, the alpha male spent the same amount of time at the den (Friedman test statistic=0.04, 1df, p= 0.84) while in 1998 his attendance decreased significantly (Friedman test statistic=27.65, 2df, p<0.000). In 1996 he was predominantly present in the afternoon while in 1997 and 1998 he was just as likely to be present at any time of day. This behavior was similar to that expressed over the entire sampling period for all years. Overall, the alpha female spent the same amount of time at the den in 1996, 1997 and 1998 (Friedman test statistic=4.02, 2df, p= 0.13) (Appendix V). However, her behavior was characterized by daytime attendance in 1996 and 1997 while in 1998 she was just as likely to be present at any time of day. The pattern is similar when all the data are used, although in 1998, she spent significantly less time at the den than in 1996 and 1997 (Friedman test statistic=9.75, 2df, p= 0.01). The handicapped wolf (F470) had a different pattern and degree of attendance during all three years (Friedman test statistic= 40.08, 2df, p<0.000) (Appendix V) and these results were consistent with those obtained using all the data available (Friedman test statistic= 48.00, 2df, p<0.000).

Two of the yearlings present in 1996 were also present in 1997. In the case of F402, her attendance was similar over the 2 years (Friedman test statistic=3.38, 1df, p= 0.07) while F411 spent significantly more time at the den site in 1996 (Friedman test statistic=9.38, 1df, p=0.002) (Appendix V). However, when all the data available were used, both wolves were found to spend significantly more time at the den site in 1996 than in 1997 (Friedman test statistic=10.67, 1df, p= 0.001 for F402 and Friedman test statistic= 16.67, 1df, p<0.000 for F411). In 1997, there were also two yearlings that were present with the pack the following year. F253 spent a similar amount of time at the den site during these two years (Friedman test statistic= 0.38, 1df, p=0.54) whereas F370 spent significantly more time at the den site in 1997 (Friedman test statistic= 24.00, 1df, p<0.000)

(Appendix V). When all the data available were used, both wolves were found to spend significantly more time at the den site in 1997 than in 1998 (Friedman test statistic= 12.04, 1df, $p=0.001$ for F253 and Friedman test statistic= 24.00, 1df, $p<0.000$ for F370). This discrepancy between patterns during a portion of the sample period and the entire sample could indicate that behavior for maturing wolves was more variable than that of the alphas throughout the season, or could simply be a factor of a small sample size.

Days were divided into four six-hour time blocs as described for arrivals and departures to determine whether there was any type of daily pattern in attendance. In 1996, both alpha male and female spent significantly more time at the den site during the day (10:00 am to 10:00 pm) ($x^2=12.00$, 3df, $p=007$ and $x^2=12.50$, 3df, $p=0.006$ respectively). Meanwhile, all of the yearlings were just as likely to be present at any time of day ($x^2>0.05$ for all wolves). In 1997, all wolves except for the adult F411 and yearling F331 had a random attendance throughout the day ($x^2=12.84$, 3df, $p=0.005$ and $x^2=14.48$, 3df, $p=0.002$ respectively). However, F411's attendance was characterized by nighttime attendance while F331 was more likely to be present from 4:00 am to 4:00 pm. In 1998, the attendance of all wolves was random throughout the day ($x^2>0.05$) (Appendix V).

Once wolves arrived at the den site, they remained there for varying durations of time (Table 3). There was no significant difference for either the alpha male ($x^2 = 0.501$, 2df, $p= 0.778$) (note that $n=6$ for 1998) or female ($x^2 = 1.258$, 2df, $p=0.533$) in the mean duration of attendance from 1996 to 1998. When all the available data were used, mean survival time for the alpha male was significantly longer in 1998 than in 1996 and 1997. On the other hand, the handicapped wolf's attendance bouts were twice as long in 1996 and 1998 as they were in 1997 ($x^2 = 11.233$, 2df, p=0.004). Bout length for the four female yearlings was not significantly different from their first to their second year (p>0.05). However, sample sizes for 1998 were much smaller than for 1996 and 1997 because, overall, wolves in 1998 stayed for longer durations resulting in a smaller number of bouts. There were no significant differences in the mean bout lengths of any age classes within the same year in 1996 and 1997, but there was not enough data to compare individuals in 1998.

The distributions of arrivals and departures among the four time blocs were similar among years for all wolves for which there was more than one season of data ($x^2>0.05$)(Appendix VI). However, these results should be treated with caution since the number of arrivals and departures for most wolves do not meet the minimum requirement of one-fifth of cells having frequencies above 5. Due to this small sample size, and since the distribution of arrivals and departures seems to be relatively constant for individual wolves, wolves having more than a season's worth of data were compared using events combined over several years. In this way, we compared seven wolves for which there was more than one season of data (M450, F381, F470, F402, F411, F253, F370). The distributions of both arrivals and departures were similar among the seven wolves ($x^2 = 16.95$, 18df, p=0.53 for arrivals, and $x^2 = 16.95$, 18df, p= 0.53 for departures). Comparisons between similarly ranked individuals within the same season were done in 1996 and 1997 (most comparisons do not meet the minimum requirement of not fewer than 5 events in one fifths of the cells), but not in 1998 due to the small sample size. In 1996, the distribution of arrivals and departures for the four female yearlings (F470, F402, F411, F421) were alike ($x^2= 5.29$, 9df, p= 0.81 for arrivals and $x^2 = 8.13$, 9df, p=0.51 for departures) and similar to the pack behavior described for that year. In 1997, this was also the case for three of the four wolves which were still with the pack (F470, F402, F411) but were now two years old ($x^2 = 4.64$, 6df, p=0.59 for arrivals, and $x^2 = 5.46$, 6df, p= 0.49 for departures). On the other hand, the distributions of arrivals and departures for the three yearlings present in 1997 (F331, F253, F370) were different from one individual to the other ($x^2 = 14.11$, 6df, p= 0.03 for arrivals and $x^2 = 13.05$, 6df, p=0.04 for departures), and while overall their arrivals occurred more often between 10:00pm and 10:00am ($x^2 = 12.80$, 3df, p=0.005), they were just as likely to depart at any portion of the day ($x^2 = 7.40$, 3df, p=0.06) (Appendix VI).

A cluster analysis was performed on the arrivals and departures of the individual wolves to determine if certain wolves tended to arrive or depart together and if this behavior was consistent from one year to the next (Appendix VII). In 1996, when the pack consisted of alphas and yearlings, arrivals of all wolves, except for F421, were clustered together while only wolves M450, F470 and F402 tended to depart together. The following year, the wolves which were more likely to arrive together were M450, F402, F253 and F370; other pack members tended to arrive alone. Clustering of departures resulted in a four-cluster solution. Interestingly, all two-year old wolves were clustered with the alpha male. In 1998, the two wolves which tended to depart together most often were the alpha male and female and they were clustered together with one yearling (F180) and a two-year old female (F253).

In 1996, there was no significant difference in the actual and expected time individuals spent with each other at the densite (x^2=5.32, 14df, p=0.98) and no clustering was evident. In 1997, there was a significant difference between the actual and expected times wolves spent together (x^2=102.07, 2df, p<0.000) and subordinate pack members spent significantly more time than expected with the alpha male (x^2=13.10, 5df, p=0.02) but not with the alpha female (x^2=8.92, 5df, p=0.11). Only two clusters containing more than a single wolf were formed. The first consisted of the alpha female (F381) and two yearlings (F253 and F370) and the second was composed of two two-year-old wolves (handicapped F470 and F411). In 1998, there was also a significant difference between actual and expected times wolves spent together (x^2=53.74, 20df, p<0.000). However, subordinates spent significantly more time with both the alpha male (x^2=16.40, 4df, p=0.003) and alpha female (x^2=8.89, 4df, p=0.06). Cluster analysis revealed a three-cluster solution with only two clusters containing more than one wolf. The first contained the alpha male and a two-year old (F370) while the second contained the alpha female, the three-year-old handicap (F470), a two-year-old (F253) and a yearling (F180). Overall, the alpha male and female were not avoiding each other and spent more time together than would be expected by random attendance but this value was not significant (x^2=3.71, 2df, p=0.16). However, they were never clustered together over the three years (Appendix VIII).

In 1996, the alpha male and female were more likely than the yearlings to return to the den site accompanied by at least one other wolf. The alpha male was the wolf that departed from the den site accompanied most often (Table 4). In 1997, the two subordinate wolves (F402 and F411) were the wolves that departed from the den site accompanied most often, while in 1998, the alpha male was significantly more likely to depart with at least one other wolf than any other pack member (x^2=22.24, 6df, p=0.001).

In 1996, the attendance at the densite of all wolves except for the alpha female decreased significantly over time; attendance of the alpha female decreased but this value was not significant (Table 5). In 1997, the attendance of all wolves decreased significantly over time except for yearling F253, whose attendance increased but not significantly over time. In 1998, the attendance of all wolves decreased significantly over time (Appendix IX).

2.6 Discussion

During the denning period, most studies have found that wolves are less active throughout the day (Vila et al. 1995), during which time they are more likely to be at the den site (Murie 1944; Kolenoski and Johnston 1967; Mech 1970; Ballard et al. 1991, Potvin et al. 2000). Only Harrington and Mech (1982) found a different pattern characterized by nighttime attendance. Over the three years of observation on the Malbaie pack, there was variation in both the relative frequency of different group sizes occurring at the den as well as the time of day in which they occurred. Our attendance results from 1997 and 1998 are similar to those observed by Harrington and Mech (1982). However, in 1996, larger groups were more likely to be found during the day than observed in other studies. Another interesting point is the fact that the frequency of larger groups of wolves at the den site was highest in 1996 when the pack consisted of the least number of wolves.

Mech and Merrill (1998) found arrival times to be random, however this could be due to the absence of night at 80 latitude. Our results are constant over the three years and similar to those observed in Alaska (Ballard et al. 1991), with wolves arriving more frequently during the night. Most studies also found that departures from the den site occur mostly in the evening (Murie 1944; Kolenoski and Johnston 1967; Mech 1970; Ballard et al. 1991), regardless of latitude (Mech and Merrill 1998). Once again, these results differed from the Minnesota study where wolves tended to leave at dawn (Harrington and Mech 1982). In the Malbaie pack, departures were random in 1996, most likely from 22:00 to 4:00 in 1997, and three times more likely between 4:00 and 10:00

than during any other time period in 1998. It was also during this year that wolves stayed away from the den for longer durations and then remained at the den site for longer periods once they returned. Therefore, our results suggest that departure times are not as easily predicted as has been suggested (Mech and Merrill 1998).

The general attendance pattern of the pack was quite variable across years with 1996 and 1997 being similar and durations of attendance and absence being longer in 1998. Although the pack used a different den site in 1998, it was only located 10 km from the previous one, within a very large territory, and should have had little effect on the overall behavior of the pack. The differences in behavior seen between study sites have been attributed to daytime temperatures, latitude and prey base (Harrington and Mech 1982, Ballard et al. 1991). In our case, the first factor remained relatively constant, and the second did not change. Although it is difficult to eliminate environment conditions and more specifically prey availability as factors, there was no drastic change in the density of moose, their primary prey, during the study making this an unlikely explanation for the variability observed. This does not imply that these factors have no effect on behavior, simply that they alone do not explain the variation we observed among the three years. Behavioral patterns observed are likely greatly affected by pack structure and their success in securing prey. If, as our data suggest, behavioral patterns can vary to such an extent within a single pack over only three years in similar ecological circumstances, then generalizations made at the pack level become quite questionable and a closer look at individual behavior becomes necessary.

Generally, our data suggest greater variability among years than between similarly ranked individuals within a particular year. For example, in the case of overall attendance, individual yearlings' attendance within a particular year were similar. Three out of four yearlings in 1996 and all the yearlings in 1997 spent the same amount of time at the den site. Although the alpha female spent close to twice as much time at the den site as the alpha male, they both had similar attendance rates from 1996 to 1997 and then a decrease in 1998 while they retained their alpha status. Yearlings, on the other hand, tended to spend more time at the den site in their first year compared to the second and this degree of attendance did not follow the pattern of the alphas, which suggests that social status, as well pack composition, could affect overall attendance.

This pattern was also observed in the duration of bouts that wolves spent at the den site. Although it was not the case for all individuals, there was a significant difference in bout length among years for both the alpha male and F470 when all the available data were used. However, there was no significant difference in similarly ranked individuals within the same year.

These results seem to suggest that overall attendance and the extent to which wolves remain at the den site are affected by pack structure and social status. This seems valid since groups of yearlings are usually unsuccessful in killing large prey on their own and require the assistance of more experienced individuals, usually the alpha male (Ballard et al. 1987). In the Malbaie pack, where moose comprise the principle food, the change in attendance patterns among years could be a function of the number of experienced wolves in the pack, and the associations most frequently observed to maximize hunting success.

This may be reflected in the size and composition of groups departing from the den site. When the pack was composed of the alpha couple and four yearling females in 1996, the frequency of large groups at the den was higher than during any other year. In 1996, the alpha male was the wolf that left the den accompanied by at least one other wolf most frequently (72% of all departures) followed by the alpha female (62% of all her departures). Departures were more randomly distributed throughout the day in 1996 than during the two following years and the association of different wolves with each other was random, possibly because of the similar hunting capabilities of the subordinate wolves (all yearlings). This randomness could be attributed to wolves waiting until a group was formed before departing. It would also seem that groups would "wait" to a certain extent for the alpha male before departing, since his bouts of attendance were shorter than those of any of the other wolves and he was most likely to depart accompanied. Additionally, all three healthy yearlings were just as likely to depart as part of a group.

In 1997, when there were two healthy adults in the pack (it is unlikely that F470 was a factor in killing moose), there was a substantial difference in the frequency of group departures between adults and yearlings (59% lone departures for yearlings and 40% for adults) and the alpha male departed with two of the adult females more often than would be expected by chance. In 1998, the adult male was again the wolf that departed accompanied most often (76% of all departures) and did so most often with the alpha female (F381), the non-injured adult female (F253) and one of the yearlings. It is also interesting that the two injured wolves (F470 and F370) were most likely to depart from the den site with each other. This pattern of non-injured adults clumping with the alpha male, and in some cases the alpha female, suggests a possible maximization of hunting experience and stresses the advantages of having adults in areas where moose are the primary prey. However, confirmation of this hypothesis would require information on the actual contribution of subordinate wolves in securing prey.

Yearlings could be spending more time at the den site to benefit from food being brought back by adults, as suggested by Harrington and Mech (1982). However subordinates in the Minnesota study spent close to 50% of their time at the den site and their attendance increased throughout the denning period (Harrington and Mech 1982). This was not the case in the Malbaie pack, where subordinate attendance varied between 3.3 and 36.5 % and in all cases but one, decreased throughout the summer. In captivity, yearling wolves are often fed by adults (Fentress and Ryon 1982). However, behavior of captive wolves, artificially kept together and unable to disperse, are not always representative of those occurring in the wild (Mech 1999). In fact, Mech et al. (1999) found that auxiliaries rarely received regurgitations but often fed the pups. In 1996, when there were no adults present, the three yearlings were just as likely not to depart alone (approximately 60% of departures were as part of a group). The fact that yearlings were less likely to depart as part of a group when there were adults present could indicate that they did not participate to the extent of the more experienced wolves, that they are learning to hunt, or that they are observers. Ballard et al. (1991) suggested that in large packs, yearlings could maximize time at the den to beg excess food but his data did not allow him to differentiate between yearlings and older wolves. Additionally, this diminished role in hunting would be advantageous to the pack if yearlings were to remain at the den site to guard the pups. This, however, was not observed in the Malbaie pack as pups were left alone more often than would be expected by chance during all three years. Furthermore, yearlings present in 1997 and 1998 spent less time at the den site than in 1996 when there were no adults. Therefore, although it is difficult to draw conclusions on yearling behavior without having direct observations, our results do not support the pup-tending hypothesis but neither did they spend as much time at the den site as reported in other studies where begging and intercepting food from adults was suggested (Harrington and Mech 1982, Ballard et al. 1991).

While the movements of the alpha male are a direct consequence of hunting success (Harrington and Mech 1982), those of the alpha female are most likely a combination of hunting necessity and caring for the pups. In smaller packs, the alpha female would probably have to play a more important role in foraging than in packs with other adults present (Ballard et al. 1991). Interestingly, the Malbaie alpha female spent the same total amount of time at the den site over the three years but her pattern of attendance was more predictable in 1996 than in 1997 or 1998, when she was just as likely to be present at any time of day. She was most likely to depart as part of a group in 1996 when there were no adults present but her departures were not clustered with those of the alpha male. In 1997, approximately half of her departures were as part of a group but not with any wolf in particular. However, in 1998, the wolves that were most likely to depart together were the alpha male and female. The alpha female departed as part of a group 50% of the time during that year and over half of those departures included the alpha male. If the alpha female was purposely waiting for the alpha male before departing, this could explain the greater variability in her attendance over that summer. However, it is unclear what could have caused her den site attendance pattern to change from daytime attendance in 1996 to random presence in 1997 and 1998.

Most studies have found a pattern of daytime attendance at den sites (Murie 1944; Joslin 1967, Kolenosky and Johnston 1967; Peterson 1977; Potvin et al. 2000) while Harrington and Mech (1982) found wolves to be present more often at night. The fact that attendance was variable in general over the three years and for most individuals could suggest that attendance, in our case, is simply a result of the hunting pattern of the alpha male and possibly the female since they are the ones that most often depart as part of a group.

The alpha wolves and the handicapped wolf F470 demonstrated variation in their behaviors from one year to the next even though their status within the pack remained the same. Furthermore, behaviors were relatively similar across like-ranked individuals. Therefore, it would seem that pack structure in combination with rank plays a determining role in affecting behavior. It is also important to consider individual variability between wolves which adds to the variability and difficulty in establishing specific patterns. One pattern which deserves notice is the difference in behavior between yearlings and two-year-old wolves. In most studies, due to the difficulty of establishing the exact age of studied wolves and also to increase sample size, they fall under the category of auxiliaries (Harrington et al. 1983; Mech 1999) and no discrimination is made as far as the relative contribution that they make to the pack. If, as our data suggest, behavior is influenced by pack structure, then observations made about any age category should also be accompanied by the exact composition of packs for comparisons across study sites.

The behaviors observed at the Malbaie pack den site are not necessarily representative of packs elsewhere, and more data are needed before any definitive conclusions can be drawn. The Malbaie pack is heavily exploited (approximately 50% mortality/year) and feeds almost exclusively on adult moose throughout the summer (Tremblay et al. in prep.). However, this study clearly demonstrates the variability and flexibility of individual wolf behavior and cautions against making conclusions based in a single season of data and extrapolating to other study sites.

Environmental factors are often cited as reasons for differences between study sites, but it is clear that the complete makeup of a pack must be considered if we are to make generalizations. For example, Potvin et al (2000) did not find a relationship between overall attendance and prey density but compared individuals from different packs of various composition. Only by increasing the sample size of such observations will we be able to tease out the relative importance of various factors on the behavioral patterns of individual wolves. This type of information, and specifically the roles played by auxiliaries of various ages, could have important management implications in areas where wolves prey on large ungulates and the removal of key individuals could affect both pack hunting behavior and the care of pups (Haber 1996).

2.7 Tables and Figures

Table 1. Mean times of attendance and absence (calculated using Survival Analysis) of the Malbaie pack between years (data from all individual wolves is combined excluding pups).

	Attendance		Absence	
Year	Mean duration (hrs)	N	Mean duration (hrs)	N
1996	10.9	87	19.9	79
1997	9.5	110	23.5	101
1998	14.8	53	41.5	49

Table 2. Proportion of time individual wolves present at densite (%) from 06/07 to 07/01.

	Year		
Wolf	1996	1997	1998
M450	26.1	25.1	13.5
F381	43.5	50.9	43.6
F470	30.7	15.9	32.4
F402	36.5	34.0	
F411	33.6	22.8	
F421	29.9		
F331		24.5	
F253		26.0	61.0*
F370		29.5	9.8
F180			43.8
F552			3.3

* Monitoring of F253 was stopped on 06/15 due to collision with car in 1998. Her attendance during the equivalent period in 1997 was 32%.

Table 3. Mean duration of attendance in hours (calculated using Survival Analysis) at the densite for individual wolves.

	Year		
Wolf	1996	1997	1998
M450	8.5	8.0	11.0
F381	11.5	13.9	10.0
F470	14.5	7.2	15.8
F402	9.7	12.2	
F411	11.2	9.8	
F421	11.5		
F331		8.1	
F253		7.1	21.5
F370		8.5	7.0
F180			23.0
F552			*

* insufficient data for analysis

Table 4. Frequency of group sizes for arrivals and departures of individual wolves in a) 1996, b) 1997, and c) 1998.

a) 1996

	Arrivals				Departures			
Wolf	% Alone	% with 1 other wolf	% with more than 1 wolf	N	% Alone	% with 1 other wolf	% with more than 1 wolf	N
M450	44.1	41.2	14.7	34	27.8	30.6	41.7	36
F381	44.1	41.2	14.7	42	38.5	25.6	35.9	39
F470	56.0	24.0	20.0	25	28.0	36.0	36.0	25
F402	61.9	21.4	16.7	42	38.5	23.1	38.5	39
F411	60.0	10.0	30.0	30	42.4	21.2	36.4	33
F421	78.8	9.1	12.1	33	42.4	24.2	33.3	33

b) 1997

	Arrivals				Departures			
Wolf	% Alone	% with 1 other wolf	% with more than 1 wolf	N	% Alone	% with 1 other wolf	% with more than 1 wolf	N
M450	58.3	25.0	16.7	24	45.8	25.0	29.2	24
F381	57.1	21.4	21.4	28	48.3	27.6	24.1	29
F470	65.0	15.0	20.0	20	57.9	15.8	26.3	19
F402	60.9	26.1	13.0	23	39.1	30.4	30.4	23
F411	63.2	15.8	21.1	19	30.0	45.0	25.0	20
F331	57.1	35.7	7.1	28	50.0	36.0	14.0	28
F253	50.0	32.1	17.9	28	40.0	36.0	24.0	25
F370	67.9	17.9	14.3	28	60.0	16.0	24.0	25

c) 1998

	Arrivals				Departures			
Wolf	% Alone	% with 1 other wolf	% with more than 1 wolf	N	% Alone	% with 1 other wolf	% with more than 1 wolf	N
M450	55.6	38.9	5.6	18	23.5	47.1	29.4	17
F381	63.6	27.3	9.1	22	50.0	25.0	25.0	24
F470	62.5	33.3	4.2	24	47.8	26.1	26.1	23
F370	66.7	20.0	13.3	15	56.3	25.0	18.8	16
F253	60.0	33.3	6.7	15	42.9	21.4	35.7	14
F180	73.7	15.8	10.5	19	47.6	19.0	33.3	21
F552	81.8	18.2	0.0	11	66.7	8.3	25.0	12

Table 5. Regression results on the three-day moving average of daily attendance of individual wolves in a) 1996, b) 1997, and c) 1998.

a) 1996

Wolf	Slope	R^2	F	P
M450	-0.40	0.28	22.35	0.00
F381	-0.06	0.00	0.21	0.65
F470	-0.48	0.22	16.46	0.00
F402	-0.72	0.42	43.28	0.00
F411	-0.52	0.41	40.96	0.00
F421	-0.28	0.13	9.12	0.00

b) 1997

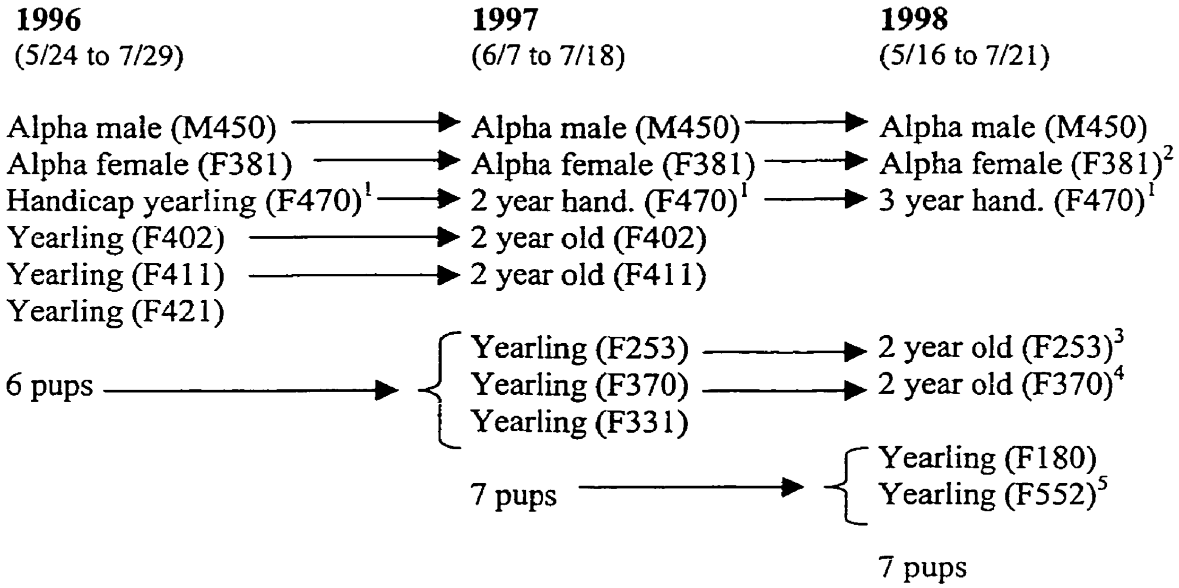
Wolf	Slope	R^2	F	P
M450	-0.70	0.16	7.03	0.01
F381	-0.65	0.19	8.25	0.01
F470	-0.43	0.17	7.59	0.01
F402	-1.03	0.60	53.44	0.00
F411	-0.59	0.43	26.89	0.00
F253	0.35	0.10	3.81	0.06
F370	-0.57	0.12	4.72	0.04
F331	-0.78	0.29	14.46	0.00

c) 1998

Wolf	Slope	R^2	F	P
M450	-0.22	0.07	4.48	0.04
F381*	-0.70	0.24	13.77	0.00
F470	-0.82	0.48	56.33	0.00
F253*	-0.15	0.00	0.13	0.72
F370	-0.33	0.17	12.83	0.00
F180	-1.13	0.48	58.12	0.00
F552	-0.40	0.18	13.33	0.00

* reduced data set due to death of wolf

Figure 1. Malbaie pack structure and duration of monitoring from 1996 to 1998.



[1] had one foot missing, probably from being caught in a snare

[2] died on 7/1/98 from collision with a car

[3] died on 6/15/98 from collision with a car

[4] had a fractured femur during the winter of 1997/98 and spent most of the winter away from the rest of the pack until the spring of 1998.

[5] dispersed from pack shortly after denning season.

Figure 2. Frequency of different group sizes (1-4 wolves not including pups) at the Malbaie densite from 06/07 to 07/01 in 1996 (a), 1997 (b), and 1998 (c).

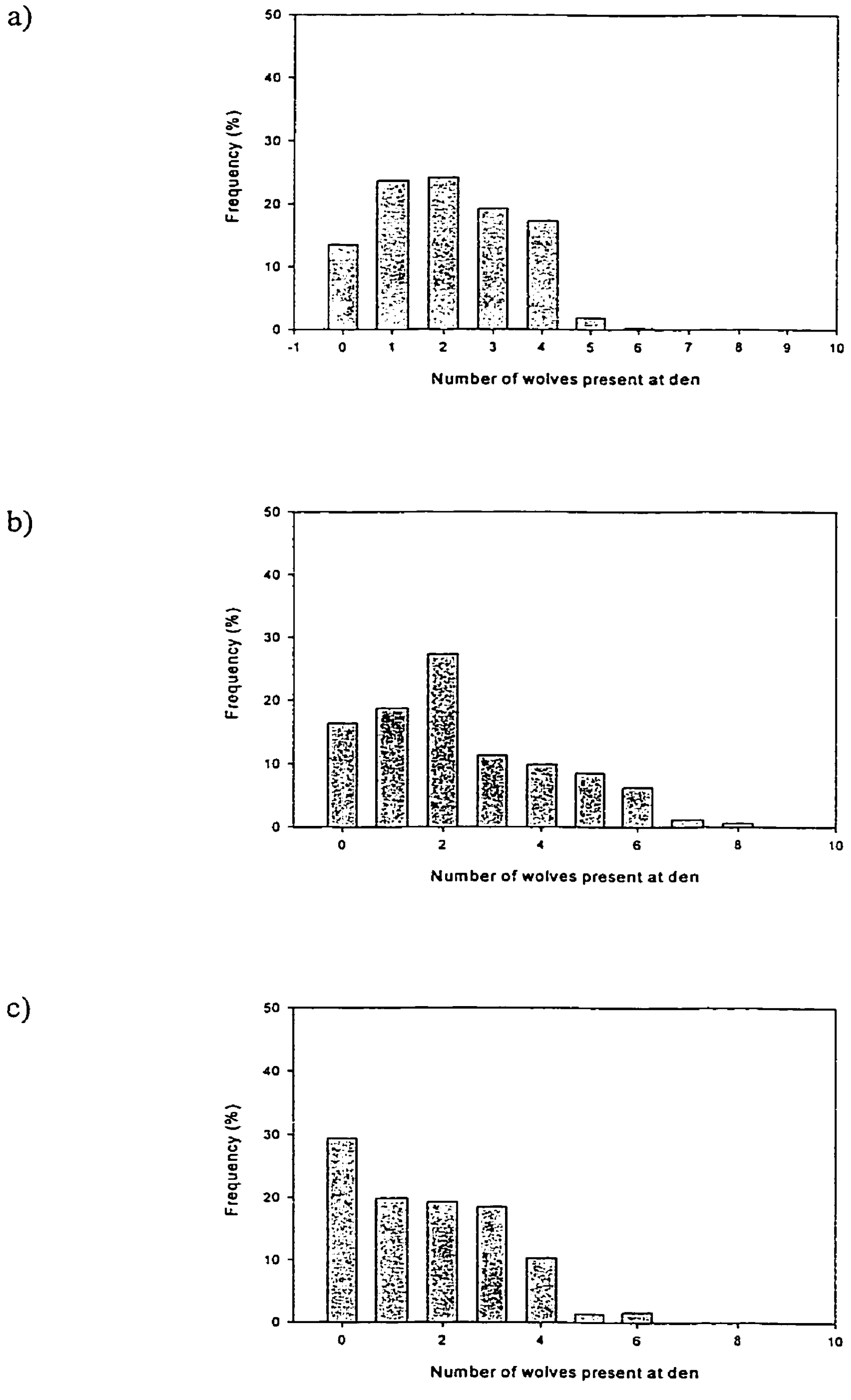


Figure 3. Frequency of more than two wolves present at the den as a function of the time of day from 1996 to 1998.

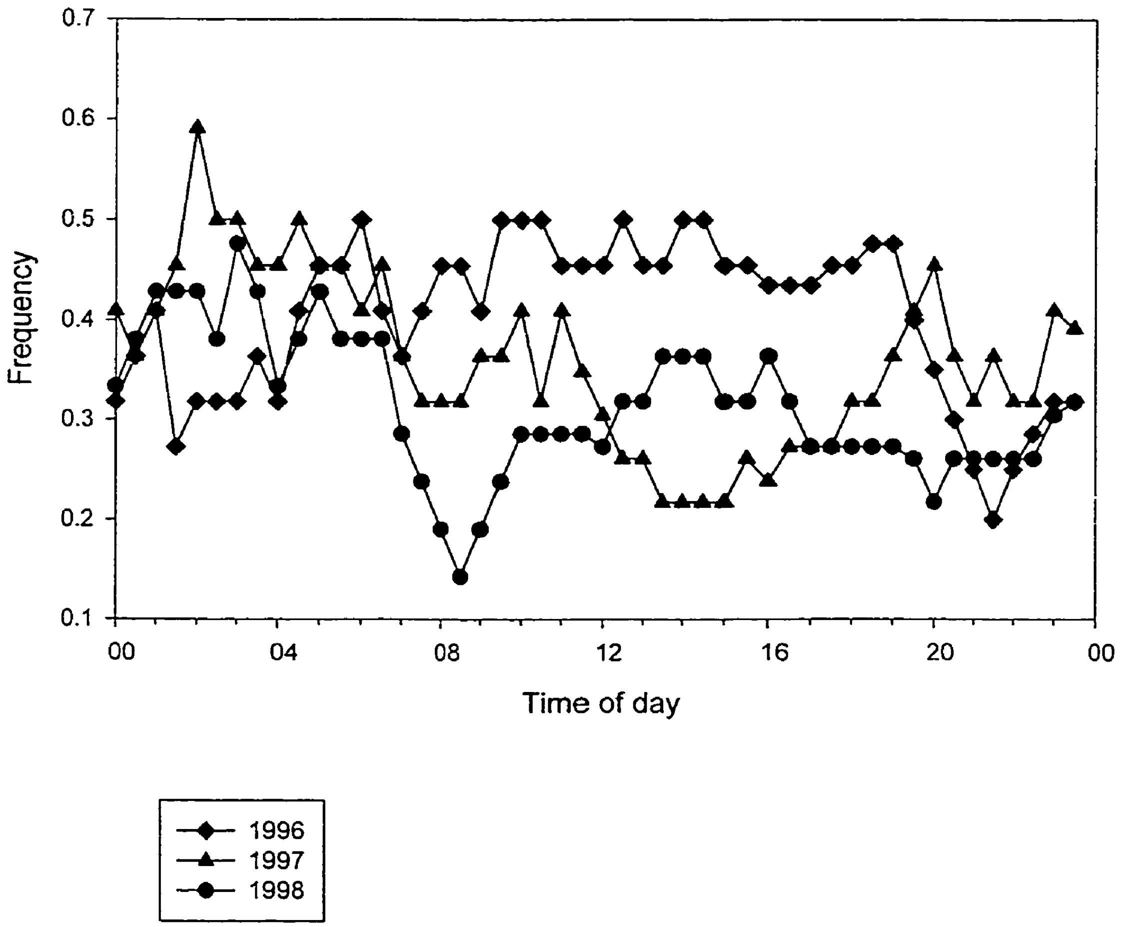
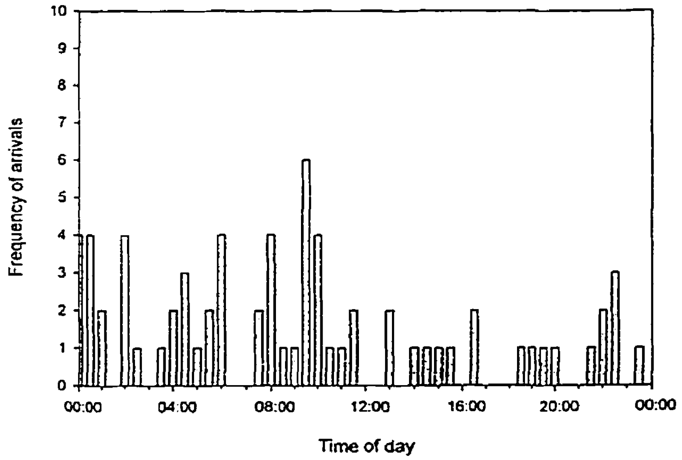
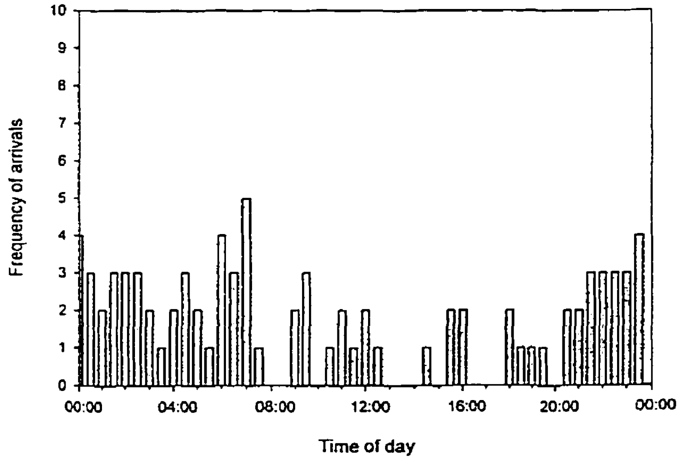


Figure 4. Distribution of 1) arrival times and 2) departure times of groups of wolves at the densite in a) 1996, b) 1997, and c) 1998 (all data used). Wolves were considered to be a group when arrivals were within 30 minutes of one another.

