BEHAVIORAL CHOICES OF MALE HUMPBACK WHALES

(*MEGAPTERA NOVAEANGLIAE*) ON THE HAWAI'IAN

WINTERING GROUNDS

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAI'I IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

MASTER OF ARTS

IN

PSYCHOLOGY

August 2004

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CHAPTER 1. GENERAL INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are a migratory species, feeding in high latitude, cooler waters during the summer, and then traveling to low latitude, warmer waters during the winter months to calve and presumably, though it has never been documented, to mate. The North Pacific has three main wintering grounds: Hawaii, Mexico/California, and Japan (Dawbin, 1966, Darling and Jurasz, 1983; Baker, Herman, Perry, Lawton, Straley, Wolman, Kaufman, Winn, Hall, Reinke, and Ostman, 1986).

Currently, approximately 4,500 humpback whales migrate down to Hawaiian waters, primarily from Alaskan waters, between the months of November and April (Calambokidis et al., 2001). According to whaling records and field observations, humpback whales do not feed during this time; their blubber layer decreases in thickness from January to April as their energy is directed towards reproductive efforts and their fat reserves are metabolized for energy (Nishiwaki 1959, Dawbin 1966, Chittleborough, 1965).

The objective of this thesis is to advance our understanding of the behavioral choices available to, and made by, adult male humpback whales on the Hawaiian wintering grounds.

Male competition

While in Hawaiian waters, the males engage at times in violent, physical competition for access to females (Tyack and Whitehead, 1983; Baker and Herman 1984). The aggressive behaviors demonstrated by the males, ranging from displays such

as s-shaped postures to physical attacks such as charge-strikes, are seen most often in large groups of whales containing one adult female and multiple males. The goal of the aggressive males seems to be to defend or gain proximity to the female (Clapham, Palsboll, and Mattila, 1992). Recent work correlating the length of whales to their social role indicates that the males seen occupying the position closest to the female (called the "principal escort" position) are, on average, significantly larger than the "secondary escorts" in the group (Spitz, Herman, Pack and Deakos, 2002). These findings suggest that size may assist in securing an advantageous position near the female and that the position is energetically demanding to hold. Another indication that maintaining the position is costly is the frequency with which the principal escorts have to defend their position from numerous challengers. Tyack and Whitehead (1983) reported that challenges were made to the principal escort approximately every 48 minutes and that 9% of these challenges were successful.

Because humpback whales do not feed while on the wintering grounds, and it is unlikely that they are feeding to any large degree during migration, the decision to invest energy in competing for proximity to a female is a decision to incur an energetic cost that may possibly limit the male's success in any additional competitive groups in which he participates that season.

Fluid social structure

On the wintering grounds humpback whales interact with one another within a very fluid social system. Unlike members of several well-studied odontocetes, (pilot whales, sperm whales, killer whales) there is no stable social structure (Kasuya and

Marsh, 1984; Magnusson and Kasuya, 1997). Rather, the affiliations between humpback whales (other than the mother/calf bond) are short-lived, rarely lasting for more than one day (Mobley and Herman, 1985; Perry, Baker and Herman, 1990). In a paper documenting the transience of social affiliations, Mobley and Herman (1985) reported that 14% of the groups examined underwent a change in membership within the course of one hour. Groups with calves were more likely to gain escorts than lose escorts, and groups without calves gained and lost members at the same rate. These results suggested to the authors that a group with a calf was a more enduring attractive unit than the group without a calf. The authors suggested that an escort may join and stay with a mother long enough to determine whether or not she was ovulating postpartum or whether she had already mated. If she was ovulating, the escort would presumably remain affiliated with her, or if she was not, he would disaffiliate. If she had already mated, they suggested that the escort may stay for an additional mating attempt.

Migratory timing

Data from historic whaling records, obtained principally along the migration routes to and from the winter grounds, have indicated that migratory timing varies according to behavioral role. What is commonly referred to as "the migratory parade" (Table 1) shows that the females who are accompanied by their yearlings are, on average, the first to arrive on the wintering grounds, followed by the immature whales, and then the adult males and "resting" females. Resting females are those that were neither pregnant nor lactating. The last group to arrive is the females in late pregnancy. This order is largely reversed on the return to the feeding grounds. The first groups to leave

the wintering grounds are the newly pregnant and resting females, and the immature whales. Then the mature males leave, followed by the new mothers with their newborn calves (Dawbin, 1966; Nishiwaki, 1966). A more recent study conducted by Craig et al. (2003) on the Hawaiian wintering grounds found supporting evidence for the migratory order documented in whaling records. Off the island of Maui the group with the earliest arrival date (where arrival is counted as the date of first photo identification) were the immature whales, then the females without calves, then the males and finally the females with calves. These behavioral groups correspond well with the data from whaling records. The females with calves in the Hawaiian winter grounds presumably would be identified as "late pregnant" along the migratory route.

The dates of earlier identification vary slightly off the Big Island where the group with the earliest mean date of first identification was the females without calves; these were followed by the juveniles, the males, and then the females with calves. The dates are given as Julian dates, i.e. number of days after January 1. Craig et al. reported the mean date of first identification to be 56.82 for males off the Big Island and 69.99 for males off Maui. For the Big Island and Maui respectively, the mean dates of first identification for females without calves were 42.21 and 60.10; for females with calves they were 59.02 and 71.33 and for juveniles the dates were 46.66 and 42.43.

Length of residency on the wintering grounds

Hypothetically, the length of a male's residency is largely dependent on his energy reserves, possibly indicating his level of fitness, but it also may reflect a reproductive strategy. In theory, a male who chooses to engage in competition for the

most attractive female will have to spend more energy and subsequently have to leave the wintering grounds earlier than a male who hypothetically opted to escort females surrounded by less fierce competition (i.e. slightly less attractive). A limited amount of information is already available on residency times of humpback whales on the wintering grounds. Craig et al. (2001) showed that the median interval between first and last sighting for 97 males off Maui was 13 days, with a minimum of 1 day, maximum of 64 days, and an interquartile range of 20 days. As noted earlier, according to whaling data, and confirmed by more current literature on migratory timing, juvenile whales are among the first groups to leave the wintering grounds. This shorter residency period may reflect their smaller body size and consequent lesser energy reserves. Similarly, the number of dyads (pairs) decreases as the season progresses. Spitz et al.(2002) showed that a large percentage of the whales found in dyads were of immature size.

For the residency times reported by Craig et al. (2001), the median interval between first and last sighting within the same season off Maui for females with calves was 5 days (range = 1 to 33 days), and for females without calves it was 2 days (range = 1 to 3 days). Females without calves are thus apparently present on the wintering grounds for a much shorter period of time than are mothers. Though we do not know how long the period of receptivity is for humpback females, the fact that mothers are often present on the wintering grounds for up to 10 times as long as non-calf females indicates that the mothers spend a significant amount of time in Hawaii when they are not receptive. An adult male choosing against escorting a mother may be because she is not receptive rather than her being less attractive because of the presence of a calf.

The goal of this thesis is to fill in certain gaps in understanding of humpback whale reproductive behaviors. Because whales only spend a small portion of their lives at the surface of the ocean, making observations difficult, a comprehensive description of their reproductive strategies is slow to evolve. The second chapter covers general methods and the data set. The third chapter presents data that suggests that while mothers as a group have a lower reproductive potential than females without calves, they should not be overlooked as members in the pool of potential mates, especially for less fit males. The fourth chapter demonstrates the existence of male mate choice, but does not make a distinction between fit and less fit males. The fifth chapter begins to sort out differences between groups of males using behavioral roles to make differentiations.

CHAPTER 2. GENERAL METHODS AND DATA SET

The Kewalo Basin Marine Mammal Lab (KBMML) has been conducting

behavioral surveys and collecting fluke photographs of humpback whales off the

Hawaiian Islands each year since1976. The resulting catalog of over 18,000 fluke

photographs spanning 26 years and documenting at least 4000 individual whales was the

primary source of data for this thesis. The photographs were collected off the waters of

Maui and the Big Island from small outboard motor boats, using Canon single lens reflex

cameras fitted with 100-300 mm zoom lenses. Each photograph is labeled with the date,

location, behavioral role and group composition, and cataloged in a Filemaker database.

The ventral face of the flukes of humpback whales have unique, permanent

pigmentation patterns that can be used to identify individuals, and to match sightings of

the same whale within and across years. KBMML has an ongoing fluke-matching

program that has resulted in identifying 1,920 individual whales that have been sighted

on more than one occasion. These numerous sightings of each individual may include

sightings within the same season, or across seasons, or both.

Different data sets extracted from the main fluke database were utilized to answer

the various questions presented in this thesis. The number of photographs collected

approximately doubled beginning in 1996, which also translated into a higher number of

within-season matches. Also, secondary behavioral roles, such as the distinction between

a principal and secondary escort, only began to be recorded beginning in 1996. For these

reasons, only data from 1996-2001 were used for most of the analyses. The full database

was queried for sightings of females in consecutive-years because this question did not

require knowledge of secondary behavioral roles. Additionally, only data from 2000-2003 was used for the head lunging analysis presented in Chapter 4. This set was chosen because I was present on the boats for those years and witnessed and participated in the behavioral data collection.

The group compositions described were based on the number of animals in the group and the presence or absence of a calf. Table 2 gives the nomenclature used throughout this study. The various abbreviations distinguish between the compositions or social groups according to the number of escorts accompanying a lone female (NA) or a mother (M) with calf. Primary escorts (1E) are distinguished from secondary escorts (2E), and escorts accompanying a lone female are further identified by the prefix N (e.g. N1E vs. N2E). If multiple escorts are accompanying a mother the prefix is not used.

CHAPTER 3. CONTEXT AND RESOURCES:

FEMALE HUMPBACK WHALE REPRODUCTIVE CHARACTERISTICS

Introduction

In order to understand the context and the resources for which males are

competing, this chapter gives a temporal description of the group compositions found

throughout the season. Additionally, mothers and females without calves (non-calf

females) are compared for residency times and the interval between consecutive year

sightings. Although these two reproductive classes of females differ in their current

reproductive potential, the attractiveness of individual mothers who may be entering post-

partum estrous should not be underestimated.

Seasonal trends in humpback whale group density and characteristics in Hawaii

have been reported from aerial surveys (Herman, Forestell, and Antinoja, 1980; Baker

and Herman, 1981; Mobley, Bauer and Herman, 1999), shore station observations (Craig,

2001), and combined boat and shore observations (Mobley and Herman, 1985). Most of

the data focuses on an increase in total whale abundance, peaking in late February/ early

March. Herman, Forestell, and Antinoja (1980) reported a peak in calf abundance in

February, and a high percentage of MCE groups among the calf groups (48% of calf

groups in 1996 and 45% in 1977). Craig (2001) describes the seasonal trends in

abundance according to group size and presence of a calf. For two years of data

collection from Maui, the number of calves peaked in Fortnight 6 in 1997 and in

Fortnight 5 in 1998.

Humpback whales have an interbirth interval of approximately two years (Baker et al., 1987; Clapham and Mayo, 1987). Again because of the great energy investment of supporting a calf while fasting, most female humpbacks have at least two years in between births. Thus, there are two reproductive classes of females visiting the wintering grounds: those who have just given birth and are accompanied by a calf, and those females who will not have a calf that year. Craig, Herman and Pack (2002) argue that the two groups differ in reproductive potential; there was a 10% probability that a female seen with a calf will be seen with a calf the following year, while there was a 75% probability that a female seen without a calf one year will be seen with a calf the second year. This highlights the difference in reproductive potential between these two classes of female.

There are no available data on estrous length in humpback whales. The only concrete data for cetaceans comes from captive toothed whales. The estrous cycle of captive killer whales ranged from 23 to 49 days and those of captive bottlenose dolphins from 24 to 35 days (as reported in Magnusson and Kasuya, 1997). A model was created by Magnusson and Kasuya that utilized an indirect estimate of receptivity time for short-finned pilot whales of 6 days (Magnusson and Kasuya, 1997). Whether any of these estrous lengths reflect that of humpback whales is of course uncertain.

Evidence for post-partum estrous has been found in whaling records, and in records of consecutive-year mothers (Chittleborough 1958; Nishiwaki, 1959; Glockner-Ferrari, 1990; Straley, Gabriele, and Baker, 1994; Weinrich, Boye and Miller, 1993). The occurrence of post-partum estrus may be limited to a small portion of the females with calves, with many mothers seen on the wintering grounds never entering into post-

partum estrous, and of those that do, few mating and bringing a fetus to term. Chittleborough (1958) reports data from Norwegian observers documenting 19 lactating females, 8 (42%) of which were also pregnant. Glockner-Ferrari (1990) reported annual births by a single female on the breeding grounds, and Weinrich et al.(1993) and Straley et al. (1994) documented the survival to at least six months by the calves of consecutive-year mothers.

A terrestrial comparison reveals that in bison, only 15% of lactating females were reported to be fertile (Kirkpatrick, Gudermuth, Flagan, McCarthy and Lasley, 1993). A study on anestrous and infertility in postpartum beef cattle showed that the major factors affecting the postpartum anestrous , or postpartum interval, were suckling and nutrition (Short, Bellows, Staigmiller, and Berardinelli, 1990). Fertility would return to normal in the beef cattle between 20 to 40 days after calving, but this was presumably in cows that were not suckling their calves for long. Nutrition also played a role, with cows with a better body condition returning to normal estrous cycles more quickly.

In her paper on male mate choice, the data of Craig et al. (2002) indicate that as a group, females without calves are much more likely to produce a calf the following season than are lactating females. The question remains though, as to whether an individual lactating female who does enter postpartum estrous on the wintering grounds would be any less attractive to males than a female without a calf.

In a review of baleen whale reproduction, Lockyer (1984) states that the energy investments in early pregnancy "are minimal, and costs only become important in the last half or third of gestation." With calf mortality rate as high as 24% (Gabriele et al., 2001), it may make biological sense that a female mate, and if her current calf survives the

migration back to the feeding grounds, the fetus would be aborted or reabsorbed. Observations from whaling ships of pre-natal mortality in baleen whales showed peaks in dead, prenatal fetuses in both the early and late stages of pregnancy (Ichihara, 1962). These data represent only fetuses that were being reabsorbed as no evidence remains for aborted fetuses. Additionally, data from Nishiwaki (1959) on fetus growth rates showed a logarithmic increase in size in which the dramatic increase in size does not begin until May/June, approximately 2 to 5 months after conception . This also supports the finding that initial investment in a fetus is small for a mother.

While Craig et al.'s (2002) hypothesis of male choosiness based on the presence of a calf remains viable, an alternate scenario is that males are escorting females who signal their receptivity. If there is a choice to be made between receptive females it is based on a measure of fitness other than the lack of a calf (i.e. girth, strength of signal etc.). A non-calf female may in many cases appear more fit than a mother.

To understand what choices escorts have available, we need to understand the reproductive status and availability of females on the wintering grounds. In this chapter I describe the seasonal pattern in group types primarily to establish, through the photographic record, the abundance of females in different reproductive states. Additional data are presented on residency times of females and the consecutive-year sightings of individual females to further illustrate differences in the length of time non-calf females spend on the wintering grounds as compared to mothers.

Methods

Temporal distribution

To answer questions about the temporal distribution of group types throughout the season, a subset of photographs from 1996-2001 was used. Beginning in 1996 the survey effort moved from the Big Island to Maui and the number of fluke photographs captured by KBMML researchers doubled due to larger population of humpback whales off Maui. To be counted, each group had to be represented by at least one photograph. Each group was only counted once, even if more than one photo was taken of different members of that group. The data from years 1996-2001 were collapsed to show the average trends across seasons. Groups containing yearlings were omitted.

The winter season was divided into two-week periods (fortnights) with Fortnight 1 starting on January 9 and Fortnight 7 ending on April 16. The start and end dates for each fortnight are listed in Table 3. January 9th was chosen because data collection had begun in all five years (96-01) by that date. Data collection had ended in year 1997 on April 15th, and on April 14th in year 2000 meaning there are fewer data points in fortnight 7 than would be fully representative.

Residency times of females

Craig et al. (2001) presented residency data on humpback whales in Hawaii utilizing the data from 1976-1996. To expand on these residency time data, the fluke matching database from 1996-2001 was examined for further within-season resights of mothers and non-calf females. The non-calf females were further divided into whales that had been designated nuclear animals (i.e. they had been seen in competitive groups and

therefore had a high probability of being sexually mature) and those females that had not been seen as a nuclear animal. The interval between first and last sighting within the same season was then calculated for 51 mothers, 14 nuclear animals and 8 females without calves that had not been seen as nuclear animals.

Consecutive-year sightings

The across-year matching data was available for years 1976-1999. For the purposes of this study, the females from this 23-year set were categorized as either females with a calf (FC) or females without a calf (FNC) each time they were sighted. Reproductive histories of female humpback whales from the Hawaiian population are documented in both Baker et al. (1987) and Craig et al. (2000), but neither address the number of days between the consecutive-year sightings and both are restricted to data obtained prior to 1995.

Each consecutive-year sighting from this data set was treated as a separate sample, and these were divided into four categories: FNC/FC (females seen the first year without a calf, and the following year with a calf), FNC/FNC (females seen both years without a calf), FC/FNC (females seen the first year with a calf, and the second year without a calf), and FC/FC (females seen in consecutive years with a calf). The intervals (measured in days) between the last sighting the first year, and the first sighting the second year, were calculated for each sample. Only whales that had been seen at least once during their sighting history as a mother were considered female. Additionally, whales were only considered a mature FNC if they had produced a calf in the past, or did so the following year.

Four of the females were seen in more than two years consecutively, which placed them in more than one category. A within-subject comparison of the categories is discussed regarding these four individuals.

<u>Results</u>

Temporal distribution

The total number of groups (excluding groups containing yearlings) photographed between Jan 9th and April 16th during the years 1996-2001 were examined for temporal trends in the types of group compositions seen throughout a season. There were 1103 groups photographed containing calves, and 1876 groups not containing calves. Figure 1 illustrates the average trends across a season for groups based on the presence of a calf. The regression lines showed an increase in the number of calf groups across the season (y= 24.429x + 59.857, $\underline{F}(1,5) = 9.60$, $p = 0.027$) and a negative trend in the number of non-calf groups across the season (y= -26.464x + 373.86, $\underline{F}(1,5) = 17.12$, $p = 0.009$). Figure 2 illustrates the different calf group compositions across season in more detail. The number of groups containing calves peaked in Fortnight 5 (March 6-March 19) and then decreased to Fortnight 7 (April 3-April 16). By far the most common group composition containing a calf was the MCE (Mother, calf, and escort) outnumbering the other group types by at least 4 times. The MCE's also peaked in Fortnight 5, decreasing then through Fortnight 7. Groups containing 2 or more escorts were considered competitive groups. The number of competitive groups containing calves doubled after Fortnight 2 (January 23-February 5). Calf groups containing three or more escorts

increased in Fortnight 4 (February 20-March 5) and remained relatively high through the end of the season.

The relative number of calf groups increased steadily across the season as illustrated in Figure 3 (y = 6.519x +10.744, $\underline{F}$ (71,5) = 90.41, p = .0002). Again, there was a general decrease in non-calf groups across the season as illustrated in Figure 1. Figure 4 shows the composition of non-calf groups in more detail across the season. The number of singletons photographed remained fairly constant. Dyads (two whales) were the most numerous group type. Both dyads and groups containing three whales were the most plentiful in the first fortnight and then decreased in number throughout the season. Competitive groups containing between two and five escorts were more common in the first four fortnights and then gradually decreased in number. Larger competitive groups containing six or more escorts were very few in number in the first two fortnights and increased in number for the last five fortnights.

Residency times of females

The 14 nuclear animals sighted within the same season from 1996-2001 had a mean within-season sighting interval of 7.21 days with a median of 5 days, ranging from 2-16 days. Non-calf females, who had not been designated as nuclear animals, had a mean within season sighting interval of 11.25 days, with a median of 7.5 days, ranging from 1-26 days.

There were 51 mothers resighted within the same season from 1996-2001. The mean interval between first and last sighting within the same season was 13.55 days, with a median of 10 days and ranging from 1 to 51 days. Eight of the mothers had intervals

greater than 26 days; 26 had intervals greater than 9.05 days and 29 had intervals

greater than 7.5 days. The comparison of the median intervals for each group of females

is illustrated in Figure 5.

The mean interval between first and last sightings for mothers was significantly

greater than the interval for nuclear animals (one-tailed t (61) = 1.91, p =.03). However,

when the nuclear animals were combined with the non-calf females and then compared to

the mothers, the difference in interval just failed significance (one-tailed t (69) = 1.62, p

= .055).

Consecutive-year sightings

Figure 6 documents the twenty-nine occurrences of Consecutive-year sightings

for females. Fourteen fell into the FNC/FC category. Each of these fourteen females had

more than a year's interval between the last date she was sighted without a calf, and the

first date she was sighted with a calf. The mean interval was 396 days, with a median of

394 days and a range of 373 to 439 days.

One female was found who was seen in consecutive years with a calf (FC/FC).

The span between the last sighting the first year and the first sighting the second year was

325 days (Table 4).

There were thirteen examples of FC/FNC sightings. The intervals between the last

sighting of the first year and first sighting the second year ranged from 303 to 378, with a

mean of 334 days and median of 329 days. This interval was significantly less than that

of the FNC/FC females (t (25) = 7.25, p = .00000006).

One female was found who was seen in consecutive years without a calf. The interval between the last sighting the first year and the first sighting the second year was 390 days.

Four individual females were resighted across more than two years and also, subsequently, fell into more than one of the Consecutive-year categories. However, every interval referred to indicates the interval from the last day the whale was sighted one year to the first day the whale was sighted the following year.

Female #71 was seen in1980 as a mother (FC) and in 1981 was seen without calf (FNC). The interval between the last sighting in 1980 and the first sighting in 1981 was 344 days and this fell into the FC/FNC category. Whale #71 was then seen in 1982 as a mother again, placing her in the FNC/FC category for years 1981 and 1982. The interval between the last sighting in 1981 and first sighting in 1982 was considerably longer, at 401 days.

Whale #228 was seen in 1982 as an adult (FNC) and again in 1983 as a mother, placing her in the FNC/FC category with an interval of 379 days. She was then seen in 1984 as a FNC placing her in the FC/FNC category with and between year interval of 378 days.

Whale #245 was seen in 1981 as a mother and in 1982 as a FNC placing her in the FC/FNC group with an interval of 371 days. She was then seen in 1983 as a mother again, putting her in the FNC/FC group for 1982/1983 with a between year interval of 378 days.

Whale # 1569 was seen in 1996 as a mother and in 1997 as a FNC. The interval

for this FC/FNC sighting was 307 days. She was then seen in1998 as a FNC placing her

in the FNC/FNC group for 1997/98 with an interval of 390 days.

It is unlikely that any of the females classified as adults (FNCs) in the

Consecutive-year analysis gave birth later the same season. Between 1977 and 2001, 136

females were seen more than twice within the same season. One hundred five females

(77%) were sighted consistently as mothers; 27 (20%) confirmed females were seen at

least twice the same season as FNC's (females without calves) and only four (3%)

females were seen first as a FNC and later as a mother.

Discussion

The number of groups containing calves increased throughout the season, peaking

in Fortnight 5. This trend was present in 1980 (Herman, Forestell, and Antinoja) with the

peak in calf groups occurring in February, only slightly earlier in the season. That the

trend in relative calf abundance across a season has not changed in over twenty years

indicates a level of stability in the population characteristics in Hawaiian waters.

Additionally, Herman, Forestell and Antinoja (1980) reported that the number of MCE's

accounted for a majority of the calf groups throughout the season. This also has not

changed with the number of MCE groups outnumbering other calf group compositions by

as many as four times.