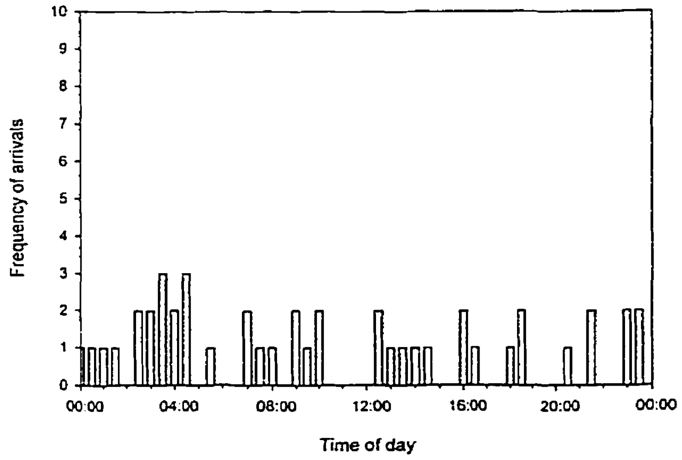
1a) Distribution of arrival times of groups of wolves in 1996



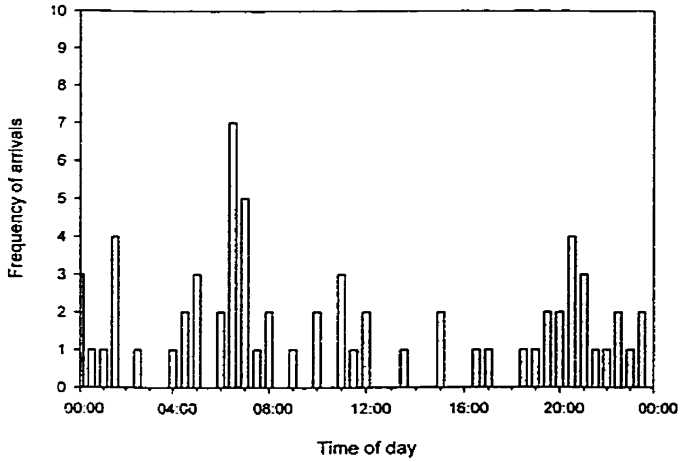
1b) Distribution of arrival times of groups of wolves in 1997



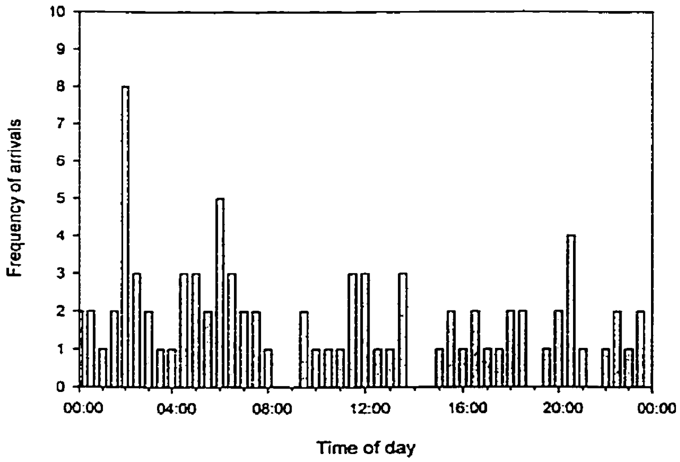
1c) Distribution of arrival times of groups of wolves in 1998



2a) Distribution of departure times of groups of wolves in 1996



2b) Distribution of departure times of groups of wolves in 1997



2c) Distribution of departure times of groups of wolves in 1998

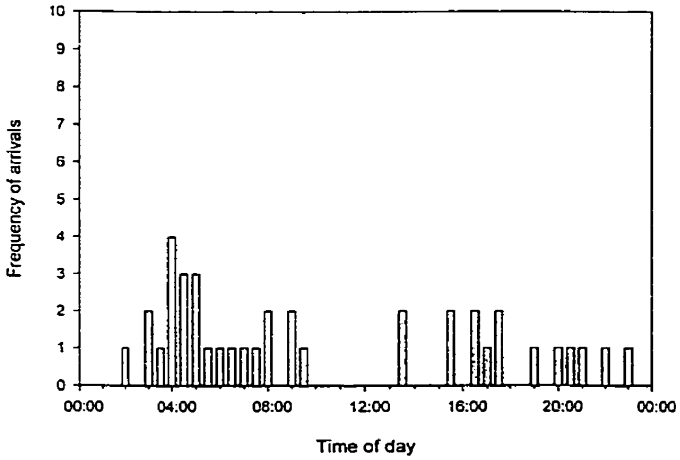
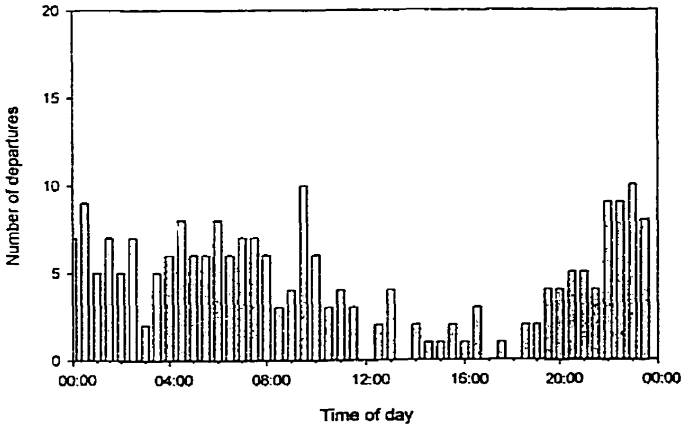
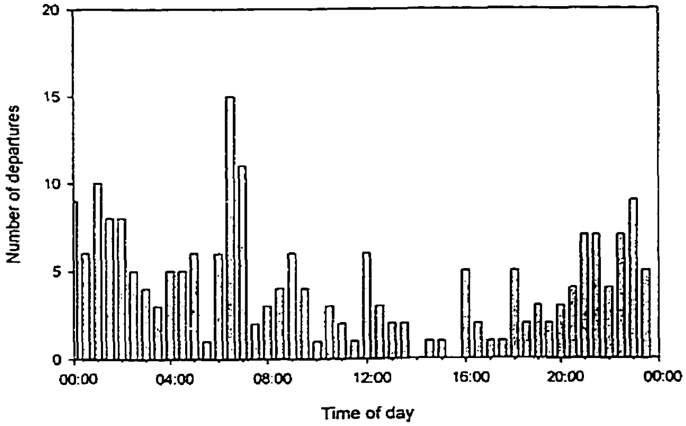


Figure 5. Distribution of 1) arrival times and 2) departure times of individual wolves at the densite in a) 1996, b) 1997, and c) 1998 (all data used).

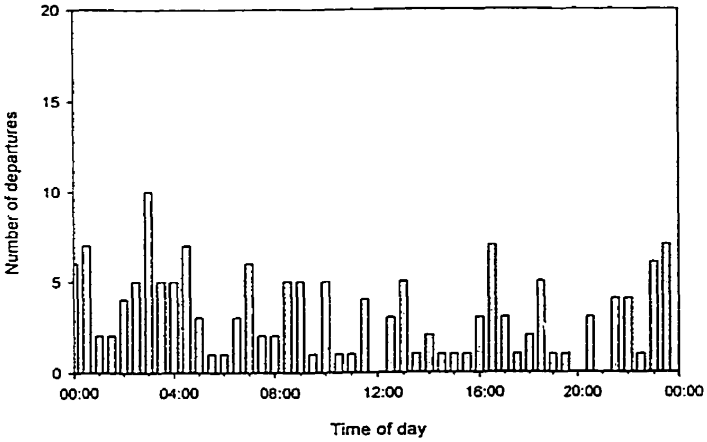
1a) Distribution of arrival times of individual wolves in 1996



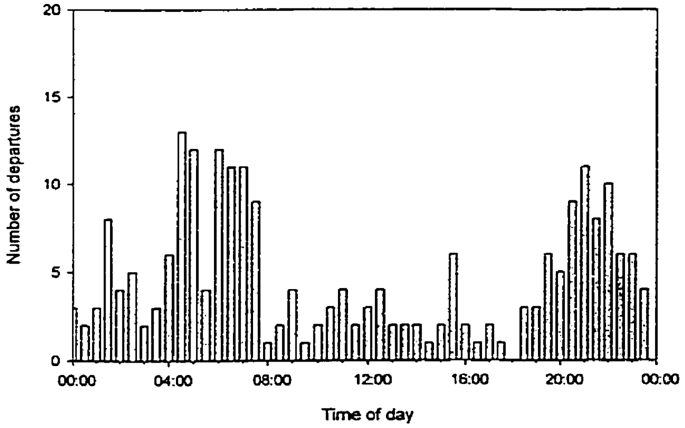
1b) Distribution of arrival times of individual wolves in 1997



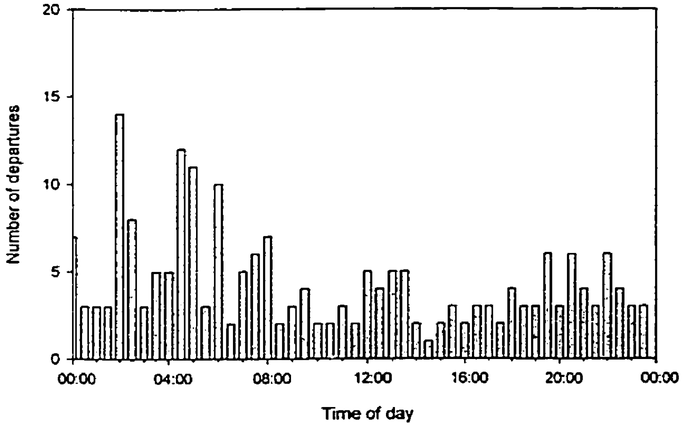
1c) Distribution of arrival times of individual wolves in 1998



2a) Distribution of departure times of individual wolves in 1996



2b) Distribution of departure times of individual wolves in 1997



2c) Distribution of departure times of individual wolves in 1998

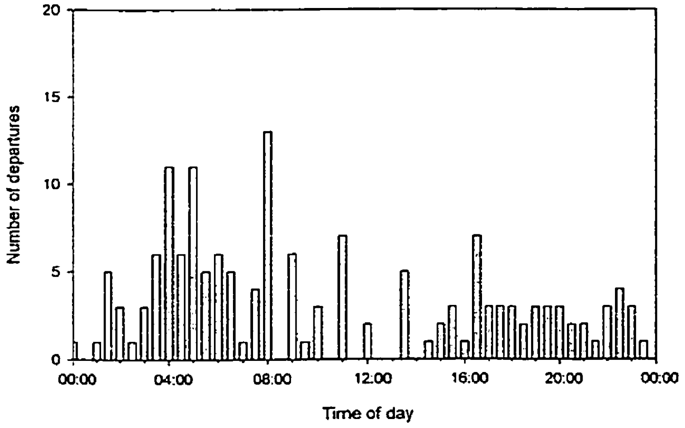
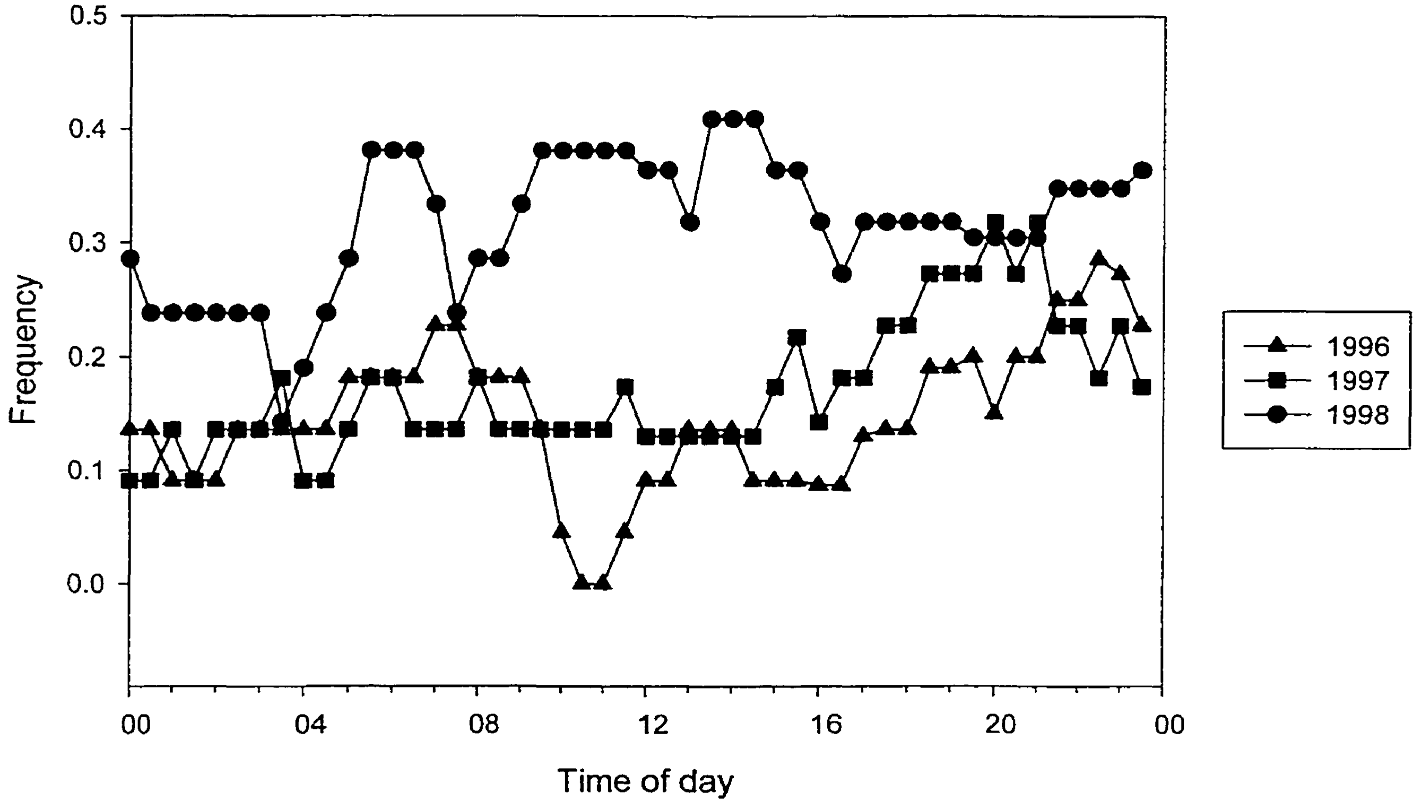


Figure 6. Frequency of Malbaie pack pups being left alone at the den as a function of the time of day from 1996 to 1998



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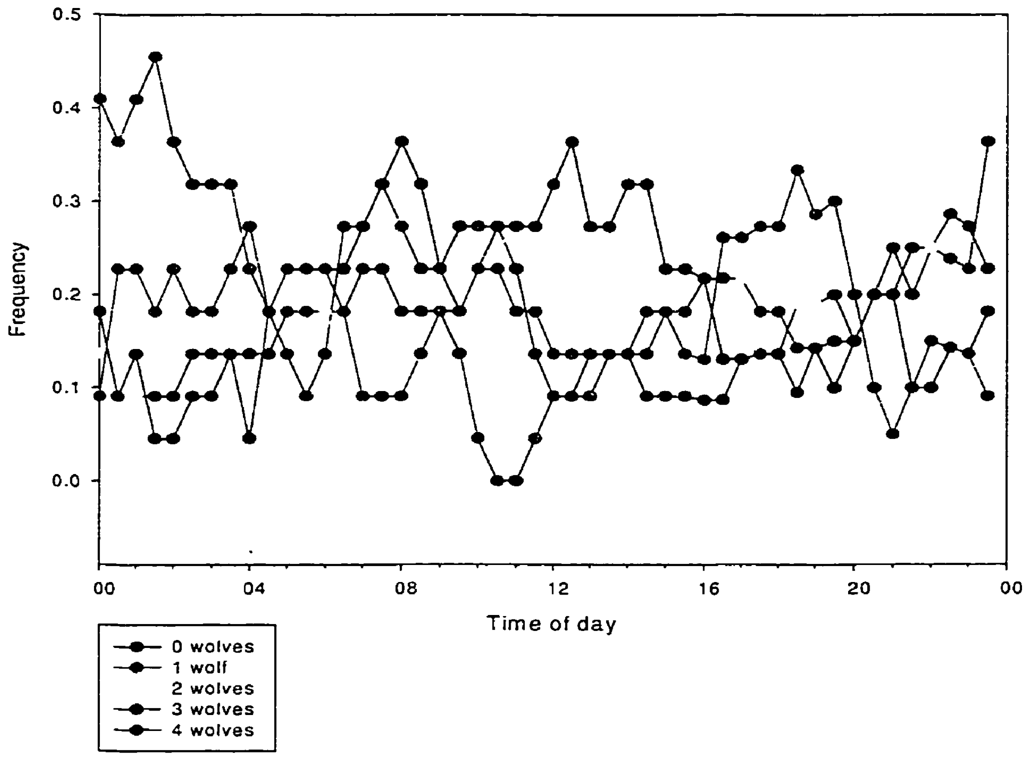
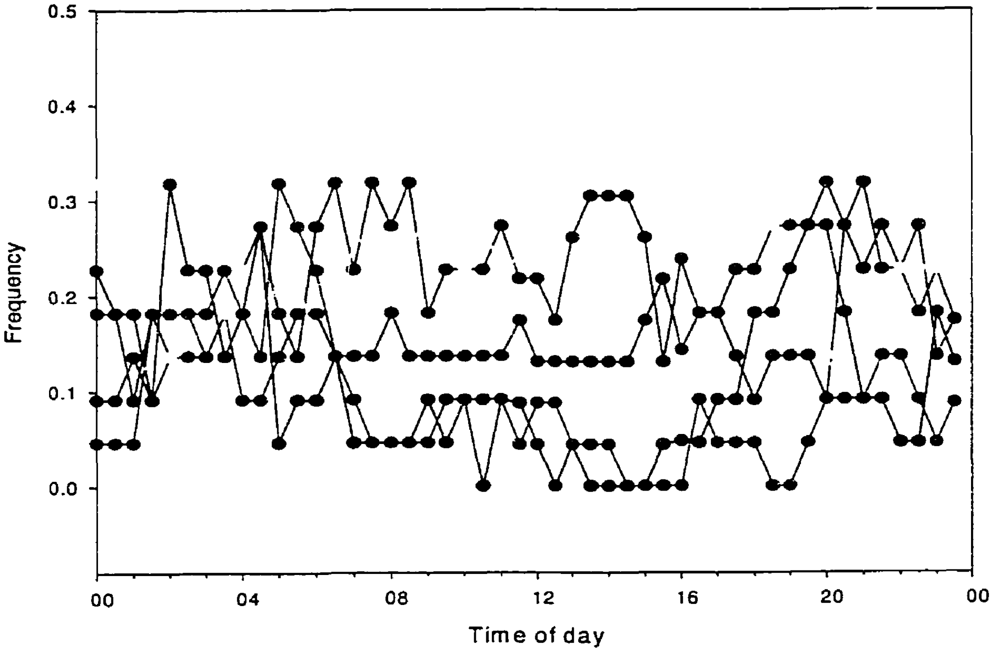
Appendix I

1) Figures of probabilities of finding different group sizes at the Malbaie densite at the half-hour throughout the day from 6/7 to 7/1 in a) 1996, b) 1997, and c) 1998.

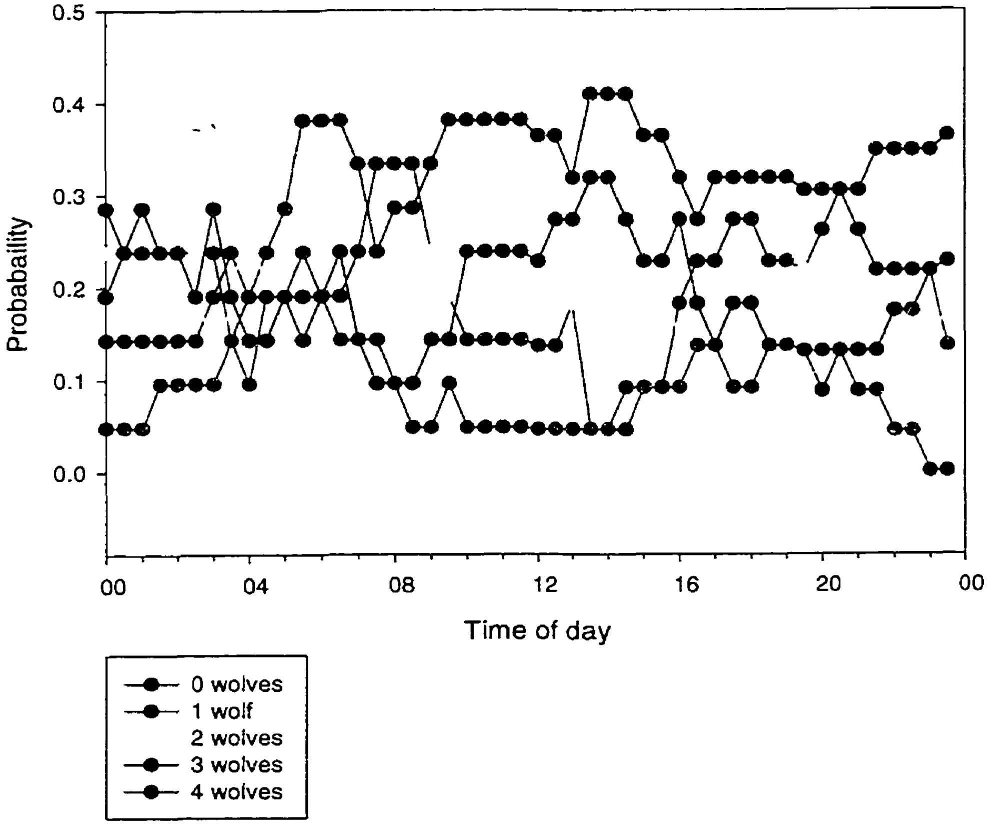
a)



b)


0.5
0.4
0.3
0.2
0.1
0.0
Frequency
00
04
08
12
16
20
00
Time of day

c)


0.5
0.4
0.3
0.2
0.1
0.0
Probability
00
04
08
12
16
20
00
Time of day
0 wolves
1 wolf
2 wolves
3 wolves
4 wolves

2) Table of probabilities of finding different group sizes at the Malbaie densite throughout the day from 6/7 to 7/1 in a) 1996, b) 1997, and c) 1998.

a)

Time	0 wolves	1 wolf	2 wolves	3 wolves	4 wolves	5 wolves	6 wolves
0:00	0.14	0.41	0.14	0.18	0.09	0.05	0.00
0:30	0.14	0.36	0.14	0.09	0.23	0.05	0.00
1:00	0.09	0.41	0.09	0.14	0.23	0.05	0.00
1:30	0.09	0.45	0.18	0.05	0.18	0.05	0.00
2:00	0.09	0.36	0.23	0.05	0.23	0.05	0.00
2:30	0.14	0.32	0.23	0.09	0.18	0.05	0.00
3:00	0.14	0.32	0.23	0.09	0.18	0.05	0.00
3:30	0.14	0.32	0.18	0.14	0.23	0.00	0.00
4:00	0.14	0.23	0.32	0.05	0.27	0.00	0.00
4:30	0.14	0.18	0.27	0.18	0.18	0.05	0.00
5:00	0.18	0.14	0.23	0.23	0.23	0.00	0.00
5:30	0.18	0.09	0.27	0.23	0.23	0.00	0.00
6:00	0.18	0.14	0.18	0.23	0.23	0.05	0.00
6:30	0.18	0.27	0.14	0.23	0.18	0.00	0.00
7:00	0.23	0.27	0.14	0.27	0.09	0.00	0.00
7:30	0.23	0.32	0.05	0.32	0.09	0.00	0.00
8:00	0.18	0.27	0.09	0.36	0.09	0.00	0.00
8:30	0.18	0.23	0.14	0.32	0.14	0.00	0.00
9:00	0.18	0.23	0.18	0.23	0.18	0.00	0.00
9:30	0.14	0.18	0.18	0.27	0.18	0.05	0.00
10:00	0.05	0.23	0.23	0.27	0.23	0.00	0.00
10:30	0.00	0.27	0.23	0.27	0.23	0.00	0.00
11:00	0.00	0.23	0.32	0.27	0.18	0.00	0.00
11:30	0.05	0.14	0.36	0.27	0.18	0.00	0.00
12:00	0.09	0.09	0.36	0.32	0.14	0.00	0.00
12:30	0.09	0.09	0.32	0.36	0.14	0.00	0.00
13:00	0.14	0.09	0.32	0.27	0.14	0.05	0.00
13:30	0.14	0.14	0.27	0.27	0.14	0.05	0.00
14:00	0.14	0.14	0.23	0.32	0.14	0.05	0.00
14:30	0.09	0.18	0.23	0.32	0.14	0.05	0.00
15:00	0.09	0.18	0.27	0.23	0.18	0.05	0.00
15:30	0.09	0.18	0.27	0.23	0.14	0.09	0.00
16:00	0.09	0.22	0.26	0.22	0.13	0.09	0.00
16:30	0.09	0.22	0.26	0.13	0.26	0.04	0.00
17:00	0.13	0.22	0.22	0.13	0.26	0.04	0.00
17:30	0.14	0.18	0.23	0.14	0.27	0.05	0.00
18:00	0.14	0.18	0.23	0.14	0.27	0.05	0.00
18:30	0.19	0.14	0.19	0.10	0.33	0.05	0.00
19:00	0.19	0.14	0.19	0.14	0.29	0.05	0.00
19:30	0.20	0.15	0.25	0.10	0.30	0.00	0.00
20:00	0.15	0.15	0.35	0.15	0.20	0.00	0.00
20:30	0.20	0.20	0.30	0.20	0.10	0.00	0.00
21:00	0.20	0.25	0.30	0.20	0.05	0.00	0.00
21:30	0.25	0.20	0.35	0.10	0.10	0.00	0.00
22:00	0.25	0.25	0.25	0.10	0.15	0.00	0.00
22:30	0.29	0.24	0.19	0.14	0.14	0.00	0.00
23:00	0.27	0.23	0.18	0.14	0.14	0.00	0.05
23:30	0.23	0.36	0.09	0.18	0.09	0.00	0.05

b)

Time	0 wolves	1 wolf	2 wolves	3 wolves	4 wolves	5 wolves	6 wolves	7 wolves	8 wolves
0:00	0.09	0.18	0.32	0.23	0.05	0.05	0.05	0.00	0.05
0:30	0.09	0.18	0.36	0.18	0.05	0.05	0.05	0.00	0.05
1:00	0.14	0.09	0.36	0.18	0.05	0.09	0.05	0.00	0.05
1:30	0.09	0.18	0.27	0.09	0.18	0.14	0.00	0.00	0.05
2:00	0.14	0.14	0.14	0.32	0.18	0.09	0.00	0.00	0.00
2:30	0.14	0.18	0.18	0.23	0.18	0.09	0.00	0.00	0.00
3:00	0.14	0.14	0.23	0.23	0.18	0.09	0.00	0.00	0.00
3:30	0.18	0.18	0.18	0.14	0.23	0.09	0.00	0.00	0.00
4:00	0.09	0.23	0.23	0.18	0.18	0.09	0.00	0.00	0.00
4:30	0.09	0.27	0.14	0.27	0.14	0.09	0.00	0.00	0.00
5:00	0.14	0.18	0.23	0.05	0.32	0.09	0.00	0.00	0.00
5:30	0.18	0.14	0.23	0.09	0.27	0.09	0.00	0.00	0.00
6:00	0.18	0.27	0.14	0.09	0.23	0.05	0.05	0.00	0.00
6:30	0.14	0.32	0.09	0.14	0.14	0.14	0.05	0.00	0.00
7:00	0.14	0.23	0.27	0.05	0.09	0.14	0.09	0.00	0.00
7:30	0.14	0.32	0.23	0.05	0.05	0.09	0.14	0.00	0.00
8:00	0.18	0.27	0.23	0.05	0.05	0.09	0.14	0.00	0.00
8:30	0.14	0.32	0.23	0.05	0.05	0.09	0.14	0.00	0.00
9:00	0.14	0.18	0.32	0.09	0.05	0.09	0.14	0.00	0.00
9:30	0.14	0.23	0.27	0.05	0.09	0.09	0.14	0.00	0.00
10:00	0.14	0.23	0.23	0.09	0.09	0.09	0.14	0.00	0.00
10:30	0.14	0.23	0.32	0.00	0.09	0.09	0.14	0.00	0.00
11:00	0.14	0.27	0.18	0.09	0.09	0.09	0.09	0.05	0.00
11:30	0.17	0.22	0.26	0.09	0.04	0.09	0.09	0.04	0.00
12:00	0.13	0.22	0.35	0.04	0.09	0.09	0.04	0.04	0.00
12:30	0.13	0.17	0.43	0.00	0.09	0.04	0.09	0.04	0.00
13:00	0.13	0.26	0.35	0.04	0.04	0.04	0.09	0.04	0.00
13:30	0.13	0.30	0.35	0.00	0.04	0.09	0.09	0.00	0.00
14:00	0.13	0.30	0.35	0.00	0.04	0.09	0.04	0.04	0.00
14:30	0.13	0.30	0.35	0.00	0.00	0.13	0.04	0.04	0.00
15:00	0.17	0.26	0.35	0.00	0.00	0.13	0.09	0.00	0.00
15:30	0.22	0.13	0.39	0.04	0.00	0.17	0.04	0.00	0.00
16:00	0.14	0.24	0.38	0.05	0.00	0.14	0.05	0.00	0.00
16:30	0.18	0.18	0.36	0.05	0.09	0.09	0.05	0.00	0.00
17:00	0.18	0.18	0.36	0.09	0.05	0.09	0.05	0.00	0.00
17:30	0.23	0.14	0.36	0.09	0.05	0.09	0.05	0.00	0.00
18:00	0.23	0.09	0.36	0.18	0.05	0.05	0.05	0.00	0.00
18:30	0.27	0.14	0.27	0.18	0.00	0.09	0.05	0.00	0.00
19:00	0.27	0.14	0.23	0.23	0.00	0.09	0.05	0.00	0.00
19:30	0.27	0.14	0.18	0.27	0.05	0.05	0.05	0.00	0.00
20:00	0.32	0.09	0.14	0.27	0.09	0.05	0.05	0.00	0.00
20:30	0.27	0.27	0.09	0.18	0.09	0.00	0.09	0.00	0.00
21:00	0.32	0.23	0.14	0.09	0.09	0.05	0.05	0.05	0.00
21:30	0.23	0.27	0.14	0.09	0.14	0.05	0.05	0.05	0.00
22:00	0.23	0.23	0.23	0.05	0.14	0.00	0.09	0.05	0.00
22:30	0.18	0.27	0.23	0.05	0.09	0.05	0.09	0.05	0.00
23:00	0.23	0.14	0.23	0.18	0.05	0.05	0.09	0.00	0.05
23:30	0.17	0.17	0.26	0.13	0.09	0.04	0.09	0.00	0.04

c)

Time	0 wolves	1 wolf	2 wolves	3 wolves	4 wolves	5 wolves	6 wolves	7 wolves
0:00	0.29	0.14	0.24	0.19	0.05	0.05	0.05	0.00
0:30	0.24	0.14	0.24	0.24	0.05	0.05	0.05	0.00
1:00	0.24	0.14	0.19	0.29	0.05	0.05	0.05	0.00
1:30	0.24	0.14	0.19	0.24	0.10	0.05	0.05	0.00
2:00	0.24	0.14	0.19	0.24	0.10	0.05	0.05	0.00
2:30	0.24	0.14	0.24	0.19	0.10	0.05	0.05	0.00
3:00	0.24	0.19	0.10	0.29	0.10	0.05	0.05	0.00
3:30	0.14	0.24	0.19	0.19	0.14	0.05	0.05	0.00
4:00	0.19	0.19	0.29	0.14	0.10	0.05	0.05	0.00
4:30	0.24	0.19	0.19	0.14	0.19	0.00	0.05	0.00
5:00	0.29	0.19	0.10	0.19	0.19	0.00	0.05	0.00
5:30	0.38	0.19	0.05	0.14	0.24	0.00	0.00	0.00
6:00	0.38	0.19	0.05	0.19	0.19	0.00	0.00	0.00
6:30	0.38	0.19	0.05	0.24	0.14	0.00	0.00	0.00
7:00	0.33	0.24	0.14	0.14	0.14	0.00	0.00	0.00
7:30	0.24	0.33	0.19	0.10	0.14	0.00	0.00	0.00
8:00	0.29	0.33	0.19	0.10	0.10	0.00	0.00	0.00
8:30	0.29	0.33	0.24	0.10	0.05	0.00	0.00	0.00
9:00	0.33	0.24	0.24	0.14	0.05	0.00	0.00	0.00
9:30	0.38	0.19	0.19	0.14	0.10	0.00	0.00	0.00
10:00	0.38	0.14	0.19	0.24	0.05	0.00	0.00	0.00
10:30	0.38	0.14	0.19	0.24	0.05	0.00	0.00	0.00
11:00	0.38	0.14	0.19	0.24	0.05	0.00	0.00	0.00
11:30	0.38	0.14	0.19	0.24	0.05	0.00	0.00	0.00
12:00	0.36	0.14	0.23	0.23	0.05	0.00	0.00	0.00
12:30	0.36	0.14	0.18	0.27	0.05	0.00	0.00	0.00
13:00	0.32	0.18	0.18	0.27	0.05	0.00	0.00	0.00
13:30	0.41	0.05	0.18	0.32	0.05	0.00	0.00	0.00
14:00	0.41	0.05	0.18	0.32	0.05	0.00	0.00	0.00
14:30	0.41	0.05	0.18	0.27	0.09	0.00	0.00	0.00
15:00	0.36	0.09	0.23	0.23	0.09	0.00	0.00	0.00
15:30	0.36	0.09	0.23	0.23	0.09	0.00	0.00	0.00
16:00	0.32	0.18	0.14	0.27	0.09	0.00	0.00	0.00
16:30	0.27	0.23	0.18	0.18	0.14	0.00	0.00	0.00
17:00	0.32	0.23	0.18	0.14	0.14	0.00	0.00	0.00
17:30	0.32	0.27	0.14	0.18	0.09	0.00	0.00	0.00
18:00	0.32	0.27	0.14	0.18	0.09	0.00	0.00	0.00
18:30	0.32	0.23	0.18	0.14	0.14	0.00	0.00	0.00
19:00	0.32	0.23	0.18	0.14	0.14	0.00	0.00	0.00
19:30	0.30	0.22	0.22	0.13	0.13	0.00	0.00	0.00
20:00	0.30	0.26	0.22	0.09	0.13	0.00	0.00	0.00
20:30	0.30	0.30	0.13	0.13	0.13	0.00	0.00	0.00
21:00	0.30	0.26	0.17	0.13	0.09	0.04	0.00	0.00
21:30	0.35	0.22	0.17	0.13	0.09	0.04	0.00	0.00
22:00	0.35	0.22	0.17	0.17	0.04	0.00	0.04	0.00
22:30	0.35	0.22	0.17	0.17	0.04	0.00	0.04	0.00
23:00	0.35	0.22	0.13	0.22	0.00	0.04	0.04	0.00
23:30	0.36	0.14	0.18	0.23	0.00	0.05	0.05	0.00

Appendix II

Details of arrivals, departures, and durations of bouts of attendance and absence for individual wolves at rendezvous sites in a) 1996, b) 1997, and c) 1998. (Bouts with missing data are omitted)

a)

Alpha male (M450)				Alpha female (F381)			
Status	Date and time	Duration of attendance	Duration of absence	Status	Date and time	Duration of attendance	Duration of absence
Arrival	5/25/96 4:30	17:00:00		Arrival	5/24/96 22:00	6:30:00	
Departure	5/25/96 21:30		10:00:00	Departure	5/25/96 4:30		8:00:00
Arrival	5/26/96 7:30	11:00:00		Arrival	5/25/96 12:30	15:30:00	
Departure	5/26/96 18:30		9:00:00	Departure	5/26/96 4:00		3:00:00
Arrival	5/27/96 3:30	18:30:00		Arrival	5/26/96 7:00	25:30:00	
Departure	5/27/96 22:00			Departure	5/27/96 8:30		14:00:00
Departure	5/29/96 16:30		4:00:00	Arrival	5/27/96 22:30		
Arrival	5/29/96 20:30	2:30:00		Arrival	5/30/96 5:00	2:00:00	
Departure	5/29/96 23:00		30:30:00	Departure	5/30/96 7:00		18:30:00
Arrival	5/31/96 5:30	15:30:00		Arrival	5/31/96 1:30	12:30:00	
Departure	5/31/96 21:00		32:00:00	Departure	5/31/96 14:00		19:30:00
Arrival	6/2/96 5:00	17:00:00		Arrival	6/1/96 9:30	15:00:00	
Departure	6/2/96 22:00		13:30:00	Departure	6/2/96 0:30		26:00:00
Arrival	6/3/96 11:30	11:30:00		Arrival	6/3/96 2:30	2:30:00	
Departure	6/3/96 23:00		28:00:00	Departure	6/3/96 5:00		22:30:00
Arrival	6/5/96 3:00	19:00:00		Arrival	6/4/96 3:30	17:30:00	
Departure	6/5/96 22:00		48:30:00	Departure	6/4/96 21:00		13:00:00
Arrival	6/7/96 22:30	4:00:00		Arrival	6/5/96 10:00	11:30:00	
Departure	6/8/96 2:30		17:30:00	Departure	6/5/96 21:30		26:00:00
Arrival	6/8/96 20:00	2:30:00		Arrival	6/6/96 23:30	17:00:00	
Departure	6/8/96 22:30		34:30:00	Departure	6/7/96 16:30		5:00:00
Arrival	6/10/96 9:00	10:00:00		Arrival	6/7/96 21:30	5:00:00	
Departure	6/10/96 19:00		34:30:00	Departure	6/8/96 2:30		7:00:00
Arrival	6/12/96 5:30	4:30:00		Arrival	6/8/96 9:30	2:30:00	
Departure	6/12/96 10:00		5:30:00	Departure	6/8/96 12:00		8:00:00
Arrival	6/12/96 15:30	13:00:00		Arrival	6/8/96 20:00	5:30:00	
Departure	6/13/96 4:30			Departure	6/9/96 1:30		31:00:00
Arrival	6/14/96 6:00	15:00:00		Arrival	6/10/96 8:30	12:00:00	
Departure	6/14/96 21:00		25:00:00	Departure	6/10/96 20:30		13:00:00
Arrival	6/15/96 22:00	9:00:00		Arrival	6/11/96 9:30	10:00:00	
Departure	6/16/96 7:00		2:30:00	Departure	6/11/96 19:30		13:30:00
Arrival	6/16/96 9:30	2:30:00		Arrival	6/12/96 9:00		
Departure	6/16/96 12:00		6:30:00	Arrival	6/14/96 6:00	15:30:00	
Arrival	6/16/96 18:30	6:00:00		Departure	6/14/96 21:30		33:30:00
Departure	6/17/96 0:30		55:30:01	Arrival	6/16/96 7:00	14:00:00	
Arrival	6/19/96 8:00	15:30:00		Departure	6/16/96 21:00		9:00:00
Departure	6/19/96 23:30		49:00:00	Arrival	6/17/96 6:00	16:30:00	

a) (cont.)

Alpha male (M450) (cont.)				Alpha female (F381) (cont.)			
Status	Date and time	Duration of attendance	Duration of absence	Status	Date and time	Duration of attendance	Duration of absence
Arrival	6/22/96 0:30	1:00:00		Departure	6/17/96 22:30		25:30:00
Departure	6/22/96 1:30		2:30:00	Arrival	6/19/96 0:00	19:30:00	
Arrival	6/22/96 4:00	3:00:00		Departure	6/19/96 19:30		2:30:00
Departure	6/22/96 7:00		5:30:00	Arrival	6/19/96 22:00	2:00:00	
Arrival	6/22/96 12:30	11:00:00		Departure	6/20/96 0:00		6:00:00
Departure	6/22/96 23:30		8:00:00	Arrival	6/20/96 6:00	14:30:00	
Arrival	6/23/96 7:30	9:30:00		Departure	6/20/96 20:30		7:30:00
Departure	6/23/96 17:00		17:00:00	Arrival	6/21/96 4:00	24:00:00	
Arrival	6/24/96 10:00	12:00:00		Departure	6/22/96 4:00		27:30:00
Departure	6/24/96 22:00		17:00:00	Arrival	6/23/96 7:30	4:00:00	
Arrival	6/25/96 15:00	8:30:00		Departure	6/23/96 11:30		34:30:00
Departure	6/25/96 23:30			Arrival	6/24/96 22:00	22:00:00	
Arrival	6/29/96 3:30	2:30:00		Departure	6/25/96 20:00		
Departure	6/29/96 6:00		4:00:00	Arrival	6/29/96 0:00	6:00:00	
Arrival	6/29/96 10:00			Departure	6/29/96 6:00		5:00:00
Arrival	7/1/96 2:00	19:00:00		Arrival	6/29/96 11:00		
Departure	7/1/96 21:00		26:30:00	Departure	7/1/96 23:00		3:30:00
Arrival	7/2/96 23:30	6:30:00		Arrival	7/2/96 2:30	2:30:00	
Departure	7/3/96 6:00			Departure	7/2/96 5:00		3:30:00
Arrival	7/8/96 22:00	4:30:00		Arrival	7/2/96 8:30	21:30:00	
Departure	7/9/96 2:30			Departure	7/3/96 6:00		
Arrival	7/11/96 1:00	11:30:00		Arrival	7/4/96 20:30	7:30:00	
Departure	7/11/96 12:30		35:30:00	Departure	7/5/96 4:00		2:30:00
Arrival	7/13/96 0:00	7:00:00		Arrival	7/5/96 6:30		
Departure	7/13/96 7:00		40:30:00	Arrival	7/7/96 13:00	20:00:00	
Arrival	7/14/96 23:30	5:30:00		Departure	7/8/96 9:00		6:30:00
Departure	7/15/96 5:00		41:30:00	Arrival	7/8/96 15:30	10:30:00	
Arrival	7/16/96 22:30	10:30:00		Departure	7/9/96 2:00		4:30:00
Departure	7/17/96 9:00		12:00:00	Arrival	7/9/96 6:30		
Arrival	7/17/96 21:00	4:30:00		Arrival	7/11/96 1:30	17:30:00	
Departure	7/18/96 1:30		38:30:00	Departure	7/11/96 19:00		4:30:00
Arrival	7/19/96 16:00	6:00:00		Arrival	7/11/96 23:30	20:30:00	
Departure	7/19/96 22:00		6:30:00	Departure	7/12/96 20:00		34:30:00
Arrival	7/20/96 4:30	3:00:00		Arrival	7/14/96 6:30	17:30:00	
Departure	7/20/96 7:30			Departure	7/15/96 0:00		34:00:00
Departure	7/21/96 23:00		23:00:00	Arrival	7/16/96 10:00	40:00:00	
Arrival	7/22/96 22:00	7:30:00		Departure	7/18/96 2:00		
Departure	7/23/96 5:30		43:30:00	Arrival	7/21/96 23:00	7:00:00	
Arrival	7/25/96 1:00	14:30:00		Departure	7/22/96 6:00		16:00:00
Departure	7/25/96 15:30		5:30:00	Arrival	7/22/96 22:00	7:30:00	
Arrival	7/25/96 21:00	2:00:00		Departure	7/23/96 5:30		#VALUE!
Departure	7/25/96 23:00			Arrival	7/25/1996 8:0+C	#VALUE!	
				Departure	7/25/96 22:30		6:30:00
				Arrival	7/26/96 5:00	15:30:00	
				Departure	7/26/96 20:30		60:30:01
				Arrival	7/29/96 9:00	10:00:00	
				Departure	7/29/96 19:00		

a) (cont.)