The number of competitive groups surrounding mothers also peaked in Fortnight

5. The fact that more mothers are being escorted in the second half of the season can be

explained by the increase in the number of mothers and decrease in number of FNC's, and may not be a result of males becoming less choosy as the season progresses. Additionally, the portion of lactating females that are entering post-partum estrus may increase as the season progresses if there is any delay after parturition before the female becomes receptive. The increase in mothers being escorted may be a function of a greater number of receptive mothers available nearer the end of the season, and not necessarily reflect a shift in male mate choice.

Females who were sighted in consecutive years showed different yearly sighting intervals, depending on their reproductive status. The main point of interest is whether a female who is pregnant will ever be sighted on the wintering grounds. Without yet having a reliable pregnancy test, but knowing the gestation period of 11.5 – 12 months, I made the assumption that any female sighted on the wintering grounds less than a year before she is first seen with a calf, would be pregnant (Chittleborough, 1958). Of the fourteen females who were FNC's one year and mothers the following year, none had sighting intervals of less than a year, indicating that soon after conception the females return to their feeding grounds and thus are not present on the breeding grounds long while pregnant. Whether the newly pregnant females are responding to biological changes brought about by pregnancy, have a residency time limited by their period of receptivity, or simply return to the feeding grounds once they have mated is not known. The thirteen females who were seen the first year as mothers and the second year as females without calves had many sighting intervals of less than a year. Because mothers spend more time on the winter grounds and return to the feeding grounds much later in the season than non-calf females on average, it is not surprising that these sighting intervals are shorter.

The additional residency data presented simply reinforce what has been shown before (Craig et al. 2002): that mothers spend a longer period of time on the wintering grounds than do non-calf females. In light of the data from Consecutive-year sightings of females, it is probable that the non-calf females stay only as long as necessary to become pregnant, and thus are receptive for a majority of their time spent on the wintering grounds. Conversely, mothers have additional priorities (a calf to nurse) and, since their length of stay is longer, are spending a portion of their residency (if not their entire residency) in a period of non-receptivity. Thus, the portion of mothers who are not escorted, may simply not be receptive. This could indicate that males are responding to females who are receptive, regardless of the presence of a calf. Additionally, males may be choosing females based on an indicator of fitness other than presence of a calf, such as girth or strength of a signal (unknown to us at this time), but only selecting between those females who are receptive. Females without calf (FNC's) should in theory be more fit than a receptive FC because of the energy drain of lactation and bringing a fetus to term, so FNC's may always be more attractive than FC's.

CHAPTER 4. EXPANDING ON MALE CHOICE

Introduction

This chapter presents two sets of evidence for the existence of male mate choice. First, male mate choice is investigated on an individual level. Resight histories of males seen twice within the same season are examined for a pattern of choice between escorting calf or non-calf groups. Secondly, data are presented that answer the question of whether head lunging is an indicator of female attractiveness. These data show the proportion of groups seen head lunging, comparing groups that have a calf to groups that do not, while controlling for group size.

The traditional view of reproductive behavior (Trivers, 1972) emphasized male competition and female choice. The energy that a female invests in offspring was believed to far outweigh the investment of males (ova vs. sperm) and therefore she had more to lose from having a less fit mate and would be the choosier of the two sexes. Males were thought to benefit the most from a large number of mating opportunities, rather than discriminating between potential mates. Evidence now suggests that the energy devoted by males has been underestimated (Dewsbury, 1982). The traditional measurement of cost was the gamete and because a single egg is much more costly to produce than a single sperm, male investment in each mating occurrence was thought low; however, the correct unit of measurement is the ejaculate which is made up of millions of sperm and is therefore much more costly. In the case of the humpback whales, animals are fasting during their migration to and from the breeding grounds in

addition to not feeding during their residency in Hawaii. This lack of energy input, added to the costs of searching for available females, and then engaging in physically demanding contests for access to the females should make it rewarding for males to exercise choice in what female they pursue. Evidence from several species ranging from zebra finches to lekking fish to bison supports the fact that males are evaluating the fitness of their female counterparts.

In a study by Jones, Monaghan, and Nager (2001), male zebra finches were experimentally exposed to standard females and females who had been receiving food supplements that led to increased fecundity. Females in the two groups were matched in size and there were no noticeable behavioral differences between the standard females and the supplemented females, yet the males preferred the supplemental females indicating that they were able to judge fecundity. The females were not exposed to one another and so female-female competition can be ruled out (Jones et al., 2001).

In a promiscuous species of lekking fish (*Astatotilapia flaviijosephi*) males showed choice for larger females in a laboratory setting. The males spent more time courting the larger females (Werner and Lotem, 2003).

The behavior of bison presents an interesting terrestrial comparison to the behavior of humpback whales. Both species exist within loose, fluid social systems and exploit relatively undefendable food resources (Rutberg, 1986; Perry, Baker and Herman, 1990). Females and males mate promiscuously and the reproductive potential of females, based on whether they gave birth the previous year, is remarkably similar to the rates cited by Chittleborough (1958) for female humpbacks in the southern hemisphere. Ninety percent of bison who did not have a calf one year produced a calf the following year,

while 38% of lactating bison produced a calf the following year (Berger, 1989).

Similarly, 89.3% of humpback whales that did not have a calf one year produced a calf

the following year while 42% of lactating humpback whales produced a calf the

following year (Craig et al., 2002; Chittleborough, 1958).

Berger points out that females producing calves early in the season are likely to

have heavier calves, and are therefore "are a more valuable resource" than females

producing calves later in the season (Berger, 1989).

Older male bison when faced with a choice between two females of different

reproductive potentials (calculated by whether she was without calf or lactating) would

choose to approach the female with higher reproductive potential regardless of whether

she was already being "tended" or not. The term "barren" in this case refers to a female

without a calf, the equivalent of a humpback FNC, and a female who is "tended" is

interpreted as the equivalent of a humpback female being escorted. Younger males, when

faced with choosing a female who was already tended, would preferentially choose

nulliparous females, but when able to choose between untended females, would choose a

barren female over a female with a calf (Berger, 1989).

A study by Craig et al. (2002) supported the existence of male mate choice in

humpback whales. She documented the difference in reproductive potential between

mothers and non-calf females as discussed in the previous chapter, and also that the

females without calves are less often alone and more likely to be found in large groups.

One line of evidence Craig et al. present in support of males choosing non-calf females

was the much higher proportion of non-calf groups than calf groups in 27 groups where

head lunging was observed. Head lunging is a very common behavior in competitive

pods and is very often performed by the principal escort and sometimes by the

challenger (personal observation). It is an indication of an intense level of competition,

and therefore seems a good indicator of the attractiveness of a given female. Craig et al.

(2002) presented data obtained from a shore observation station where head lunging was

observed in 27 groups. Twenty-three of these groups did not contain a calf, and 4 did;

however, as the number of adults in a group can not always be confirmed from a shore

platform, the study did not control for group size. This current study examines the

proportion of calf and non-calf groups seen head lunging while controlling for group size

by examining data obtained from a boat observations.

In this chapter I examine whether individual males exhibit choice in the type of

group they escort (calf or non-calf) and whether or not males become less choosy as the

reproductive season progresses.

Methods

Choice by individual males

To answer questions about individual male behavioral roles, I used a data set of

males who were photographically identified on more than one occasion within the same

season. Within-season resights from the years 1996-2001 were utilized. Differentiation

between principal and secondary escorts only began to be recorded in 1996, and the

within season matching has only been completed through 2001. The within season

matches were then compiled across the years, resulting in 176 pairs of photographs of

male whales. The group composition, and the presence or absence of a calf at the time of

sighting were recorded on each photograph. Only whales that had been classified at least

once in the past as an escort, or identified by an underwater observer as male were included in this dataset.

The 176 pairs were divided into two categories based on the presence or not of a calf in the first sighting. These two structural categories were then subdivided according to the presence or absence of a calf in the second sighting, resulting in four unique categories across two sightings: C/C, C/NC, NC/C, and NC/NC where C=calf group, and NC= non-calf group. A whale that was seen in a group containing a calf for both sightings was put into the C/C category. A whale that was seen the first time in a calf group and the second time in a group without a calf was put into the C/NC group, etc. A chi-square test was used to determine if the males seen initially in non-calf groups differed in the distribution of their second sightings than would be expected if males randomly associated with the calf and non-calf groups available. A similar chi-square test was performed for the males seen initially with calf groups.

The expected distribution was derived from the number of groups larger than one animal, but excluding groups containing yearlings, that were photographed from 1996-2001. There were 2551 such groups. The percentage of calf to non-calf groups in this set was multiplied against the number of males in the dataset in order to calculate the expected distribution.

Head lunging

In addition to collecting fluke identification photographs from the boat, detailed behavioral notations were made for each group of whales tracked. A log of each group tracked is cataloged in a Filemaker database. This database was queried for records

between the years 2000-2003 for all groups containing 3 or more adults. Records were

categorized according to the presence of a calf, and any occurrence of head lunging. The

correlation between the occurrence of head lunging and increasing group size was

plotted. Also, while controlling for pod size, the occurrence of head lunging was

compared for pods with calves and pods without calves.

Comparison of large competitive groups across a season

To determine how the presence of a calf may affect group size and whether males

become less choosy as the season progresses, the same dataset examined in Chapter 3

was used to compare the trends in large competitive groups across a season. Competitive

groups with four or more escorts were divided into two categories: those calves and those

not containing calves. The trend across the season of the proportion of calf to non-calf

groups for the two competitive categories was compared.

Results

Choice by individual males

One hundred seventy-six individual males were sighted twice within the same

season in groups larger than one animal between 1996 and 2001. Figure 7 shows how the

males were divided into the four categories: C/NC, C/C, NC/C and NC/NC. One hundred

five of the males were seen in non-calf groups on their first sighting; seventy-one of them

were seen in calf groups on their first sighting. The earliest sighting recorded for these

males was January 6th (Julian day 6, temporary rs 1999.1) and the latest recorded first

sighting was April 16 (temporary resight #1998.3). Figure 8 illustrates the observed and

expected counts for the males in the four categories: C/NC, C/C, NC/C and NC/NC. Of the 105 males seen initially in a non-calf group, 76 (72%) were seen again in a non-calf group, and 29 (28%) were seen the second time in a calf group. Of the 71 males seen initially in a calf group, 37 (52%) were seen again in a calf group and 34 (48%) were seen the second time in a non-calf group. The C/NC and C/C bars are grouped together on Figure 6 and there is little difference between the expected and observed counts for these categories: $\chi^2 (1, \underline{N} = 71) = 2.27$, $\underline{p} > 0.05$, However, the males who had escorted a non-calf group in their first sighting were significantly more likely to escort a non-calf group the second time than would be expected by random association with the available groups: $\chi^2 (1, \underline{N} = 105) = 12.61$, $\underline{p} < .0005$.

The earliest date of a second sighting was January 9th (rs 1784) and the latest was April 25th (rs 1473). The shortest interval between first and second sightings for the 179 males was 1 day, the longest interval was 68 days (rs 2000.29, first seen 1/18/00, second sighting 3/27/00).

Head lunging

All the groups tracked by the boat between 2000 and 2003 were divided into the number of adults present in each group, whether or not a calf was present, and whether or not head lunging was observed. Because head lunging was being considered as a signifier of competition around a female, only groups containing three or more adults are included in this analysis.

For the initial analysis of effects of group size on head lunging frequency, all four groups were pooled together. Figure 9 illustrates the trend of increasing head lunging as

group size increased. The value of R^2 was 0.8493. Hence, a larger proportion of the behavior is explained by group size. Additionally, Figure 8 illustrates that when controlling for group size, the ratio of head lunging groups to non-head lunging groups was not different between calf and non-calf groups. The data are organized according to number of adults in a group with the ratio of calf to non-calf groups not differing significantly between groups found head lunging and groups where head lunging was absent. Because of a small sample size, chi-square tests were performed on combined data of groups of 3 and 4 adults, of 5 and 6 adults, and of 7+ adults: 3 and 4 adults: $\chi^2(1, \underline{N} = 374) = 0.2$, $\underline{p} > .05$; 5 and 6 adults: $\chi^2(1, \underline{N} = 115) = 0.94$, $\underline{p} > .05$; 7 or more adults: $\chi^2(1, \underline{N} = 101) = 0.49$, $\underline{p} > .05$.