Yearling F402				Yearling 470			
Status	Date and time	Duration of attendance	Duration of absence	Status	Date and time	Duration of attendance	Duration of absence
Arrival	5/25/96 1:30	20:00:00		Arrival	5/27/96 1:00	21:30:00	
Departure	5/25/96 21:30		5:00:00	Departure	5/27/96 22:30		42:00:00
Arrival	5/26/96 2:30	2:00:00		Arrival	5/29/96 16:30	4:00:00	
Departure	5/26/96 4:30		3:00:00	Departure	5/29/96 20:30		13:00:00
Arrival	5/26/96 7:30	11:00:00		Arrival	5/30/96 9:30	15:30:00	
Departure	5/26/96 18:30		11:30:00	Departure	5/31/96 1:00		25:30:00
Arrival	5/27/96 6:00	16:00:00		Arrival	6/1/96 2:30	22:30:00	
Departure	5/27/96 22:00		49:00:00	Departure	6/2/96 1:00		121:30:01
Arrival	5/29/96 23:00	5:30:00		Arrival	6/7/96 2:30	24:00:00	
Departure	5/30/96 4:30		19:30:00	Departure	6/8/96 2:30		22:30:00
Arrival	5/31/96 0:00	7:30:00		Arrival	6/9/96 1:00	24:30:00	
Departure	5/31/96 7:30		3:30:00	Departure	6/10/96 1:30		52:30:01
Arrival	5/31/96 11:00	10:00:00		Arrival	6/12/96 6:00	21:30:00	
Departure	5/31/96 21:00		26:30:00	Departure	6/13/96 3:30		
Arrival	6/1/96 23:30	70:00:01		Arrival	6/15/96 9:30	21:30:00	
Departure	6/4/96 21:30		9:30:00	Departure	6/16/96 7:00		3:00:00
Arrival	6/5/96 7:00	15:00:00		Arrival	6/16/96 10:00	9:30:00	
Departure	6/5/96 22:00		28:00:00	Departure	6/16/96 19:30		58:00:01
Arrival	6/7/96 2:00	4:30:00		Arrival	6/19/96 5:30	1:00:00	
Departure	6/7/96 6:30		6:30:00	Departure	6/19/96 6:30		26:00:00
Arrival	6/7/96 13:00	13:30:00		Arrival	6/20/96 8:30	12:00:00	
Departure	6/8/96 2:30		17:30:00	Departure	6/20/96 20:30		8:00:00
Arrival	6/8/96 20:00	8:00:00		Arrival	6/21/96 4:30	21:00:00	
Departure	6/9/96 4:00		28:00:00	Departure	6/22/96 1:30		3:30:00
Arrival	6/10/96 8:00	21:00:00		Arrival	6/22/96 5:00	1:30:00	
Departure	6/11/96 5:00		23:30:00	Departure	6/22/96 6:30		5:00:00
Arrival	6/12/96 4:30	2:30:00		Arrival	6/22/96 11:30	18:30:00	
Departure	6/12/96 7:00		2:30:00	Departure	6/23/96 6:00		67:00:01
Arrival	6/12/96 9:30			Arrival	6/26/96 1:00		
Arrival	6/14/96 2:30	4:00:00		Arrival	7/1/96 6:00	4:00:00	
Departure	6/14/96 6:30		21:30:00	Departure	7/1/96 10:00		43:30:00
Arrival	6/15/96 4:00	5:00:00		Arrival	7/3/96 5:30		
Departure	6/15/96 9:00		5:00:00	Departure	7/5/96 3:30		
Arrival	6/15/96 14:00	17:00:00		Arrival	7/6/96 20:30	5:00:00	
Departure	6/16/96 7:00		2:30:00	Departure	7/7/96 1:30		
Arrival	6/16/96 9:30	5:30:00		Arrival	7/12/96 23:00	8:00:00	
Departure	6/16/96 15:00		3:30:00	Departure	7/13/96 7:00		94:00:01

a) (cont.)

Yearling F402 (cont.)

Status	Date and time	Duration of attendance	Duration of absence
Arrival	6/16/96 18:30	3:00:00	
Departure	6/16/96 21:30		22:00:00
Arrival	6/17/96 19:30	15:30:00	
Departure	6/18/96 11:00		37:30:00
Arrival	6/20/96 0:30	7:00:00	
Departure	6/20/96 7:30		21:00:00
Arrival	6/21/96 4:30	6:30:00	
Departure	6/21/96 11:00		5:30:00
Arrival	6/21/96 16:30	3:30:00	
Departure	6/21/96 20:00		28:30:00
Arrival	6/23/96 0:30	16:30:00	
Departure	6/23/96 17:00		31:30:00
Arrival	6/25/96 0:30	23:00:00	
Departure	6/25/96 23:30		
Arrival	6/29/96 0:30	5:00:00	
Departure	6/29/96 5:30		
Departure	6/30/96 21:00		9:30:00
Arrival	7/1/96 6:30	8:30:00	
Departure	7/1/96 15:00		4:00:00
Arrival	7/1/96 19:00	10:00:00	
Departure	7/2/96 5:00		20:30:00
Arrival	7/3/96 1:30	3:00:00	
Departure	7/3/96 4:30		
Departure	7/5/96 4:30		
Arrival	7/6/96 19:00	12:30:00	
Departure	7/7/96 7:30		45:00:00
Arrival	7/9/96 4:30		
Arrival	7/13/96 10:30	25:30:00	
Departure	7/14/96 12:00		13:00:00
Arrival	7/15/96 1:00	3:30:00	
Departure	7/15/96 4:30		109:00:01
Arrival	7/19/96 17:30	3:30:00	
Departure	7/19/96 21:00		23:30:00
Arrival	7/20/96 20:30	1:30:00	
Departure	7/20/96 22:00		7:30:00
Arrival	7/21/96 5:30		
Arrival	7/21/96 21:00	6:00:00	
Departure	7/22/96 3:00		19:30:00
Arrival	7/22/96 22:30	7:00:00	
Departure	7/23/96 5:30		17:00:00
Arrival	7/23/96 22:30	7:30:00	
Departure	7/24/96 6:00		17:00:00
Arrival	7/24/96 23:00	16:30:00	
Departure	7/25/96 15:30		16:00:00
Arrival	7/26/96 7:30	6:30:00	
Departure	7/26/96 14:00		

Yearling 470 (cont.)

Status	Date and time	Duration of attendance	Duration of absence
Arrival	7/17/96 5:00	3:30:00	
Departure	7/17/96 8:30		13:00:00
Arrival	7/17/96 21:30	4:00:00	
Departure	7/18/96 1:30		52:00:01
Arrival	7/20/96 5:30	2:00:00	
Departure	7/20/96 7:30		3:00:00
Arrival	7/20/96 10:30	4:00:00	
Departure	7/20/96 14:30		
Departure	7/22/96 6:00		16:00:00
Arrival	7/22/96 22:00	7:00:00	
Departure	7/23/96 5:00		26:00:00
Arrival	7/24/96 7:00	3:30:00	
Departure	7/24/96 10:30		13:30:00
Arrival	7/25/96 0:00	15:30:00	
Departure	7/25/96 15:30		

a) (cont.)

Yearling F421				Yearling F411			
Status	Date and time	Duration of attendance	Duration of absence	Status	Date and time	Duration of attendance	Duration of absence
Departure	5/25/96 17:30			Departure	5/24/96 22:30		
Arrival	5/25/96 19:30	8:30:00		Arrival	5/25/96 2:00	19:00:00	
Departure	5/26/96 4:00		3:00:00	Departure	5/25/96 21:00		4:30:00
Arrival	5/26/96 7:00	12:30:00		Arrival	5/26/96 1:30	2:30:00	
Departure	5/26/96 19:30		42:30:00	Departure	5/26/96 4:00		3:00:00
Arrival	5/28/96 14:00			Arrival	5/26/96 7:00	12:30:00	
Arrival	5/29/96 22:30	7:30:00		Departure	5/26/96 19:30		35:00:00
Departure	5/30/96 6:00		25:30:00	Arrival	5/28/96 6:30		
Arrival	5/31/96 7:30	3:00:00		Arrival	5/29/96 23:00	8:30:00	
Departure	5/31/96 10:30		2:30:00	Departure	5/30/96 7:30		14:30:00
Arrival	5/31/96 13:00	8:30:00		Arrival	5/30/96 22:00	23:00:00	
Departure	5/31/96 21:30		32:30:00	Departure	5/31/96 21:00		28:30:00
Arrival	6/2/96 6:00	13:30:00		Arrival	6/2/96 1:30	20:00:00	
Departure	6/2/96 19:30		7:30:00	Departure	6/2/96 21:30		33:00:00
Arrival	6/3/96 3:00	2:00:00		Arrival	6/4/96 6:30	14:30:00	
Departure	6/3/96 5:00		48:00:00	Departure	6/4/96 21:00		60:30:01
Arrival	6/5/96 5:00	15:30:00		Arrival	6/7/96 9:30	13:00:00	
Departure	6/5/96 20:30		31:30:00	Departure	6/7/96 22:30		36:30:00
Arrival	6/7/96 4:00	16:30:00		Arrival	6/9/96 11:00	33:30:00	
Departure	6/7/96 20:30		29:30:00	Departure	6/10/96 20:30		11:30:00
Arrival	6/9/96 2:00	4:30:00		Arrival	6/11/96 8:00	19:30:00	
Departure	6/9/96 6:30		16:00:00	Departure	6/12/96 3:30		
Arrival	6/9/96 22:30	10:30:00		Arrival	6/14/96 0:00	7:30:00	
Departure	6/10/96 9:00		42:30:00	Departure	6/14/96 7:30		16:00:00
Arrival	6/12/96 3:30	20:30:00		Arrival	6/14/96 23:30	11:30:00	
Departure	6/13/96 0:00		28:30:00	Departure	6/15/96 11:00		5:30:00
Arrival	6/14/96 4:30	3:30:00		Arrival	6/15/96 16:30	4:00:00	
Departure	6/14/96 8:00		23:30:00	Departure	6/15/96 20:30		37:30:00
Arrival	6/15/96 7:30	23:00:00		Arrival	6/17/96 10:00	3:30:00	
Departure	6/16/96 6:30		13:00:00	Departure	6/17/96 13:30		18:30:00
Arrival	6/16/96 19:30	2:30:00		Arrival	6/18/96 8:00	3:30:00	
Departure	6/16/96 22:00		58:00:01	Departure	6/18/96 11:30		3:00:00
Arrival	6/19/96 8:00	15:00:00		Arrival	6/18/96 14:30	11:00:00	
Departure	6/19/96 23:00		3:00:00	Departure	6/19/96 1:30		51:00:01
Arrival	6/20/96 2:00	5:30:00		Arrival	6/21/96 4:30	2:30:00	
Departure	6/20/96 7:30		16:30:00	Departure	6/21/96 7:00		4:00:00
Arrival	6/21/96 0:00	5:00:00		Arrival	6/21/96 11:00	9:00:00	

a) (cont.)

Yearling F421 (cont.)

Status	Date and time	Duration of attendance	Duration of absence
Departure	6/21/96 5:00		19:30:00
Arrival	6/22/96 0:30	6:00:00	
Departure	6/22/96 6:30		6:30:00
Arrival	6/22/96 13:00	22:00:00	
Departure	6/23/96 11:00		35:30:00
Arrival	6/24/96 22:30	21:30:00	
Departure	6/25/96 20:00		
Arrival	6/29/96 11:30		
Arrival	6/30/96 22:30	6:00:00	
Departure	7/1/96 4:30		23:30:00
Arrival	7/2/96 4:00	3:00:00	
Departure	7/2/96 7:00		18:30:00
Arrival	7/3/96 1:30	9:00:00	
Departure	7/3/96 10:30		
Arrival	7/5/96 23:00	7:30:00	
Departure	7/6/96 6:30		2:30:00
Arrival	7/6/96 9:00	6:30:00	
Departure	7/6/96 15:30		12:30:00
Arrival	7/7/96 4:00	5:30:00	
Departure	7/7/96 9:30		37:30:00
Arrival	7/8/96 23:00	3:00:00	
Departure	7/9/96 2:00		
Arrival	7/12/96 21:00	10:00:00	
Departure	7/13/96 7:00		115:30:01
Arrival	7/18/96 2:30	19:30:00	
Departure	7/18/96 22:00		
Arrival	7/22/96 3:30	2:30:00	
Departure	7/22/96 6:00		13:30:00
Arrival	7/22/96 19:30	9:30:00	
Departure	7/23/96 5:00		16:30:00
Arrival	7/23/96 21:30	7:30:00	
Departure	7/24/96 5:00		26:00:00
Arrival	7/25/96 7:00	0:30:00	
Departure	7/25/96 7:30		16:00:00
Arrival	7/25/96 23:30	5:00:00	
Departure	7/26/96 4:30		

Yearling F411 (cont.)

Status	Date and time	Duration of attendance	Duration of absence
Departure	6/21/96 20:00		14:30:00
Arrival	6/22/96 10:30	20:00:00	
Departure	6/23/96 6:30		40:30:00
Arrival	6/24/96 23:00	7:30:00	
Departure	6/25/96 6:30		
Departure	6/28/96 18:30		
Departure	7/1/96 6:00		42:30:00
Arrival	7/3/96 0:30	4:00:00	
Departure	7/3/96 4:30		
Departure	7/5/96 3:00		
Arrival	7/7/96 9:30	4:00:00	
Departure	7/7/96 13:30		31:30:00
Arrival	7/8/96 21:00	5:00:00	
Departure	7/9/96 2:00		
Departure	7/11/96 4:30		20:00:00
Arrival	7/12/96 0:30	12:00:00	
Departure	7/12/96 12:30		10:30:00
Arrival	7/12/96 23:00	7:30:00	
Departure	7/13/96 6:30		18:00:00
Arrival	7/14/96 0:30	4:00:00	
Departure	7/14/96 4:30		67:00:01
Arrival	7/16/96 23:30	6:30:00	
Departure	7/17/96 6:00		14:30:00
Arrival	7/17/96 20:30	4:30:00	
Departure	7/18/96 1:00		
Arrival	7/22/96 21:30	7:30:00	
Departure	7/23/96 5:00		42:00:00
Arrival	7/24/96 23:00	6:00:00	
Departure	7/25/96 5:00		15:00:00
Arrival	7/25/96 20:00	8:30:00	
Departure	7/26/96 4:30		

b)

Alpha male (M450)				Alpha female (F381)			
Status	Date and time	Duration of attendance	Duration of absence	Status	Date and time	Duration of attendance	Duration of absence
Departure	6/8/97 2:30			Departure	6/9/97 6:00		
Arrival	6/9/97 20:00	3:30:00		Arrival	6/10/97 5:00	3:00:00	
Departure	6/9/97 23:30		19:30:00	Departure	6/10/97 8:00		8:30:00
Arrival	6/10/97 19:00	11:00:00		Arrival	6/10/97 16:30	10:00:00	
Departure	6/11/97 6:00		18:00:00	Departure	6/11/97 2:30		4:30:00
Arrival	6/12/97 0:00	20:30:00		Arrival	6/11/97 7:00	13:30:00	
Departure	6/12/97 20:30		5:30:00	Departure	6/11/97 20:30		9:00:00
Arrival	6/13/97 2:00			Arrival	6/12/97 5:30	8:00:00	
Arrival	6/16/97 1:30	22:30:00		Departure	6/12/97 13:30		17:30:00
Departure	6/17/97 0:00		57:00:00	Arrival	6/13/97 7:00		
Arrival	6/19/97 9:00	2:30:00		Arrival	6/15/97 12:00	51:00:00	
Departure	6/19/97 11:30		34:30:00	Departure	6/17/97 15:00		3:00:00
Arrival	6/20/97 22:00	6:30:00		Arrival	6/17/97 18:00	3:00:00	
Departure	6/21/97 4:30		18:00:00	Departure	6/17/97 21:00		7:30:00
Arrival	6/21/97 22:30	3:30:00		Arrival	6/18/97 4:30	1:30:00	
Departure	6/22/97 2:00		26:00:00	Departure	6/18/97 6:00		28:30:00
Arrival	6/23/97 4:00	6:30:00		Arrival	6/19/97 10:30	11:30:00	
Departure	6/23/97 10:30		35:30:00	Departure	6/19/97 22:00		50:30:00
Arrival	6/24/97 22:00	20:00:00		Arrival	6/22/97 0:30	23:30:00	
Departure	6/25/97 18:00			Departure	6/23/97 0:00		6:30:00
Departure	6/27/97 3:30		12:30:00	Arrival	6/23/97 6:30	4:00:00	
Arrival	6/27/97 16:00	6:30:00		Departure	6/23/97 10:30		15:00:00
Departure	6/27/97 22:30		54:30:00	Arrival	6/24/97 1:30	20:30:00	
Arrival	6/30/97 5:00	2:30:00		Departure	6/24/97 22:00		2:30:00
Departure	6/30/97 7:30		1:30:00	Arrival	6/25/97 0:30	2:00:00	
Arrival	6/30/97 9:00	0:30:00		Departure	6/25/97 2:30		4:30:00
Departure	6/30/97 9:30		3:00:00	Arrival	6/25/97 7:00	29:00:00	
Arrival	6/30/97 12:30	0:30:00		Departure	6/26/97 12:00		14:00:00
Departure	6/30/97 13:00		2:30:00	Arrival	6/27/97 2:00	1:30:00	
Arrival	6/30/97 15:30	2:00:00		Departure	6/27/97 3:30		21:30:00
Departure	6/30/97 17:30		12:30:00	Arrival	6/28/97 1:00	29:00:00	
Arrival	7/1/97 6:00	12:00:00		Departure	6/29/97 6:00		24:00:00
Departure	7/1/97 18:00		12:30:00	Arrival	6/30/97 6:00	11:30:00	
Arrival	7/2/97 6:30	14:30:00		Departure	6/30/97 17:30		30:30:00
Departure	7/2/97 21:00		36:30:00	Arrival	7/2/97 0:00	32:00:00	
Arrival	7/4/97 9:30	4:00:00		Departure	7/3/97 8:00		13:00:00
Departure	7/4/97 13:30		1:30:00	Arrival	7/3/97 21:00	25:00:00	
Arrival	7/4/97 15:00	1:00:00		Departure	7/4/97 22:00		3:00:00
Departure	7/4/97 16:00		1:00:00	Arrival	7/5/97 1:00	4:00:00	
Arrival	7/4/97 17:00	1:00:00		Departure	7/5/97 5:00		12:30:00
Departure	7/4/97 18:00		7:30:00	Arrival	7/5/97 17:30	2:00:00	
Arrival	7/5/97 1:30	3:30:00		Departure	7/5/97 19:30		4:00:00
Departure	7/5/97 5:00		23:30:00	Arrival	7/5/97 23:30	3:00:00	
Arrival	7/6/97 4:30	15:30:00		Departure	7/6/97 2:30		27:30:00
Departure	7/6/97 20:00		35:00:00	Arrival	7/7/97 6:00	21:30:00	
Arrival	7/8/97 7:00	6:30:00		Departure	7/8/97 3:30		19:00:00
Departure	7/8/97 13:30		3:00:00	Arrival	7/8/97 22:30	6:00:00	

b) (cont.)

Alpha male (M450) (cont.)				Alpha female (F381) (cont.)			
Status	Date and time	Duration of attendance	Duration of absence	Status	Date and time	Duration of attendance	Duration of absence
Arrival	7/8/97 16:30	9:00:00		Departure	7/9/97 4:30		28:30:00
Departure	7/9/97 1:30		10:30:00	Arrival	7/10/97 9:00	8:00:00	
Arrival	7/9/97 12:00	1:00:00		Departure	7/10/97 17:00		
Departure	7/9/97 13:00		5:30:00	Arrival	7/14/97 3:10	20:00:00	
Arrival	7/9/97 18:30	1:30:00		Departure	7/14/97 23:10		1:00:00
Departure	7/9/97 20:00		11:00:00	Arrival	7/15/97 0:10	4:40:00	
Arrival	7/10/97 7:00	7:30:00		Departure	7/15/97 4:50		1:40:00
Departure	7/10/97 14:30			Arrival	7/15/97 6:30	1:20:00	
Arrival	7/16/97 7:20	14:30:00		Departure	7/15/97 7:50		41:00:00
Departure	7/16/97 21:50			Arrival	7/17/97 0:50	6:10:00	
				Departure	7/17/97 7:00		

b) (cont.)

Adult Female (402)

Status	Date and time	Duration of attendance	Duration of absence
Departure	6/8/97 2:30		
Arrival	6/9/97 9:30	20:00:00	
Departure	6/10/97 5:30		10:30:00
Arrival	6/10/97 16:00	14:00:00	
Departure	6/11/97 6:00		24:30:00
Arrival	6/12/97 6:30	10:00:00	
Departure	6/12/97 16:30		
Arrival	6/15/97 23:00	25:00:00	
Departure	6/17/97 0:00		24:00:00
Arrival	6/18/97 0:00	2:00:00	
Departure	6/18/97 2:00		3:00:00
Arrival	6/18/97 5:00	8:30:00	
Departure	6/18/97 13:30		33:00:00
Arrival	6/19/97 22:30	15:00:00	
Departure	6/20/97 13:30		8:00:00
Arrival	6/20/97 21:30	7:00:00	
Departure	6/21/97 4:30		42:30:00
Arrival	6/22/97 23:00	2:00:00	
Departure	6/23/97 1:00		4:00:00
Arrival	6/23/97 5:00	13:30:00	
Departure	6/23/97 18:30		42:30:00
Arrival	6/25/97 13:00	23:00:00	
Departure	6/26/97 12:00		47:00:00
Arrival	6/28/97 11:00	15:00:00	
Departure	6/29/97 2:00		2:30:00
Arrival	6/29/97 4:30	12:00:00	
Departure	6/29/97 16:30		9:30:00
Arrival	6/30/97 2:00	4:00:00	
Departure	6/30/97 6:00		42:30:00
Arrival	7/2/97 0:30	7:00:00	
Departure	7/2/97 7:30		10:30:00
Arrival	7/2/97 18:00	2:30:00	
Departure	7/2/97 20:30		26:30:00
Arrival	7/3/97 23:00	8:30:00	
Departure	7/4/97 7:30		13:30:00
Arrival	7/4/97 21:00	4:00:00	
Departure	7/5/97 1:00		2:30:00
Arrival	7/5/97 3:30	1:30:00	
Departure	7/5/97 5:00		51:00:00
Arrival	7/7/97 8:00	13:30:00	
Departure	7/7/97 21:30		51:00:01
Arrival	7/10/97 0:30	0:30:00	
Departure	7/10/97 1:00		11:00:00
Arrival	7/10/97 12:00		
Arrival	7/14/97 22:50	6:00:00	
Departure	7/15/97 4:50		

Adult Female (470)

Status	Date and time	Duration of attendance	Duration of absence
Arrival	6/7/97 21:00	5:00:00	
Departure	6/8/97 2:00		43:00:00
Arrival	6/9/97 21:00	7:00:00	
Departure	6/10/97 4:00		21:00:00
Arrival	6/11/97 1:00	5:00:00	
Departure	6/11/97 6:00		
Arrival	6/16/97 7:30	16:30:00	
Departure	6/17/97 0:00		6:00:00
Arrival	6/17/97 6:00	1:00:00	
Departure	6/17/97 7:00		41:00:00
Arrival	6/19/97 0:00	0:30:00	
Departure	6/19/97 0:30		3:30:00
Arrival	6/19/97 4:00	1:00:00	
Departure	6/19/97 5:00		4:00:00
Arrival	6/19/97 9:00	3:30:00	
Departure	6/19/97 12:30		12:30:00
Arrival	6/20/97 1:00	19:00:00	
Departure	6/20/97 20:00		111:00:00
Arrival	6/25/97 11:00	2:00:00	
Departure	6/25/97 13:00		9:30:00
Arrival	6/25/97 22:30	13:30:00	
Departure	6/26/97 12:00		42:30:00
Arrival	6/28/97 6:30	13:00:00	
Departure	6/28/97 19:30		
Arrival	7/4/97 8:00	21:00:00	
Departure	7/5/97 5:00		73:30:00
Arrival	7/8/97 6:30	1:30:00	
Departure	7/8/97 8:00		15:30:00
Arrival	7/8/97 23:30	2:30:00	
Departure	7/9/97 2:00		
Arrival	7/13/97 21:50	1:30:00	
Departure	7/13/97 23:20		48:50:00
Arrival	7/16/97 0:10	5:50:00	
Departure	7/16/97 6:00		0:30:00
Arrival	7/16/97 6:30	0:10:00	
Departure	7/16/97 6:40		12:10:00
Arrival	7/16/97 18:50	0:40:00	
Departure	7/16/97 19:30		37:10:00
Arrival	7/18/97 8:40	1:00:00	
Departure	7/18/97 9:40		1:00:00
Arrival	7/18/97 10:40	0:30:00	
Departure	7/18/97 11:10		

c) (cont.)

Adult Female (411)			
Status	Date and time	Duration of attendance	Duration of absence
Arrival	6/7/97 18:30	7:30:00	
Departure	6/8/97 2:00		44:00:00
Arrival	6/9/97 22:00	10:00:00	
Departure	6/10/97 8:00		13:00:00
Arrival	6/10/97 21:00	9:00:00	
Departure	6/11/97 6:00		
Arrival	6/16/97 9:00	15:30:00	
Departure	6/17/97 0:30		33:30:00
Arrival	6/18/97 10:00	1:30:00	
Departure	6/18/97 11:30		21:00:00
Arrival	6/19/97 8:30	28:30:00	
Departure	6/20/97 13:00		79:30:00
Arrival	6/23/97 20:30	10:30:00	
Departure	6/24/97 7:00		14:00:00
Arrival	6/24/97 21:00	6:30:00	
Departure	6/25/97 3:30		20:00:00
Arrival	6/25/97 23:30		
Arrival	6/28/97 4:30	11:00:00	
Departure	6/28/97 15:30		54:00:00
Arrival	6/30/97 21:30	5:00:00	
Departure	7/1/97 2:30		4:30:00
Arrival	7/1/97 7:00	2:30:00	
Departure	7/1/97 9:30		14:00:00
Arrival	7/1/97 23:30	5:00:00	
Departure	7/2/97 4:30		50:00:00
Arrival	7/4/97 6:30	4:30:00	
Departure	7/4/97 11:00		9:00:00
Arrival	7/4/97 20:00	2:00:00	
Departure	7/4/97 22:00		3:00:00
Arrival	7/5/97 1:00	3:30:00	
Departure	7/5/97 4:30		78:00:00
Arrival	7/8/97 10:30	2:00:00	
Departure	7/8/97 12:30		10:00:00
Arrival	7/8/97 22:30	6:00:00	
Departure	7/9/97 4:30		37:30:00
Arrival	7/10/97 18:00		
Arrival	7/17/97 2:40	4:20:00	
Departure	7/17/97 7:00		14:40:00
Arrival	7/17/97 21:40	0:30:00	
Departure	7/17/97 22:10		3:30:00
Arrival	7/18/97 1:40	2:20:00	
Departure	7/18/97 4:00		

Yearling Female (331)			
Status	Date and time	Duration of attendance	Duration of absence
Arrival	6/7/97 20:30	5:30:00	
Departure	6/8/97 2:00		25:00:00
Arrival	6/9/97 3:00	15:30:00	
Departure	6/9/97 18:30		36:00:00
Arrival	6/11/97 6:30	34:30:00	
Departure	6/12/97 17:00		10:00:00
Arrival	6/13/97 3:00		
Arrival	6/16/97 0:00	9:00:00	
Departure	6/16/97 9:00		18:00:00
Arrival	6/17/97 3:00	1:00:00	
Departure	6/17/97 4:00		29:30:00
Arrival	6/18/97 9:30	6:00:00	
Departure	6/18/97 15:30		7:00:00
Arrival	6/18/97 22:30	0:30:00	
Departure	6/18/97 23:00		5:00:00
Arrival	6/19/97 4:00	1:30:00	
Departure	6/19/97 5:30		22:00:00
Arrival	6/20/97 3:30	16:00:00	
Departure	6/20/97 19:30		62:00:00
Arrival	6/23/97 9:30	9:00:00	
Departure	6/23/97 18:30		
Arrival	6/28/97 0:30	1:00:00	
Departure	6/28/97 1:30		5:30:00
Arrival	6/28/97 7:00	17:00:00	
Departure	6/29/97 0:00		4:00:00
Arrival	6/29/97 4:00	1:30:00	
Departure	6/29/97 5:30		3:30:00
Arrival	6/29/97 9:00	0:30:00	
Departure	6/29/97 9:30		40:30:00
Arrival	7/1/97 2:00	3:00:00	
Departure	7/1/97 5:00		50:00:00
Arrival	7/3/97 7:00	1:00:00	
Departure	7/3/97 8:00		4:00:00
Arrival	7/3/97 12:00	1:00:00	
Departure	7/3/97 13:00		15:30:00
Arrival	7/4/97 4:30	5:30:00	
Departure	7/4/97 10:00		20:30:00
Arrival	7/5/97 6:30	10:00:00	
Departure	7/5/97 16:30		11:30:00
Arrival	7/6/97 4:00	15:00:00	
Departure	7/6/97 19:00		36:00:00
Arrival	7/8/97 7:00	1:00:00	
Departure	7/8/97 8:00		17:30:00
Arrival	7/9/97 1:30	3:00:00	
Departure	7/9/97 4:30		19:30:00
Arrival	7/10/97 0:00	3:00:00	
Departure	7/10/97 3:00		

b) (cont.)

Adult Female (411) (cont.)				Yearling Female (331)			
Status	Date and time	Duration of attendance	Duration of absence	Status	Date and time	Duration of attendance	Duration of absence
				Arrival	7/13/97 3:20	2:30:00	
				Departure	7/13/97 5:50		16:50:00
				Arrival	7/13/97 22:40	5:30:00	
				Departure	7/14/97 4:10		21:10:00
				Arrival	7/15/97 1:20	3:40:00	
				Departure	7/15/97 5:00		1:20:00
				Arrival	7/15/97 6:20	6:00:00	
				Departure	7/15/97 12:20		61:30:00
				Arrival	7/18/97 1:50	5:50:00	
				Departure	7/18/97 7:40		6:00:00
				Arrival	7/18/97 13:40	0:30:00	
				Departure	7/18/97 14:10		

b) (cont.)

Yearling Female (253)				Yearling Female (370)			
Status	Date and time	Duration of attendance	Duration of absence	Status	Date and time	Duration of attendance	Duration of absence
Departure	6/8/97 2:00			Arrival	6/7/97 23:00	3:00:00	
Arrival	6/9/97 20:00	11:00:00		Departure	6/8/97 2:00		41:30:00
Departure	6/10/97 7:00		53:30:00	Arrival	6/9/97 19:30	6:30:00	
Arrival	6/12/97 12:30			Departure	6/10/97 2:00		52:30:00
Arrival	6/15/97 12:00	8:30:00		Arrival	6/12/97 6:30		
Departure	6/15/97 20:30		45:30:00	Arrival	6/16/97 2:30	23:30:00	
Arrival	6/17/97 18:00	2:30:00		Departure	6/17/97 2:00		17:30:00
Departure	6/17/97 20:30		43:00:00	Arrival	6/17/97 19:30	1:00:00	
Arrival	6/19/97 15:30	11:30:00		Departure	6/17/97 20:30		100:30:00
Departure	6/20/97 3:00		46:00:00	Arrival	6/22/97 1:00	23:30:00	
Arrival	6/22/97 1:00	4:00:00		Departure	6/23/97 0:30		22:30:00
Departure	6/22/97 5:00		42:00:00	Arrival	6/23/97 23:00	7:30:00	
Arrival	6/23/97 23:00	22:00:00		Departure	6/24/97 6:30		11:30:00
Departure	6/24/97 21:00		0:30:00	Arrival	6/24/97 18:00	3:00:00	
Arrival	6/24/97 21:30	1:00:00		Departure	6/24/97 21:00		0:30:00
Departure	6/24/97 22:30		13:30:00	Arrival	6/24/97 21:30	1:00:00	
Arrival	6/25/97 12:00	6:00:00		Departure	6/24/97 22:30		16:00:00
Departure	6/25/97 18:00		4:00:00	Arrival	6/25/97 14:30	11:00:00	
Arrival	6/25/97 22:00			Departure	6/26/97 1:30		4:30:00
Arrival	6/28/97 2:30	2:00:00		Arrival	6/26/97 6:00	6:00:00	
Departure	6/28/97 4:30		0:30:00	Departure	6/26/97 12:00		12:00:00
Arrival	6/28/97 5:00	10:00:00		Arrival	6/27/97 0:00	3:30:00	
Departure	6/28/97 15:00		34:30:00	Departure	6/27/97 3:30		23:00:00
Arrival	6/30/97 1:30	6:00:00		Arrival	6/28/97 2:30	24:30:00	
Departure	6/30/97 7:30		4:00:00	Departure	6/29/97 3:00		23:00:00
Arrival	6/30/97 11:30	0:30:00		Arrival	6/30/97 2:00	5:30:00	
Departure	6/30/97 12:00		42:30:00	Departure	6/30/97 7:30		14:00:00
Arrival	7/2/97 6:30	2:30:00		Arrival	6/30/97 21:30	5:00:00	
Departure	7/2/97 9:00		31:00:00	Departure	7/1/97 2:30		21:00:00
Arrival	7/3/97 16:00	3:00:00		Arrival	7/1/97 23:30	2:30:00	
Departure	7/3/97 19:00		4:00:00	Departure	7/2/97 2:00		28:00:00
Arrival	7/3/97 23:00	0:30:00		Arrival	7/3/97 6:00	22:30:00	
Departure	7/3/97 23:30		2:30:00	Departure	7/4/97 4:30		3:30:00
Arrival	7/4/97 2:00	0:30:00		Arrival	7/4/97 8:00	0:30:00	
Departure	7/4/97 2:30		18:30:00	Departure	7/4/97 8:30		16:30:00
Arrival	7/4/97 21:00	0:30:00		Arrival	7/5/97 1:00	3:30:00	
Departure	7/4/97 21:30		3:30:00	Departure	7/5/97 4:30		69:00:00
Arrival	7/5/97 1:00	1:00:00		Arrival	7/8/97 1:30	9:30:00	
Departure	7/5/97 2:00		4:30:00	Departure	7/8/97 11:00		4:30:00
Arrival	7/5/97 6:30	3:30:00		Arrival	7/8/97 15:30	0:30:00	
Departure	7/5/97 10:00		15:00:00	Departure	7/8/97 16:00		3:00:00
Arrival	7/6/97 1:00	18:00:00		Arrival	7/8/97 19:00	5:00:00	
Departure	7/6/97 19:00		36:00:00	Departure	7/9/97 0:00		21:30:00
Arrival	7/8/97 7:00	8:30:00		Arrival	7/9/97 21:30	1:30:00	
Departure	7/8/97 15:30		0:30:00	Departure	7/9/97 23:00		
Arrival	7/8/97 16:00	12:30:00		Arrival	7/15/97 1:50	0:10:00	
Departure	7/9/97 4:30		28:00:00	Departure	7/15/97 2:00		5:10:00

b) (cont.)

Yearling Female (253) (cont.)			
Status	Date and time	Duration of attendance	Duration of absence
Arrival	7/10/97 8:30	0:30:00	
Departure	7/10/97 9:00		7:00:00
Arrival	7/10/97 16:00	1:00:00	
Departure	7/10/97 17:00		
Arrival	7/13/97 8:20	0:20:00	
Departure	7/13/97 8:40		3:50:00
Arrival	7/13/97 12:30	15:50:00	
Departure	7/14/97 4:20		18:40:00
Arrival	7/14/97 23:00	5:50:00	
Departure	7/15/97 4:50		1:30:00
Arrival	7/15/97 6:20	13:00:00	
Departure	7/15/97 19:20		1:00:00
Arrival	7/15/97 20:20	1:20:00	
Departure	7/15/97 21:40		52:40:00
Arrival	7/18/97 2:20	5:40:00	
Departure	7/18/97 8:00		5:40:00
Arrival	7/18/97 13:40	0:30:00	
Departure	7/18/97 14:10		

Yearling Female (370) (cont.)			
Status	Date and time	Duration of attendance	Duration of absence
Arrival	7/15/97 7:10	5:20:00	
Departure	7/15/97 12:30		0:30:00
Arrival	7/15/97 13:00	6:30:00	
Departure	7/15/97 19:30		1:00:00
Arrival	7/15/97 20:30	1:50:00	
Departure	7/15/97 22:20		2:10:00
Arrival	7/16/97 0:30	3:40:00	
Departure	7/16/97 4:10		24:50:00
Arrival	7/17/97 5:00	19:00:00	
Departure	7/18/97 0:00		

c)

Alpha Male (450)				Alpha Female (381)			
Status	Date and time	Duration attendance	Duration absence	Status	Date and time	Duration attendance	Duration absence
Arrival	5/19/98 8:30	17:00:00		Departure	5/17/98 4:00		
Departure	5/20/98 1:30		47:59:59	Arrival	5/18/98 0:00	30:30:00	
Arrival	5/22/98 1:30	5:50:00		Departure	5/19/98 6:30		20:30:00
Departure	5/22/98 7:20		19:10:00	Arrival	5/20/98 3:00	13:00:00	
Arrival	5/23/98 2:30	9:30:00		Departure	5/20/98 16:00		25:09:59
Departure	5/23/98 12:00		59:40:00	Arrival	5/21/98 17:10	17:40:00	
Arrival	5/25/98 23:40	2:10:00		Departure	5/22/98 10:50		13:30:00
Departure	5/26/98 1:50		9:20:00	Arrival	5/23/98 0:20	11:40:00	
Arrival	5/26/98 11:10	20:40:00		Departure	5/23/98 12:00		15:00:00
Departure	5/27/98 7:50		51:50:00	Arrival	5/24/98 3:00	26:40:00	
Arrival	5/29/98 11:40	15:30:00		Departure	5/25/98 5:40		37:20:00
Departure	5/30/98 3:10		26:00:00	Arrival	5/26/98 19:00	42:20:00	
Arrival	5/31/98 5:10			Departure	5/28/98 13:20		17:10:00
Arrival	6/1/98 13:10	20:40:00		Arrival	5/29/98 6:30	52:30:00	
Departure	6/2/98 9:50		14:50:00	Departure	5/31/98 11:00		
Arrival	6/3/98 0:40	10:10:00		Departure	6/3/98 10:50		6:30:00
Departure	6/3/98 10:50		5:50:00	Arrival	6/3/98 17:20	47:10:00	
Arrival	6/3/98 16:40	16:30:00		Departure	6/5/98 16:30		24:10:00
Departure	6/4/98 9:10		7:10:00	Arrival	6/6/98 16:40	16:30:00	
Arrival	6/4/98 16:20	17:50:00		Departure	6/7/98 9:10		13:50:00
Departure	6/5/98 10:10		6:10:00	Arrival	6/7/98 23:00	19:50:00	
Arrival	6/5/98 16:20	0:10:00		Departure	6/8/98 18:50		9:20:00
Departure	6/5/98 16:30		49:50:00	Arrival	6/9/98 4:10	23:50:00	
Arrival	6/7/98 18:20	10:00:00		Departure	6/10/98 4:00		48:30:00
Departure	6/8/98 4:20		47:00:00	Arrival	6/12/98 4:30	22:50:00	
Arrival	6/10/98 3:20	0:40:00		Departure	6/13/98 3:20		10:10:00
Departure	6/10/98 4:00		77:50:00	Arrival	6/13/98 13:30	15:40:00	
Arrival	6/13/98 9:50	19:20:00		Departure	6/14/98 5:10		11:10:00
Departure	6/14/98 5:10			Arrival	6/14/98 16:20		
Arrival	6/20/98 0:20	7:50:00		Departure	6/19/98 13:20		11:40:00
Departure	6/20/98 8:10		96:50:00	Arrival	6/20/98 1:00	7:10:00	
Arrival	6/24/98 9:00	7:40:00		Departure	6/20/98 8:10		5:00:00
Departure	6/24/98 16:40		134:50:00	Arrival	6/20/98 13:10	15:00:00	
Arrival	6/30/98 7:30	20:20:00		Departure	6/21/98 4:10		28:00:00
Departure	7/1/98 3:50			Arrival	6/22/98 8:10	18:50:00	
Arrival	7/9/98 7:10	12:30:00		Departure	6/23/98 3:00		48:30:00
Departure	7/9/98 19:40		81:30:00	Arrival	6/25/98 3:30	2:00:00	
Arrival	7/13/98 5:10	24:00:00		Departure	6/25/98 5:30		21:40:00
Departure	7/14/98 5:10		48:00:00	Arrival	6/26/98 3:10	25:30:00	
Arrival	7/16/98 5:10	22:00:00		Departure	6/27/98 4:40		2:20:00
Departure	7/17/98 3:10		23:00:00	Arrival	6/27/98 7:00	2:00:00	
Arrival	7/18/98 2:10	5:50:00		Departure	6/27/98 9:00		14:50:00
Departure	7/18/98 8:00		43:00:00	Arrival	6/27/98 23:50	8:10:00	
Arrival	7/20/98 3:00	15:40:00		Departure	6/28/98 8:00		49:50:00
Departure	7/20/98 18:40			Arrival	6/30/98 9:50	18:00:00	
				Departure	7/1/98 3:50		

c) (cont.)

Adult Female (370)			
Status	Date and time	Duration attendance	Duration absence
Arrival	5/17/98 7:00	20:30:00	
Departure	5/18/98 3:30		28:30:00
Arrival	5/19/98 8:00	17:30:00	
Departure	5/20/98 1:30		96:19:59
Arrival	5/24/98 1:50	21:30:00	
Departure	5/24/98 23:20		25:20:00
Arrival	5/26/98 0:40	22:10:00	
Departure	5/26/98 22:50		53:10:00
Arrival	5/29/98 4:00	14:00:00	
Departure	5/29/98 18:00		12:50:00
Arrival	5/30/98 6:50	15:30:00	
Departure	5/30/98 22:20		
Departure	6/1/98 21:20		53:20:00
Arrival	6/4/98 2:40	0:40:00	
Departure	6/4/98 3:20		47:30:00
Arrival	6/6/98 2:50	2:10:00	
Departure	6/6/98 5:00		33:50:00
Arrival	6/7/98 14:50	0:50:00	
Departure	6/7/98 15:40		80:00:00
Arrival	6/10/98 23:40	7:00:00	
Departure	6/11/98 6:40		45:10:00
Arrival	6/13/98 3:50	10:50:00	
Departure	6/13/98 14:40		6:00:00
Arrival	6/13/98 20:40	8:30:00	
Departure	6/14/98 5:10		
Arrival	6/19/98 16:00	4:20:00	
Departure	6/19/98 20:20		106:50:00
Arrival	6/24/98 7:10	9:30:00	
Departure	6/24/98 16:40		79:30:00
Arrival	6/28/98 0:10	7:50:00	
Departure	6/28/98 8:00		
Arrival	7/5/98 0:40	18:30:00	
Departure	7/5/98 19:10		74:20:00
Arrival	7/8/98 21:30	22:10:00	
Departure	7/9/98 19:40		

Adult Female (253)			
Status	Date and time	Duration attendance	Duration absence
Arrival	5/18/98 23:30	26:00:00	
Departure	5/20/98 1:30		57:09:59
Arrival	5/22/98 10:40	11:40:00	
Departure	5/22/98 22:20		29:10:00
Arrival	5/24/98 3:30	26:10:00	
Departure	5/25/98 5:40		17:50:00
Arrival	5/25/98 23:30	32:20:00	
Departure	5/27/98 7:50		26:00:00
Arrival	5/28/98 9:50	12:00:00	
Departure	5/28/98 21:50		12:00:00
Arrival	5/29/98 9:50	20:00:00	
Departure	5/30/98 5:50		20:00:00
Arrival	5/31/98 1:50		
Arrival	6/1/98 23:20	10:30:00	
Departure	6/2/98 9:50		36:00:00
Arrival	6/3/98 21:50	48:40:00	
Departure	6/5/98 22:30		
Arrival	6/6/98 20:30	11:00:00	
Departure	6/7/98 7:30		5:20:00
Arrival	6/7/98 12:50	0:30:00	
Departure	6/7/98 13:20		9:40:00
Arrival	6/7/98 23:00	5:20:00	
Departure	6/8/98 4:20		22:20:00
Arrival	6/9/98 2:40	91:20:00	
Departure	6/12/98 22:00		3:20:00
Arrival	6/13/98 1:20	3:10:00	
Departure	6/13/98 4:30		17:10:00
Arrival	6/13/98 21:40	7:30:00	
Departure	6/14/98 5:10		

c) (cont.)

Yearling Female (180)				Yearling Female (552)			
Status	Date and time	Duration attendance	Duration absence	Status	Date and time	Duration attendance	Duration absence
Departure	35932.1875			Arrival	5/24/98 4:40	25:00:00	
Arrival	5/18/98 0:00	30:30:00		Departure	5/25/98 5:40		19:00:00
Departure	5/19/98 6:30		2:00:00	Arrival	5/26/98 0:40	31:10:00	
Arrival	5/19/98 8:30	17:00:00		Departure	5/27/98 7:50		22:30:00
Departure	5/20/98 1:30		40:19:59	Arrival	5/28/98 6:20	8:40:00	
Arrival	5/21/98 17:50	4:20:00		Departure	5/28/98 15:00		5:20:00
Departure	5/21/98 22:10		5:50:00	Arrival	5/28/98 20:20	12:50:00	
Arrival	5/22/98 4:00	12:30:00		Departure	5/29/98 9:10		9:20:00
Departure	5/22/98 16:30		6:30:00	Arrival	5/29/98 18:30	11:10:00	
Arrival	5/22/98 23:00	23:40:00		Departure	5/30/98 5:40		13:40:00
Departure	5/23/98 22:40		12:50:00	Arrival	5/30/98 19:20	10:30:00	
Arrival	5/24/98 11:30	16:20:00		Departure	5/31/98 5:50		
Departure	5/25/98 3:50		5:00:00	Arrival	6/1/98 13:10	0:10:00	
Arrival	5/25/98 8:50	47:10:00		Departure	6/1/98 13:20		253:20:00
Departure	5/27/98 8:00		41:10:00	Arrival	6/12/98 2:40	1:10:00	
Arrival	5/29/98 1:10	28:50:00		Departure	6/12/98 3:50		152:30:00
Departure	5/30/98 6:00		20:00:00	Arrival	6/18/98 12:20	5:10:00	
Arrival	5/31/98 2:00			Departure	6/18/98 17:30		179:10:00
Departure	6/4/98 4:00		4:20:00	Arrival	6/26/98 4:40	1:20:00	
Arrival	6/4/98 8:20	71:10:00		Departure	6/26/98 6:00		104:10:00
Departure	6/7/98 7:30		15:30:00	Arrival	6/30/98 14:10	8:50:00	
Arrival	6/7/98 23:00	106:40:00		Departure	6/30/98 23:00		
Departure	6/12/98 9:40		8:50:00	Arrival	7/6/98 18:30	0:40:00	
Arrival	6/12/98 18:30	8:50:00		Departure	7/6/98 19:10		7:30:00
Departure	6/13/98 3:20		13:00:00	Arrival	7/7/98 2:40	1:20:00	
Arrival	6/13/98 16:20	12:50:00		Departure	7/7/98 4:00		67:30:00
Departure	6/14/98 5:10			Arrival	7/9/98 23:30	3:00:00	
Departure	6/18/98 16:20		5:00:00	Departure	7/10/98 2:30		1:30:00
Arrival	6/18/98 21:20	7:40:00		Arrival	7/10/98 4:00	4:50:00	
Departure	6/19/98 5:00		22:10:00	Departure	7/10/98 8:50		29:10:00
Arrival	6/20/98 3:10	5:00:00		Arrival	7/11/98 14:00	7:10:00	
Departure	6/20/98 8:10		40:00:00	Departure	7/11/98 21:10		77:40:00
Arrival	6/22/98 0:10	29:00:00		Arrival	7/15/98 2:50	1:30:00	
Departure	6/23/98 5:10		72:20:00	Departure	7/15/98 4:20		4:00:00
Arrival	6/26/98 5:30	14:30:00		Arrival	7/15/98 8:20	2:30:00	
Departure	6/26/98 20:00		32:20:00	Departure	7/15/98 10:50		6:20:00
Arrival	6/28/98 4:20	3:40:00		Arrival	7/15/98 17:10	0:50:00	
Departure	6/28/98 8:00		47:20:00	Departure	7/15/98 18:00		
Arrival	6/30/98 7:20	18:50:00					
Departure	7/1/98 2:10		50:20:00				
Arrival	7/3/98 4:30	1:50:00					
Departure	7/3/98 6:20						
Arrival	7/4/98 11:40	4:00:00					
Departure	7/4/98 15:40		30:20:00				
Arrival	7/5/98 22:00	6:30:00					
Departure	7/6/98 4:30		13:30:00				

c) (cont.)

Yearling Female (180) (cont.)				Yearling Female (552) (cont.)			
Status	Date and time	Duration attendance	Duration absence	Status	Date and time	Duration attendance	Duration absence
Arrival	7/6/98 18:00	5:10:00					
Departure	7/6/98 23:10		15:10:00				
Arrival	7/7/98 14:20	5:50:00					
Departure	7/7/98 20:10		88:10:00				
Arrival	7/11/98 12:20	8:00:00					
Departure	7/11/98 20:20		15:10:00				
Arrival	7/12/98 11:30	18:40:00					
Departure	7/13/98 6:10		3:50:00				
Arrival	7/13/98 10:00	6:50:00					
Departure	7/13/98 16:50		7:00:00				
Arrival	7/13/98 23:50	5:20:00					
Departure	7/14/98 5:10		21:40:00				
Arrival	7/15/98 2:50	3:00:00					
Departure	7/15/98 5:50		90:40:00				
Arrival	7/19/98 0:30	10:30:00					
Departure	7/19/98 11:00						

c) (cont.)

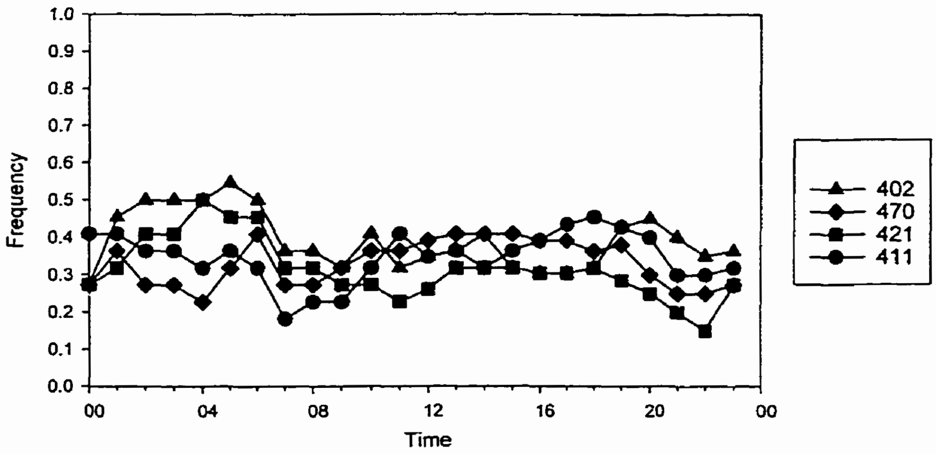
Adult Female (470)

Status	Date and time	Duration attendance	Duration absence
Arrival	35931.64583	4:00:00	
Departure	35931.8125		11:00:00
Arrival	5/17/98 6:30	21:00:00	
Departure	5/18/98 3:30		14:30:00
Arrival	5/18/98 18:00	31:30:00	
Departure	5/20/98 1:30		39:39:59
Arrival	5/21/98 17:10	0:30:00	
Departure	5/21/98 17:40		4:10:00
Arrival	5/21/98 21:50	9:30:00	
Departure	5/22/98 7:20		23:30:00
Arrival	5/23/98 6:50	54:30:00	
Departure	5/25/98 13:20		19:00:00
Arrival	5/26/98 8:20	23:30:00	
Departure	5/27/98 7:50		25:10:00
Arrival	5/28/98 9:00	6:10:00	
Departure	5/28/98 15:10		12:10:00
Arrival	5/29/98 3:20	14:30:00	
Departure	5/29/98 17:50		28:40:00
Arrival	5/30/98 22:30		
Arrival	6/1/98 23:10	25:40:00	
Departure	6/3/98 0:50		11:50:00
Arrival	6/3/98 12:40	4:20:00	
Departure	6/3/98 17:00		4:40:00
Arrival	6/3/98 21:40	35:30:00	
Departure	6/5/98 9:10		7:10:00
Arrival	6/5/98 16:20	0:10:00	
Departure	6/5/98 16:30		46:40:00
Arrival	6/7/98 15:10	15:50:00	
Departure	6/8/98 7:00		16:10:00
Arrival	6/8/98 23:10	18:10:00	
Departure	6/9/98 17:20		16:10:00
Arrival	6/10/98 9:30	21:00:00	
Departure	6/11/98 6:30		26:40:00
Arrival	6/12/98 9:10	18:10:00	
Departure	6/13/98 3:20		12:40:00
Arrival	6/13/98 16:00	13:10:00	
Departure	6/14/98 5:10		
Arrival	6/19/98 18:40	20:50:00	
Departure	6/20/98 15:30		59:50:00
Arrival	6/23/98 3:20	13:40:00	
Departure	6/23/98 17:00		16:00:00
Arrival	6/24/98 9:00	11:50:00	
Departure	6/24/98 20:50		30:20:00
Arrival	6/26/98 3:10	16:50:00	
Departure	6/26/98 20:00		27:40:00
Arrival	6/27/98 23:40	8:20:00	
Departure	6/28/98 8:00		92:40:00
Arrival	7/2/98 4:40	13:40:00	
Departure	7/2/98 18:20		
Arrival	7/9/98 22:00	2:00:00	
Departure	7/10/98 0:00		6:10:00
Arrival	7/10/98 6:10	28:40:00	
Departure	7/11/98 10:50		77:10:00
Arrival	7/14/98 16:00	21:20:00	
Departure	7/15/98 13:20		61:30:00
Arrival	7/18/98 2:50	1:20:00	
Departure	7/18/98 4:10		57:00:00
Arrival	7/20/98 13:10	12:40:00	
Departure	7/21/98 1:50		

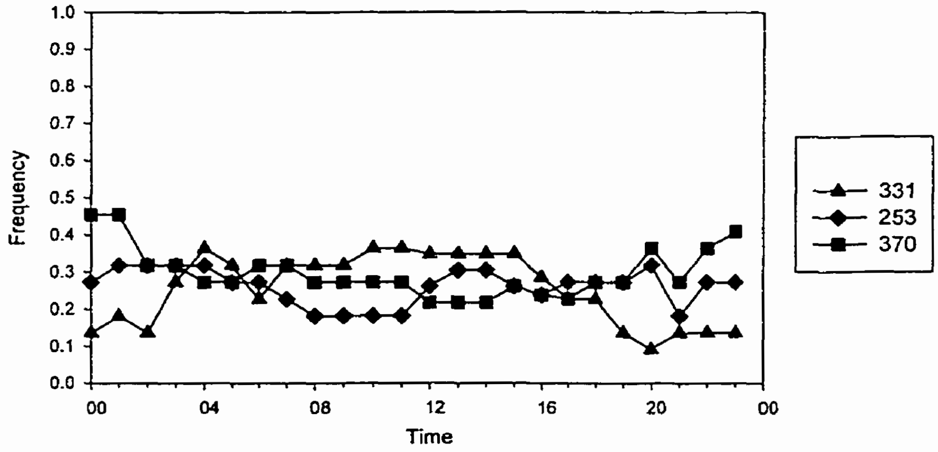
Appendix III

1) Frequency of attendance of individual yearling wolves as a function of the time of day in a) 1996, b) 1997, and c) 1998.

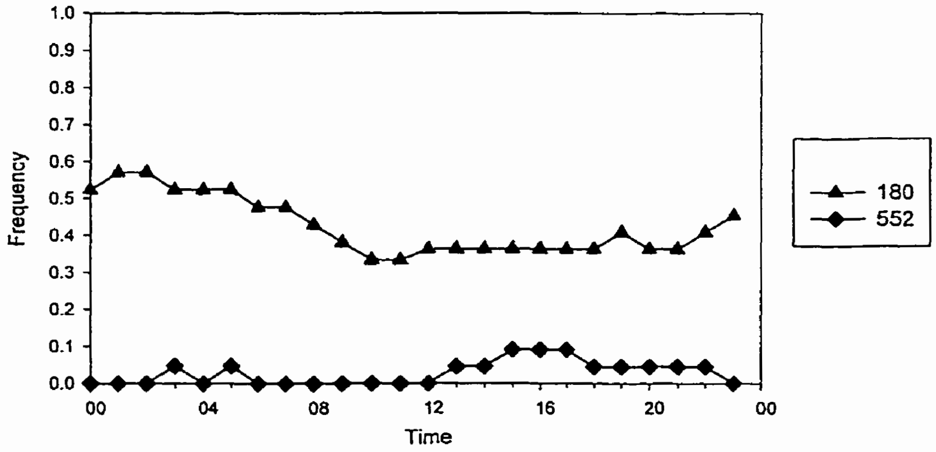
a)



b)



c)



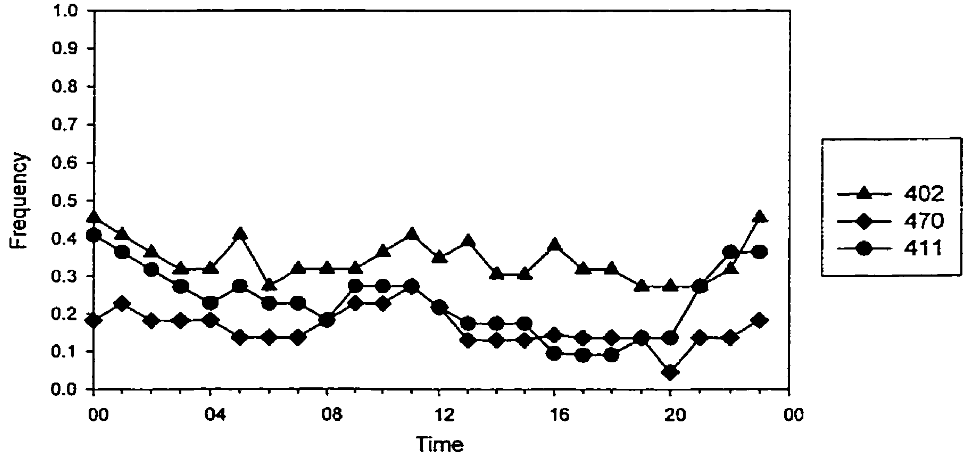
2) Table of attendance of individual yearling wolves as a function of the time of day in 1996, 1997, and 1998.

	1996				1997			1998	
Time	F402	F470	F421	F411	F331	F253	F370	F180	F552
0:00	0.27	0.27	0.27	0.41	0.14	0.27	0.45	0.52	0.00
1:00	0.45	0.36	0.32	0.41	0.18	0.32	0.45	0.57	0.00
2:00	0.50	0.27	0.41	0.36	0.14	0.32	0.32	0.57	0.00
3:00	0.50	0.27	0.41	0.36	0.27	0.32	0.32	0.52	0.05
4:00	0.50	0.23	0.50	0.32	0.36	0.32	0.27	0.52	0.00
5:00	0.55	0.32	0.45	0.36	0.32	0.27	0.27	0.52	0.05
6:00	0.50	0.41	0.45	0.32	0.23	0.27	0.32	0.48	0.00
7:00	0.36	0.27	0.32	0.18	0.32	0.23	0.32	0.48	0.00
8:00	0.36	0.27	0.32	0.23	0.32	0.18	0.27	0.43	0.00
9:00	0.32	0.32	0.27	0.23	0.32	0.18	0.27	0.38	0.00
10:00	0.41	0.36	0.27	0.32	0.36	0.18	0.27	0.33	0.00
11:00	0.32	0.36	0.23	0.41	0.36	0.18	0.27	0.33	0.00
12:00	0.35	0.39	0.26	0.35	0.35	0.26	0.22	0.36	0.00
13:00	0.36	0.41	0.32	0.36	0.35	0.30	0.22	0.36	0.05
14:00	0.41	0.41	0.32	0.32	0.35	0.30	0.22	0.36	0.05
15:00	0.32	0.41	0.32	0.36	0.35	0.26	0.26	0.36	0.09
16:00	0.30	0.39	0.30	0.39	0.29	0.24	0.24	0.36	0.09
17:00	0.30	0.39	0.30	0.43	0.23	0.27	0.23	0.36	0.09
18:00	0.32	0.36	0.32	0.45	0.23	0.27	0.27	0.36	0.05
19:00	0.43	0.38	0.29	0.43	0.14	0.27	0.27	0.41	0.05
20:00	0.45	0.30	0.25	0.40	0.09	0.32	0.36	0.36	0.05
21:00	0.40	0.25	0.20	0.30	0.14	0.18	0.27	0.36	0.05
22:00	0.35	0.25	0.15	0.30	0.14	0.27	0.36	0.41	0.05
23:00	0.36	0.27	0.27	0.32	0.14	0.27	0.41	0.45	0.00

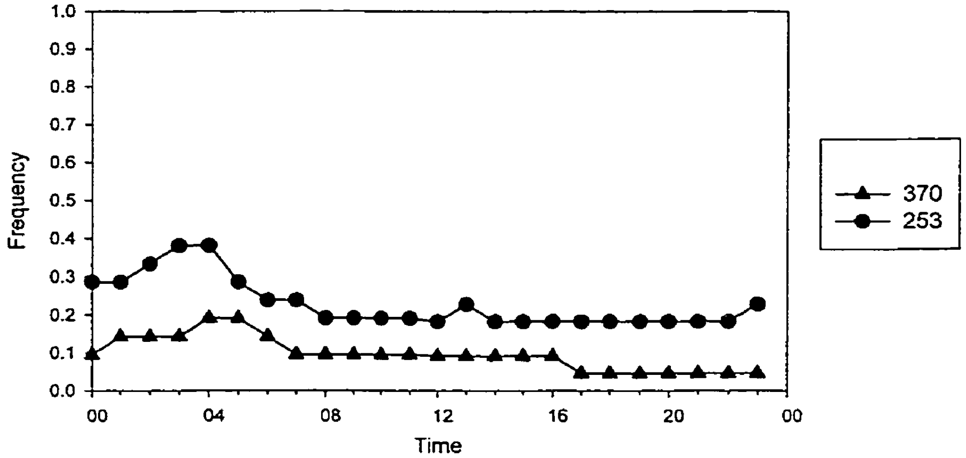
Appendix IV

1) Figures of attendance of individual two-year-old wolves as a function of the time of day in a) 1997, and b) 1998.

a)



b)

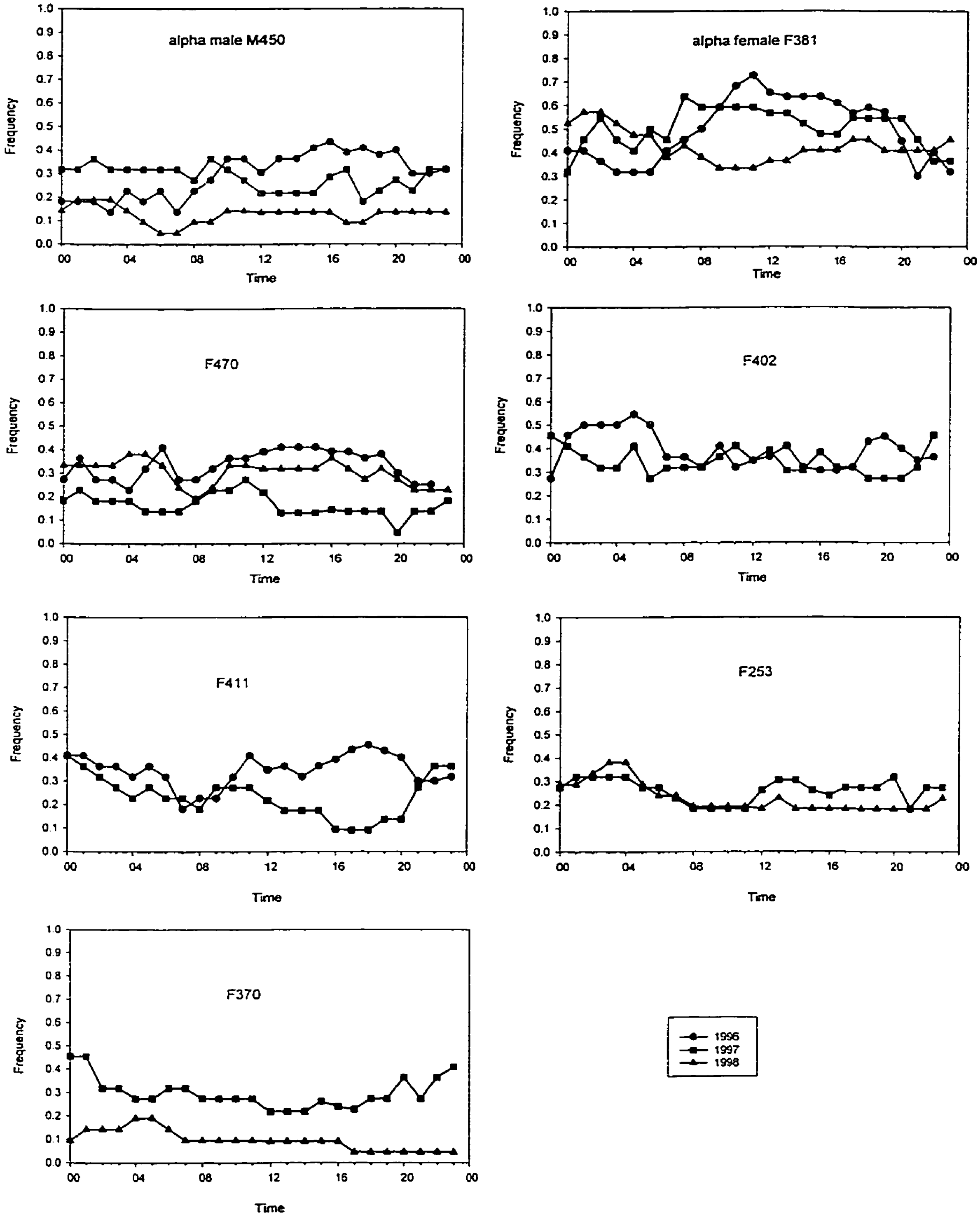


2) Table of attendance of individual two-year-old wolves as a function of the time of day in 1997 and 1997.

	1997			1998	
Time	F402	F470	F411	F370	F253
0:00	0.45	0.18	0.41	0.10	0.29
1:00	0.41	0.23	0.36	0.14	0.29
2:00	0.36	0.18	0.32	0.14	0.33
3:00	0.32	0.18	0.27	0.14	0.38
4:00	0.32	0.18	0.23	0.19	0.38
5:00	0.41	0.14	0.27	0.19	0.29
6:00	0.27	0.14	0.23	0.14	0.24
7:00	0.32	0.14	0.23	0.10	0.24
8:00	0.32	0.18	0.18	0.10	0.19
9:00	0.32	0.23	0.27	0.10	0.19
10:00	0.36	0.23	0.27	0.10	0.19
11:00	0.41	0.27	0.27	0.10	0.19
12:00	0.35	0.22	0.22	0.09	0.18
13:00	0.39	0.13	0.17	0.09	0.23
14:00	0.30	0.13	0.17	0.09	0.18
15:00	0.30	0.13	0.17	0.09	0.18
16:00	0.38	0.14	0.10	0.09	0.18
17:00	0.32	0.14	0.09	0.05	0.18
18:00	0.32	0.14	0.09	0.05	0.18
19:00	0.27	0.14	0.14	0.05	0.18
20:00	0.27	0.05	0.14	0.05	0.18
21:00	0.27	0.14	0.27	0.05	0.18
22:00	0.32	0.14	0.36	0.05	0.18
23:00	0.45	0.18	0.36	0.05	0.23

Appendix V

1) Figures of hourly frequency of attendance for individual wolves across years.



2) Table of hourly frequency of attendance for individual wolves across years from June 7th to July 1st:

	Alpha male (M450)			**Alpha female (F381)**			**Handicap (F470)**			**F402**		**F411**		**F253**		**F370**	
Time	1996	1997	1998	1996	1997	1998	1996	1997	1998	1996	1997	1996	1997	1997	1998	1997	1998
0:00	0.18	0.32	0.14	0.41	0.32	0.52	0.27	0.18	0.33	0.27	0.45	0.41	0.41	0.27	0.29	0.45	0.10
1:00	0.18	0.32	0.19	0.41	0.45	0.57	0.36	0.23	0.33	0.45	0.41	0.41	0.36	0.32	0.29	0.45	0.14
2:00	0.18	0.36	0.19	0.36	0.55	0.57	0.27	0.18	0.33	0.50	0.36	0.36	0.32	0.32	0.33	0.32	0.14
3:00	0.14	0.32	0.19	0.32	0.45	0.52	0.27	0.18	0.33	0.50	0.32	0.36	0.27	0.32	0.38	0.32	0.14
4:00	0.23	0.32	0.14	0.32	0.41	0.48	0.23	0.18	0.38	0.50	0.32	0.32	0.23	0.32	0.38	0.27	0.19
5:00	0.18	0.32	0.10	0.32	0.50	0.48	0.32	0.14	0.38	0.55	0.41	0.36	0.27	0.27	0.29	0.27	0.19
6:00	0.23	0.32	0.05	0.41	0.45	0.38	0.41	0.14	0.33	0.50	0.27	0.32	0.23	0.27	0.24	0.32	0.14
7:00	0.14	0.32	0.05	0.45	0.64	0.43	0.27	0.14	0.24	0.36	0.32	0.18	0.23	0.23	0.24	0.32	0.10
8:00	0.23	0.27	0.10	0.50	0.59	0.38	0.27	0.18	0.19	0.36	0.32	0.23	0.18	0.18	0.19	0.27	0.10
9:00	0.27	0.36	0.10	0.59	0.59	0.33	0.32	0.23	0.24	0.32	0.32	0.23	0.27	0.18	0.19	0.27	0.10
10:00	0.36	0.32	0.14	0.68	0.59	0.33	0.36	0.23	0.33	0.41	0.36	0.32	0.27	0.18	0.19	0.27	0.10
11:00	0.36	0.27	0.14	0.73	0.59	0.33	0.36	0.27	0.33	0.32	0.41	0.41	0.27	0.18	0.19	0.27	0.10
12:00	0.30	0.22	0.14	0.65	0.57	0.36	0.39	0.22	0.32	0.35	0.35	0.35	0.22	0.26	0.18	0.22	0.09
13:00	0.36	0.22	0.14	0.64	0.57	0.36	0.41	0.13	0.32	0.36	0.39	0.36	0.17	0.30	0.23	0.22	0.09
14:00	0.36	0.22	0.14	0.64	0.52	0.41	0.41	0.13	0.32	0.41	0.30	0.32	0.17	0.30	0.18	0.22	0.09
15:00	0.41	0.22	0.14	0.64	0.48	0.41	0.41	0.13	0.32	0.32	0.30	0.36	0.17	0.26	0.18	0.26	0.09
16:00	0.43	0.29	0.14	0.61	0.48	0.41	0.39	0.14	0.36	0.30	0.38	0.39	0.10	0.24	0.18	0.24	0.09
17:00	0.39	0.32	0.09	0.57	0.55	0.45	0.39	0.14	0.32	0.30	0.32	0.43	0.09	0.27	0.18	0.23	0.05
18:00	0.41	0.18	0.09	0.59	0.55	0.45	0.36	0.14	0.27	0.32	0.32	0.45	0.09	0.27	0.18	0.27	0.05
19:00	0.38	0.23	0.14	0.57	0.55	0.41	0.38	0.14	0.32	0.43	0.27	0.43	0.14	0.27	0.18	0.27	0.05
20:00	0.40	0.27	0.14	0.45	0.55	0.41	0.30	0.05	0.27	0.45	0.27	0.40	0.14	0.32	0.18	0.36	0.05
21:00	0.30	0.23	0.14	0.30	0.45	0.41	0.25	0.14	0.23	0.40	0.27	0.30	0.27	0.18	0.18	0.27	0.05
22:00	0.30	0.32	0.14	0.40	0.36	0.41	0.25	0.14	0.23	0.35	0.32	0.30	0.36	0.27	0.18	0.36	0.05
23:00	0.32	0.32	0.14	0.32	0.36	0.45	0.27	0.18	0.23	0.36	0.45	0.32	0.36	0.27	0.23	0.41	0.05

Appendix VI

Arrivals and departure events for individual wolves by 6-hour time bloc in a) 1996, b) 1997, and c) 1998. (all available data for each year used)

a)

1) Arrivals:

Blocs	M450	F381	F402	F470	F421	F411
22:00-3:59	15	15	16	7	16	14
4:00-9:59	12	20	13	12	12	8
10:00-15:59	6	6	4	3	4	5
16:00-21:59	6	3	9	3	5	5

2) Departures:

Blocs	M450	F381	F402	F470	F421	F411
22:00-3:59	18	10	6	10	5	7
4:00-9:59	10	13	19	11	20	15
10:00-15:59	4	3	7	4	4	5
16:00-21:59	8	14	9	3	7	9

b)

1) Arrivals:

Blocs	M450	F381	F402	F470	F411	F331	F253	F370
22:00-3:59	7	12	10	6	7	14	8	12
4:00-9:59	11	11	6	9	5	13	7	6
10:00-15:59	4	2	3	2	2	2	7	3
16:00-21:59	6	4	4	4	8	1	8	8

2) Departures:

Blocs	M450	F381	F402	F470	F411	F331	F253	F370
22:00-3:59	7	10	7	5	6	5	6	15
4:00-9:59	5	10	8	9	9	13	11	6
10:00-15:59	7	4	3	4	5	5	5	3
16:00-21:59	10	5	5	3	0	6	10	4

c)

1) Arrivals:

Blocs	M450	F381	F370	F253	F180	F552	F470
22:00-3:59	8	9	8	8	11	5	9
4:00-9:59	8	6	5	2	9	5	9
10:00-15:59	3	2	1	2	6	4	4
16:00-21:59	4	5	3	3	5	5	8

2) Departures:

Blocs	M450	F381	F370	F253	F180	F552	F470
22:00-3:59	5	3	6	4	7	3	6
4:00-9:59	10	12	4	8	16	9	8
10:00-15:59	3	5	2	1	2	3	5
16:00-21:59	4	3	6	1	6	4	10

Appendix VII

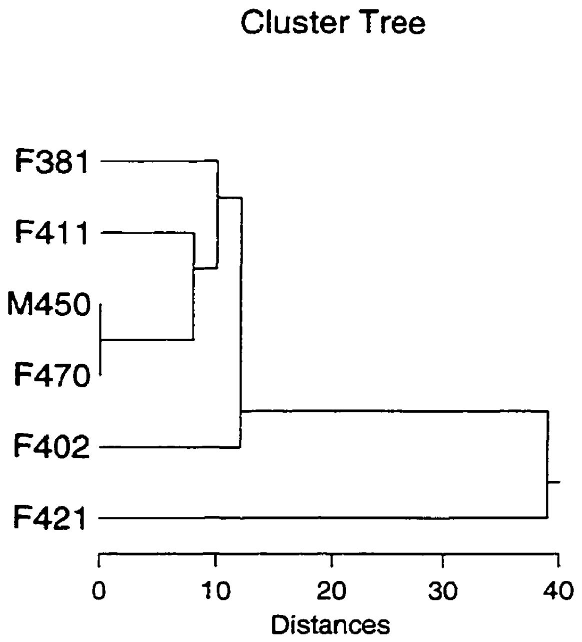
Single linkage cluster analysis of the frequency of individual wolves arriving and departing together in a) 1996, b) 1997, and c) 1998. Wolves were considered to have arrived together when events occurred within a time frame of 30 minutes.

a) 1996

1) Similarity matrix of arrivals for individual wolves where similarity = (xy/x+y)*1000.