Comparison of large competitive groups across a season

Craig et al. (2002) reported that head lunging occurred more often in groups not containing a calf than in those with calves, but did not control for group size. Because the above results indicate that a larger group size leads to a higher occurrence of head lunging, and that when controlling for group size there is no difference in potential for head lunging between calf and non-calf groups, the results reported by Craig et al., could be explained if in her data set, there were, on average, larger groups existing around non-calf females than around mothers. Craig et al.'s data were obtained from a shore station where 27 groups were observed head lunging, 23 of these groups did not contain calves while 4 did. The shore station data were obtained between January 14 and April 17, 1998 (Craig et al., 2002). The unit of interest is the competitive group because escorts are already competing for proximity to the female. Figure 11 illustrates the higher proportion

of non-calf groups in the category of competitive groups with four or more escorts.

The comparison showed a significantly larger number of groups of four or more escorts that did not contain calves as opposed to those that did ($\underline{t}$ (6) = -11.93, $\underline{p}$ = .00002). Even as the season progressed and the non-calf females presumably leave for the feeding grounds, these large competitive groups are forming most often around non-calf females.

Discussion

Individual males appear to choose to escort non-calf females over mothers. The resight histories of 105 individual males who were sighted initially in a non-calf group showed them to have a significant tendency to be seen again in a non-calf group (χ^2 (1, $\underline{N}$ = 105) = 12.61, $\underline{p}$ < .0005). This same consistency was not shown by males initially seen escorting mothers.

This influence is based on the presumption that all groups of two or more contain a female who was available to be escorted. It is possible that a portion of the non-calf groups consisted only of male whales. Clapham, Palsboll, Mattila, and Vasquez (1992) conducted a study where skin biopsies determined the sexes of all group members. Seven of 21 groups (33%) consisted of only males. Also, mothers who are not currently receptive may discourage escorts.

Because there is currently no way to determine female receptivity, the question regarding whether a receptive female without a calf is more attractive than a receptive mother is addressed here using a combination of boat observations and photographic records. Craig et al. (2002), used head lunging as an indication that males were more

aggressive, and therefore more interested in non-calf females, but the study did not control for group size. While the existence of head lunging did not appear to be a direct effect of the lack of a calf in a group, it did illustrate a striking difference between competitive groups of varying sizes.

When controlling for size, there was no difference between calf and non-calf groups in the percentage of groups displaying head lunging. However, head lunging increased as group size increased (calf and non-calf groups combined), and the proportion of non-calf to calf groups is heavily skewed towards non-calf groups when there are four or more escorts present. Therefore, Craig et al.'s results can possibly be explained by the tendency for head lunging to occur in larger groups, and for these groups to form primarily (even through the end of the season) around non-calf females.

Though mothers may be entering post-partum estrus, and may be receptive to male escorts, the females without calves are still attracting the largest number of escorts on average. This indicates that these non-calf females are still highly attractive to males at the end of the season, meaning that the males have not become less choosy as the season progresses as suggested by Craig et al. (2002). Any increase in the number of mothers being escorted may be a result of a higher number of mothers who are available and the fewer number of available females without calf, and may not indicate a tendency for males to shift their preferences.

CHAPTER 5. BEHAVIORAL ROLES

Introduction

Since we cannot truly assess fitness of males without paternity information, our best estimate comes from those males seen in the closest proximity to females, particularly those females without calves. This chapter looks at males seen in the position closest to the female, the principal escort, and whether they are exhibiting different behavioral choices than males who have never been seen in these roles. (Behavioral role descriptions can be found in Table 2). The two specific questions asked are: do the principal escorts arrive earlier on the wintering grounds? And, do the males seen as principal escorts have different residency periods than males never seen as principal escorts? Furthermore, to give evidence showing that singing is a behavior engaged in by males irrespective of age or behavioral status, two questions are answered. First, are the principal escorts seen more or less often as singers than males never seen as principal escorts? And secondly, do males with long-term resight histories who have been sighted as singers show a correlation between being seen as a singer and their age?

The overall residency and migratory timing patterns of male humpbacks have been described, but examining such patterns of subgroups of males may show the presence of alternative mating strategies occurring in the same population (Craig et al., 2001; Craig et al., 2003).

The residency and migratory timing data places all adult males into one category, but evidence from Spitz et al. (2002) size data shows that there is a difference in length

between males who are seen in different behavioral roles. Levels of fitness presumably differ for the males as well as the females, and some males will be better able to compete for access to the fittest females than others. Alternative mating strategies could include altering migratory timing in order to arrive on the wintering grounds after the prime males have spent much of their energy, or when the competition may not be as fierce, or when a different set of females are available. Some males may be able to exercise control over how long they stay on the wintering grounds by spending less energy per female and staying longer, while other males may opt to shorten their stay but invest their energy in fewer but more aggressive competitive groups. Additionally, perhaps males who are not able to compete successfully for access to a female without a calf will preferentially choose to escort the lactating females who are more accessible.

Finally, much attention has been given to humpback whale song as a secondary mating strategy (Chu and Harcourt, 1986; Mobley, Herman and Frankel, 1988; Frankel, Clark, Herman and Gabriele, 1995). Is it a strategy employed by males who are not successful at other strategies? While this is a current hypothesis, no clear evidence exists supporting that song directly attracts females, and the function of song remains speculative. Size data indicates that there is no difference in the sizes of males seen as singers and males seen in other behavioral roles (Spitz et al., 2002). Working under the assumption that males sing to attract the attention of females, two questions were asked. First: Are males who are seen in the dominant, principal escort roles seen less often as singers? And secondly: Is there a pattern in males' life histories as to when they are seen as singers? (i.e. do males sing more often late in life than early?).

Methods

Principal Escorts

Beginning in 1996 KBMML began recording secondary behavioral roles; prior to 1996, differentiation between a principal and secondary escort was not recorded. The fluke photograph database from 1996-2001 was queried for males who had been seen more than once within a season. This resulted in a subset of 247 males. These males were divided into two categories: those who had been seen at least once occupying the nuclear principal escort role (the closest position to a female without a calf when there was more than one escort present), and those whales who had never been sighted as a nuclear principal escort. These two subgroups were compared for their average arrival time on the wintering grounds, their average and range of residency, and the percentage seen at another time as a singer.

Life Histories of Singers

The entire fluke database from 1976-2001 was queried for whales that had resight histories and who had been sighted at least once as singers. One hundred and two whales met these criteria and the number of years each whale was sighted, and the span of their sighting histories were plotted in Figure 12. The span of sightings is offset from the number of years seen because a whale seen in only one year would have a span of zero. Most of the whales were seen in three or fewer years. The span between sightings decreases from 0 to 7 years, then there is a spike in the number of whales who's resight histories spanned 8 or more years. Because this analysis pertains most to long-term

resights, only those animals with histories spanning at least 8 years were analyzed for life history trends (n=42).

Each of these 42 males were assigned a number (or numbers) representing when in their sighting history they were seen as a singer. This number is referred to as each whales' singer index. For example: Whale A was seen in 1980, 1985 and 1989 and he was seen as a singer in 1980 and 1985. There are 10 years in his sighting history, and he was seen as a singer in year 1 and year 5. One divided by 10 is 0.1 and 5 divided by 10 is 0.5, so Whale A is assigned singer indexes 0.1 and 0.5.

The whales' singer indexes were plotted to illustrate the presence or lack of trends in singing across a whale's resight history.

Results

Principal Escorts

Between 1996 and 2001 there were 247 males seen more than once within the same season. The average day of the first sighting was day 56 (Feb 25th), the median was Day 57. The average interval between first and last sighting was 16.5 days, with a range of 1-78 days.

This subset of whales was divided into three categories: those males who had been seen at least once as a nuclear principal escort (principal escort to a female without a calf- N1E; n=25), those males seen at least once as a principal escort to a mother (1E; n=22), and those males never seen as a N1E or 1E (n=198). These three subsets were compared against one another for differences in Julian day of first sighting, interval between first and last sighting within the same season, and the percent also seen as a

singer (Table 5). Two males sighted at different times in both the N1E and 1E roles were not included in any of the subsets.

The median day of first sighting for the males who had never been seen as a principal escort was Day 59.5 (Feb 28th). The median day of first sighting for the N1E's was Day 37, and the median day of first sighting for the 1E's was Day 51.5 (Figure 11). The day of first sighting for N1E's varied significantly from the first day for males never seen as principal escorts (t (221) = 2.39, p < .05). The day of first sighting for 1E's did not vary significantly from the first day for males never seen as principal escorts (t (218) = 0.80, p > .05).

The average and median intervals between first and last sighting within the same season are reported in Table 5 for N1E's, 1E's and males never seen as N1E's or 1E's. The median interval for 1E's was longer than intervals for any other category but an ANOVA showed that the difference was not significant (F(2, 242) = 3.03, p > .05). The two whales (resights 2001.21 and 1852) that had been seen both as a 1E and N1E had intervals of 27 and 15 days and were first seen on Day 44, and Day 94. Again, these whales were not included in any of the sub-categories.

Of the males seen at least once as a N1E, 12% of them had additional sightings as singers. Of the males seen at least once as 1E's, 9% of them had additional sightings as singers; and 14% of the males never seen as a principal escort had been sighted at least once as a singer.

Life histories of singers

The entire fluke database contained 133 records of whales who had been seen at least once as singers and who had been photographed on more than one occasion. A majority of these whales were sighted in four or fewer years, with most being seen in two separate years (n=32). The interval between first and last sighting (across years) ranged from 0 years (within season resight) to 21 years (Figure 10). There is a peak in whales whose sightings spanned 0-2 years, and another smaller peak in the number of whales sighted across 8-11 years. Because the presence of a trend in singing across the whales' life histories was the question being addressed, a subset of 42 males with sighting histories spanning 8 or more years was analyzed further.

The singer indexes from the sighting histories of the 42 males are listed in Table 6 and illustrated in Figure 14. There is no trend towards singer sightings occurring in the early or the late portion of a whale's sighting history; rather, they are universally distributed.

Discussion

Males seen as nuclear principal escorts (principal escorts to non-calf females), were shown to arrive earlier on the wintering grounds than males who had been seen as principal escorts to calf groups, or males who had never been sighted as a principal escort. That there is a difference in arrival time between the two categories of principal escort supports the hypothesis that different mating strategies are being pursued by different individual males (as grouped by behavioral role). The nuclear principal escorts

appear to be selecting for females who are available earlier in the season, or for the fact that more females are available at the beginning of the season.

Information on the interval between first and last sighting is less conclusive. The males seen as principal escorts to calf groups had a longer average interval between sightings than either the nuclear principal escorts or those whales never seen as principal escorts, but this was not significant. It is possible that 1E's were either fit enough to stay for longer periods of time, or were choosing a strategy (escorting mothers) that was less physically challenging and therefore effectively rationed energy resources allowing them to stay for a longer period of time than nuclear principal escorts. The fact that the males never seen as principal escorts were seen for a shorter length of time could be influenced by the possible inclusion of juvenile whales in this group.

There was no indication that singing was a behavior engaged in more by less fit males than fit males. The males seen as principal escorts were just as likely to be seen singing as males who had never been sighted as principal escorts. A chi-square comparison between the number of whales seen singing for each behavioral category showed no significance (χ^2 (2, $\underline{N}$ = 245) = 0.38, $\underline{p}$ > .05).