	450	402	381	470	421	411
450						
402	79					
381	92	71				
470	102	90	30			
421	45	53	27	0		
411	94	83	69	91	63	

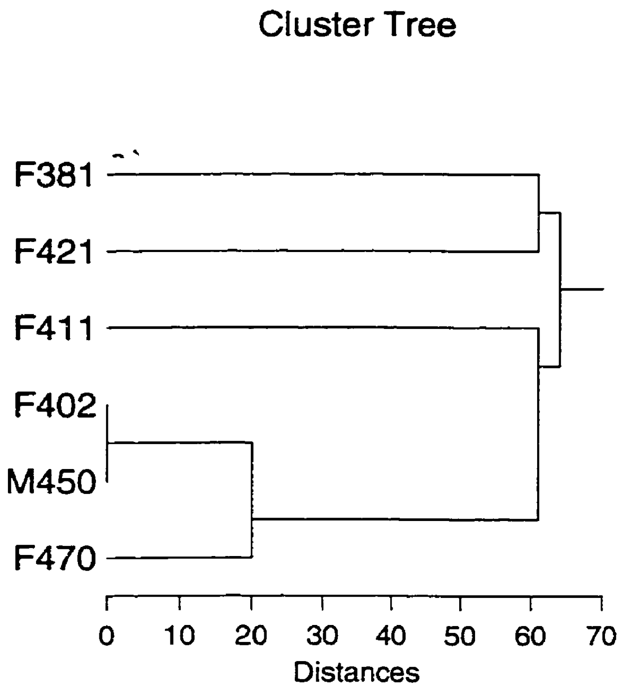
Single linkage cluster analysis solution for arrivals:



2) Similarity matrix of departures for individual wolves where similarity = (xy/x+y)*1000.

	450	402	381	470	421	411
450						
402	200					
381	133	128				
470	180	94	125			
421	101	111	139	86		
411	130	139	125	86	136	

Single linkage cluster analysis solution for arrivals:



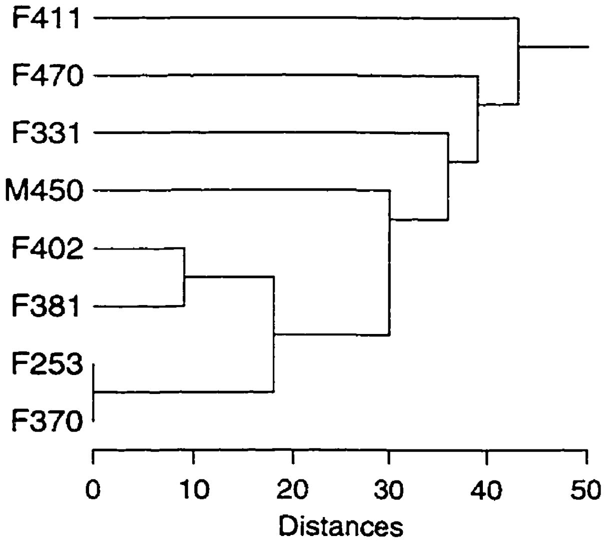
b) 1997

1) Similarity matrix of arrivals for individual wolves where similarity = (xy/x+y)*1000.

	450	381	402	470	411	331	253	370
450								
381	38							
402	43	98						
470	68	21	0					
411	47	64	24	51				
331	58	36	39	63	42			
253	77	89	20	63	21	71		
370	38	54	39	21	43	0	107	

Single linkage cluster analysis solution for arrivals:

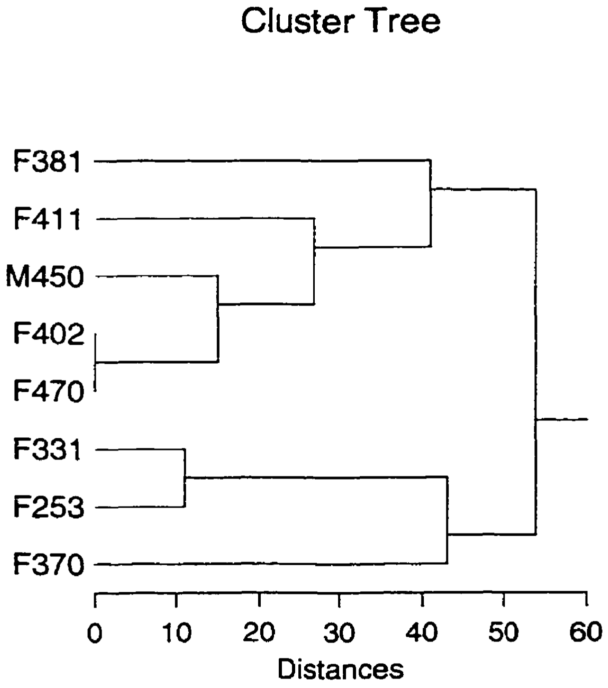
Cluster Tree



2) Similarity matrix of departures for individual wolves where similarity = (xy/x+y)*1000.

	450	381	402	470	411	331	253	370
450								
381	75							
402	128	77						
470	93	42	143					
411	114	102	116	103				
331	38	70	78	85	63			
253	82	74	42	23	89	132		
370	61	74	83	45	44	19	100	

Single linkage cluster analysis solution for arrivals:

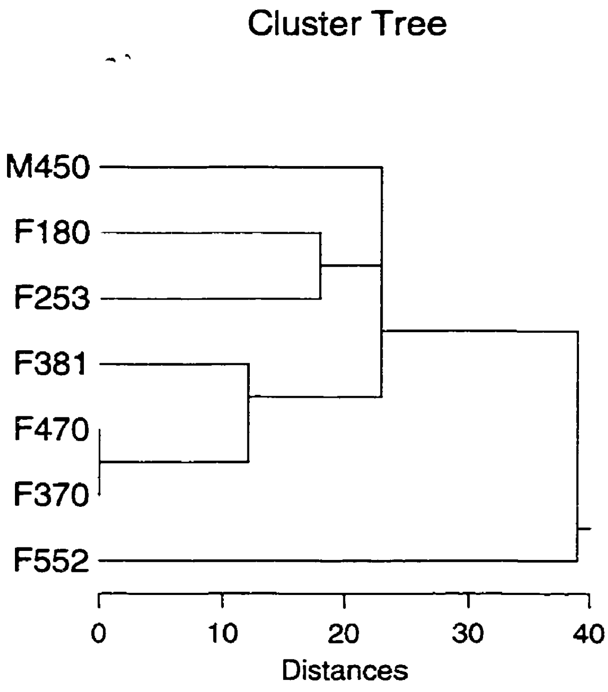


c) 1998

1) Similarity matrix of arrivals for individual wolves where similarity = (xy/x+y)*1000.

	450	381	370	253	180	552	470
450							
381	50						
370	30	27					
253	30	54	0				
180	54	49	29	59			
552	34	0	38	0	0		
592	48	65	77	51	0	0	

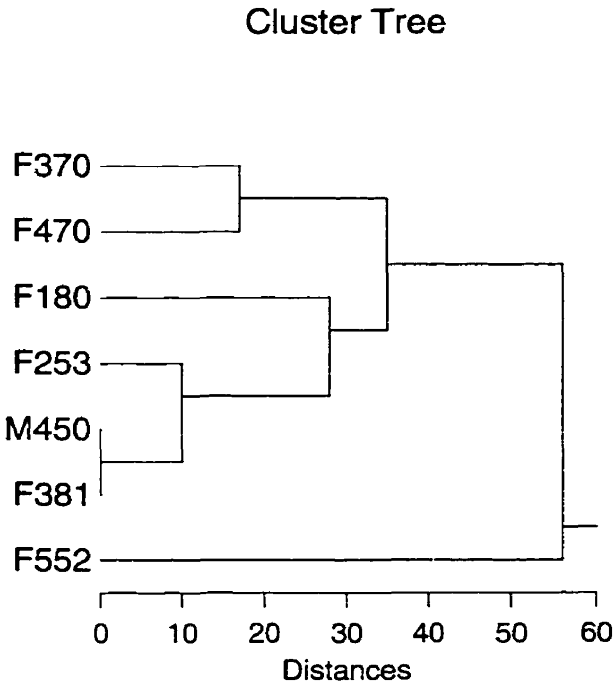
Single linkage cluster analysis solution for arrivals:



2) Similarity matrix of departures for individual wolves where similarity = (xy/x+y)*1000.

	450	381	370	253	180	552	592
450							
381	171						
370	91	50					
253	161	53	133				
180	105	133	81	143			
552	34	28	0	115	61		
592	125	85	154	81	136	57	

Single linkage cluster analysis solution for arrivals:



Appendix VIII

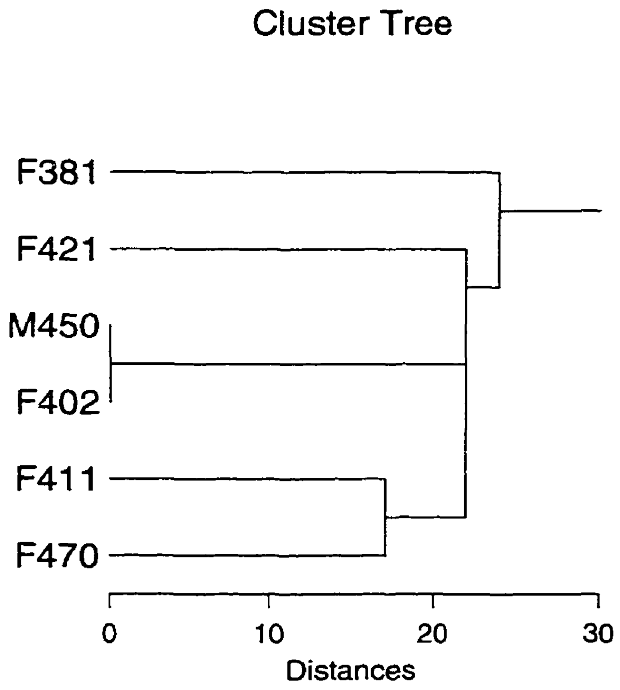
Single linkage cluster analysis of attendance of individual wolves at the densite in a) 1996, b) 1997, and c) 1998.

a) 1996

Similarity matrix of attendance for individual wolves where similarity = (xy/x+y)*1000.

	450	402	381	470	421	411
450						
402	247					
381	206	223				
470	152	171	156			
421	222	213	162	168		
411	180	225	207	230	225	

Single linkage cluster analysis solution for arrivals:



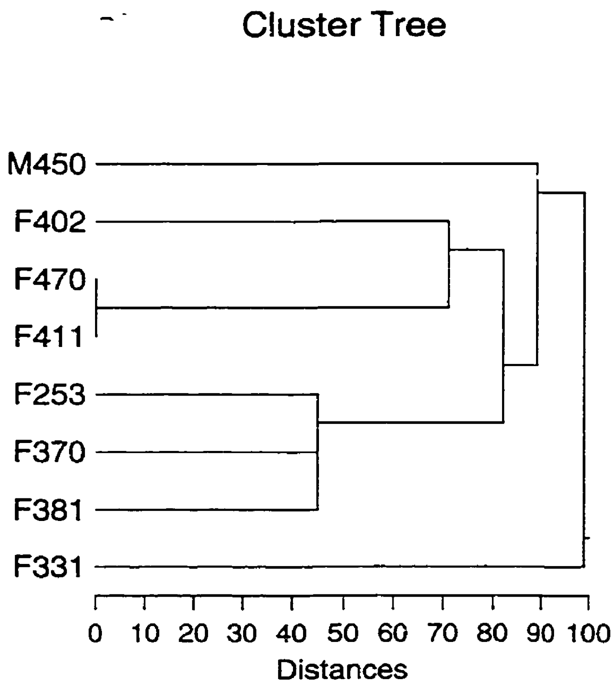
Cluster Tree

b) 1997

Similarity matrix of attendance for individual wolves where similarity = (xy/x+y)*1000.

	450	381	402	470	411	331	253	370
450								
381	203							
402	236	218						
470	150	153	254					
411	159	192	238	325				
331	163	171	226	163	100			
253	162	237	170	163	243	113		
370	228	280	232	190	196	119	280	

Single linkage cluster analysis solution for arrivals:

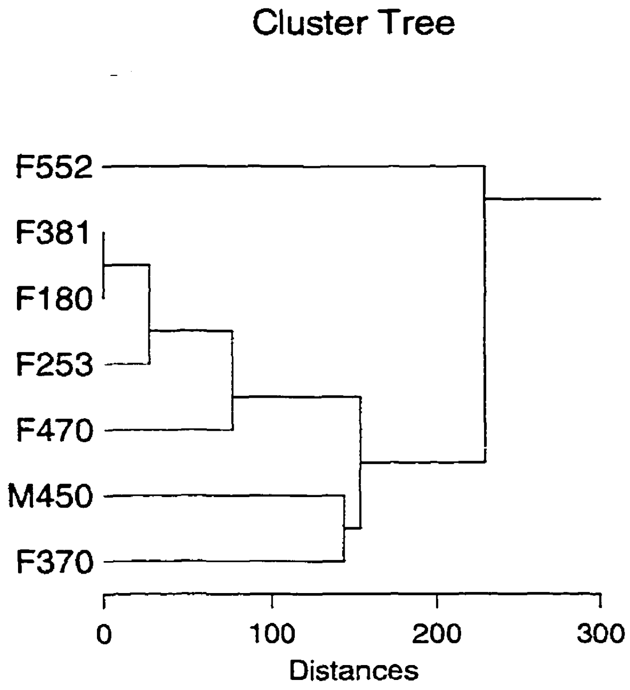


c) 1998

Similarity matrix of attendance for individual wolves where similarity = (xy/x+y)*1000.

	450	381	370	253	180	552	592
450							
381	171						
370	188	67					
253	78	176	97				
180	154	333	73	306			
552	104	64	0	8	62		
470	178	236	157	240	257	5	

Single linkage cluster analysis solution for arrivals:



Appendix IX

Three-day moving average and regression analysis on daily attendance of individual wolves at the densite in a) 1996, b) 1997, and c) 1998.

Only days that were monitored for at least 70% of the time were used for the analysis and missing values were interpolated by local quadratic smoothing.

a) 1996

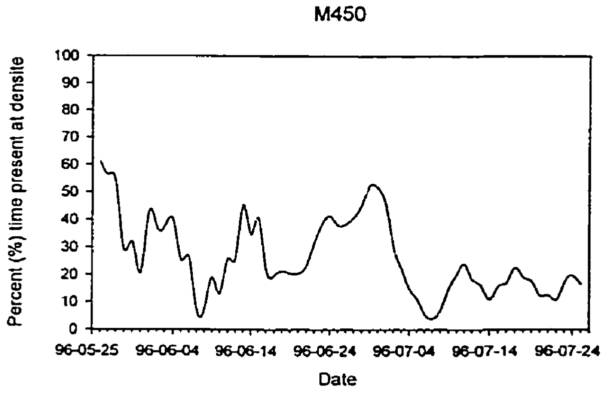
Table of attendance of individual wolves after smoothing with three-day moving average. (highlighted sections represent days interpolated by local quadratic smoothing).

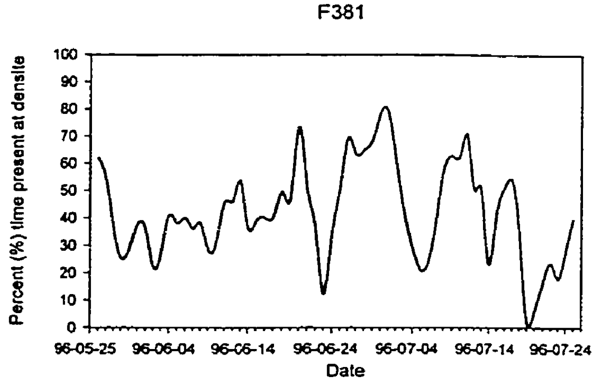
Date	M450	F402	F381	F470	F421	F411
5/26/96	61.22	63.95	61.90	34.01	51.02	44.22
5/27/96	56.39	55.60	54.15	47.95	28.30	27.03
5/28/96	**53.68**	**53.80**	**36.42**	**65.11**	**14.63**	**19.24**
5/29/96	**29.19**	**38.83**	**25.54**	**55.59**	**22.79**	**31.49**
5/30/96	31.98	43.09	28.53	37.57	30.54	52.08
5/31/96	20.41	28.57	37.41	48.98	22.45	40.82
6/01/96	42.86	55.10	36.05	31.29	31.97	55.10
6/02/96	37.41	65.31	22.45	29.93	19.73	26.53
6/03/96	37.41	94.56	26.53	1.36	19.73	45.58
6/04/96	40.14	81.63	40.82	0.00	22.45	19.05
6/05/96	25.17	48.98	38.10	0.00	20.41	19.05
6/06/96	26.53	39.46	40.14	28.57	42.18	17.01
6/07/96	7.48	27.89	36.05	31.97	21.77	17.01
6/08/96	7.48	33.33	38.10	62.59	28.57	34.01
6/09/96	19.05	34.69	28.57	36.05	19.05	44.90
6/10/96	12.93	33.33	30.61	32.65	19.05	65.99
6/11/96	25.93	47.40	45.64	23.99	38.26	55.48
6/12/96	25.77	38.83	46.08	32.72	39.39	38.13
6/13/96	**45.50**	**36.79**	**53.56**	**32.72**	**43.47**	**26.57**
6/14/96	34.53	36.32	36.49	29.81	39.23	39.79
6/15/96	40.82	43.54	38.78	40.82	37.41	29.25
6/16/96	21.77	44.22	40.14	40.82	33.33	23.81
6/17/96	19.73	40.14	40.14	21.77	11.56	20.41
6/18/96	21.09	20.41	49.66	0.68	19.73	22.45
6/19/96	20.41	23.81	46.94	16.33	26.53	18.37
6/20/96	20.41	21.09	73.47	42.18	32.65	16.33

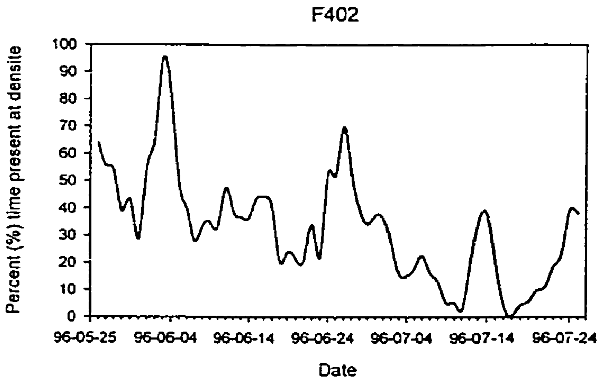
Table of attendance of individual wolves after smoothing with three-day moving average. (cont.)

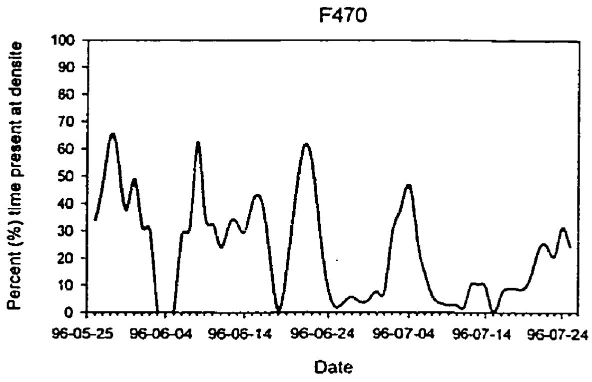
Date	M450	F402	F381	F470	F421	F411
6/21/96	18.37	21.09	51.02	61.22	34.69	31.97
6/22/96	30.61	34.01	36.73	53.74	42.86	40.82
6/23/96	46.26	21.77	12.24	27.89	38.10	27.21
6/24/96	38.78	52.38	34.01	8.16	43.54	18.37
6/25/96	38.76	51.88	50.52	1.71	48.28	16.29
6/26/96	**36.18**	**69.82**	**69.35**	**3.79**	**64.06**	**21.22**
6/27/96	**40.17**	**53.05**	**63.59**	**5.54**	**51.27**	**15.97**
6/28/96	**45.96**	**39.89**	**64.85**	**3.83**	**43.27**	**9.21**
6/29/96	50.58	34.14	68.63	4.71	35.80	7.47
6/30/96	**60.87**	**37.30**	**78.47**	**7.73**	**27.50**	**12.03**
7/01/96	42.85	36.00	79.07	7.73	19.19	12.03
7/02/96	33.33	27.21	62.59	29.25	21.09	12.93
7/03/96	14.73	15.81	43.20	38.13	25.15	8.32
7/04/96	**18.79**	**15.18**	**29.29**	**46.66**	**33.43**	**10.82**
7/05/96	**10.63**	**17.91**	**21.13**	**26.25**	**38.88**	**6.05**
7/06/96	4.06	22.51	23.50	14.65	35.49	7.26
7/07/96	2.04	16.33	37.41	6.12	24.49	8.16
7/08/96	5.80	12.87	56.88	3.40	10.54	12.72
7/09/96	**12.88**	**5.08**	**62.75**	**2.62**	**6.30**	**13.81**
7/10/96	**25.81**	**5.08**	**62.75**	**2.62**	**5.62**	**16.54**
7/11/96	22.05	2.42	70.49	1.94	5.96	28.31
7/12/96	23.81	17.69	50.34	10.20	12.93	31.29
7/13/96	8.84	34.01	50.34	10.20	12.93	29.93
7/14/96	15.65	38.10	23.13	9.52	9.52	13.61
7/15/96	8.16	20.41	41.50	0.00	0.00	4.76
7/16/96	23.81	4.08	51.02	6.80	0.00	12.24
7/17/96	19.05	0.00	53.74	8.84	25.85	13.61
7/18/96	25.17	4.08	35.37	8.84	25.85	13.61
7/19/96	12.93	5.44	2.72	8.84	25.85	1.36
7/20/96	14.82	9.70	5.67	13.92	4.77	2.12
7/21/96	**9.37**	**11.06**	**15.88**	**24.12**	**12.94**	**4.84**
7/22/96	13.46	18.54	23.36	24.12	22.46	11.65
7/23/96	9.52	23.13	17.69	21.09	24.49	10.20
7/24/96	28.57	38.78	26.53	31.29	16.33	19.05
7/25/96	21.09	38.10	39.46	24.49	12.93	18.37

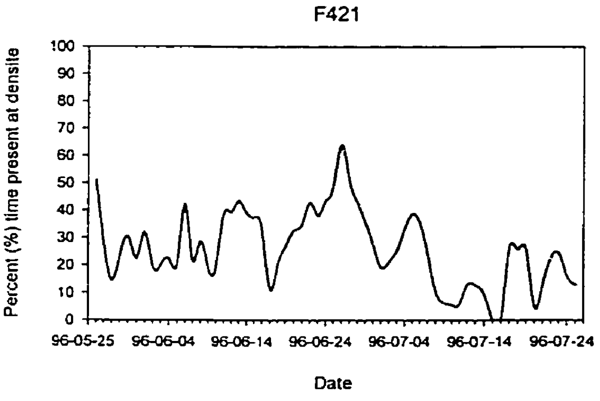
Figures of attendance of individual wolves after smoothing with three-day moving average for 1996.

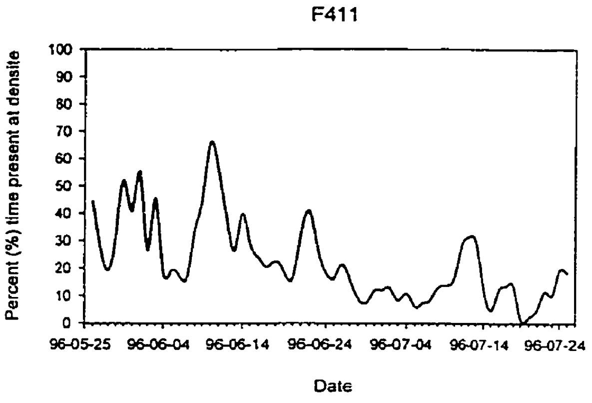












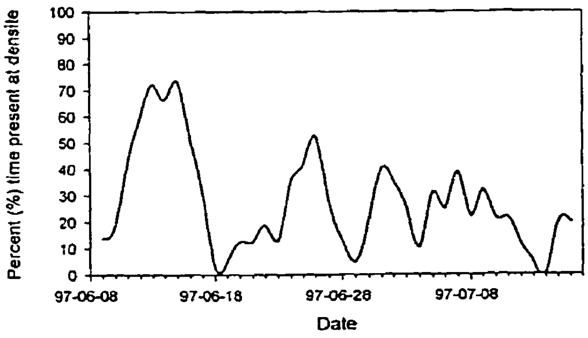
b) 1997

Table of attendance of individual wolves after smoothing with three-day moving average. (highlighted sections represent days interpolated by local quadratic smoothing).

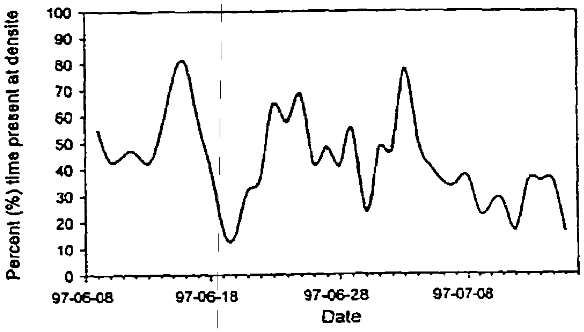
Date	M450	F381	F402	F470	F411	F331	F253	F370
6/9/97	13.89	54.86	40.97	11.81	19.44	23.61	17.36	11.11
6/10/97	18.75	43.06	45.83	15.28	25.00	44.44	14.58	8.33
6/11/97	42.36	45.14	39.58	11.81	22.92	47.22	25.00	26.39
6/12/97	59.16	46.28	35.84	9.94	12.41	67.12	25.86	42.92
6/13/97	**72.18**	**42.25**	**43.76**	**10.36**	**10.98**	**60.14**	**33.66**	**61.48**
6/14/97	**66.23**	**54.74**	**51.27**	**21.89**	**22.14**	**49.84**	**22.80**	**57.94**
6/15/97	**73.74**	**73.74**	**70.28**	**40.42**	**38.19**	**41.75**	**12.22**	**67.79**
6/16/97	52.39	80.55	54.03	34.45	31.99	25.81	7.20	52.70
6/17/97	30.56	59.03	46.53	22.92	22.22	20.14	2.78	32.64
6/18/97	2.78	40.97	14.58	5.56	22.92	9.72	13.89	3.47
6/19/97	4.86	16.67	36.11	30.56	40.28	30.56	15.28	0.00
6/20/97	12.50	15.28	29.17	30.56	38.89	22.92	15.28	0.00
6/21/97	12.50	31.94	28.47	25.69	18.06	21.53	9.03	31.25
6/22/97	18.75	36.81	26.39	0.00	4.17	11.81	5.56	32.64
6/23/97	13.19	64.58	20.14	0.00	17.36	11.81	35.42	45.83
6/24/97	35.42	57.64	34.03	3.47	22.22	11.81	40.28	27.08
6/25/97	41.54	68.42	22.69	6.22	22.43	2.36	47.05	36.04
6/26/97	**52.65**	**42.03**	**22.69**	**6.22**	**9.23**	**2.36**	**17.19**	**27.02**
6/27/97	27.65	48.28	25.47	20.11	18.95	25.98	22.75	43.68
6/28/97	13.19	40.97	36.11	17.36	14.58	25.00	15.28	37.50
6/29/97	4.86	54.86	40.97	17.36	17.36	25.00	22.92	43.06
6/30/97	20.83	23.61	23.61	0.00	9.03	4.86	7.64	17.36
7/1/97	40.28	47.92	16.67	0.00	15.28	3.47	10.42	15.97
7/2/97	35.42	47.22	12.50	0.00	12.50	4.86	6.25	30.56
7/3/97	25.69	77.78	26.39	21.53	13.89	8.33	6.25	33.33
7/4/97	10.42	52.08	17.36	28.47	11.81	21.53	8.33	34.72
7/5/97	31.25	40.97	16.67	28.47	11.81	40.28	29.17	10.42
7/6/97	25.00	34.72	20.83	6.94	4.17	33.33	29.17	4.17
7/7/97	38.89	34.03	18.06	1.39	3.47	20.83	45.83	17.36
7/8/97	22.22	36.81	18.06	4.17	9.72	4.17	27.78	18.75
7/9/97	32.37	23.37	15.22	4.17	16.24	7.79	28.50	18.75
7/10/97	21.58	26.41	24.08	3.57	17.25	11.17	12.87	3.07
7/11/97	**21.80**	**27.45**	**29.22**	**1.94**	**13.57**	**12.29**	**16.44**	**3.21**
7/12/97	**11.66**	**16.59**	**14.00**	**3.80**	**7.04**	**13.52**	**31.69**	**3.21**
7/13/97	4.39	34.84	6.53	3.00	2.57	15.23	32.97	1.53
7/14/97	0.00	35.42	8.33	1.85	0.00	23.61	48.84	18.29
7/15/97	19.91	35.42	8.33	8.56	0.00	18.75	32.87	23.15
7/16/97	19.91	16.20	6.94	8.56	6.25	12.96	25.69	49.31

Figures of attendance of individual wolves after smoothing with three-day moving average for 1997.

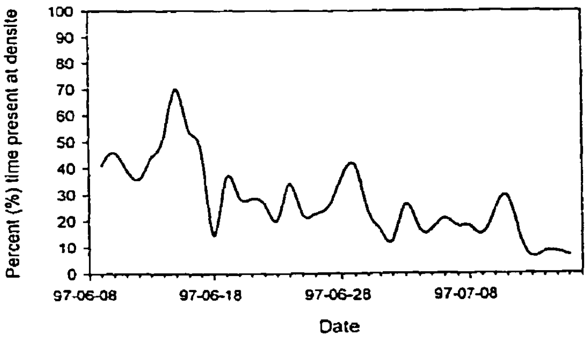
M450



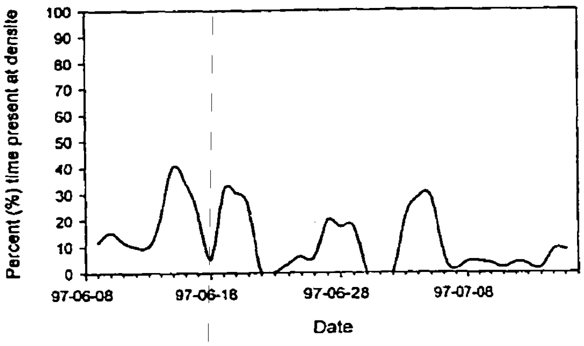
F381



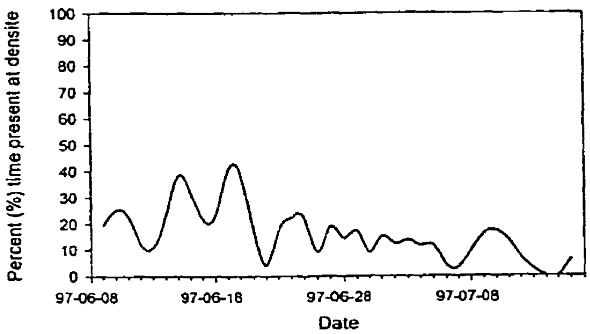
F402



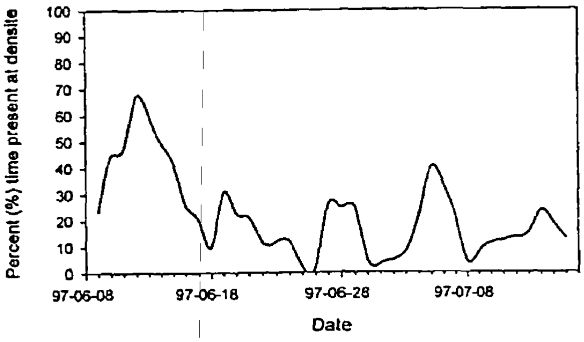
F470



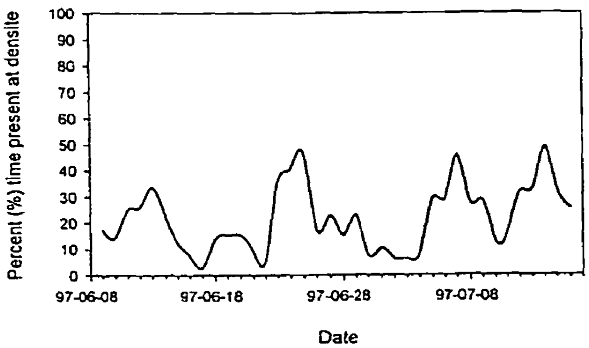
F411



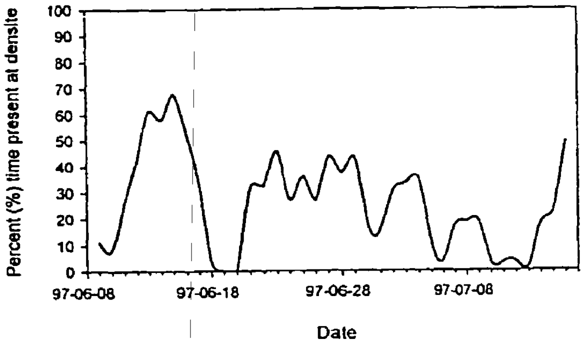
F331



F253



F370



c) 1998

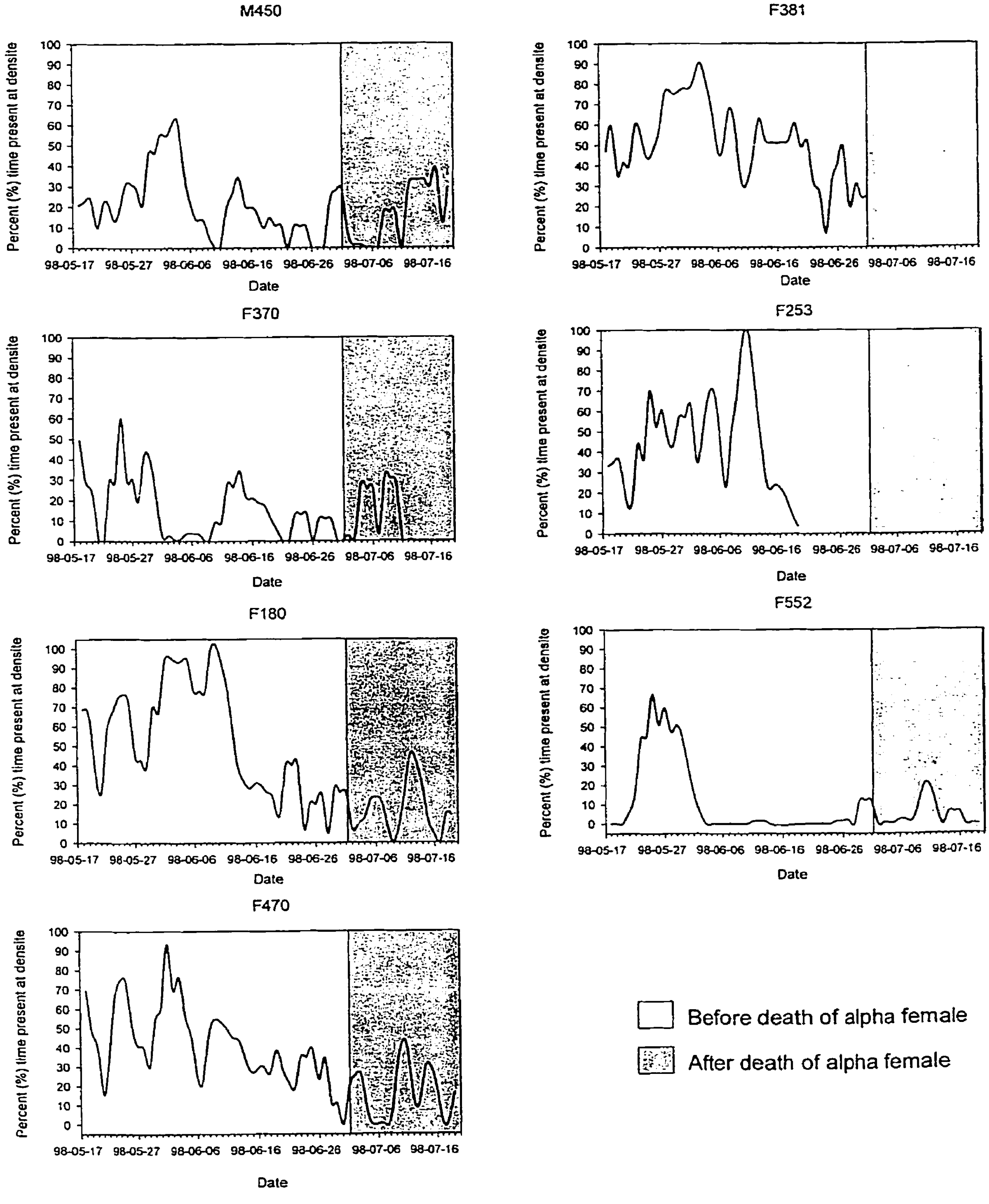
Table of attendance of individual wolves after smoothing with three-day moving average. (highlighted sections represent days interpolated by local quadratic smoothing).

Date	M450	F381	F370	F253	F180	F552	F470
5/18/98	20.83	47.22	49.31	33.33	68.75	0.00	69.44
5/19/98	22.92	59.03	28.47	35.42	64.58	0.00	47.92
5/20/98	22.92	35.52	23.61	35.42	37.65	0.00	38.61
5/21/98	9.95	41.54	2.08	18.06	26.08	6.48	15.46
5/22/98	20.83	40.15	0.00	15.97	55.48	17.36	36.99
5/23/98	20.83	59.95	29.63	44.21	66.90	43.98	67.13
5/24/98	13.19	52.78	29.63	36.57	74.77	45.37	75.46
5/25/98	20.37	43.52	60.19	69.91	76.62	66.67	73.38
5/26/98	31.25	47.92	30.56	52.55	70.60	50.93	50.93
5/27/98	31.02	58.56	30.56	60.65	44.44	59.72	40.74
5/28/98	27.78	75.93	19.21	46.76	42.59	47.69	39.12
5/29/98	21.30	75.93	40.51	43.98	39.81	50.93	30.09
5/30/98	45.67	75.89	40.51	57.52	69.51	44.06	55.09
5/31/98	46.10	77.97	23.89	57.30	67.04	29.66	61.83
6/01/98	**55.36**	**77.97**	**2.59**	**62.85**	**92.04**	**15.54**	**93.31**
6/02/98	54.83	83.56	2.59	35.66	95.68	5.73	69.93
6/03/98	60.65	90.74	0.69	49.77	93.75	0.00	76.62
6/04/98	61.11	80.32	0.69	67.36	93.75	0.00	56.02
6/05/98	37.27	66.20	3.47	69.21	93.75	0.00	46.06
6/06/98	21.76	46.76	3.70	47.92	78.24	0.00	24.77
6/07/98	13.66	50.00	3.70	22.69	78.24	0.00	22.69
6/08/98	13.66	67.36	0.93	47.45	78.24	0.00	46.76
6/09/98	6.71	59.03	0.23	68.75	100.00	0.00	54.63
6/10/98	0.69	32.87	9.49	96.06	100.00	0.00	53.01
6/11/98	0.69	32.41	9.49	97.22	87.50	1.39	49.31
6/12/98	19.44	45.83	28.47	71.06	69.21	1.39	44.91
6/13/98	26.77	63.09	26.54	45.06	43.21	1.39	43.21
6/14/98	34.28	53.37	34.31	23.08	32.69	-0.14	32.49
6/15/98	**21.55**	**51.33**	**22.16**	**23.65**	**28.07**	**-0.36**	**26.88**
6/16/98	**19.92**	**51.05**	**21.04**	**22.54**	**30.73**	**-0.58**	**29.48**
6/17/98	**16.41**	**51.48**	**18.62**	**17.69**	**29.38**	**-0.58**	**29.47**
6/18/98	**9.70**	**53.06**	**17.34**	**9.94**	**25.90**	**-0.36**	**26.74**

Table of attendance of individual wolves after smoothing with three-day moving average. (cont.)