Furthermore, there were no trends in the occurrence of singing through a male's resight history. Males are heard singing throughout their resight history, with no trend towards singing more often early or late in their resight histories. This supports the hypothesis that song is a behavior engaged in by all males, at all times of their life, and is not part of an alternative mating strategy.

CHAPTER 6. SUMMARY AND GENERAL DISCUSSION

Issues in male humpback whale reproductive behavior include the question of "choosiness" (Craig et al, 2002). Do males act promiscuously and indiscriminately or do they exercise preferences and choice in mate selection? Male humpbacks whales have a choice between two reproductive classes of females: those who are accompanied by a calf, and those who are not.

Data from carcasses examined by whaling biologists and from successive year observations of live animals indicate that, in general, mothers are less likely than females without a calf to produce a calf the succeeding year. Thus, Chittleborough (1958) reported on data collected by Norwegian observers documenting that 67 of 75 (89%) of non-lactating females were pregnant, while only 8 of 19 (42%) lactating females were pregnant. Observations of females followed over several years show that successive year births are rare (Baker et al.,1987; Glockner-Ferrari and Ferrari, 1984; and Clapham and Mayo, 1987). Finally, and more pertinent to this study, are the findings of Craig et al. (2002) that females having a calf in one year had only a 10% probability of being seen with a calf the following year, whereas females without calves in one year had a 75% probability of being seen with a calf the following year. Thus, on the wintering grounds, females without calf have a higher reproductive potential than do females with calf.

The data presented on male mate choice gave evidence that, on the whole, males do appear to be choosing females without calves over lactating females. Individual males who were seen initially in groups without calves are more likely to be consistent in that choice than are males seen initially in calf groups. Craig et al. (2002) reported that head lunging was seen more often in non-calf groups than calf groups. However, data presented here showed that when controlling for group size (which was difficult if not impossible from the shore station used in Craig's study) the difference in the presence of head lunging between calf and non-calf groups disappeared. There was, though, a positive correlation between competitive group size and the presence of head lunging, and far more large competitive groups (four or more escorts) occurring around non-calf

females than around mothers (t(12) = -3.02, p = 0.0106). The prevalence of larger groups forming around non-calf females then indicates that these females are preferred over mothers. This preference continued through to the end of the season.

The above evidence suggests that non-calf females are chosen over mothers as potential mates; however, is this based on the attractiveness of the female, or the fact that she is in a receptive state? While both Chittleborough (1958) and Craig et al., (2002) showed that mothers had a lesser chance of being either pregnant or seen with a calf the following season, there is a discrepancy between the 10% of females seen with consecutive year calves (this 10% being based on the fact that in KBMML's 29-year photo id database from 1976-1996 there was only one example of a consecutive year mother) and the Chittleborough data where 42% of the lactating females are pregnant. So why are we not seeing more consecutive year mothers? Are these concurrently pregnant and lactating females not bringing the fetus to term? As suggested earlier in this thesis, it is possible that a certain percentage of lactating, receptive females mate, become pregnant, and then either abort or resorb the fetus if the current calf survives the migration back to the feeding grounds. This could explain the discrepancy between the receptivity/reproductive potential reported by Chittleborough (1958) and the low percentage of consecutive year mother reported by Craig et al. (2002).

Although further data are required, the data presented here on context and resources allow us to speculate that males might be choosing females based on her reproductive state (i.e. ovulating or not), rather than on her potential to successfully rear a calf. As opposed to females without a calf, who most likely will enter a receptive state (ovulate) while on the wintering grounds, there is possibly much variation in receptivity of mothers, with still perhaps less than half of mothers becoming receptive. This indicates that a proper comparison (for attractiveness) of available females should be between those who are ovulating, eliminating those who are not currently receptive.

Mothers, in general, spend a longer time on the wintering grounds than do females without calves. The maximum within-season interval between first and last sighting for 14 females (nuclear animals) without calves was 16 days, while the

maximum interval for 51 mothers was 56 days. Nineteen mothers (37%) had intervals that were greater than the 16 day maximum for non-calf females. Therefore, although we do not know the length of receptivity for female humpback whales, we can assume that the mothers on the wintering grounds are spending a larger portion of their time (perhaps all of it) in an unreceptive state than are females without calves. Using the maximum interval for females without calves as an indicator, we could hypothesize that the receptivity period is shorter than 16 days. Any comparison of the attractiveness of mothers versus non-calf females should take into account the possibility that the non-calf females have a higher probability of being receptive.

The data from whaling biologists (Chittleborough, 1958) show that a percentage of mothers do enter post-partum estrous. There is also evidence of this from sightings of consecutive-year mothers (Glockner-Ferrari, 1990; Straley, Gabriele and Baker, 1994; Weinrich, Boye, and Miller, 1993). These observations, in conjunction with the presence of mothers in competitive groups, indicate that certain mothers may represent advantageous mating opportunities for some males.

Nonetheless, mothers are likely to be less biologically fit because of the energetic demands of lactation, and the lingering effects of pregnancy (Lockyer 1981). There may be cues to fitness level that are recognized by males such as girth, or behavioral cues. Hence, though a mother may be receptive, she may be less desirable than a non-calf female. Support for this contention was found in the data discussed earlier showing that larger competitive groups formed around non-calf females than around lactating females. The competitive group seems a proper unit of measurement to compare the attractiveness of mothers with non-calf females. The presence of multiple escorts around a female

suggests that the female may be in a receptive state. The considerably larger male aggregations forming around nuclear animals rather than around mothers provides evidence for the greater attractiveness of the nuclear animal. Thus, it still appears that males prefer, in general, non-calf females to mothers.

So, why would a male choose to escort a mother? At least two possibilities exist. First, the number of non-calf females decreases across the season so the choices for males become limited. Some mothers may enter post-partum estrous late in the season providing an opportunity for males to find a receptive mate. Second, not all males may be able to compete successfully for access to non-calf females with a greater reproductive potential. The relatively reduced competition around a mother may allow that same male to mate with her. Therefore, there may be two alternative mating strategies followed by different groups of males: some who are more fit may be able to compete successfully for access to females without calves, and others that are less fit may focus on competing for access to receptive mothers. The data comparing nuclear principal escorts to principal escorts in calf groups, and to males never seen in either role, show that nuclear principal escorts are arriving earlier on the wintering grounds. According to migratory data (Dawbin, 1966; Craig et al., 2003) mature females (without calves) who have recently mated are among the earliest to leave the wintering grounds (and therefore were among the earliest to arrive). It therefore follows that males must arrive early enough to compete for mating opportunities with these females. It is possible that the males seen as nuclear principal escorts represent a group of males who are more fit, and therefore are able to leave the feeding grounds earlier than other males.

In summary, when analyzed as a group, males may preferentially choose to escort females without calves. Nuclear principal escorts apparently arrive earlier on the wintering grounds and therefore are possibly gaining the most mating opportunities with non-calf females who soon return to the feeding grounds. At the end of the season large competitive groups still form more often around non-calf females than mothers. It is possible though, if alternative mating strategies exist in this population, that there is a group of males preferentially escorting mothers, but this will require further investigation.

APPENDIX A: TABLES

Table 1: Migratory Parade, (Dawbin, 1966)

Arriving on Wintering Grounds	Leaving Wintering Grounds
Lactating females, then	Newly pregnant females, then
Immature whales, then	Immature Whales, then
Mature males, then	Mature males, then
Resting females	Lactating females (new calves)

Table 2: Behavioral Roles

- NA- nuclear animal. Whale in center of competitive group. Assumed to be the female until underwater observations can confirm sex. Also referred to as FNC in this thesis (Female No Calf).

- N1E- nuclear principal escort. The whale with closest proximity to the NA.

- N2E- nuclear secondary escort. Any whale in a non-calf competitive group who is not the principal escort or the NA.

- Mother- whale with calf in close proximity. Also referred to as FC (Female with calf) in this thesis.

- E- escort. A male who is accompanying a mother.

- 1E- principal escort. A whale who is the closest to the mother when there is more than one escort present.

- 2E- secondary escort. A whale in a calf group who is not the principal escort or the mother.

Table 3: Fortnights

Fortnight	Start Date	End Date
1	January 9	January 22
2	January 23	February 5
3	February 6	February 19
4	February 20	March 5
5	March 6	March 19
6	March 20	April 2
7	April 3	April 16

Table 4: Consecutive Year Females

Category	Resight	First 1st yr sighting	Last 1st Yr. Sighting	1st 2nd Yr. Sighting	Last 2nd yr. Sighting	Interval in days
FNC ->FNC	1569	1/12/97	1/12/97	2/6/98	2/16/98	390
FNC -> FC	71	2/13/81	2/15/81	2/22/82	3/22/82	373
	228	2/24/82	2/24/82	3/10/83	3/10/83	379
	245	3/9/82	3/9/82	3/22/83	3/22/83	378
	346	2/23/82	2/23/82	3/27/83	3/27/83	397
	355	2/7/83	2/7/83	2/17/84	2/17/83	375
	1241	2/19/95	2/19/95	4/8/96	4/8/96	414
	1289	1/17/91	1/17/91	3/6/92	3/6/92	414
	1384	2/20/97	2/20/97	4/8/98	4/8/98	412
	1550	3/8/96	3/16/96	3/27/97	3/27/97	376
	1556	1/29/97	1/29/97	2/26/98	2/26/98	393
	1701	3/10/97	3/10/97	3/31/98	3/31/98	386
	1712	2/16/97	2/16/97	3/18/98	3/18/98	395
	1850	2/7/98	2/7/98	3/25/99	4/8/99	411
	1909	1/11/97	1/11/97	3/26/98	3/26/98	439
FC-> FNC	71	3/6/80	3/6/80	2/13/81	2/15/81	344
	228	3/10/83	3/10/83	3/22/84	3/22/84	378
	245	3/3/81	3/3/81	3/9/82	3/9/82	371
	540	3/18/83	3/18/83	2/3/84	2/3/84	322
	570	4/13/86	4/13/86	3/10/87	3/10/87	329
	1056	3/7/89	3/28/89	2/6/90	2/6/90	315
	1093	3/22/87	3/22/87	3/7/88	3/7/88	351
	1240	3/25/97	3/25/97	1/8/98	1/8/98	314
	1569	3/11/96	3/11/96	1/12/97	1/12/97	307
	1660	4/16/96	4/16/96	2/21/97	2/21/97	311
	1685	2/12/97	4/3/97	1/31/98	1/31/98	303
	1688	2/8/97	2/8/97	1/16/98	1/16/98	342
	1758	4/2/98	4/16/98	4/4/99	4/4/99	353
FC->FC	442	3/11/83	3/11/83	1/30/84	1/30/84	325

Table 5: 247 Males Seen More Than Once Within a Season (1996-2001)

	Julian date of first sighting	Median Julian date	Mean Interval btwn 1st and last sighting w/in season	Median interval	% seen as a singer
N1E (n=25)	44 Feb 13th	37	15.24 (1-57)	10	12%
1E (n=22)	53 Feb 22nd	51.5	23.05 (1-78)	19	9%
Never a N1E or 1E (n=198)	58 Feb 27th	59.5	15.91 (1-68)	12	14%
All males (n=247)	56 Feb 25th	57	16.52 (1-78)	13	13%

Table 6: Singer Index Scores: Occurrence of Singing in Whales' Life
Histories

whale	Singer index 1	Singer Index 2	Singer Index 3
7	0.07	0.67	0.93
1385	0.08		
408	0.09	0.73	1.00
976	0.09	1.00	
433	0.10		
555	0.10	0.60	
1103	0.10		
95	0.11		
1576	0.11	1.00	
134	0.13		
949	0.18	0.73	
89	0.19		
311	0.22		
1079	0.22		
1094	0.22		
51	0.24	0.29	0.59
497	0.31	1.00	
847	0.43		
336	0.45		
1118	0.50	1.00	
1034	0.50		
1036	0.55		
183	0.67		
105	0.72		
1642	0.74		
1173	0.75		
48	0.79	0.86	
82	0.82		
120	0.83	0.94	
419	1.00		
1016	1.00		
320	1.00		
509	1.00		
1062	1.00		
998	1.00		
69	1.00		
431	1.00		
512	1.00		
361	1.00		
427	1.00		
1492	1.00		
905	1.00		

Figure 1: Number of calf and non-calf groups across seasons

$y = -26.464x + 373.86$
$R^2 = 0.774$

$y = 24.429x + 59.857$
$R^2 = 0.6576$

# of groups

Fortnight

calf groups — nc groups — Linear (nc groups) — Linear (calf groups)
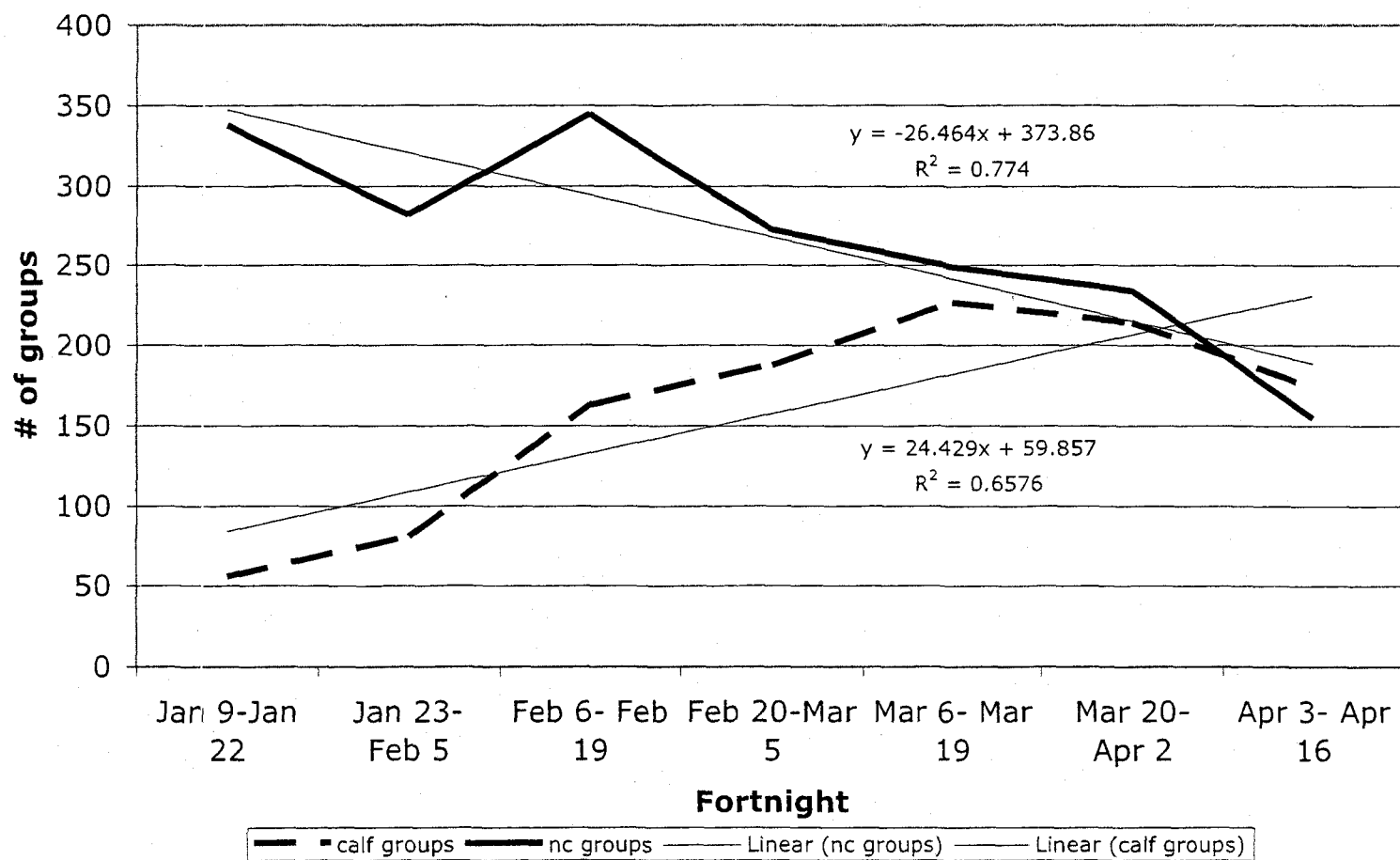
Figure 2: All calf groups across season (1996-2001)
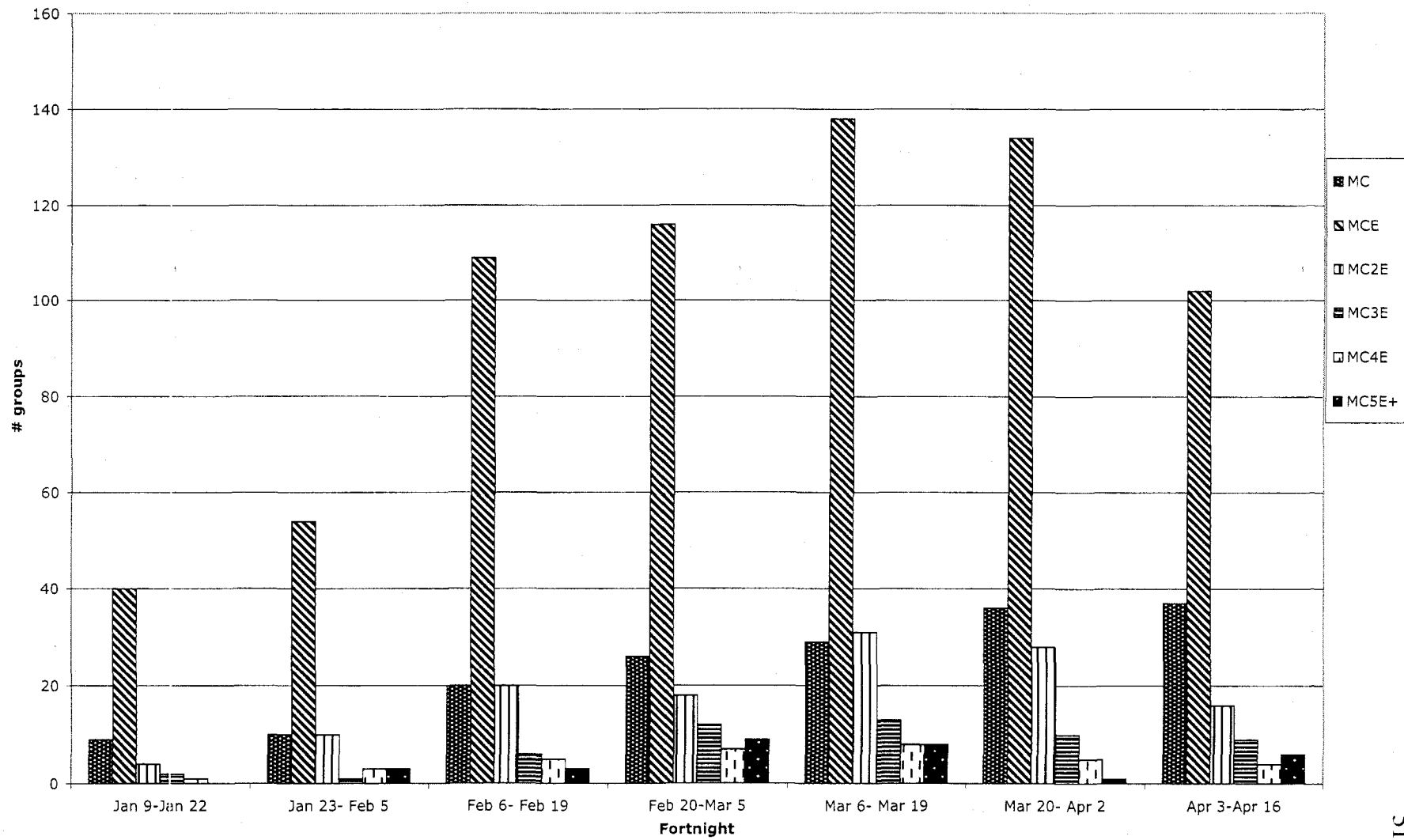
Figure 3: Percent groups with calf (1996-2001)

$y = 6.519x + 10.744$

$R^2 = 0.9476$

Legend:
- % grps w/ calf
- Linear (% grps w/ calf)

x-axis (Fortnight): Jan 9-Jan 22, Jan 23- Feb 5, Feb 6- Feb 19, Feb 20-Mar 5, Mar 6- Mar 19, Mar 20- Apr 2, Apr 3- Apr 16