Date	M450	F381	F370	F253	F180	F552	F470
6/19/98	14.65	60.63	11.14	3.73	22.62	-0.14	38.33
6/20/98	10.65	48.84	5.79	-	13.66	0.00	28.70
6/21/98	10.65	52.08	0.00	-	39.58	0.00	21.53
6/22/98	0.00	31.71	0.00	-	40.05	0.00	18.75
6/23/98	10.42	25.93	12.96	-	40.05	0.00	34.95
6/24/98	10.42	6.71	12.96	-	7.18	0.00	34.95
6/25/98	10.42	31.25	12.96	-	19.91	1.62	39.35
6/26/98	0.00	40.28	0.00	-	19.91	1.62	23.38
6/27/98	0.00	48.84	10.65	-	24.77	1.62	34.49
6/28/98	0.00	20.14	10.65	-	4.86	0.00	11.34
6/29/98	22.69	30.56	10.65	-	27.78	12.04	11.11
6/30/98	28.01	24.77	0.00	-	25.93	12.04	0.00
7/01/98	28.01	24.77	0.00	-	25.93	12.04	18.75
7/02/98	6.66	-	2.35	-	7.02	0.55	25.57
7/03/98	**1.34**	**-**	**2.35**	**-**	**10.09**	**0.55**	**25.57**
7/04/98	1.34	-	27.82	-	12.64	0.55	6.82
7/05/98	0.00	-	25.46	-	21.83	0.69	0.00
7/06/98	0.00	-	25.46	-	23.61	2.31	0.00
7/07/98	0.00	-	3.24	-	21.06	2.31	0.00
7/08/98	17.13	-	30.56	-	7.87	2.08	2.55
7/09/98	17.13	-	30.56	-	0.00	10.42	27.08
7/10/98	17.13	-	27.31	-	10.88	20.14	42.13
7/11/98	0.00	-	0.00	-	28.01	19.68	39.58
7/12/98	25.93	-	0.00	-	45.83	9.72	15.05
7/13/98	33.10	-	0.00	-	42.13	0.00	10.88
7/14/98	33.10	-	0.00	-	28.94	6.02	29.40
7/15/98	33.10	-	0.00	-	11.11	6.02	29.40
7/16/98	30.32	-	0.00	-	3.94	6.02	18.52
7/17/98	38.19	-	0.00	-	0.00	0.00	1.62
7/18/98	12.27	-	0.00	-	14.35	0.00	1.62
7/19/98	29.40	-	0.00	-	14.35	0.00	16.44

Figure of attendance of individual wolves after smoothing with three-day moving average for 1998.



3. Vocal and behavioral responses of wolves to two different types of simulated howling

S. Czetwertynski[a], P. McLeod[a]

a Biology Department, Horton Hall, Acadia University
Wolfville, Nova Scotia, Canada
B0P 1X0

Corresponding author:

Sophie Czetwertynski
5797 Ave de la Terrasse
Rawdon, PQ
J0K 1S0

3.1 Abstract:

Two wolf packs equipped with radio collars in the Laurentide reserve, Quebec, were subjected to a regime of simulated howls near their respective rendezvous sites in 1996 and 1997 to examine the factors affecting howling response rate and subsequent movements of all wolves within hearing distance of the broadcast howls. Two types of simulated howls were used; one consisting of howls of an unknown pack of wolves, and another recorded from a single coyote. The number of wolves present at the rendezvous site was found to be the most important factor affecting response rate. Wolves responded more readily to the simulated wolf howls than to the coyote howl, regardless of the number of wolves present. Both simulated howls and those of packmates at rendezvous sites were found to affect the behavior of distant wolves and often caused individuals to immediately return to rendezvous sites. Wolves' behavior was found to be less affected by stimulation from the coyote howl than when recorded wolf howls were played. These results are of importance to both the ecotourism industry and wildlife officials using howling surveys to estimate wolf population densities.

3.2 Introduction:

Wolves are social carnivores (Mech 1970) which implies the need for a sophisticated or developed vocal repertoire for intra-pack communication. Although many different types of vocalizations have been identified (Harrington and Mech 1978b; Lehner 1978), only howling can be heard over long enough distances to also serve in inter-pack communication (Joslin 1967; Harrington and Mech 1978b). Howls have been described as continuous sounds with a fundamental pitch from 150 to 780 Hz (Theberge and Falls 1967; Harrington and Mech 1978a) and, under good atmospheric conditions and in relatively level landscapes, can be heard from 9 to 16 km away (Henshaw and Stephenson 1974, Harrington and Mech 1979).

Wolves have a complex spatial organization (Mech 1972) which is maintained through a combination of auditory (Harrington and Mech 1979; Harrington and Mech 1983) and olfactory (Peters and Mech 1975) cues. Because howling can be heard over long distances, it can be used as a territory-independent method of advertising and defending a territory from alien conspecifics (Harrington and Mech 1983). Furthermore, wolves have the potential to discriminate between howls of pack members and those of foreign wolves (Theberge and Falls 1967; Tooze et al. 1990). Therefore, howling can provide information not only on the number of wolves and their location but also about their identity. In this way, wolves may be able to avoid encounters with unfamiliar animals

(Harrington and Mech 1979) which often result in fighting, injuries, and even deaths (Van Ballenberghe and Erikson 1973; Mech 1977).

Within a pack, howling also serves to bring together members of the pack (Murie 1944, Mech 1966; Rutter and Pimlott 1968) and may also announce the approach of wolves to den and rendezvous sites (Harrington and Mech 1978b). Because wolves are able to produce and distinguish between a wide variation in sound, they have the potential to convey motivational information in intra-pack communication (Fentress 1967; Theberge and Falls 1967), although evidence for this is lacking.

Spontaneous howling can be heard at all times of the day and year (Joslin 1967; Mech 1970) but there are both daily and seasonal trends in howling frequency (Joslin 1967; Harrington and Mech 1978a,b). This seasonal variation has also been observed in the long-range vocalizations of coyotes (Laundre 1981; Okoniewski and Chambers 1984; Gese and Ruff 1998), dingos (Corbett and Newsome 1975) and golden jackals (Jaeger et al. 1996). Wolves tend to howl more often at dusk and dawn (Rutter and Pimlott 1968; Harrington and Mech 1978b) and howling frequency increases around the breeding season and during July and August in both captive (Fentress 1967; Klinhammer and Laidlaw 1979; Zimen 1975) and wild packs (Joslin 1967; Harrington and Mech 1978a).

Wolf howls have recently become a tool in population estimation and education. When recorded howls are played, wild wolves seem to respond in an inter-pack context, do not readily habituate to the simulations (Harrington and Mech 1979), and the frequency of eliciting a response is correlated to the daily and seasonal trends described for spontaneous howling (Harrington and Mech 1978b). Although time consuming and inherently biased (Crête and Messier 1987; Fuller and Sampson 1988), simulated howling has been used as a method of estimating wolf population numbers when detailed information from radio-telemetry and aerial counts are not available (Joslin 1967; Theberge and Strickland 1978; Harrington and Mech 1982; Gaines et al. 1995). In addition, due to the general appeal of hearing "the call of the wild", ecotourism companies have begun organizing "wolf-howling" excursions, as early as 1963, where people are taken near den and rendezvous sites to listen to wolves respond to simulated howling (Carbyn 1979). These excursions have become increasingly popular in recent years.

Apart for the seasonal variation, other factors have also been suggested to influence whether or not wolves will respond to simulated howling. Joslin (1967) offers some information on factors that might influence response rate but results are vague since it was not known whether there were any wolves within hearing distance of the stimulations and the context within which wolves responded was unknown (ie. at kill sites, rendezvous sites, travelling). Harrington and Mech (1979) looked at responses to simulated howling at rendezvous and kill sites of two wolf packs over two years and one pack during a single season. They found that response rate per session (RR/S), the time to response, and the duration of howls were positively correlated with pack size. Wolves respond to simulated howling in an intra-specific fashion (Harrington and Mech 1979) and therefore their rate of response will depend on factors surrounding to that particular situation. Harrington (1975) compared the response rates of wolves in different situations and found that the response rate was highest at kill and rendezvous sites because these represented valuable resources that are not easily moved. Therefore, the wolves are better off responding than potentially encountering the intruder(s) (Harrington 1975, 1979).

Harrington (1987) found that the howls of wolves approaching the site of the simulated howls were lower pitched that those of wolves not approaching and suggested that these lower pitched howls designate a greater level of hostility. Therefore the fact that responses to simulated howling tend to be lower in pitch than spontaneous ones in both wild and captive wolves (Theberge and Falls 1967; Harrington and Mech 1978b), suggests that repeated simulated wolf howling by humans could have a detrimental effect on the recipient animals. In keeping with this, repeated howling stimulations have recently been found to have a long-term effect on wolves' attendance patterns at rendezvous sites (Manseau et al. in preparation).

The present study examines the responses to simulated howling of two wolf packs in the Laurentide wildlife reserve, Quebec, Canada. Because the pitch of howls is believed to convey the degree of aggressiveness, two types of howls were used for stimulation to observe whether they might elicit different vocal and behavioral results. The first consisted of howls recorded from a pack of wolves, deemed the "more aggressive" stimulus, while the second consisted of a recording of a single coyote, considered to be "less aggressive'. More specifically, we examine factors that might affect the response rate of wolves to simulated howling, including the type of howl, and its immediate effect on specific wolves' behaviors at and away from rendezvous sites.

Because all individual wolves in both studied packs were collared, we examined not only the influence that environmental factors might have on response (Bender et al. 1996; Harrington and Mech 1982) but also used detailed information about number, age, and social status of wolves present at the time of stimulation to determine factors most affecting the odds of a vocal response. This is an improvement over previous studies where this type of information was not available because not all of the wolves in studied packs were collared (Joslin 1967, Harrington and Mech 1982). The ability to tease apart the relative influence of both social and environmental factors will provide valuable information not only for ecotourism companies wanting to increase the success of their activities, but will also contribute to a better interpretation of the results of howling surveys used to estimate wolf abundance.

Using data from the same study area and packs presented here, Manseau et al. (in prep.) found a long-term effect of wolf howling simulations on the attendance patterns of wolves at rendezvous sites, although there were no such measurable effects on the short-term attendance of wolves, nor were there any effects from coyote howls. However, these results were based only on the amount of time that individual wolves are present at the rendezvous site with pups. To further this work, the movements of individual wolves was monitored at a finer scale, at and away from these sites, several hours before and after stimulations, to detect immediate behavioral changes. Because all of the pack members were collared, we are able to examine these movements on an individual basis. Such information may be useful in better understanding the effect that howling activities may have on wolves and, if necessary, how they might be minimized. We will also use these data to examine whether wolves respond directly to the stimulations or if their activities are only affected by the howls of packmates at rendezvous sites.

3.3 Study area and Methods:

The data presented were collected in conjunction with a large-scale three-year wolf ecology project conducted by the Quebec Ministry of Environment and Fauna (MEF) in the Laurentide wildlife reserve and surrounding area located in southern Quebec, Canada (Jolicoeur 1999). The reserve is divided into 111 exclusive trapping territories on which wolves can be trapped without limit from mid-October to the 1st of March. Only one pack (Malbaie) was studied in 1996 while in 1997, two packs were monitored (Malbaie and Grands-Jardins (GJ)).

The Malbaie pack's territory (1 092 km^2) lies near the center of the Laurentide Wildlife reserve (7 932 km^2) where the altitude is highest (800 meters) and the vegetation is characterized by coniferous forest (*Picea mariana* and *Abies balsamea*). The area is heavily logged and easily accessible due to a high density of logging roads. Throughout the study, the pack fed mostly on moose (*Alces alces*) during the summer and fall (Tremblay et al. in prep). Moose density in this area is estimated at 0.4 moose/10 km^2 (Frenette 1990, St-Onge et al. 1995).

The territory occupied by the GJ pack (1 089 km^2) consisted of the eastern side of the Laurentide reserve, the adjacent GJ park (310 km^2), the Terres du Seminaire (land used by a private hunting and trapping club) as well as public and private land. Because this pack traveled over so many areas outside the reserve where there were no exclusive trapping territories and trapping pressure is higher in general, this pack experienced high mortality and disruption of pack structure on a yearly basis. Their territory was characterized by a mix of deciduous (*Acer* spp. and *Betula alleghaniensis*) and coniferous forest (*Picea mariana* and *Abies balsamea*). Neither logging nor trapping was permitted within the GJ park but there was a well established road system for tourists. Throughout the study, the summer diet of the pack consisted mostly of a combination of moose and beaver (*Castor canadensis*) (Trembay et al. in prep). A more detailed description of the area is available in Jolicoeur et al. (1999).

Wolves were captured in modified leg-hold traps (see technical paper) in summer and fall and by helicopter in winter using net-guns and tranquilizer darts (Tiletamine-zolazepam (Telazol) at 5 mg˙kg body weight^{-1}). Age and social status were determined through tooth wear, size of testes/teats and behavior (Van Ballenberghe et al. 1975). All individual members of the packs studied were collared. We did not observe any behavioral changes due to manipulations and wolves were usually located with their respective packs within the same day of capture. Between two and three pups were captured from the Malbaie pack in the summers of 1996 and 1997, before the densite was abandoned, in order to relocate rendezvous sites quickly when the pack moved. All the tagged animals were recaptured in winter to readjust their collars. There were no pups collared in the GJ pack in 1997 because the animals did not venture far from the densite and traps were placed at least 1 km away in order not to disturb the site.

Simulated howling sessions took place at rendezvous sites, once pups had been moved away from the densite. The Malbaie pack was studied from August 4th to the 27th in 1996 and used only one rendezvous site, which was the kill site of an adult moose. In 1997, the Malbaie and GJ packs were studied from July 22nd to September 27th and July 31st to August 27th, respectively. The Malbaie pack used five different rendezvous sites during this time that were all moose kill sites (site 1: 21.07.97 to 03.08.97 at 13:00; site 2: 03.08.97 to 14.08.97 at 20:40; site 3: 15.08.97 to 23.08.97 at 4:00; site 4: 24.08.97 to 22.09.97 at 00:30; site 5: 23.09.97 to 28.09.97); the GJ pack moved the pups only 1 km from the densite where the pups had access to fields of blueberries throughout this entire period.

In 1996, the experimental treatment consisted of four days of simulated wolf howls alternating with four days of no stimulation. The recording used was from a group of wolves consisting of adults and pups (extract from a sound track made by Bob Maxwell, *The Language and Music of the Wolves*, Columbia). In 1997, the howls of a single coyote were added and were used in alternation with wolf howls (Appendix I). Wolf howls were considered more threatening for two reasons. First of all, the wolf howls used for stimulation were those many animals (adults and pups howling and barking) while the coyote recording consisted of a single animal howling. Secondly, lower pitched howls reflect greater aggressivity (Harrington 1987) and there is a wide variation between the howls of the two species (Harrington 1975, McCarley 1975, Harrington and Mech 1978b, Lehner 1978). Whereas the presence of a large pack producing lower pitched howls likely represents a challenge to the resident pack, the higher pitched howl of a single coyote likely represents little threat. Two stimulations took place on stimulation nights and were played 30 minutes apart until wolves responded for a maximum of 60 seconds. For consistency in the analysis of factors affecting response, when there were several groups of wolves within range of the stimulation, a positive response was noted only if the group of wolves present with the collared pups responded as these are the individuals which would be stimulated by ecotourism companies. Responses of distant wolves will be discussed separately.

Wildlife callers (specialized animal call players used by hunters to attract game) were used at maximum strength to play recorded howls. Due to the high level of access in the area occupied by the Malbaie pack, stimulations were played from a distance of 300 meters from the rendezvous sites. Stimulations of the GJ pack took place from 700 meters of the rendezvous site due to the lack of access in that area.

In 1996, the first simulated howls were played between 21:30 and 22:00 while a wolf located away from the rendezvous site was followed by radio-telemetry from 19:00 to 2:00. On occasions where the wolf being followed was definitely not within hearing distance of either the stimulation or the pack's response, it was stimulated from 200 meters of its location and it's behavioral and vocal response was monitored. Behavioral monitoring as well as recordings of response were only taken during the last three days of each treatment (pre-determined design). Telemetry in 1996 consisted of locating an individual wolf not at the rendezvous site (preferably one that had recently departed from the site based on data from the monitoring station) two hours before the first stimulation (approximately 19:00) and following it until the end of monitoring at 2:00. Radio-tracking was done from a truck equipped with a 9-element antennae on a 7' rotating mast connected to an electronic compass and GPS. Locations of wolves were taken by triangulating every half-hour and individual triangulations were usually done within 10 minutes. Because wolves were usually followed from a distance of 0.5 km, vocal responses of followed wolves were also monitored. On occasions where the wolf being followed was clearly not within hearing distance of either the stimulation or the pack's response (either 5 km away or closer depending on the landscape), it was stimulated from approximately 200 meters of its location and its behavioral and vocal response was monitored. Therefore, on these evenings, stimulations occurred both at the rendezvous site and near the location of the animal being followed.

In 1997, the first stimulation was played between 21:00 and 23:00 and a second stimulation was broadcast 30 minutes later. The reason for the wider time range is that wolves away from the rendezvous site were not followed by radio-telemetry. Therefore, an attempt was made to stimulate the wolves at the rendezvous site approximately 30 minutes after a wolf departed from the site. This enabled us to monitor whether a wolf, known to be within hearing distance of the stimulation and/or pack's howling, would return to the rendezvous site. Movement and vocalizations near the rendezvous site were monitored from 19:00 until 1:00 daily.

During both 1996 and 1997, environmental conditions including temperature, precipitation, wind speed, lunar phase, and cloud cover were monitored from 8:00 pm to 2:00 am in 1996 and to 1:00 am in 1997.

A logistic regression analysis was performed to determine the factors that influence whether or not wolves present at a rendezvous site will respond to simulated howling. This analysis is preferable to other multivariate techniques because it makes no assumptions about the distribution of the independent variables and the independent variables of interest can be a mixture of categorical and continuous variables. This analysis was performed for wolf stimulations at the GJ pack as well as both wolf and coyote stimulations at the Malbaie pack.

3.4 Pack Structures:

3.4.1 Malbaie pack

In 1994, the pack was composed of the alpha pair (M450 and F381) and a minimum of three pups. It is believed that this is the first year that these wolves bred in this area. None of the pups borne in 1994 survived the winter and in 1995, the pack consisted of the alpha pair (M450 and F381) and 7 pups. Four of these pups survived to the following year (table 1). Of the four yearlings present in 1996, all remained with the pack into their second year except for F421 who dispersed. Of the six pups born to the alpha female (F381) in 1996, only three survived to the following year.

3.4.2 Grands-Jardins pack (GJ)

Due in part to the fact that its territory extended outside of the park and reserve, this pack was exposed to a higher degree of trapping pressure than the Malbaie pack. Prior to 1995, this pack was almost completely eliminated in the fall on a yearly basis in an effort to reduce predation pressure on a reintroduced caribou herd. Therefore, the turnover in individuals was much higher than for the Malbaie pack, particularly in the case of the alpha females. In 1995, the GJ pack consisted of a two-year old alpha female (AF1) and alpha male (M361), two subadults (M290 and F135) of unknown age but believed to be yearlings based on weight) and 3 pups. The alpha female and three pups were caught in snares in the fall and the pack was reduced to three wolves by the end of the trapping season (M361, M290, F135). The two-year old female F135 then became the alpha female. In the spring of 1996, she had 4 pups (2 uncollared, F020, M060), which brought the pack to a total of 7 wolves. Only two of the pups survived the winter (F020 and M060). In the spring of 1997, the pack was composed of 13 wolves (table 2). Just after the opening of the trapping season in 1997, alpha female F135 was killed in a snare and the pack was reduced to 2-3 individuals by the end of the 1997-98 trapping season.

3.5 Results:

3.5.1 Responses to simulated howling:

In 1996, wolves in the Malbaie pack were stimulated twice with wolf howls on 16 nights, 12 of which were monitored (table 3). Wolves responded to 8 out of 12 first stimulations (67%) and 10 out of 12 of the second stimulations (83%). The alpha male was present with the pups on four occasions during the first stimulation and there was a response on 50% of those occasions. He was present with pups during 7 of the second stimulations and wolves responded on 6 of those nights (86%). The alpha female was present on 6 occasions during the first stimulation and a response was heard on 4 nights (67%). There was a response to 4 of the 7 times she was present during the second stimulation. Pups were unattended once during the first stimulation and did not respond (August 27th). However, they were also alone once during a second stimulation and did howl back (August 14th).

In 1997, wolves in the Malbaie pack were stimulated with wolf howls on 18 nights and coyote howls on 16 nights. However, due to equipment failure, only 15 of the 16 second stimulations of coyote howls took place (table 4). Wolves responded to 12 of the 18 (67%) first wolf stimulations and 12 of the 18 second wolf stimulations while responses to coyote stimulations occurred on 6 out of 16 first stimulations (38%) and 5 of the 15 (33%) second stimulations. When the alpha male was present during wolf stimulations, there was a response in 7 out of 8 (88%) occasions during the first stimulations and on 8 of the 9 (89%) times during the second stimulations. He was only present on two nights during coyote stimulations and there was no response to either the first or the second playback. When the alpha female was present, wolves responded to 6 of the 7 (86%) first and 6 of the 9 (67%) second wolf stimulations. Of the 5 nights when she was present during first and second coyote stimulations there was only one response (20%) to the first playback and 2 (40%) to the second. On occasions when only pups were present during wolf stimulations, there was a response to 1 of the 3 (33%) first stimulations and 1 of the 2 (50%) second stimulations. During coyote stimulations, unattended pups responded to 3 of 6 (50%) first and 2 of 5 (40%) second stimulations.

In 1997, the GJ pack was stimulated alternatively with wolf and coyote howls from July 31st to August 27th (table 5). The wolves were stimulated with wolf howls on 7 nights and coyote howls on 8 nights (the night of August 18th was removed because the rendezvous site was not confirmed). Wolves responded to 2 of the 7 (29%) of both first and second wolf stimulations (not on the same nights) and responded to 2 of the 8 (25%) first and 1 of the 8 (13%) second coyote stimulations. On all nights where there was a response to a stimulation (coyote or wolf), either the alpha male or female was present or had just departed from the site. The pups never responded when there were no other wolves present.

3.5.2. Factors affecting response rate:

Because of the multiple factors possibly affecting the response rate, a logistic regression analysis was performed to determine the influence of several parameters on the probability of a howling response. The model has the form:

$$\text{Logit (P)} = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + ... + \beta_k X_k$$

Where logit (P) = ln (p/1-p) and X_1, X_2, ..., X_k are the independent variables. The variables considered in the analysis include a seasonal effect (days since pack left the den), the type of stimulation (wolf vs. coyote), days since the last moose kill (only available for the Malbaie pack in 1997), the presence of the alpha male, the presence of the alpha female, and the presence of more than 2 wolves with the pups. When several groups of wolves were within range of the rendezvous site, only the response of the group present with the pups was considered.

A first analysis was performed with only data from the Malbaie pack in 1997 because this is the only data set large enough to interpret individually and this also allowed us to compare the effect of wolf vs. coyote stimulations. The analysis was performed separately for the first and second stimulation (tables 6 and 7) (For a detailed description of model building see Appendix 1). The overall fit of the reduced model with variables season, type of stimulation, and more than 2 wolves was not significantly different from the full model (p = 0.50 and p = 0.32 for the first and second stimulations). The variance accounted for by the models (McFadden's rho-squared) was 0.40 and 0.45 for the first and second stimulations respectfully (values between 0.20 and 0.40 are considered very satisfactory)(Hensher and Johnson, 1981). This type of analysis, where a priori set of models are tested against each other avoids many of the problems encountered when drawing conclusions based solely on p-values (Anderson et al. 2000). Therefore, once the seasonal effect was taken into account, wolves were more likely to respond to a wolf stimulation (OR = 3.83 and 7.08) when there were more than 2 individuals present (OR = 10.04 and 3.49).

In order to compare results between years for the same pack and because the sample size for the Malbaie pack in 1996 is small, we combined this data set with information from nights of wolf howling stimulation in 1997. Again, for both the first and second stimulations, only the variable 'total number of wolves' was found to significantly influence the response rate. This same analysis was repeated with the addition of data from the GJ pack where once again, the total number of wolves was the variable that most affected the response rate (For a more detailed description of this analysis and models see Appendix II)

All of these models were also tested with the inclusion of environmental parameters which included precipitation, wind (above and below 50 km/hour), presence of full moon (considered full 2 days before and after actual full moon), and cloud cover (above or below 50%). None of these factors significantly affected response and were not included in final models. However, high winds did occur on two nights during which there was no response.

3.5.3 Behaviors and movement associated with changes in response from the first to the second stimulation:

Although the vocal responses to the first and second stimulations were not always the same, there was no significant difference in the overall response rate from first to second stimulation for either wolf (1996 and 1997) or coyote stimulations in 1997 ($p>0.5$) for the Malbaie pack (The binomial test was used instead of the McNemar test to assess the difference between the 2 stimulations because of the small sample sizes). More specifically, there were only four nights in 1996 and three nights in 1997 where there was a change is response from the first stimulation to the second. For the GJ pack, there were only two nights on which there was a change in response from the first to the second stimulation. These nights are of particular interest since most variables between the two stimulations remained constant, so a closer examination of events occurring between the two stimulations could offer additional insights into factors affecting response rate.

In 1996, Malbaie wolves changed their responsiveness between stimulations on only 4 nights, responding to the first stimulation on 2 nights and to the second on 2 other nights. The first instance occurred on August 5th when there was only one yearling female (F411) present with at least 2 pups at the rendezvous site. Both alphas and the 3 other yearlings were approximately 1 km from the site and had at least 1 pup with them. There had been howling between the two groups so we know that they were aware of each other's presence. There was no response to the first stimulation. Half an hour later when the wolves were stimulated a second time, there was a response followed by movement of the single yearling with the pups toward the larger group of wolves. Two hours later, there was spontaneous howling coming from the entire group.

The second instance occurred on August 12th. The alpha female and the handicapped yearling (F470) were present at the rendezvous site with at least 2 pups when the first stimulation took place. The third collared pup had started to distance himself from the rendezvous site and his signal had not been heard for an hour prior to the first stimulation. There was a response from the wolves at the rendezvous site which lasted under a minute. Half an hour later, when the second stimulation took place, the pup had returned to the group and there was no response.

The third occasion took place on August 26th when there were two yearling females (F402 and F411) present with at least 2 of the pups at the rendezvous site (collar on 3rd pup failed). They did not respond to the first stimulation, but there was a response from both alphas and the other 2 yearlings located approximately 2 km west of the rendezvous site. When the second stimulation took place, the alpha male and the handicap yearling had moved to the rendezvous site and there was a response from the 4 wolves and the pups at the rendezvous site. The alpha female and one of the yearlings (F421) were situated about 2 km from the rendezvous site and did not respond. However, they returned to the rendezvous site minutes after the second stimulation.

The fourth occasion occurred on August 27th when at least 2 pups were present at the rendezvous site. Sometime after 2:00 on the 27th, all the wolves except the pups left the rendezvous site. At 19:00 they were located together approximately 2.8 km from the rendezvous site. They were moving away from the rendezvous site at an approximate speed of 3.38±0.16 km/hour (straight line speed), based on triangulations every half hour. Immediately prior to the first stimulation, the wolves were located 6 km from the rendezvous site. Neither the pups at the rendezvous site nor the wolves away from the site responded to the first stimulation. The pack, however, changed direction and made it back (except the handicapped wolf) to the rendezvous site 33 minutes, increasing their speed 3 fold (12km/hr) and reversing their direction of travel in response to the first stimulation. The wolves vocally responded to the 2nd stimulation (all present except the handicap) followed by 3 spontaneous group howls during the 10 min following the stimulation. The handicapped wolf arrived at the rendezvous site 30 minutes after the other wolves. All the wolves remained at the rendezvous site until 7:30 the next morning.

In 1997, there were three nights on which there was a change in response in the Malbaie pack during wolf stimulations and one instance during coyote stimulation. The first instance during wolf stimulation occurred on August 9th when the alpha female (381), two adults (402, 470), and two yearlings (331, 370) were present with most of the pups. The wolves responded to the first but not to the second stimulation 30 minutes later. During the inter-stimulation interval, there were no arrivals or departures from the site.

The second occasion occurred on August 10th when most pups were present at the rendezvous site but the signals of the alpha male (450), alpha female (381), two adults (402, 470), and a yearling (331) were all east of the site. The pups did not respond to the first stimulation. The second stimulation took place 30 minutes later at which time all the wolves mentioned had arrived at the site and responded for approximately 1 minute. It is not clear whether the first stimulation caused the wolves to return to the site because most of them had been gone since 5:00 that morning and may have been heading back to the rendezvous site prior to the stimulation (no ground tracking in 1997).

The third instance occurred on August 25th. The alpha female (381), the handicapped wolf (470) and a yearling (331) were present until 19:50 at which time F381 and F470 left the rendezvous site. The first stimulation took place at 22:30 and there was no response. Only the yearling (331) was present with the pups but F381 and F470 were still within 2 km of the rendezvous site. Within 10-20 minutes, both wolves returned to the site and when the second stimulation took place at 23:00, there was a response. Additionally, after the first response another adult's signal (402) was detected for the first time that night and she arrived at the densite at 23:20. However, it is difficult to conclude whether her return was caused by the stimulation because she had been gone since at least 7:00 pm (no data were available since 9:00 that day due to technical difficulties).

On September 1st, during a coyote howl stimulation night, there were only pups present at the rendezvous site and they responded to the first but not the second stimulation. They had been unattended since 5:00 that morning and there were no signals heard from any of the adult wolves in the vicinity throughout the evening.

In the GJ pack, the one occasion during which there was a change in response from the first to the second stimulation occurred during a night of stimulaition with coyote howls. On August 10th, only one yearling was present with the pups during the first stimulation. The wolves responded together after which the yearling howled twice alone and departed from the rendezvous site. Because the pups were not collared it is not known whether she left alone or took the pups with her. However, there was no response to the second stimulation.

3.5.4. Wolf Movement:

3.5.4.1. Movements of wolves on nights of stimulation with wolf howls

In 1996, movements of wolves were recorded both in the vicinity of and when away from the rendezvous site. In 1997, only movements of wolves near the rendezvous site were monitored. For the purpose of this paper, movement in response to wolf stimulation was defined as any trajectory initiated within 5 minutes of the broadcast and was devided into 2 basic types: 1) movement of individuals or groups of wolves in response to howls broadcast at the rendezvous site; and 2) movement of individuals or groups of wolves in response to howls broadcast away from the rendezvous sites. (For a detailed description of movement and response for individual days see appendices III, IV, and V)

1) Movements of wolves in response to broadcasts near the rendezvous site:

Movements of groups of wolves occurred on four nights in 1996, twice when there was a response from wolves located at the rendezvous site (August 5th and 13th) and twice when wolves remained silent (August 25th and 26th). On August 5th and 13th, there was only one yearling present with at least one pup at the rendezvous site during the first stimulation. During this time, other pack members were in a group (both alphas and 3 yearlings on August 5th, the alpha male and 2 yearlings on August 13th) located approximately 1 km from the rendezvous site and had some of the pups with them. There had been howling between the groups before the first stimulation on both evenings so they were aware of each others' locations. On August 5th, there was no response to the first stimulation but both groups responded vocally to the second stimulation and then the yearling located at the rendezvous site moved the pups to the larger group of wolves. On August 13th, both groups responded vocally to the first stimulation and began moving toward each other. When the second stimulation took place, wolves from both groups were located together and responded vocally again.

On August 25th, there were 3 yearlings present at the rendezvous site (it is not known whether any pups were with them) and they did not respond vocally to either the first or second stimulation. However, after the second stimulation, 2 of the yearlings departed to join both alphas, a yearling, and at least 2 pups located 6 km from the rendezvous site at that time. On August 26th, there were 2 yearlings present with at least 2 pups at the rendezvous site and they did not respond vocally to the first stimulation. However, there was a vocal response from both of the alphas and 2 yearlings that were located approximately 2 km from the rendezvous site followed by movement of the alpha male and one of the yearlings to the rendezvous site. The 4 wolves and pups at the rendezvous site responded vocally to the second stimulation. There was no vocal response from the alpha female and yearling located 2 km from the site but they returned to the rendezvous site minutes after the second stimulation.

In 1997, there was one occasion (August 25th Malbaie) where a group of two wolves returned to the rendezvous site after a stimulation. Only a yearling was present with pups at the site during the first stimulation since the alpha female and another adult had left the site 40 minutes before (still within hearing distance). The yearling and pups did not respond to the stimulation and the alpha female and adult returned to the site within 10-20 minutes of the stimulation. When the second stimulation occurred, all the wolves responded.

Movements of individual wolves in response to howling at the rendezvous site were particularly interesting and are described separately by age and rank. There are several examples of movements of alpha individuals affected by howling. On August 4th 1996, the alpha female departed from the rendezvous site in the evening leaving all other pack members behind and moved north-west. An hour later, she was almost 4 km from the rendezvous site and continuing to distance herself from the pack when wolves at the rendezvous site howled (we believe due to our presence). She immediately changed directions and began to retrace her steps back toward the rendezvous site but did not respond vocally. In all, she was only away from the rendezvous site for 3 hours and was taking a well known trail to a feeding site before changing directions. A similar situation occurred in 1997 (August 26th Malbaie) when 6 wolves who were present with the pups, including both alphas, all suddenly departed from the rendezvous site. Approximately 40 minutes after their departure, the pups, alone at the site, were stimulated and did not respond. Twenty minutes later, the alpha female had left the group of wolves and had returned to the pups where she remained until 2:40 the following morning.

A similar disruption of ongoing movement occurred to the GJ alpha on August 19th, 1997. The alpha male (M361), the adult male (M290), and a yearling (M130) were at the rendezvous site during the first stimulation at 23:00 and there was no vocal response. Ten minutes before the second stimulation at 23:29 the alpha male (M361) left the rendezvous site. The two other wolves were still at the rendezvous site during the second stimulation and there was no response. However, the alpha male (M361) immediately returned to the rendezvous site and remained there until 1:00 on the following day.

The handicapped wolf (F470) was away from the rendezvous site but within hearing distance on one occasion (he was located in a valley below the broadcast location). On August 8th 1997, the alphas, an adult and a yearling were present with the pups at the rendezvous site. The wolves responded to the first stimulation and F470, who had left the site 50 minutes before, returned.

Because three of the seven pups were collared it was also possible to monitor their behavior during stimulations. One night in 1996 (August 12th), at least one of the collared pups left the rendezvous site unaccompanied by any adult wolves. When the first stimulation took place, the pup was located approximately 2 km from the rendezvous site and the wolves present at the site (alpha female, handicap and some pups) responded to the stimulus. Immediately after this response, the pup returned to the rendezvous site. Half an hour later, the wolves did not respond to the second stimulation.

2) Movements of individuals or groups of wolves in response to howls broadcast away from the rendezvous sites:

On two occasions in 1996, individuals or groups of wolves being radio-tracked were too far from the rendezvous site to hear stimulations and responses, and where therefore stimulated near their location. In one instance (August 14th), the pack was divided into two groups, one consisting of two yearlings and several pups at the rendezvous site and another composed of the alpha couple, a yearling, and at least 2 pups. Although the group at the rendezvous site responded to both stimulations, it was unlikely that the alpha group heard the response as they were located 15 km away. When the alpha group was stimulated at 00:30, the alpha female left the group and made a direct trip back to the rendezvous site alone. On another occasion (August 19th) the alpha male had left the rendezvous site one hour before the first stimulation and was located almost 5 km from the rendezvous site 20 min after the first stimulation. Because it was unlikely that he heard the stimulation or the response of the wolves at the rendezvous site (alpha female, handicap and pups) due to the topography of the area (moved behind mountains higher than broadcast location), he was stimulated approximately 200 meters from his location. He immediately changed direction and returned to the rendezvous site in under 30 minutes without responding vocally.

In 1997, when stimulations occurred approximately 30 minutes after a departure of an individual or group of wolves from the Malbaie pack's rendezvous site, there were four instances where the departing wolves did not return. On three of the occasions (July 22nd, August 11th, and September 12th), one or more wolves remained with the pups, including at least 1 alpha, after the departures occurred. Only on one occasion did all the adults, including both alphas, depart and continue distancing themselves after two wolf stimulations (July 23rd). On this night, the first stimulation took place 15 minutes after the wolves had departed from the rendezvous site. There was a vocal response from the departing wolves adult wolves but not from the pups at the rendezvous site. When the second stimulation took place 30 minutes later, the adult group was located approximately 0.5 km from the rendezvous site. There was a first vocal response from the pups, then howling from the adult group, followed by final howling from the pups at the rendezvous site. After this exchange, all of the departing wolves continued to distance themselves from the rendezvous site. In the GJ pack, there was one instance where two non-alpha individuals continued to distance themselves after wolf stimulations leaving the pups unattended (August 17th). Although their exact location was not known, the first stimulation took place 40 minutes after their departure from the rendezvous site, making it likely that they were still within hearing distance.

3.5.4.2. Movements of wolves on nights of stimulation with coyote howls

During the 16 nights of coyote stimulation in 1997, there were no observations of wolves returning to the rendezvous site after stimulation in the Malbaie pack. However, this was not because there were no wolves departing from rendezvous sites during the stimulation period. Rather, there were four cases (July 31st, August 1st, 19th, September 2nd) where individual or groups of wolves were stimulated approximately 30 minutes after their departures from the rendezvous site yet they continued to distance themselves and on two occasions (August 19th and September 2nd) left the pups unattended.

In the case of the GJ pack, there were also two examples of departing wolves not returning after being stimulated with coyote howls, leaving pups either unattended or with a single yearling. The first occurred on August 8th, when the alpha male (M361) and two yearlings (M060 and F020) were present with the pups. The alpha male and M060 began distancing themselves from the rendezvous site and were stimulated 20 minutes later. There was a response by the female yearling and pups to the two consecutive stimulations but neither of the two departing wolves returned. The second occasion occurred on August 10th, when only yearling 020 was present with the pups at the rendezvous site. The wolves present at the rendezvous site responded to the first stimulation and then the yearling left the rendezvous site. Because there was no response to the second stimulation, it is not known whether the yearling left with the pups. However, we believe this to be unlikely since the pups were known to be at the site the following day.

The only example of a wolf returning to the rendezvous site after a coyote stimulation was on the night of August 26th. The GJ alpha female (F135), an adult (M060), and a yearling (M130) were present with the pups. The first stimulation was played 30 minutes after the female had left the site, travelling alone. There was no vocal response from any of the wolves, but the alpha female immediately returned to the rendezvous site. There was no response to the second stimulation and the wolves remained at the rendezvous site until at least 1:00.

One example of aggressive behavior in response to a coyote stimulation movement toward the source of the stimulation. On the 9th of August, the adult male (M290) and a yearling (F020) were with the pups during both stimulations and there was no response. During this time, however, the adult male moved to within 100 meters of the source of the stimulation and began barking and howling 8 minutes after the second stimulation. From that time until midnight, there was continuous howling alternating between the adult male, still near the broadcast location, and the wolves at the rendezvous site. It is important to note that there was no immediate vocal response to the stimulation and that the male only howled after he had approached 6 humans at the source of the stimulation. After this, the adult male returned to the rendezvous site.

3.6 Discussion

3.6.1 Factors affecting response rate to simulated wolf howls

Since the howling of a group of wolves within close proximity of a resident packs' rendezvous site is most likely perceived as a threat, resident wolves should respond in a way that would increase the safety of pups. Therefore it is logical that most studies have found that pack size influences response rate (Harrington and Mech 1979, 1982) as a lesser number of wolves would be at a disadvantage in a conflict and would probably benefit from not revealing their location and number. In this study, because all individual wolves were collared, we were able to make the distinction between the effect of pack size and the total number and age/social status of wolves present during the stimulation within a single pack. This allows us to eliminate many of the variables that add to the uncertainty when comparing different packs (pack age and structure, prey base, large-scale environmental conditions, etc.). Based on our analysis, pack size between the three pack/year variables (number of adult wolves in packs: 6 in Malbaie 1996, 8 in Malbaie 1997, and 5 in GJ 1997) was not found to significantly affect the response rate although it should be noted that that only a small range of pack sizes were studied. On the other hand, across packs and years, the factor most influencing response was the total number of wolves present with the pups at the time of the stimulation. Of course, these two variables are interrelated since the larger the pack, the more likely that there will be a greater number of wolves present at the rendezvous site during a stimulation. However, this distinction is important because it partly explains the large degree of variation in response rate within a particular pack when submitted to a constant stimulation regime. These data also differ from results obtained in Minnesota where pack composition was not found to have an effect on response rate at rendezvous sites (Harrington 1975).

In Minnesota, stimulation sites were divided into rendezvous and non-rendezvous sites, where most non-rendezvous occasions consisted of wolves traveling or present around a kill (Harrington 1975). In the case of this study, all of the rendezvous sites used by the Malbaie pack were moose kills to which the pups were moved within a day or two. Harrington and Mech (1979) found that in general, wolves had a higher response rate at rendezvous sites than at non-rendezvous sites, that the presence of a kill significantly increased the response rate at non-rendezvous sites, and that responsiveness decreased as the prey was consumed. Both of these situations represent resources that can not easily be moved and in one of our models (using data from the Malbaie pack in 1997), we were able to combine information on the age of the kill with the other measured parameters and found that the age of the kill did not significantly affect response rate. There are several possible explanations for the present results differing from those of Harrington (1975). First of all, kill sites in Minnesota were studied in winter primarily when any effect of pups on reply rate is likely passed. Also, our sample size is relatively small and the effect could have been undetected (N=34, data on 5 rendezvous sites). Furthermore, the first few days after a kill are usually associated with most of the pack members being present, particularly when the main prey item is a large ungulate. Therefore the higher response rate could simply be a result of the large number of wolves present at that time as suggested by our model. Kill sites and rendezvous sites, when they are not the same locations, harbor not only a different type of resource, but also distinct pack compositions. Because rendezvous sites are areas where pups are left before they are strong enough to travel (Mech 1970), they are often left unattended. Kill sites on the other hand, serve to feed the adults who will bring the food back to the pups or occasionally bring some of the pups to the site to feed (Mech 1970). Therefore, the odds of encountering lone pups or a small number of adults (factors that decrease response rate) are much lower at a kill site removed from the main rendezvous site.

Alpha wolves are the most vocal individuals during the breeding season, and in Minnesota the alpha male was the wolf who initiated most of the responses (Harrington 1975). In coyotes, alpha individuals were also found to howl more frequently than subordinates and pups (Gese and Ruff 1998). Therefore, we expected that particularly the alpha male's presence would be a factor affecting the response rate of wolves at the rendezvous site. Evidence for the presence of the alpha male as a factor is the fact this variable was retained in the model with all of the data combined. Additionally, in 1997, response rates for both the GJ and Malbaie packs were higher on nights when the alphas were present compared to the overall response rate. However, the most important factor in predicting the probability of a response is clearly the number of adult wolves present with the pups.

Examples of wolf behavior on nights where wolves vocally responded to only one of the two wolf stimulations offer additional data on the influence of both total number of wolves and the presence of alphas on the odds of a response. Of the nine occasions where there was a change in response, five (August, 5th, 26th, 27th, 1996 and August 10th, 25th, 1997 Malbaie pack) occurred when there were 0-2 yearling wolves with the pups during the first stimulation and there was no response. Before the second stimulation wolves arrived at the rendezvous site and increased the number present to 3-6 wolves and in all cases included at least one of the alphas. On all of these nights, there was a response to the second stimulation. Harrington and Mech (1979) also observed that packs often did not reply to the first stimulation, but no explanation was offered. Therefore, whether or not wolves respond to simulated howling is not only a factor of the resource being defended (Harrington 1975), but also depends on whether the resident wolves are at an advantage with regard to numbers compared to the intruders. Wolves in our study were stimulated by the howls of an entire pack, therefore, revealing the location of pups would only be an advantage if there were several wolves present, otherwise it would be to their advantage not to reveal their location.

3.6.2. *Movements of wolves in response to wolf howling stimulations*

Other studies have reported the return of wolves to rendezvous sites following wolf howling simulaitons (Joslin 1967; Harrington and Mech 1979). However, because it was not known how long the returning wolf(ves) had been away from the site and what his/their behavior was before the stimulation, it was unclear whether the return was caused by the stimulation, the howling of the wolves present at the rendezvous site, or whether it was coincidental. The events on several evenings of wolf stimulations (August 27th, 1996 and August 25th, 1997 Malbaie and August 19th, GJ) clearly show that wolves do respond directly to the stimulation since there was an immediate change in behavior and no reply from any of the wolves. On both occasions in the Malbaie pack, the first stimulation took place approximately 30 minutes after several wolves began distancing themselves from the rendezvous site leaving behind unattended pups in one case and a single yearling with the pups in the other. The immediate change in direction of travel and return to the rendezvous site could only have been a direct response to the stimulaiton since there was no response from the wolves at the rendezvous site. In both of these cases, the wolves likely were aware of the number of wolves present with the pups. On these nights, all of the departing wolves returned together to the rendezvous site. Similarly, the alpha male of the GJ pack was observed to return to the rendezvous site immediately following a wolf stimulation. He had only been distancing himself for approximately 10 minutes and there had been no reply to the stimulation. These examples clearly suggest that wolves perceive the wolf howling simulations as threatening and that their reaction is a direct response to it.

The alpha female seemed to be the most responsive when the pups were possibly in danger. On one night when she departed from the rendezvous site with five other wolves (Malbaie August 26th, 1997), only she returned to the rendezvous site while the other wolves continued to distance themselves. On another evening (Malbaie August 14th, 1996), both alphas and a yearling were located 15 km from the rendezvous site and were stimulated near their location. The immediate response of the alpha female was to return to the pups at the rendezvous site. Therefore, this suggests that the alpha female's behavior is the most affected, of any pack member, by the wolf howling stimulations.

3.6.3. Movements of wolves in response to pack howling and potential information transmitted

The analysis of howls from captive wolves has shown that individuals can be discriminated based on structural characteristics, thus allowing for long-distance identification (Theberge and Falls 1967; Tooze et al 1990). Field observations support this hypothesis, since wolves rarely approach the source of unknown simulated howls (Harrington and Mech 1979). Structural analysis of howls has also shown that the variation within the howl of an individual animal offers the potential to convey information over large distances (Theberge and Falls 1967). Although wolves are able to discriminated variations in sound, there are no direct field observations of behavioral changes due to the howls of distanced pack members. The return of wolves to rendezvous sites following a response from wolves present has been observed (Joslin 1967; Harrington and Mech 1979) and we have demonstrated that wolves respond directly to simulated howls but there are no examples in the wild of wolves behavior being affected directly by the howling of packmates.

The events on several nights of our study address these questions. First of all, on August 4th 1996, the return of the alpha female to the rendezvous site is of particular interest. It is important to note that the female was taking a well-known route to a feeding site before any howling was heard. Therefore, her immediate change of direction and return to the rendezvous site at exactly the time howling was heard at the rendezvous site is unlikely to be a coincidence since she was only half way to her probable destination. Secondly, this behavioral response could only have been due to the howling of her pack, since there had been no stimulation at that time (we believe that the howling was a response to the noises from our truck).

The second example involves the events on the night of August 12th, 1996 when one of the pups had distanced himself from the rendezvous site and returned after wolves at the site had responded to the first stimulation (short response lasting under a minute). Several pieces of information can be deduced from the events of this night. First of all, it is possible that the pup was able to differentiate between the howls of his packmates and the recordings of unknown wolves, since he returned directly to the rendezvous site and did not approach us. However, it is also possible that returning to the rendezvous site is an immediate response by pups to any howling. Secondly, although we can not be certain that the return was caused by the response of the pack as opposed to a direct response to the stimulation as described in the previous section, it is important to point out that once the pup had returned to the site, there was no response to the second stimulation. It is unlikely that the sole purpose of the response was to reply to the stimulation since once the pup had returned, the wolves did not respond to the second stimulation. Generally, unless there were arrivals of wolves between the two stimulations to increase the number of wolves present, wolves reacted similarly to both stimulations. Additionaly, howling from wolves at the rendezvous site does not always cause the return of pack members nearby (July 22 and 23 1997 Malbaie). Therefore, this behavior does not seem to be an automatic response to howling.

To be able to ascertain with certainty that information is being transmitted and received through howls would have required the structural analysis of responses under various circumstances and a comparison with the responses they elicited from distant wolves. Unfortunately, this was not possible due to the distance from which howls were recorded. However, these field observations support the theory that wolves are able to send and receive motivational information through howls (Theberge and Falls 1967).

3.6.4. Behavioral responses to simulated coyote howls

Although we could not be sure what the wolves perceived the coyote stimulation to represent, the fact that the GJ alpha female returned to the rendezvous site after an unanswered stimulation (August 26th GJ) suggests that it is perceived as a potential threat. The behavior of the adult male who moved up to the source of the stimulation confirms that it could also elicit an aggressive behavioral response (August 9th GJ).

In general, however, wolves departing from the rendezvous site do not return after hearing a recorded coyote howl (July 31st, August 1st, 19th, September 2nd Malbaie; August 8th and 10th, GJ). This suggests that coyote howls, although perceived as some type of intrusion, do not represent as much of a threat as the howling of a pack of unknown wolves.

3.6.5. Response to wolf versus coyote simulated howls

Although the number of wolves present increased the odds of a response to both coyote and wolf simulated howling, wolves were not as likely to respond to coyote howls as they were to wolf howls regardless of the number of wolves present. Previous studies did not find a significant difference in response rates to a single or group stimuli (Joslin 1967; Theberge and Pimlott 1969; Harrington and Mech 1982). However, these are based only on the number of people howling and not the "type" of howl. Although there are no detailed data, the response rate of captive wolves has been found to vary with the type of howl played (Harrington and Mech 1982).

The results from this study are somewhat surprising. Based on results obtained from responses to wolf howls, wolves were more likely to respond when they were in a position of strength in numbers and, perhaps, able to intimidate the intruders. If the show of aggression were the sole purpose of the response, then we would have expected a higher response rate to the howl of a single coyote. It is impossible to determine whether the wolves recognized this howl as that of another species (there are no coyotes and there likely never were any in the Malbaie area, however, the GJ pack's territory is adjacent to agricultural land where coyotes are present) or simply considered it as a less threatening vocalization than the wolf howls. In either case, it is possible that the wolves simply did not feel the "need" to respond to this non-aggressive simulation. Wolves are known to react directly to the stimulation, hence if there is no threat of an encounter with this intruder and no information to be transmitted to pack members, wolves may choose not to respond. Other explanations are possible but more information on differences in response rates to various stimuli is needed before any type of conclusion can be drawn.

3.6.6. Conclusions and implications for industry and management:

Although the sample sizes of our models are small and many of our conclusions are based few observations, they are an important addition to the limited literature on wolf behavior in response to howling in the wild because they incorporate details not previously published.

In the case of the simulated howls of a pack of wolves, the odds of a response increased with the number of wolves present. Therefore wolves appeared to react to this howl as aggressive and responded when they were in a position of dominance. When the animals at the rendezvous site are at a disadvantage, they do not need to divulge their location since pack members respond directly to the stimulation. Responses may also occur when wolves are at a disadvantage but need to convey information to distanced individuals. The higher pitched howl of a single coyote does not elicit as much of a behavioral response as that of the howls of an unknown wolf pack and is likely considered less threatening (Harrington 1987). In addition, the response rate to coyote howls is lower than to wolf howls, regardless of the number of wolves present. The reasons behind this require closer examination but would fit with the idea that howls are used for intra-specific and not inter-specific communication.

One of the goals of ecotourism activities is to increase the odds of a response while minimizing the effects caused by the activity. While these activities usually take place in the fall when the response rate is high, organizers can further increase their chances of hearing a response by choosing larger packs and scheduling activities at times when most wolves are likely to be present at rendezvous sites. Although the use of a more aggressive recording results in a higher response rate, it has the disadvantage of causing a higher degree of disruption to the wolves' natural behavior. Therefore, more experiments using alternative methods of stimulation should be performed in order to arrive at a "standard stimulation" that would satisfy ecotourism companies while limiting the effects on wolves' behaviors. These could consist of acoustic frequencies between those used in this study and do not necessarily need to come from a canid to elicit a response (Klinghamer and Laidlaw 1979). This is particularly important since activities run by private companies will usually affect a small number of packs that will be stimulated repetitively over a prolonged period of time.

In the case of howling surveys, the temporary disruption caused to the animals is lessened by the fact that it is necessary to cover the entire area to be surveyed and the same wolves are not affected over an extended period of time. However, the response rate as such is a less important issue as is the minimization of variations in response rates between individual days/nights and packs. Harrington and Mech (1982) recommend the use of a single howl with "flat" and "breaking" segments to reduce the differences in reply rates among packs. Based on results from the Laurentide wolves, this type of howl would likely elicit a higher response rate than the coyote howls used in this study and possibly cause less of a behavioral disturbance than the howls of a pack of wolves. Because most surveys call for howling sessions to be repeated 3-5 times per trial (Harrington and Mech 1982; Fuller and Sampson 1988; Gaines et al. 1995), managers could consider the use of higher pitched wolf howls as a possible mechanism to reduce disturbance to the animals. Due to our study design, we are not able to discern between the effect of species and group size. Because we were only able to test two alternative stimulation methods we chose them such that they would represent extremes to increase the likelihood of detecting a difference in response, if one were present. Based on our results, further tests of stimulation types are warranted and are necessary before more detailed conclusions can be drawn.

3.7 Tables

Table 1. Composition of Malbaie pack during the spring and summer of the study.

1996	**1997**
Alpha male (M450)	Alpha male (M450)
Alpha female (F381)	Alpha female (F381)
Yearling (F402)	2 year old (F402)
Yearling (F411)	2 year old (F411)
Yearling (F421)	2 year old handicapped wolf (F470)[1]
Handicapped yearling (F470)[1]	Yearling (F331)
6 pups (3 collared)[2]	Yearling (F253)
	Yearling (F370)
	7 pups (3 collared)

[1] had one foot missing

[2] the collar of one of the pups failed on August 25th

Table 2. Composition of the GJ pack in the spring and summer of the study.

1997

Alpha male (M361)
Alpha female (F135)
Adult male (M290)
Adult male (M130)[1]
Yearling female (F020)
Yearling male (M060)
7 pups

[1] was only captured in August of 1997. His origin nor the length of time he had been with the pack is not known.

Table 3. Response parameters to wolf howling stimulations at rendezvous sites for the Malbaie pack in 1996*.

Date	Days since left den	Response 1	Alpha male Present	Alpha female present	Total # wolves present	Response 2	Alpha male present	Alpha female present	Total # wolves preesnt
04.08.96	5	Y	Y	N	5	Y	Y	Y	5
05.08.96	6	N	Y	Y	6	Y	Y	Y	6
06.08.96	7	Y	N	N	1	Y	Y	N	3
12.08.96	13	Y	N	Y	2	N	N	Y	2
13.08.96	14	Y	Y	N	4	Y	Y	N	4
14.08.96	15	Y	N	N	1	Y	N	N	0
17.08.96	18	Y	N	Y	3	Y	N	N	1
18.08.96	19	Y	N	Y	2	Y	N	Y	2
19.08.96	20	Y	N	Y	2	Y	N	Y	2
25.08.96	26	N	Y	Y	3	N	Y	Y	3
26.08.96	27	N	N	N	2	Y	Y	N	4
27.08.96	28	N	N	N	0	Y	Y	Y	5

* Day 1 of stimulation blocs were not monitored due to field-related constraints.

Table 4. Responses to wolf and coyote stimulations at rendezvous sites for the Malbaie pack in 1997.

Date	Days since left den	Stimulation	Response 1	Alpha male present	Alpha female present	Total # wolves present	Response 2	Alpha male present	Alpha female present	Total # wolves present
22.07.97	3	W	Y	N	N	2	Y	Y	N	3
23.07.97	4	W	Y	Y	Y	4	Y	Y	Y	4
24.07.97	5	W	Y	Y	Y	5	Y	Y	Y	5
25.07.97	6	W	Y	Y	Y	5	Y	Y	Y	5
31.07.97	12	C	Y	N	N	2	Y	N	N	2
01.08.97	13	C	Y	N	N	0	Y	N	N	0
02.08.97	14	C	Y	N	N	0	Y	N	N	0
03.08.97	15	C	Y	N	Y	5	Y	N	Y	5
08.08.97	20	W	Y	Y	Y	4	Y	Y	Y	5
09.08.97	21	W	Y	N	Y	5	N	N	Y	5
10.08.97	22	W	N	N	N	0	Y	N	N	0
11.08.97	23	W	Y	Y	N	4	Y	Y	N	3
16.08.97	28	C	N	Y	Y	7	N	Y	Y	7
17.08.97	29	C	N	N	N	0	-	N	N	0
18.08.97	30	C	N	N	N	1	N	N	N	1
19.08.97	31	C	Y	N	Y	4	Y	N	Y	4
24.08.97	36	W	Y	N	N	1	Y	N	N	1
25.08.97	37	W	N	N	N	1	Y	N	Y	4
26.08.97	38	W	N	N	N	0	N	N	Y	1
27.08.97	39	W	Y	Y	N	5	Y	Y	N	5
01.09.97	44	C	Y	N	N	0	N	N	N	0
02.09.97	45	C	N	N	N	0	N	N	N	0
03.09.97	46	C	N	N	N	2	N	N	N	2
04.09.97	47	C	N	N	N	1	N	N	N	1
09.09.97	52	W	Y	N	N	2	Y	N	N	2
10.09.97	53	W	N	N	N	2	N	N	N	2
11.09.97	54	W	N	N	Y	1	N	N	Y	1
12.09.97	55	W	N	Y	N	2	N	Y	N	2
17.09.97	60	C	N	N	N	0	N	N	N	0
18.09.97	61	C	N	N	N	1	N	N	N	1
19.09.97	62	C	N	Y	Y	5	N	Y	Y	6
20.09.97	63	C	N	N	Y	3	N	N	Y	3
25.09.97	68	W	Y	Y	Y	6	Y	Y	Y	6
27.09.97	70	W	Y	N	N	0	N	N	N	0

Table 5. Responses to wolf howling stimulations at rendezvous sites for the GJ pack in 1997.

Date	Days since left den	Stimulation	Response 1	Alpha male present	Alpha female present	Total # wolves present	Response 2	Alpha male present	Alpha female present	Total # wolves present
31.07.97	5	W	N	N	N	1	Y	N	N	1
01.08.97	6	W	N	N	N	1	N	N	N	1
02.08.97	7	W	Y	N	Y	2	Y	N	Y	2
03.08.97	8	W	Y	Y	N	2	Y	Y	N	2
08.08.97	13	C	Y	N	N	1	Y	N	N	1
09.08.97	14	C	N	N	N	2	N	N	N	1
10.08.97	15	C	Y	N	N	1	N	N	N	0
11.08.97	16	C	N	N	N	1	N	Y	Y	3
16.08.97	21	W	N	N	N	0	N	N	N	0
17.08.97	22	W	N	N	N	0	N	N	N	0
18.08.97	23	-	-	-	-	-	-	-	-	-
19.08.97	24	W	N	Y	N	3	N	Y	N	3
24.08.97	29	C	N	N	N	1	N	N	N	1
25.08.97	30	C	N	N	N	4	N	Y	Y	4
26.08.97	31	C	N	N	Y	3	N	N	Y	3
27.08.97	32	C	N	N	N	0	N	N	N	0

Table 6. Parameters of reduced model for first stimulations of Malbaie pack in 1997.

Variables:	Estimates	S.E.	t-ratio	p	Odds Ratio	95% confidence intervals Upper	Lower
Constant:	1.49	1.12	1.34	0.18	-	-	-
Season:	-0.08	0.03	-2.62	0.01	0.92	0.98	0.87
Type of Stimulation:	1.34	1.00	1.35	0.18	3.83	26.90	0.55
More than 2 wolves:	2.31	1.01	2.28	0.02	10.04	72.72	1.39

Table 7. Parameters of reduced model for second stimulations of Malbaie pack in 1997.

						95% confidence intervals	
Variables:	Estimates	S.E.	t-ratio	p	Odds Ratio	Upper	Lower
Constant:	1.93	1.24	1.55	0.12	-	-	-
Season:	-0.09	0.03	-2.77	0.01	0.91	0.97	0.86
Type of Stimulation:	1.96	1.13	1.18	0.24	7.08	65.33	0.76
More than 2 wolves:	1.25	1.06	1.18	0.24	3.49	28.03	0.44

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3.9 Appendices

Appendix I

Schedule of howling stimulations and nights of monitoring for a) the Malbaie pack in 1996 and b) for the Malbaie and GJ packs in 1997.

a)

Date	Type of stimulation (W=wolf, NS=no stimulation)	monitoring from 19:00 to 1:00 (Y/N)
03.08.96	W	N
04.08.96	W	Y
05.08.96	W	Y
06.08.96	W	Y
07.08.96	NS	N
08.08.96	NS	Y
09.08.96	NS	Y
10.08.96	NS	Y
11.08.96	W	N
12.08.96	W	Y
13.08.96	W	Y
14.08.96	W	Y
15.08.96	NS	N
16.08.96	W	N
17.08.96	W	Y
18.08.96	W	Y
19.08.96	W	Y
20.08.96	NS	N
21.08.96	NS	Y
22.08.96	NS	Y
23.08.96	NS	Y
24.08.96	W	N
25.08.96	W	Y
26.08.96	W	Y
27.08.96	W	Y

b)

Date	Malbaie stimulation (W=wolf, C=coyote, NS=no	 monitoring from 19:00 to 1:00 (Y/N)	Grands-Jardins stimulation (W=wolf, C=coyote, NS=no	 monitoring from 19:00 to 1:00 (Y/N)
22.07.97	W	Y	NS	N
23.07.97	W	Y	NS	N
24.07.97	W	Y	NS	N
25.07.97	W	Y	NS	N
26.07.97	NS	N	NS	N
27.07.97	NS	Y	NS	N
28.07.97	NS	N	NS	N
29.07.97	NS	N	NS	N
30.07.97	NS	N	NS	N
31.07.97	C	Y	W	Y
01.08.97	C	Y	W	Y
02.08.97	C	Y	W	Y
03.08.97	C	Y	W	Y
04.08.97	NS	N	NS	N
05.08.97	NS	Y	NS	Y
06.08.97	NS	Y	NS	Y
07.08.97	NS	Y	NS	Y
08.08.97	W	Y	C	Y
09.08.97	W	Y	C	Y
10.08.97	W	Y	C	Y
11.08.97	W	Y	C	Y
12.08.97	NS	Y	NS	N
13.08.97	NS	Y	NS	Y
14.08.97	NS	Y	NS	Y
15.08.97	NS	Y	NS	Y
16.08.97	C	Y	W	Y
17.08.97	C	Y	W	Y
18.08.97	C	Y	W	Y
19.08.97	C	Y	W	Y
20.08.97	NS	Y	NS	Y
21.08.97	NS	Y	NS	Y
22.08.97	NS	Y	NS	Y
23.08.97	NS	N	NS	Y

b) (cont.)

	Malbaie		Grands-Jardins	
Date	stimulation (W=wolf, C=coyote, NS=no stimulation)	monitoring from 19:00 to 1:00 (Y/N)	stimulation (W=wolf, C=coyote, NS=no stimulation)	monitoring from 19:00 to 1:00 (Y/N)
24.08.97	W	Y	C	Y
25.08.97	W	Y	C	Y
26.08.97	W	Y	C	Y
27.08.97	W	Y	C	Y
28.08.97	NS	N	NS	Y
29.08.97	NS	Y	NS	Y
30.08.97	NS	Y	NS	Y
31.08.97	NS	Y	NS	Y
01.09.97	C	Y	-	-
02.09.97	C	Y	-	-
03.09.97	C	Y	-	-
04.09.97	C	Y	-	-
05.09.97	NS	N	-	-
06.09.97	NS	N	-	-
07.09.97	NS	Y	-	-
08.09.97	NS	Y	-	-
09.09.97	W	Y	-	-
10.09.97	W	Y	-	-
11.09.97	W	Y	-	-
12.09.97	W	Y	-	-
13.09.97	NS	N	-	-
14.09.97	NS	Y	-	-
15.09.97	NS	Y	-	-
16.09.97	NS	Y	-	-
17.09.97	C	Y	-	-
18.09.97	C	Y	-	-
19.09.97	C	Y	-	-
20.09.97	C	Y	-	-
21.09.97	NS	N	-	-
22.09.97	NS	N	-	-
23.09.97	NS	Y	-	-
24.09.97	NS	Y	-	-
25.09.97	W	Y	-	-
26.09.97	W	N	-	-
27.09.97	W	Y	-	-

Appendix II

A logistic regression analysis was performed to determine the influence of several parameters on the probability of a howling response. Variables considered in the analysis included a seasonal effect (days since pack left the den), the type of stimulation (wolf vs. coyote), days since the last kill, presence of the alpha male, presence of the alpha female and the presence of more than 2 wolves with the pups. When several groups of wolves were present in proximity of the rendezvous site, only the response behavior of the group with the collared pups was considered. Therefore, the full model had the form:

$$\text{Logit (P)} = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k$$

Where logit (P) = p/1-p and X_1, X_2, …, X_k are the independent variables.

The first model used only data obtained from the Malbaie pack in 1997 (34 days of stimulation), because two variables not available in 1996 could be tested (howling stimulus used (wolf vs. coyote howls) and time since the last moose kill; each new moose kill became a rendezvous site). The first logistic regression analysis used only data from the 1st stimulation. The test of the full model with all 6 variables against a constant only model was statistically reliable (x^2 (6, N=34) = 21.17, p=0.002), indicating that the predictors, as a set, reliably contributed to the prediction of a response. According to the Wald criterion, only the number of days since the pack abandoned the den reliably predicted the pack's response (z = -2.28, p = 0.02) with response rate decreasing over time.

Taking this seasonal effect into account, the other variables were tested individually. Only 2 variables, type of stimulation (z=1.62, p= 0.11), and the presence of more than 2 wolves (z = 2.47, p = 0.01) were considered significant. Table 4 shows regression coefficients, Wald statistics, odds ratios and 95% confidence intervals and odds ratios for each of the 3 predictors in the reduced model.

The overall fit of the reduced model was not significantly different from the full model (p = 0.50). The variance accounted for by the model (McFadden's rho-squared) is 0.40 (values between 0.20 and 0.40 are considered very satisfactory)(Hensher and Johnson, 1981). The overall prediction rate of the model is moderate with an overall correct prediction rate of 71%.

The same type of analysis was performed on data from the second stimulation for the Malbaie pack in 1997. The same variables were retained in the final reduced model which was not significantly different from the full model (p = 0.32) and accounted for much of the variance (McFadden's rho = 0.45). The overall correct prediction rate was 76%. Therefore for both first and second stimulations, the presence of more than two wolves with the pups as well as the use of wolf over coyote howls significantly increased the odds of a positive response (table 5).

In order to test these predictors across years for the Malabie pack, only nights of wolf stimulation in 1997 for the Malbaie pack were combined with data from wolf stimulation nights of the Malbaie pack in 1996 (wolves were only stimulated with wolf howls in 1996). Because the pack size was different in 1996 and 1997 (6 vs. 8 wolves), the variable "more than 2 wolves present" was replaced by the "total number of wolves present" and the variable 'year' was added. Therefore, the predictors considered in this model were year, seasonal effect, presence of alpha male, presence of alpha female and the number of wolves present. A test of the full model with all 5 predictors against a constant-only model was not statistically reliable for the first stimulation, (x^2 (5, N = 30) = 10.16 and p = 0.07) meaning that these variables as a whole are not good predictors of the outcome of a stimulation. The only variable found to be a predictor of response was the total number of wolves present (z = 2.01, p = 0.04 (OR: 3.06). The addition of this variable to the constant only model was also significant, x^2 (1, N=30) = 4.43, p = 0.04. Because of the seasonal effect in 1997 and the fact that environmental factors vary from year to year, the variables 'season' and 'year' were kept in the final model although they were not significant. When the full model was compared to the reduced model with the variables season, year, and total number of wolves, they were not significantly different (x^2 (2, N=30)=2.61, p=0.27). Parameter estimates and odds ratios of variables are presented in the table below:

Variables:	Estimates	S.E.	t-ratio	p	Odds Ratio	95% confidence intervals Upper	Lower
Constant:	0.24	1.65	0.15	0.89	-	-	-
Season:	-0.03	0.03	-0.95	0.34	0.97	1.03	0.92
Year:	0.20	1.09	0.18	0.86	1.22	10.35	0.14
Total number of wolves:	0.45	0.27	1.69	0.09	1.57	2.65	0.93

A test of the first model with all 5 predictors for the second stimulation was significant [x^2 (5, N = 30) = 13.11, p = 0.02]. Only the seasonal effect was found to be significant according to the Wald criterion (z=-1.75, p=0.08) but variables 'presence of alpha female' and 'total number of wolves' were also considered for the reduced model (z= -1.50, p=1.13 and z=1.38, p=0.17 respectively). The reduced model consisting of variables year, seasonal effect, alpha female present and total number of wolves present was not significantly different from the full model (x^2 (1, N = 30) = 0.02, p = 0.89). However, the variable 'presence of the alpha female' did not affect response (OR= 0.08) and was not significant (z= -1.59, p= 0.11). The final model consisting of variables year, seasonal effect, and the total number of wolves was not significantly different from the full model (x2 (2, N=30) = 3.70, p=0.16). Parameter estimates and odds ratios of variables are presented in the table below:

Variables:	Estimates	S.E.	t-ratio	p	Odds Ratio	95% confidence intervals Upper	Lower
Constant:	0.74	2.02	0.37	0.71	-	-	-
Season:	-0.06	0.03	-1.65	0.10	0.95	1.01	0.88
Year:	0.51	1.30	0.39	0.69	1.67	21.53	0.13
Total number of wolves:	0.41	0.29	1.44	0.15	1.51	2.66	0.86

To combine data from the GJ pack to the two years of data from the Malbaie pack, only wolf stimulation nights were used and the variable year was replaced with the variable pack/year. A test of the full model against the 5 predictors was significant for the first stimulation, $x^2 (5, N = 38) = 10.16, p=0.07$. However, based on the Wald statistic, only the number of wolves present was a significant predictor of response ($z = 2.20, p=0.03$). The reduced model consisting of the variables pack/year, seasonal effect, and the total number of wolves present was not found to differ significantly from the full model [$x^2 (2, N = 38) = 1.93, p= 0.38$]. Additionally, a test of the model with all variables except the number of wolves present was found to be significantly different from the full model, $x^2 (1, N =38) = 12.19, p<0.001$. Therefore, an increase in the number of wolves present is the factor that most increases the chances of a response (OR=1.68). For parameter estimates and odds ratios of variables in the reduced model see table below:

						95% confidence intervals	
Variables:	Estimates	S.E.	t-ratio	p	Odds Ratio	Upper	Lower
Constant:	0.77	1.43	0.54	0.59	-	-	-
Season:	-0.02	0.02	-0.75	0.45	0.98	1.03	0.94
Pack/Year:	-0.49	0.53	-0.92	0.36	0.62	1.74	0.22
Total number of wolves:	0.52	0.24	2.15	0.03	1.68	2.69	1.05

A test of the full model against the 5 predictors for the second stimulation was significant ($x^2 (5, N = 38) = 13.56, p=0.02$). Only the variable pack/year was significant according to the Wald criterion ($z= -1.75, p= 0.08$). When variables pack/year and the seasonal effect were kept in the model and tested individually with the other three variables (presence of the alpha male and female and the total number of wolves), the presence of the alpha male and the total number of wolves were found to affect response (z= 2.00, p= 0.05 and z= 1.82, p= 0.07 respectively). The reduced model consisting of the constant, seasonal effect, pack/year variable, the presence of the alpha male and the total number of wolves present was not statistically different from the full model (x^2 (1, N = 38) = 0.98, p=0.32). However, none of the variables were found to significantly influence response (p>0.1). For parameter estimates and odds ratios of variables in the reduced model see table below:

						95% confidence intervals	
Variables:	Estimates	S.E.	t-ratio	p	Odds Ratio	Upper	Lower
Constant:	2.27	1.78	1.28	0.20	-	-	-
Season:	-0.03	0.02	-1.32	0.19	0.97	1.02	0.93
Pack/Year:	-1.00	0.62	-1.61	0.11	0.37	1.25	0.11
Presence of alpha male:	1.19	1.07	1.11	0.28	3.28	26.61	0.40
Total number of wolves:	0.23	0.31	0.73	0.47	1.25	2.30	0.68

Environmental parameters including precipitation, temperature, wind (above or below 50km/h), presence of full moon (considered full 2 days before and after actual full moon), cloud cover (above or below 50%) were measured during every stimulation night. None of these variables significantly predicted wolf response (p>1.0) and were not included in the model. However it should be noted that the presence of wind over 50km/h occurred on 1 occasion in 1996 and once in 1997 and on both occasions there were no vocal responses from the wolves present.

Sample sizes for the models presented above are small. However, when the seasonal effect is taken into account, the factor most influencing a response is clearly the number of wolves present as it was retained in each of the separate models.

Appendix III

Movements and responses of wolves of the Malbaie pack in 1996 on individual days:

In 1996, wolves were only stimulated using a recording of a pack of wolves which included adults and pups. Two different rendezvous sites were used and wolves were stimulated from a distance of 0.5 km from both sites. Wolves that were not present at the rendezvous site were located usually approximately two hours before the first stimulation and followed until 2:00 by ground radio tracking. Monitoring took place on 12 of the 16 nights of stimulation. The following are detailed descriptions of events taking place on these nights.

1) **August 4th**. The alpha female had left the rendezvous site at 19:25pm and headed northwest away from the rendezvous site. At 20:40 pm she was located 3.6 km from the rendezvous site (straight-line distance). All other individuals of the pack were located at the rendezvous site at this time and howled spontaneously for three minutes. The alpha female immediately changed direction and began heading back toward the rendezvous site. Whether it was the presence of technicians near the rendezvous site that initiated this howling we cannot say, but the howling definitely altered the behavior of the alpha female. She was taking a well-known route to a feeding site located approximately 20 km from their rendezvous site. The group howled again at 21:20 and at this point the alpha female was approximately 3.0 km from the rendezvous site. At 21:30 the pack was stimulated and responded 3 times between 9:30 and 9:45. During this time the alpha female continued to move toward

the direction of the rendezvous site (but took the longer route around a lake). She could not travel in a straight line due to a lake so she covered 4.2 km to make it back to the rendezvous site at 23:00 (from 20:40 to 23:00). The second stimulation took place at 23:00 and all the wolves responded. The alpha female never responded while she was away from the rendezvous site. She remained at the site for the remainder of the night.

2) **August 5th**. There was only one yearling female (F411) present with at least 2 pups at the rendezvous site. Both alphas and the 3 other yearlings were approximately 1 km from the site and had at least 1 pup with them. The two groups were located in a valley on either side of the stimulation site which was on top of a mountain. There had been howling between the 2 groups so we can assume that they were aware of each other's presence. There was no vocal response to the first stimulation. Half an hour later when the wolves were stimulated a second time, there was a vocal response followed by movement of the single yearling (F411) with the pups toward the larger group of wolves. Two hours later, there was spontaneous howling coming from the entire group.

3) **August 6th**. Only the handicapped yearling (F470) was with at least two of the pups during the first stimulation and all wolves responded. However the alpha male (M450), and three other yearlings (F402, F411, F421) and one of the collared pups were all within 1 km of that site. They did not vocally respond to the first stimulation. When the second stimulation took place, the alpha male (M450) and one of the

yearlings (F402) moved to join the handicap and pups at the rendezvous site and responded to the stimulation. The other two yearlings and collared pup did not respond but were within hearing distance of the stimulation and response. The alpha female was located over 10km from the rendezvous site at the time and so was out of range of the stimulation.

4) **August 12th**. The alpha female and the handicapped yearling were present at the rendezvous site with 2 pups when the first stimulation took place. The third collared pup had started to distance himself from the rendezvous site and his signal was not heard for an hour before the first stimulation. There was a response from the wolves at the rendezvous site, which lasted under a minute. Half an hour later, when the second stimulation took place, the pup had returned to the group and there was no response. During the time of the first stimulation the alpha male and 2 yearlings were over 14 km from the rendezvous site, were travelling in the direction of the rendezvous site and arrived around midnight. However, they were likely out of range and the wolves had been gone from the rendezvous site for over 12 hours and were already heading in the direction of the rendezvous site before the stimulation. Therefore, the return was not necessarily due to the howling.

5) **August 13th**. All of the wolves except the alpha female were near the rendezvous site. The alpha female was 16 km from the rendezvous site and most likely didn't hear the howling. The wolves were divided into 2 groups separated by approximately 1 km; one consisting of the alpha male, 2 yearling females (1 handicap) and at least 2 pups

while the other consisted of a yearling and at least one pup. There was howling between the 2 groups on 9 occasions between 21:00 and 21:45. When the 1st stimulation took place (22:00pm), the 2 groups began moving closer together while both groups vocally responded. Minutes after the 2nd stimulation half an hour later, the wolves were in one group and vocally responded.