y-axis: %
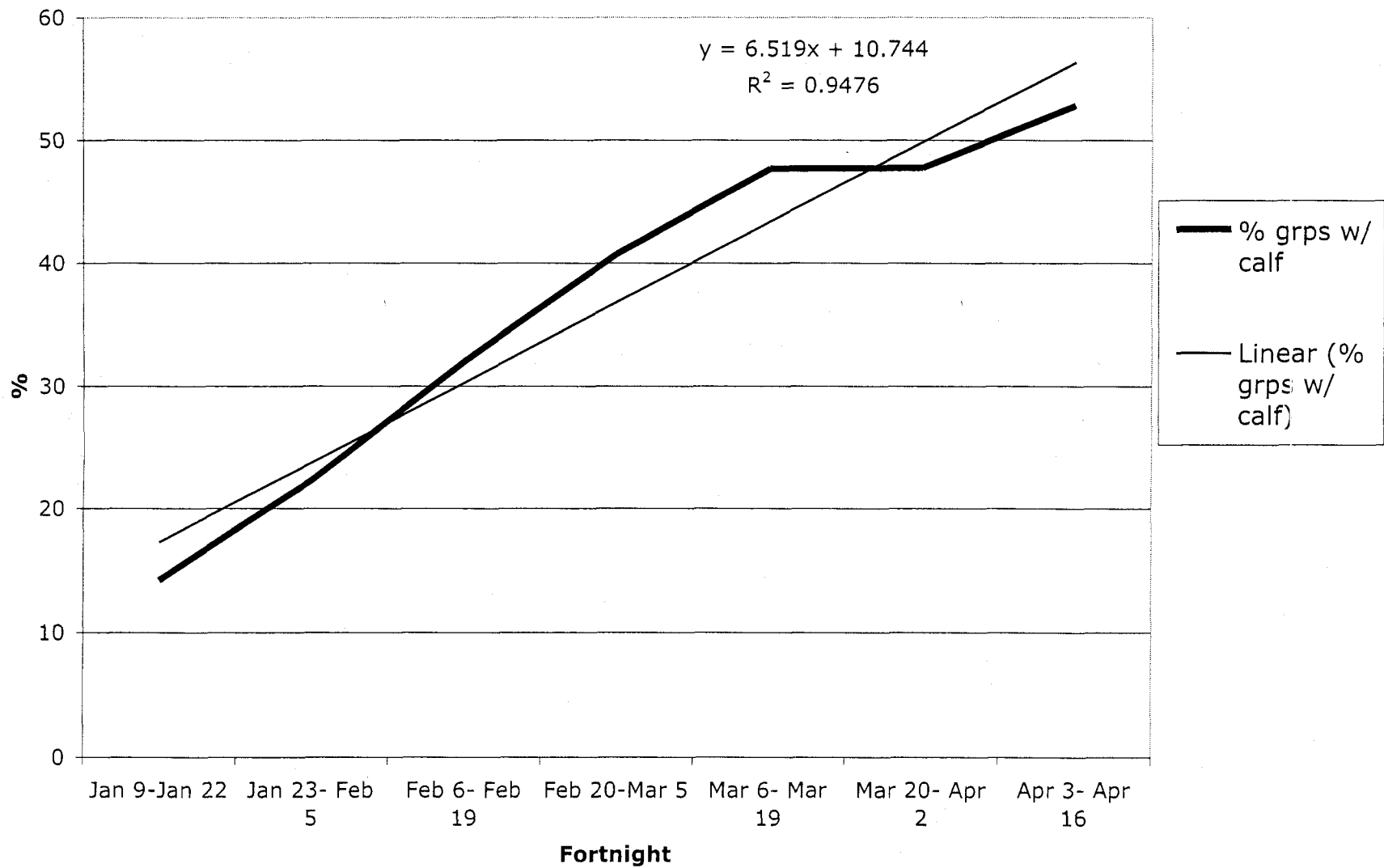
Figure 4: All non-calf groups (1996-2001)
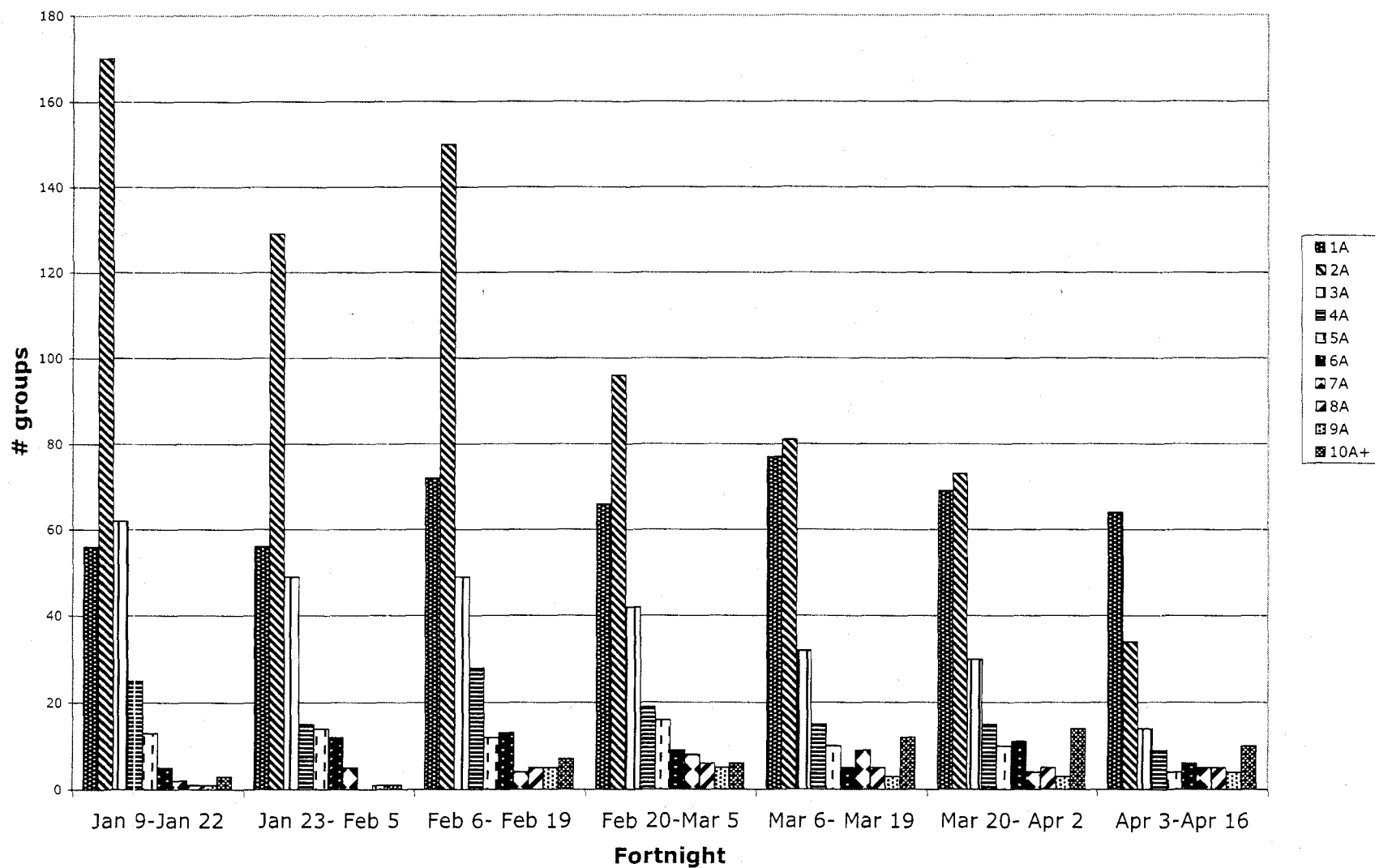
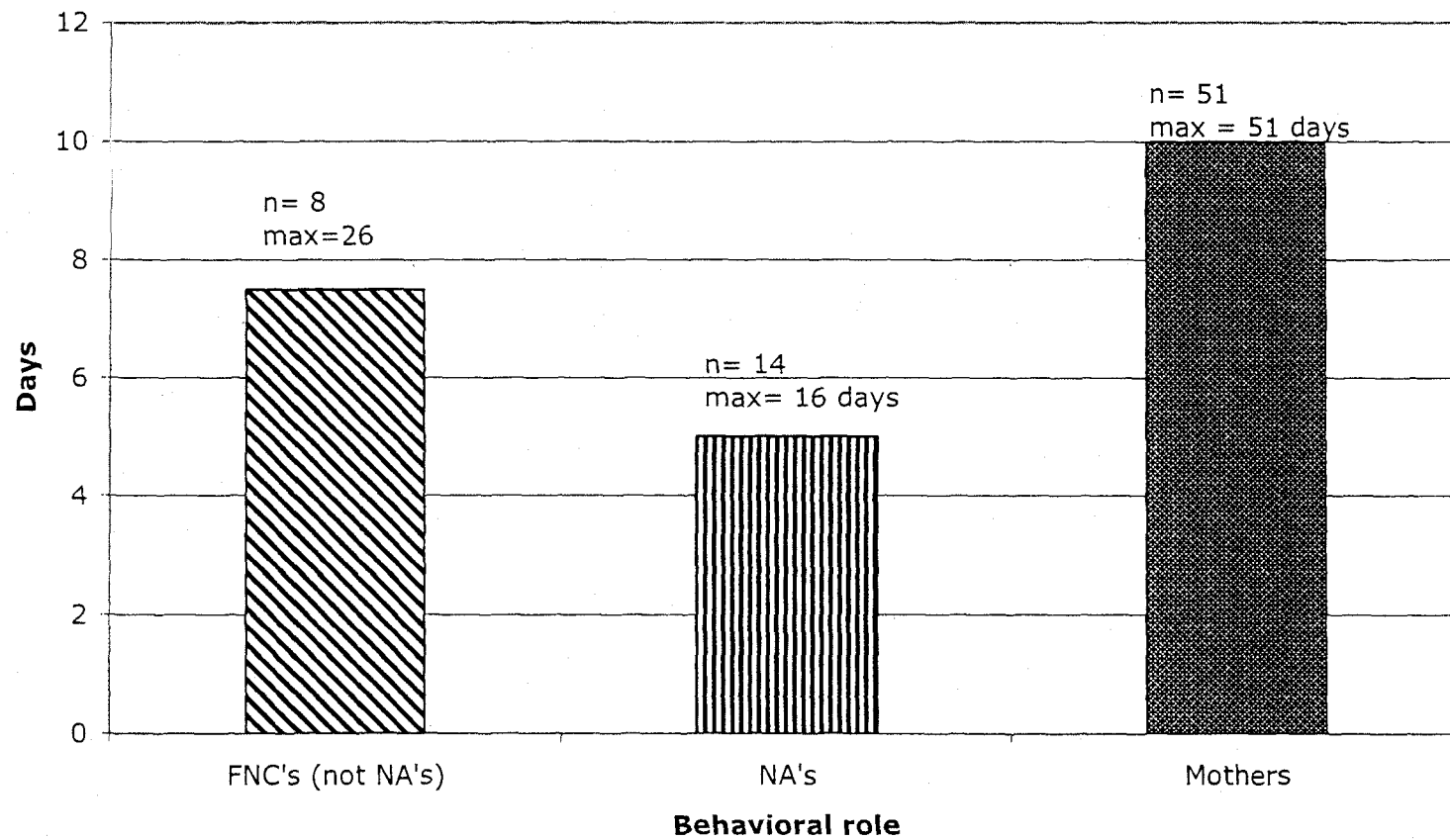**Figure 5: Median within-season interval between first and last sighting for females**

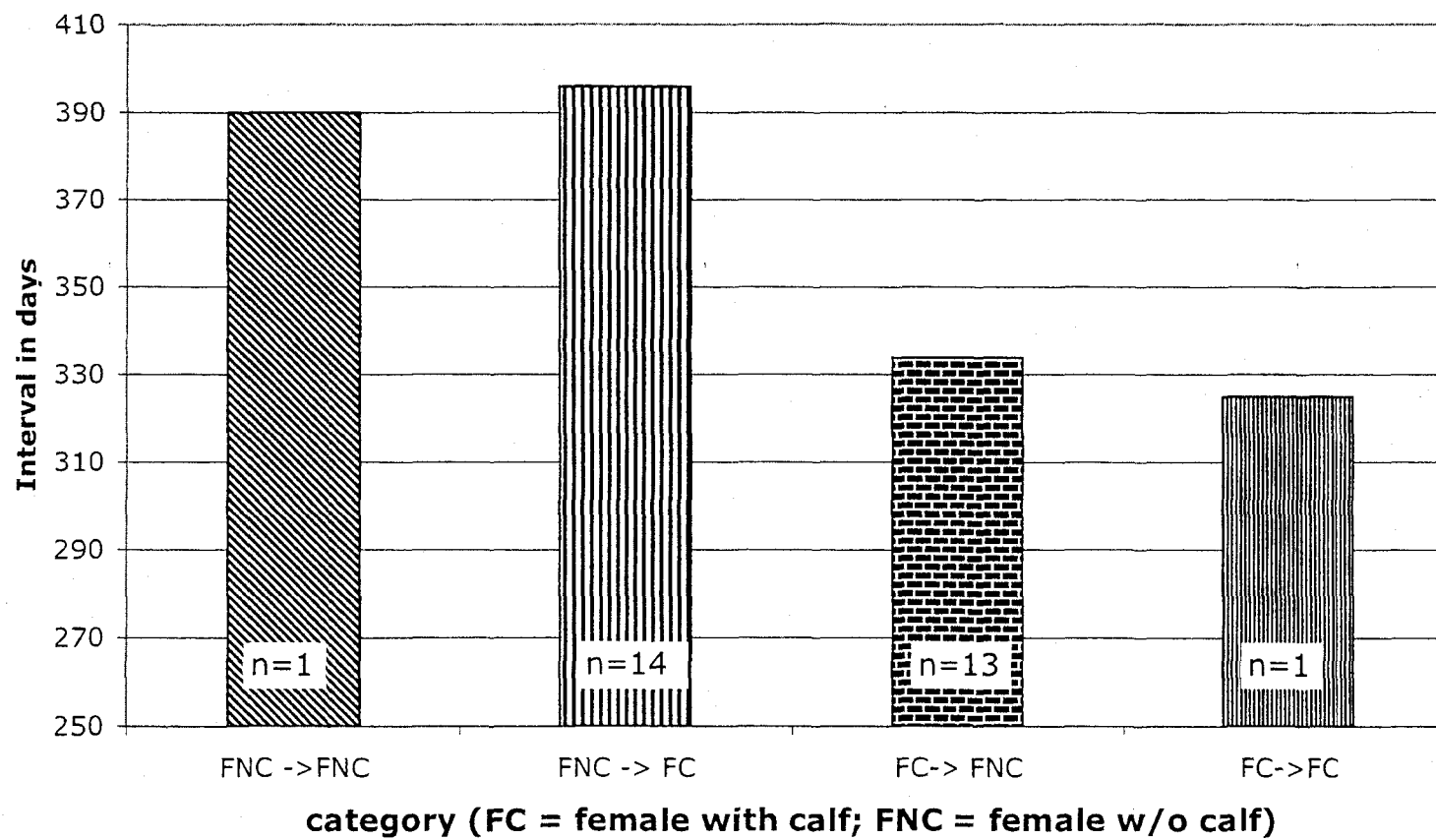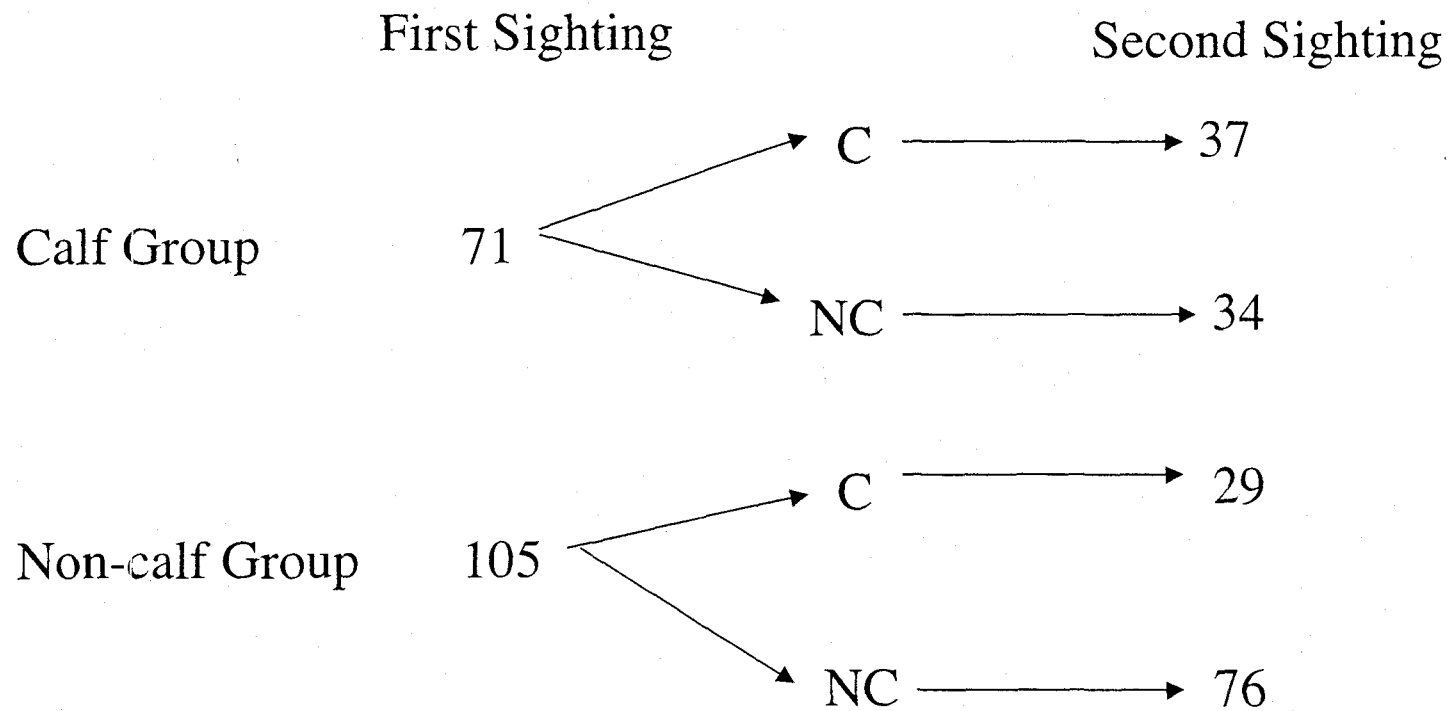# Figure 6: Intervals (in days) between years for females seen in consecutive years