6) **August 14th**. The handicapped wolf (F470) and yearling F411 were at the rendezvous site with at least 2 pups and responded to both stimulations. The alphas (F381 and M450), F402 and at least 2 pups were approximately 15 km from the rendezvous site. They were stimulated at 00:30 and responded. The alpha female left the group and returned to the rendezvous site by 4:30. The other wolves (M450 and F402) did not return until the following day.

7) **August 17th**. All of the wolves except the handicapped wolf (F470) were at the rendezvous site and vocally responded to both stimulations. F470 had left the rendezvous site at 21:15 and was within hearing range (4km) of the first stimulation half an hour later (21:42). She did not return to the rendezvous site and was located and remained 4 km from the rendezvous from midnight until 2:00 and did not return until the following night. All the wolves except the handicap remained at the rendezvous during the entire night.

8) **August 18th**. The alpha female (F381) and the handicapped wolf (F470) were with the pups during both stimulations and responded. The other wolves were not within hearing distance and did not return (they could not be found within the territory).

9) **August 19th**. The alpha female (F381) and the handicapped wolf (F470) were with the pups during both stimulations (22:20 and 23:00) and responded. The alpha male (M450) had left the rendezvous site at 21:00 and was heading south away from the rendezvous site. Twenty minutes after the first stimulation, he was 4.5 km from the rendezvous site but there were relatively high mountains separating him from the site so he probably did not hear the stimulations or the pack's vocal response. We stimulated him 200 meters from his location (4.5 km from rendezvous site) and he turned around and was back at the rendezvous site within 30 minutes.

10) **August 25th**. Three yearling females (470, 421, 411) were at the rendezvous site but with an unknown number of pups. Both alphas (M450, F381) and a yearling (F402) were with at least 2 pups and were located approximately 6 km from the rendezvous site. Due to the topography of the area, it is unclear whether they were able to hear the stimulation. There was no response to either stimulation (21:40 and 22:15), and two of the yearlings (F411 and F421) left the rendezvous site at midnight to join up with the alpha group (6 km away). F470 remained at the rendezvous until 7:30. The location that the alpha group moved the pups to then became the next rendezvous site (6 km away). The group never returned to the old rendezvous site.

11) **August 26th**. Two yearling females (F402, F411) were present with at least 2 of the pups at the rendezvous site (collar on 3rd pup had failed). They did not respond to the first stimulation, however, there was a response from both alphas (M450, F381) and the other 2 yearlings (F470, F421), approximately 2 km west of the rendezvous site. When the second stimulation took place, the alpha male (M450) and the handicapped yearling (F470) were back at the rendezvous site and there was a response from the 4 wolves and the pups. The alpha female (F381) and one of the yearlings (F421) were located approximately 2 km from the rendezvous site and did not respond vocally. However, they returned to the rendezvous site minutes after the second stimulation.

12) **August 27th**. Shortly after 2:00 on the 27th, all the wolves except the pups left the rendezvous site. At 19:00 they were located together approximately 2.8 km from the rendezvous site. They continued to move away from the rendezvous site at an approximate speed of 3.38±0.16 km/hour (straight line speed), based on triangulations every half hour. Just before the first stimulation took place, the wolves were located approximately 6 km from the rendezvous site. At least 2 pups were present at the rendezvous site. Neither the pups at the rendezvous site nor the wolves responded to the stimulation. The pack changed directions and made it back (except the handicapped wolf) to the rendezvous site 33 minutes after the stimulation. They therefore increased their speed 3 fold (12km/hr). The wolves responded to the 2nd stimulation (all had returned except the handicapped wolf) and howled 3 times during 10 minutes following the stimulation. The handicapped wolf arrived at the

rendezvous site 30 min after the other wolves. All the wolves remained at the rendezvous site until 7:30 the next morning.

Appendix IV

Behaviors and movements of Malbaie pack wolves in response to howling simulations in 1997:

a) Wolves stimulated using recordings of wolf howls (recording of a pack of wolves)

In 1997 wolf movement and behavior was only monitored within the vicinity of the rendezvous site. Wolves at the rendezvous site were stimulated from a distance of 100-200 meters. There were three occasions on which there was a change in response from the first to the second stimulation (August 9th, 10th, 25th), four nights on which there was neither a response to the first nor the second stimulation (August 26th, September 10th, 11th, and 12th) and nine evenings on which wolves present with the pups responded to both stimulations (July 22nd, 23rd, 24th, 25th, August 8th, 11th, 24th, 27th, and September 9th). Overall, there were 16 nights of wolf howling stimulations and the following are detailed descriptions of behaviors and movements of wolves at the rendezvous site and surrounding area:

1) **July 22nd**. The alpha female (F381), an adult (F402) and three yearlings (F331, F253, and F370) were at the rendezvous site at 21:00. At 21:40 the alpha female (F381), the adult (F402), and one of the yearlings (F331) left the rendezvous site. The stimulation took place at 22:00 (20 minutes later), so the departing wolves were likely within hearing distance. There was a response from the 2 yearlings (F253 and F370) and the

pups but the alpha female group (F381, F402, F331) did not respond nor did they return. The alpha male (M450) arrived 30 minutes after the stimulation and the 3 wolves (M450, F253, and F370) and pups responded to the second stimulation. The wolves howled spontaneously at 1:00 and then the three adult wolves departed leaving the pups alone.

2) **July 23rd**. The alpha male (M450), alpha female (F381), the handicapped adult (F470) and a yearling (F253) were present with the pups until 22:10. The stimulation took place 15 min after they had left the rendezvous site. All the wolves responded but continued to distance themselves from the rendezvous site. The second stimulation took place 30 minutes later. The adult wolves were about 0.5 km from the pups and responded. The pups howled after that and then the adults responded once more. However, they did not return to the rendezvous site.

3) **July 24th**. The alpha male (M450) and female (F381) and the three yearlings (F331, F370, and F253) were at the rendezvous site during the first and second stimulations and responded to both. However, all the adult wolves left the rendezvous site an hour later leaving the pups alone.

4) **July 25th**. The alpha male (M450) and female (F381), two adults (F402 and F470) and a yearling (F253) were at the rendezvous site during both stimulations and responded to both. They left the rendezvous site 3 hours later, leaving the pups alone.

5) **August 8th**. The alpha male (M450) and female (F381), an adult (F402), a yearling (F331) and at least three pups were present at the rendezvous site. The wolves responded to the first stimulation (22:20) and the handicapped adult (F470), who had left the site 50 minutes before the stimulation, returned to the rendezvous site within 20 minutes. All the wolves mentioned above were present at the rendezvous site during the second stimulation and responded vocally.

6) **August 9th**. The alpha female (F381), an adult (F402), the handicapped adult (F470), and two yearlings (F331 and F370) were present at the rendezvous site with most of the pups. The first stimulation took place at 23:02 and the wolves responded. The second stimulation occurred 32 minutes later and the wolves did not respond. There were no arrivals or departures from the site.

7) **August 10th**. Most or all of the pups were present at the rendezvous site but the alpha male (M450) and female (F381), an adult (F402), the handicapped adult (F470), and a yearling (F331) were located a maximum of 2 km east of the site. The pups did not respond to the first stimulation at 22:07. The second stimulation took place 30 minutes later at which time all the wolves had arrived back at the site and howled for approximately 1 minute. It is unclear whether the first stimulation caused the wolves to return to the site because most of them had been gone since 5:00 am that morning.

8) **August 11th**. Until 21:00, tha alpha female (F381), an adult (F402), and a yearling (F253) were present with the pups. At that time, the alpha female began distancing

herself from the rendezvous site. At 22:10 the alpha male (M450) and a yearling (F370) arrived at the rendezvous site and there was spontaneous howling at 22:40. The first stimulation took place at 22:50 and there was a response from the pups and the four wolves present with them. The alpha female did not return to the rendezvous site but it is not known whether she was within hearing distance of the howls since her signal had not been heard for approximately 90 minutes. Yearling F253 departed from the rendezvous site at 23:10. The second stimulation occurred at 23:25 and there was a response from the three wolves (M450, 402, F370) and the pups present. F253 was within hearing distance of the stimulation and response but did not respond or return to the rendezvous site.

9) **August 24th**. Only one adult wolf (F402) was present with the pups during the two stimulations and there were no movements noted. Wolves responded vocally to both stimulations.

10) **August 25th**. The alpha female (F381), the handicapped wolf (F470) and a yearling (F331) were present with the pups until 19:50 at which time F381 and F470 left the rendezvous site. The first stimulation took place at 22:30 and there was no response. Only F331 was present with the pups but F381 and F470 were still within range of the receiver. Within 10-20 minutes, both wolves returned to the site and when the second stimulation took place at 23:00 there was a response. Additionally, after the first response adult (F402)'s signal was first heard and she arrived at the rendezvous site at 23:20. However, it is difficult to say whether her return was caused by the stimulation

because she had been gone since at least 19:00 and data were not available for the 10-hour period prior to this.

11) **August 26th**. At 21:20 there were six wolves present at the rendezvous site: the alpha male (M450), the alpha female (F381), two adults (F402 and F470), and two yearlings (F331 and F370) and all of them left the site within the next 10-20 minutes. The first stimulation took place at 22:30 and there was no response but there were no adults left with the pups. Twenty minutes after the stimulation, the alpha female returned to the site and was there during the second stimulation at 23:00 but there was no response and she remained at the site until 2:40 am on the 27th of August.

12) **August 27th**. At 21:40, the alpha male (M450), an adult (F402), and three yearlings (F331, F253 and F370) were at the rendezvous site. At 21:50 F402 began moving west of the rendezvous site and our location. When the first stimulation occurred at 22:35, all the wolves at the site responded but not F402, who moved very close to our location. The second stimulation took place at 23:05 and all the wolves responded except for F402. After the response, the alpha male moved in the direction of the broadcast speakers and remained in the vicinity until midnight. All the wolves remained at the site until 5:00 am the next morning.

13) **September 9th**. The handicapped wolf (F470) and a yearling (F331) were present at the rendezvous site during the first stimulation at 23:00 and the wolves responded but

only for 7 seconds. The second stimulation occurred at 23:30 and the same wolves responded for 10 seconds. No movements were noted.

13) **September 10th**. The first stimulaiton took place at 22:30 and only the handicapped wolf (F470) and a yearling (F331) were present with the pups and there was no response. There was no movement detected around the site. The second stimulation took place 30 minutes later and again only F470 and F331 were present and there was no response.

14) **September 11th**. Only the alpha female (F381) was present with the pups during both stimulations and there was no response. The first stimulation took place at 22:30 and the second at 23:00.

15) **September 12th**. During the first stimulation at 22:30, the alpha male (M450) and the handicapped wolf (F470) were present at the rendezvous site with the pups but adult (F402) and yearling (F331) were together and within hearing distance. There was no response from either group. Twenty minutes after the stimulation F470 moved away from the site and during the second stimulation only the alpha male (M450) was with the pups, with the 3 other wolves still within hearing distance. No wolves responded. From 23:20 on, the three wolves left the area of the rendezvous site and were no longer within range of the telemetry receiver. The alpha male remained with the pups until 1:00 am on the 13th of September.

b) Wolves stimulated using recordings of a coyote howl (individual coyote)

In 1997, wolf movement and behavior was only monitored within the vicinity of the rendezvous site. There was one occasion on which there was a change in response from the first to the second stimulation (September 1st), ten nights on which there was neither a response to the first nor the second stimulation (August 16th, 17th, 18th, September 2nd, 3rd, 4th, 17th, 18th, 19th, 20th) and five evenings on which wolves present with the pups responded to both stimulations (July 31st, August 1st, 2nd, 3rd, 19th). Overall, there were 16 nights of coyote howling stimulations and the following are detailed descriptions of behaviors and movements of wolves at the rendezvous site and surrounding area:

1) **July 31st**. Adults F402 and F470 (handicapped wolf) were with the pups at the rendezvous site during the first stimulation and responded. F470 left the rendezvous site 25 minutes later. The wolves were stimulated 25 minutes after the departure of F470 (she was within hearing distance). There was no response or return by F470 but F402 and F411 vocally responded with the pups. F411 had returned to the rendezvous site between the two stimulations but had been gone for over 20 hours so her return was not necessarily due to stimulation. There was howling at the rendezvous site on and off for the next hour.

2) **August 1st**. Only pups were present during the two stimulations and they responded to both. Yearling F253 was within hearing distance of the first and maybe second stimulation but did not return.

3) **August 2nd**. Only pups were present during the two stimulations and they vocally responded to both. There were no other wolves known to be in the area.

4) **August 3rd**. The alpha female (F381), an adult (F402), the handicapped adult (F470) and two yearlings (F331 and F253) were with the pups during the two stimulations and responded to both. No movement was noted around the rendezvous site.

5) **August 16th**. All the wolves except the adult (F411) were present during both stimulations but they did not respond to either. All the wolves remained at the site until 5:00 the next morning. It is worth noting that the pack had killed an adult moose 2-3 days before and none of the individuals had left the site since the kill.

6) **August 17th**. The wolves were only stimulated once at the rendezvous site due to equipment failure. Only the pups were present and there was no response.

7) **August 18th**. Yearling (F331) arrived at the site at 22:00 where only pups were present. Stimulations occurred at 23:00 and 23:30. There was no vocal response and no movements noted.

8) **August 19th**. At 22:30, the alpha female (F381), an adult (F402), and two yearlings (F331 and F370) were at the rendezvous site but, 10 minutes later, the alpha female, F331, and F370 began moving away together. The first stimulation occurred at 23:12

and both groups answered (there were at least 2 pups with the group that left). At 23:20, the adult F402 also left the site and there were at least 2 pups left behind. When the second stimulation occurred at 23:50, only the group of wolves that had moved away answered (from about 1-2 km). There was no vocal response from the pups at the site to either the coyote stimulation or the pack's howling.

9) **September 1st**. Stimulations occurred at 22:30 and 23:00. There were only pups present at the site and they had been left unattended since 5:00 that morning. They howled in response to the first stimulation for 35 seconds but did not respond to the second stimulation. There were no movements noted.

10) **September 2nd**. The alpha female (F381), an adult (F402), a yearling (F331) and pups howled spontaneously at 19:48 and 20:01 and then the adults headed away from the site approximately half an hour later. Wolves were stimulated at 21:30 and 22:00 when they were still within hearing distance. Neither of the groups responded and none of the wolves returned to the site until after midnight. However, the alpha male's signal was heard at 22:10 (1-2 km away) and he arrived at the site at midnight; however, he had been absent for over 2 days.

11) **September 3rd**. The handicapped adult (F470) and a yearling (F370) were with the pups during both stimulations which occurred at 22:30 and 23:00. There was no response and no movement.

12) **September 4th**. Only one yearling (F331) was present with the pups during both stimulations. There was no response and no movement.

13) **September 17th**. No adults were present with the pups and there was no response to either of the two stimulations.

14) **September 18th**. Only one yearling (F331) was present with the pups during both stimulations. There was no response and no movement.

15) **September 19th**. All the wolves, except for adult F411 and yearling F331 who were already present, arrived around 1:00 am that morning and were present during both stimulations. There was no response and no particular movement to note.

16) **September 20th**. The alpha female (F381), the handicapped wolf (F470), and a yearling (F253) were present during both stimulations (F381 and F470 had not left the site since the previous stimulation on the 19th). There was no response to either stimulation. The alpha female did not leave the site until the 22nd when the rest of the pack killed an adult moose and then she moved the pups to the new rendezvous site.

Appendix V

Behaviors and movements of GJ pack wolves in response to howling simulations in 1997:

a) Wolves stimulated using recordings of wolf howls (recording of a pack of wolves)

All of the stimulations took place from approximately 700-800 meters from the rendezvous site. Movements of wolves were only followed near the vicinity of the site. There were 2 nights during which wolves responded to both stimulations (August 2nd and 3rd). There were 5 nights during which wolves did not respond to either stimulation (July 31st, August 1st, 16th, 17th, 19th). Overall, there were 8 nights of wolf howling stimulations and the following are detailed descriptions of behaviors and movements of wolves at the rendezvous site and surrounding area:

1) **July 31st**. Only the yearling F020 was with the pups during both stimulations (23:01 and 23:46) and there was no response. There were no other wolves within hearing distance of the stimulation and no movement was noted.

2) **August 1st**. Only the yearling F020 was with the pups during the two stimulations (22:48 and 23:32) and there was no response. The adult M290 was located 2-3 km from the rendezvous site during both stimulations and did not return to the site nor did he howl. However, there were technical difficulties with the broadcast speakers and it is possible that he may not have heard the stimulation.

3) **August 2nd**. The first stimulation took place at 23:00 and the alpha female (F135) and yearling F020 were present. There was a response to the stimulation by all the wolves present. The alpha female then moved toward us and was located 100 meters from the stimulation site during the second stimulation at 23:33. There was again a vocal response from all of the wolves and the alpha female (F135) left the site not long after the stimulation.

4) **August 3rd**. The alpha male (M361) and yearling F020 were at the rendezvous site with the pups during both stimulations (23:03 and 23:35) and there were responses both times. There was spontaneous howling until at least 1:00 on August 24th when monitoring ended.

5) **August 16th**. The alpha male (M361), the adult male (M290), and a yearling (M130) were present at the rendezvous site with the pups. The group howled spontaneously at 20:30 and then the three wolves began to distance themselves from the site. The stimulations took place at 23:00 and 23:31 and there was no response. Although the signals of the departing wolves were still within range, it is possible that they did not hear the stimulation due to high winds. They continued to distance themselves after both stimulations.

6) **August 17th**. The adult M290 and yearling M130 were at the rendezvous site until approximately 21:30 and then began to distance themselves from the site. When the first stimulation took place at 22:27, they had been out of range of the receivers for

approximately 40 minutes. There was no response from either group and the two wolves did not return to the rendezvous site. The second stimulation took place at 22:53. There was no response from the rendezvous site and none of the collared adult wolves were present.

7) **August 18th**. It was believed that the pups were moved to a new rendezvous site so the stimulation took place near this area. However, it was later discovered that the pups had not been moved so this stimulation in fact did not take place at the true rendezvous site. The adult M290 was at the stimulation site (not the rendezvous site) and barked 5 minutes after the first stimulation (stimulation time: 23:21). The collar frequency of the alpha male (M361) was heard in the distance but there was no reply. The second stimulation occurred at 23:52 and there was no reply from either wolf.

8) **August 19th**. The alpha male (M361), the adult male (M290), and a yearling (M130) were at the rendezvous site during the first stimulation at 23:00 and there was no response. Ten minutes before the second stimulation at 23:29 the alpha male (M361) left the rendezvous site. The two other wolves were still at the rendezvous site during the second stimulation and there was no response. However, the alpha male (M361) returned to the rendezvous site and remained there until 1:00 on the 20th of August.

b) Wolves stimulated using recordings of a coyote howl (individual coyote)

Wolf movement and behavior were only monitored within the vicinity of the rendezvous site. There was one night on which wolves responded to both stimulations (August 8th). There was one night on which there was a change in response from the first to the second stimulation (August 10th). There were six nights during which there was no response to the stimulations (August 9th, 11th, 24th, 25th, 26th, 27th). Overall, there were 8 nights of coyote howling stimulations and the following are detailed descriptions of behaviors and movements of wolves at the rendezvous site and surrounding area:

1) **August 8th**. The alpha male M361 and 2 yearlings (M060, F020) were present with the pups at the rendezvous site and howled spontaneously four times between 19:45 and 21:15. The alpha male (M361) and M060 then began distancing themselves together from the rendezvous site and when the first stimulation was played at 21:34, there was only a response from yearling F020 and the pups. The alpha male and M060 were likely within hearing distance. F020 and the pups responded to the second stimulation but both the alpha male (M361) and yearling M060 continued to distance themselves from the rendezvous site (not toward the stimulation site) and their signals were not heard until the end of monitoring at 1:00 on August 9th.

2) **August 9th**. The adult male M290 and the yearling F020 were with the pups at the rendezvous site during both stimulations (23:00 and 23:30) and there was no immediate response. During this time, M290 moved toward the stimulation site and

began howling and barking 8 minutes after the second stimulation. From that time until midnight, there was almost continuous howling alternating between M290 (near us) and F020 with the pups at the rendezvous site. During this time M290 was located <100 meters from the stimulation site and repeatedly barked at us. M290 then returned to the rendezvous site and there was a spontaneous howl at 00:40 from M290, F020, and the pups.

3) **August 10th**. The yearling F020 was present with the pups during the first stimulation at 23:00. The wolves responded to the stimulation together for a duration of approximately 4 minutes after which F020 howled twice alone and departed from the rendezvous site. Because the pups were not collared it is not known whether she left alone or took the pups with her. There was no response to the second stimulation at 23:30.

4) **August 11th**. Only the yearling F020 was present with the pups at the rendezvous site and there was no response to the first stimulation at 23:00. The alpha male (M361) and alpha female (F135) arrived at the site before the second stimulation at 23:30 but there still was no response to the second stimulation. The alpha male and female had been absent from the rendezvous site for over 24 hours.

5) **August 24th**. Only M060 was present at the rendezvous site during both stimulations (23:37 and 23:50). There was no response and no movement noted.

6) **August 25th**. Two wolves (M060, and M130) were present with the pups until 23:30. There was no response to the first or second stimulations at 21:30 and 22:00 and no movement was noted. The alpha male (M361) and female (F135) arrived at the site at approximately 23:00. It is not sure whether they returned because of the stimulation since they had been gone for at least 24 hours. The wolves were then stimulated two more times (at 23:00 and 23:30) and did not respond. At 23:56, all of the wolves present howled and did so on eight more occasions between then and 1:00 on August 26th. (note: to be conservative, the last two of the four stimulations were used in the logistic analysis because the location of adults was not known during the first).

7) **August 26th**. The alpha female (F361), the adult (M060) and one of the yearlings (M130) were at the rendezvous site. The alpha female began distancing herself from the site at approximately 21:10. The first stimulation was played at 21:40 and the alpha female (F135) returned to the site but there was no vocal response. The second stimulation was played at 22:40 and there was no vocal response. All three wolves remained at the site until at least 1:00 on August 27th.

8) **August 27th**. There were no collared wolves present at the rendezvous site during the two stimulations (21:40 and 22:16). There was no response to either stimulation and no movement noted. It is possible that the wolves had abandoned the site but impossible to verify because there were no pups collared in the pack.

4. Technical Paper

Rubber padded leg-hold traps in the capture of wolves

S. Czetwertynski[1], R. Lemieux[2]P, McLeod[1]

[1] Acadia University, Psychology Department, Wolfville, Nova Scotia. B0P 1X0.

[2] Ministère de l'Environnement et de la Faune du Québec, 675 boul. René-Lévesque Est, 11e étage, Québec, Québec. G1R 5V7.

Corresponding author:

Sophie Czetwertynski
5797 Ave de la Terrasse
Rawdon, PQ
K0K 1S0

4.1 Abstract

The trapping of mammals is an essential part of most wildlife research projects and in the case of wolves, leg-hold traps are the tools most commonly used. In this study, wolves were captured using several different models of traps in the Laurentide reserve as part of a three-year wolf ecology study (Jolicoeur 1999). Because modified Newhouse 4 and 114 traps generally used by wolf researchers were found to cause substantial injuries, Soft Catch #3 traps with rubber padded jaws were modified in an attempt to reduce capture-related injuries. These traps were found to cause significantly less damage to the animals and are presently being tested by the Canada Fur Institute to determine whether they meet the injury and behavioral threshold requirements defined by the Agreement on International Humane Trapping Standards. Trap modifications are detailed and the advantages and disadvantages of the modified Soft-Catch #3 are discussed.

4.2 Introduction

The live-trapping of mammals is an essential part of most wildlife research projects and for many larger species leg-hold traps are the most commonly used trapping tool. Tooth-jawed traps are commonly used in research projects though they have been commercially banned from North America because they were perceived as inhumane (Gilbert 1995). Public scrutiny and the demands of society concerned with the suffering of animals have placed increased pressure on the scientific community to continually improve capture methods and establish standards (Gilbert 1991). Accordingly, Canada, Russia and the European Union have signed the Agreement on International Humane Trapping Standards (AITS) in July of 1997 (Fur Institute of Canada http.). As part of this agreement, the use of all conventional leg-hold traps by trappers and biologists will be banned in these countries as of April 1st, 2001 (Fur Institute of Canada http.). Several non-conventional or modified traps are being and will be tested by the Fur Institute of Canada and only those passing the standards set by the AITS will be legalized. There is presently no restraining trap for wolves passing the standards. The US is not part of this agreement but did sign an Understanding (not legally binding) with the European Union to try and abide by the AITS but the ultimate decision will lie with individual States.

Leg-hold traps most commonly used by researchers include the Newhouse 3 and 4 (smooth-jawed) and the Newhouse 14 and 114 (toothed-jaws) which can either be offset or not (Van Ballenberghe 1984; Kuehn et al. 1986). All of these traps can be, and often are, modified in order to reduce the pressure they put on the animal's foot (Kolenosky and Johnston 1967). However, most of these traps remain quite powerful and although serious injuries are not common, most wolves sustain minor cuts and swelling when caught with these instruments (Peterson et al. 1984).

Twenty wolves were captured in the first year of a three-year study (Jolicoeur 1999) using modified Newhouse 4 and 114 offset traps (modified jaws and springs) and almost all sustained various degrees of swelling and lacerations requiring stitches. As an alternative to decreasing the strength of powerful Newhouse traps, Victor Soft Catch #3 rubber padded traps (sold commercially for the trapping of coyotes) were modified in an attempt to reduce capture-related injuries to wolves (Lemieux 1996). Soft Catch #3 traps were chosen because of their smaller size (easier installation), lower cost, and primarily their rubber padded jaws. The ideal leg-hold trap is one that will be able to retain an animal no matter its size once caught and also inflict little or no damage. Because the commercial Soft Catch #3 trap is not powerful enough to retain a wolf, certain modifications were necessary both to ensure that wolves of various sizes would be retained once caught and to minimize harm to them.

In what follows, we describe the modifications made to these traps and the results of having used them in the last two years of the study.

4.3 Study area and methods

All captures took place during a three-year wolf ecology study in the Laurentide reserve area of Quebec, Canada (Lemieux 1996, Jolicoeur 1999). The study area is characterized by boreal forest (black spruce, *Picea mariana* and balsam fir, *Abies balsamea*). There is an elaborate road system due to ongoing logging activities. Traps were usually set along logging roads known to be used by wolves. These areas had been logged and regrowth usually consisted of maple (*Acer* spp.), yellow birch (*Betula alleghaniensis*), and various shrubs that decreased the time required for wolves to get the traps tangled. Trap lines were checked on a daily basis, usually in the early morning. A more detailed description of the study areas is available in Jolicoeur (1999).

Traps were first boiled for a minimum of 30 minutes in water and logwood crystals and then dipped into a mixture of boiling water, paraffin and bees wax before being hung outside to dry. The traps were then stored in travelling containers lined with fir branches to avoid all human scent before installation. Handling of traps was done with rubber gloves at all times.

The proportion of bycatch species was reduced by carefully selecting sites and using the appropriate sexual and curiosity lures (Lemieux 1999). Careful attention was made in the placement of traps, as well as the types of baits used (Lemieux 1999) by burying meatball size portions, to prevent both theft and the accidental capture of birds of prey (Figure 1).

Trapped wolves were handled using a neck-snare constructed of thick plastic-covered cable and passed through a 1.5-meter long pipe to handle the wolf from a secure distance. The snare noose could be made large to easily slide it around the wolves' neck and then tighten it. Unlike the use of a Y-type stick, this allows the handler to keep the wolf's upper body tightly against the ground without applying direct pressure on the neck. The handler was then able to restrain the jaw and feet when required. None of the wolves captured needed to be immobilized to be handled and take the required measurements and blood samples. Stress was minimized by reducing the number of people present (usually 2) and by avoiding loud noises (motors, talking, etc.). Thus problems related to drug use such as overdoses, accidental deaths or cardiac arrhythmia were avoided (Mech 1974; Fuller and Keith 1981; Fuller and Kuehn 1983). In most cases, wolves did have elevated heart and respiration rates, but not to a level that would cause concern. Not drugging wolves was an added advantage in an area with high traffic due to logging, fishing, hunting, and tourists as released wolves that are still under the effects of sedation may not be as vigilant.

4.4 Modifications to conventional Soft Catch #3 trap

1) Solder was applied to the base of the jaws, thereby preventing adult wolves from freeing themselves by forcing the jaws out from the base of the trap (Figure 2). 2) The original coils were removed and replaced by manufactured ones twice as powerful to increase the closure speed of the trap and to retain larger wolves. 3) An additional sheet of metal was soldered to the original base of the trap to reinforce it. This also allowed for

the installation of a pivot at the center of the trap as opposed to its original position on the end (note: more recent Soft Catch traps now have the pivot at this location on the trap). This lessens the strain on the wolves' leg by offering more mobility with less torque on the captured limb and produces resistance directly underneath the foot instead of to the side (Figure 3). 4) The pad was cut to reduce its dimension in order for wolves to push their leg deeper into the jaws of the trap before it is set off. This prevents wolves from being caught by their toes which is more likely to cause lacerations (Figure 4). 5) A second trigger position was filed above the original one thus requiring more pressure to set the trap off. This also facilitated installation. 6) There is an original swivel located four chain links from the pivot. A second swivel was added four links from the first to increase the mobility of the trap once a wolf is captured, thus avoiding possible sprains and twisting of the leg. The swivel was then attached to a shock absorber (J.C. Conner's in-line shock spring), in order to minimize the abruptness of the shock and prevent shoulder injuries when a captured wolf pulls on the trap at the full extension of the chain (Figure 5). 7) An extra 3 meters of chain (3/16" diameter) was added to the original length ensuring that the wolf gets tangled as soon as possible. A wolf will usually fight with the trap as long as it can drag it and this increases the chance of injuries caused not only by the force of pulling on the trapped leg but also by sharp vegetation encountered. 9) Large pronged steel drags or grapnels (75 cm long from one prong to the other, 400 grams, 9.67 cm diameter) were twisted (3 cm distance between ground and end of prong when placed flat on the ground) and sharpened in order to "anchor" the trap, rather than using a stake, for two reasons. Firstly, the vegetation onto which the animal gets tangled serves as an extra shock absorber. Secondly, the captured wolf is more likely to be able to retreat into a secluded shaded area thus reducing the stress involved in the capture. This was especially important in our study area where there was substantial traffic on logging roads.

4.5 Results and Discussion

In the Quebec study, using the modified Victor Soft Catch #3 trap described above, 30 different wolves were captured. Weights of wolves captured ranged from 6kg (pup) to 40kg (adult male). Ninety three percent of the captures caused no observable damage to the foot (no cuts or swelling) and none of the wolves captured incurred injuries more severe than slight swelling. Swelling occurred less often in pups than in adults who tended to resist more. Even when the ambient temperature was below freezing, captured feet remained warm, indicating that circulation to the foot was not excessively restricted. Due to the rubberized jaws, animals captured rarely sustained cuts (2 wolves out of 30 captured) and almost all bycatch species could be released unharmed (porcupine, lynx, fox).

In their reviews of trap related injuries, Van Ballenberghe (1984) and Kuehn et al. (1986) classified injuries from traps into the following four categories. Class 1, no visible injuries or slight swelling. Class 2, moderate swelling with cuts < 2.5 cm in width. Class 3, cuts > 2.5 cm in width with underlying tissue damage and a maximum of 1 fractured or dislocated phalanx or metacarpal. Class 4, severe injuries including deep lacerations and severed tendons, more than one injured phalanx or metacarpal, broken bones and dislocations. In their study, across age groups and trap types they reviewed, approximately 75% of wolves experienced injuries of class 2 and higher (Van Ballenberghe 1984; Kuehn et al. 1986). The Newhouse No. 14 (custom made toothed jaws offset 1.8 cm) were found to cause the least damage with injuries of almost all of the wolves captured classified as class 2 (Kuehn et al. 1986).

Our results clearly represent a major improvement over most of the steel-jawed traps where class 3 and 4 injuries occurred in 41% of captures (Van Ballenberghe 1984). Even the least damaging No. 14 toothed trap with offset jaws, the least damaging steel-jawed trap, produced class 2 injuries to almost all of the wolves captured (Kuehn et al. 1986).

From an economic point of view, the Soft Catch #3 is much less expensive (approx. $40.00 US with all modifications) than the Newhouse models commonly used. Technically, it is also much easier to install and disseminate due to its smaller size, saving much time during trapping. This small size also makes it easier for the animal to maneuver once captured and reduced injuries caused by nearby sharp vegetation. One drawback is the need for more experience and precision during installation because of the smaller jaws relative to the Newhouse traps.

4.6 Conclusion

We found injuries caused by the modified Soft Catch #3 to be much less severe than those inflicted by steel-jawed traps, and found it to be a far superior tool for the capture of wolves than those previously used and reported in the literature. It should be noted that these traps are presently being tested by the Fur Institute of Canada to determine whether they meet the injury and behavioral threshold requirements defined by the AITS. As a result, we suggest that researchers consider these traps as a possible alternative to the commonly used modified Newhouse traps.

4.7 List of figures

Figure 1. Camouflaged trap and bait.

Figure 2. Side view. Solder (blobs) applied to the base of jaws.

Figure 3. View of bottom with soldered additional plate and centered pivot.

Figure 4. Top view. Reduced pad to force captured foot deeper into the trap.

Figure 5. Top view of changed chain, large twisted prongs and added swivel and shock-absorber.

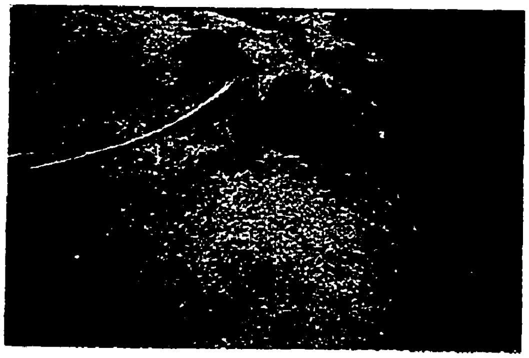

Figure 1.

Figure 2.

Figure 3.

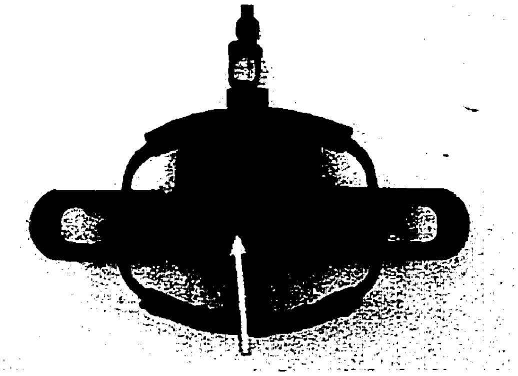

Figure 4.

Figure 5.

4.8 Literature cited

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5. General Conclusion

Information collected throughout the Laurentide wolf project has produced valuable information not only pertaining to this specific population, but also with regard to general wolf ecology and behavior. Similarly, public awareness about this population has been raised not only in the immediate area, but throughout the province in the form of documentaries and articles, and even in the United States through the spread of information by various conservation groups.

The database on the attendance patterns of individual wolves at den and rendezvous sites will likely serve in further studies and will add to the valuable information already collected on wolf behavior in the wild. Information obtained on the Malbaie pack has produced the most complete picture of wolf pack behavior at den and rendezvous sites available to date, owing to the fact that all individual wolves equipped with radio-collars during three consecutive years and were monitored 24 hours a day. These data are evidence to the great flexibility in individual wolves' behaviors in response to social factors. The attendance patterns of individual wolves were found to be influenced by both age and the composition of the pack. Additionally, specific associations of wolves and their behavioral patterns suggest that adult members play a more significant role in hunting than do yearlings. This is a concept that requires further investigation but is an indication as to the presumed importance of maintaining packs with several age classes, particularly in areas where large ungulates are the primary prey. Furthermore, this variability between wolves of various ages and social hierarchy warn against the clumping of behavioral information among these groups in the search for behavioral patterns.

Field information on vocal and behavioral responses to simulated wolf and coyote howls are an important addition to the information presently available on howling. It is also unique because the identity and social relationships of all wolves are known. Wolves were found to respond more readily to simulated howls of a pack of wolves than they were to the howls of a single coyote, while the factor most affecting the probability of a response to wolf howls was the total number of wolves present at the rendezvous site. However, while simulated wolf howls were found to elicit an immediate response from individual wolves (usually a return to the rendezvous site), particularly the alpha female, the response to coyote howls was not as clear. Although both the alpha male and female were observed to have returned to the rendezvous site following simulated coyote howling, this was not the case on the majority of stimulation nights. Behavioral changes were observed after simulated howls as well as howls originating from packmates testifying to the potential motivational information transferred via these vocalizations. Wolf howls, although they clearly cause behavioral changes in wolves movements, are more likely to evoke a response. This is valuable information for ecotourism companies for several reasons. First of all, organizers can chose to schedule their activities during periods of the day when wolves are more likely to be present. Secondly, when possible, the stimulation of packs with the highest number of individuals can increase the probability of there being numerous wolves at the rendezvous site and thus the odds of eliciting a response. Lastly, this behavioral information is important in better understanding wolf communication and hopefully will serve to further this type of research and test other possible methods of stimulation that might not be as disturbing to wolves.

In the process of carrying out fieldwork for the project, several technical advancements in the study of wolves were made. The first innovation was the replacement of traditional strip chart recorders with electronic versions that were developed specifically with monitoring den and rendezvous sites in mind (GENEQ Inc.)(Czetwertynski et al. in prep). Although similar apparati are available commercially from companies specializing in radio-tracking equipment, they are relatively expensive and therefore not feasible for most field projects with limited funding. The advantages of GENEQ decoders is the low cost (can be manufactured personally) and the reduced scanning time which allows for greater accuracy in attendance data (attendance data can be collected every 5 sec). The second improvement of interest is the modification of rubber padded leg-hold traps (Technical Paper, this Thesis) for the live-capture of wolves. The changes made to the commercially sold Soft Catch #3 traps inflicted significantly fewer and less severe injuries than traditionally used modified Newhouse traps. These traps are presently being tested by the Canada Fur Institute to determine whether they meet the requirements of the AITS, in which case they will be the first restraining trap for wolves to be accepted.

Although ecotourism affects the behavior of wolves, this is an insignificant detail compared to the greater danger of overharvesting and the lack of an official management plan. The move by ecotourism companies to reduce the impact they have on wolves is a noble endeavor, but one of the requirements for the activity is the presence of wolves. The life history of the Malbaie pack is a poignant example. The Mikin ecotourism company, after investing into the Laurentide wolf project and adjusting its activities to correspond with the research protocol, have found themselves without any wolves to use in their educational activities and have had to stop offering the program altogether. From the information available, it would seem that almost all of the established packs in the reserve have been eliminated or are left with a couple of individuals. This is not only a wildlife management tragedy but also a great loss to the thousands of people that could have benefited from the information that was conveyed about wolves, their behavior and ecology.

If there is a single big lesson to be learnt from the Laurentide wolves, it is that to study a problem is simply not enough. Based on results, concrete actions must be taken and all parties must be part of the process and the solution. Because these wolves are no longer being studied, nor are trappers asked to return carcasses any longer, the situation of the Laurentide wolves, unknown before the research project, is once again shrouded in secrecy.