Bar chart. Y-axis: Interval in days (ranging from 250 to 410). X-axis: category (FC = female with calf; FNC = female w/o calf)

- FNC ->FNC: ~390, n=1
- FNC -> FC: ~396, n=14
- FC-> FNC: ~334, n=13
- FC->FC: ~324, n=1

Figure 7: Individual male choice

First Sighting   Second Sighting

                                    C ⟶ 37
Calf Group   71
                                    NC ⟶ 34

                                    C ⟶ 29
Non-calf Group   105
                                    NC ⟶ 76

Figure 8: Observed vs. Expected for calf presence
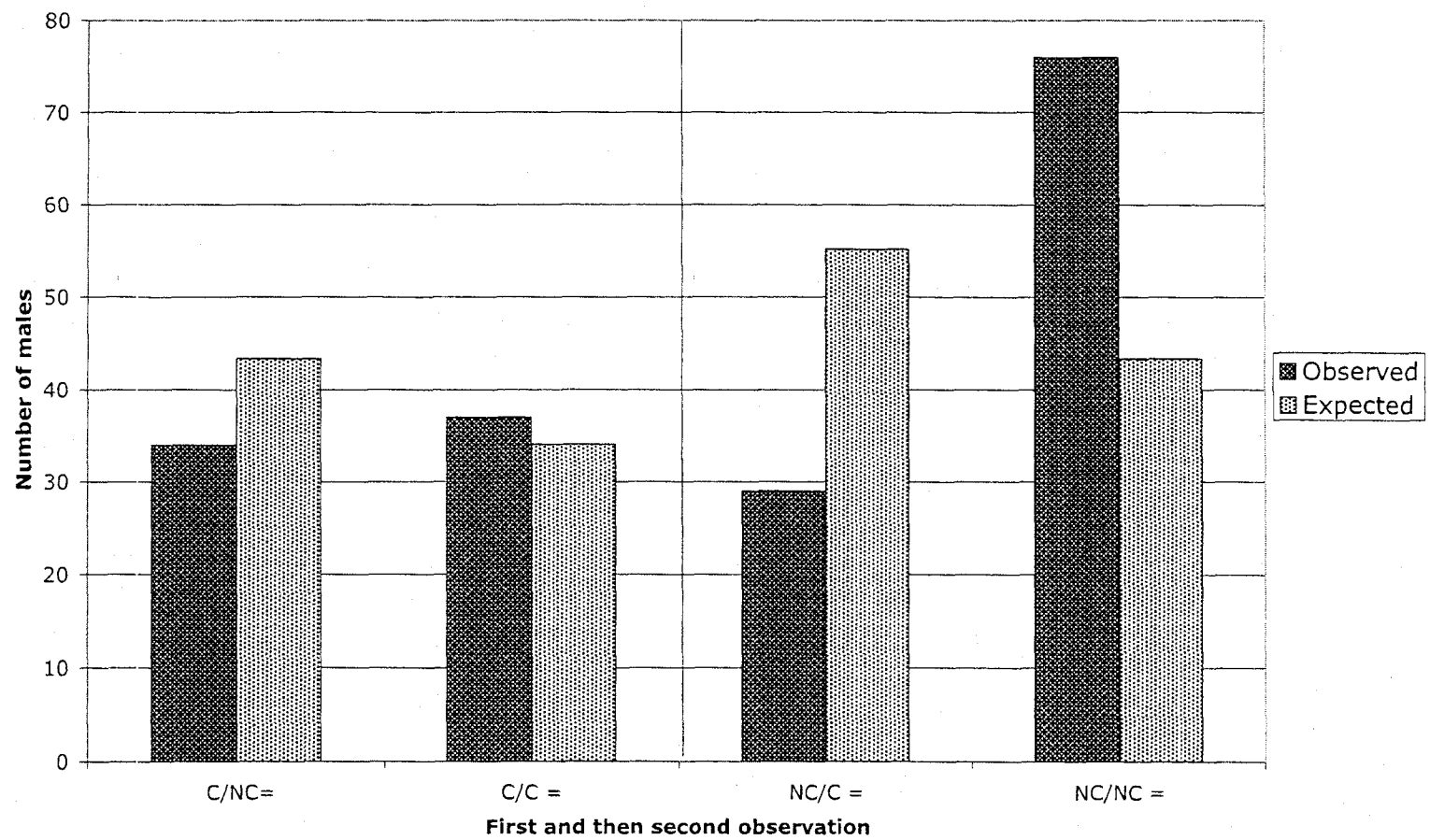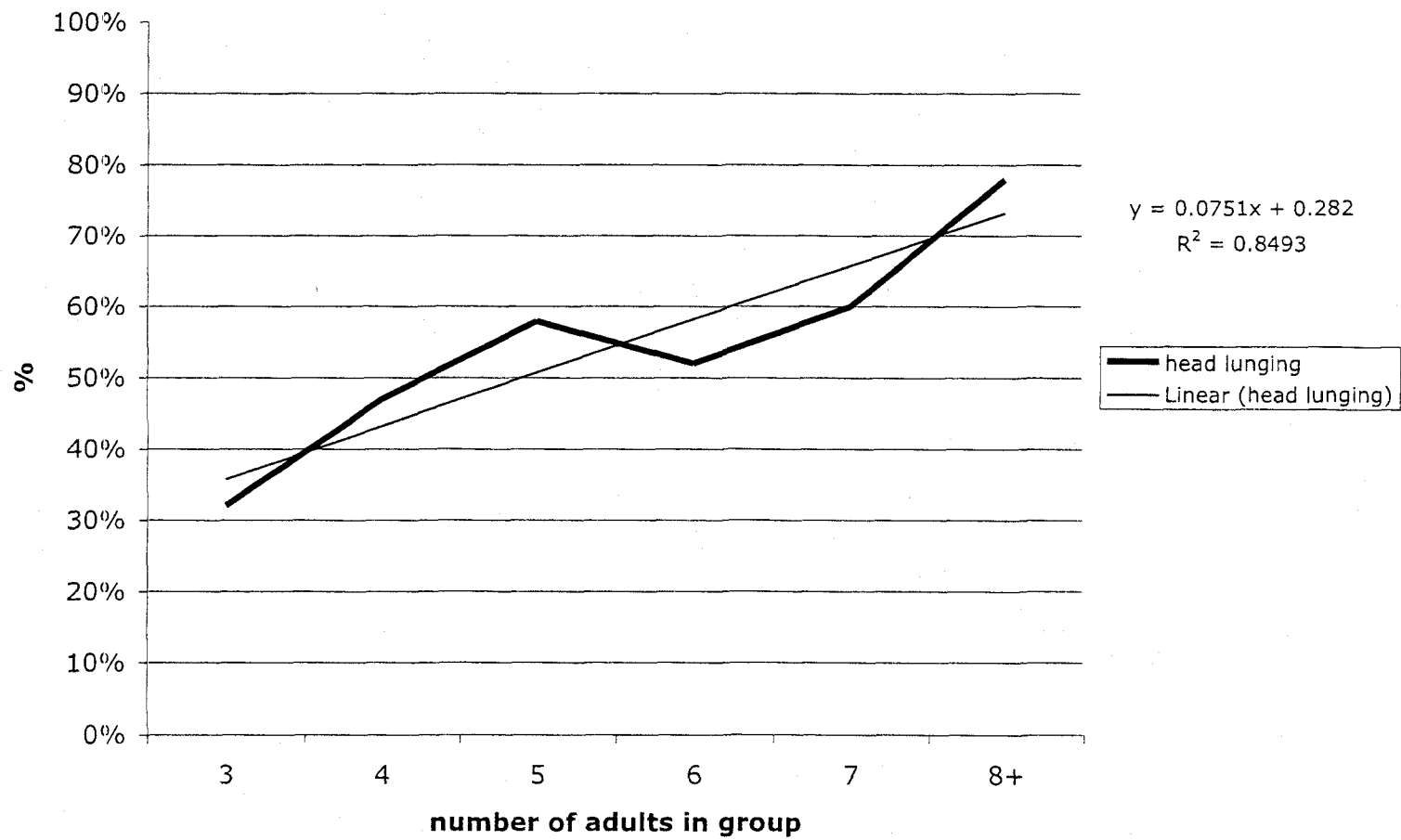
Figure 9: Percent of groups head lunging vs group size

$y = 0.0751x + 0.282$
$R^2 = 0.8493$

head lunging
Linear (head lunging)

number of adults in group

Figure 10: Percent groups head lunging controlling for group size
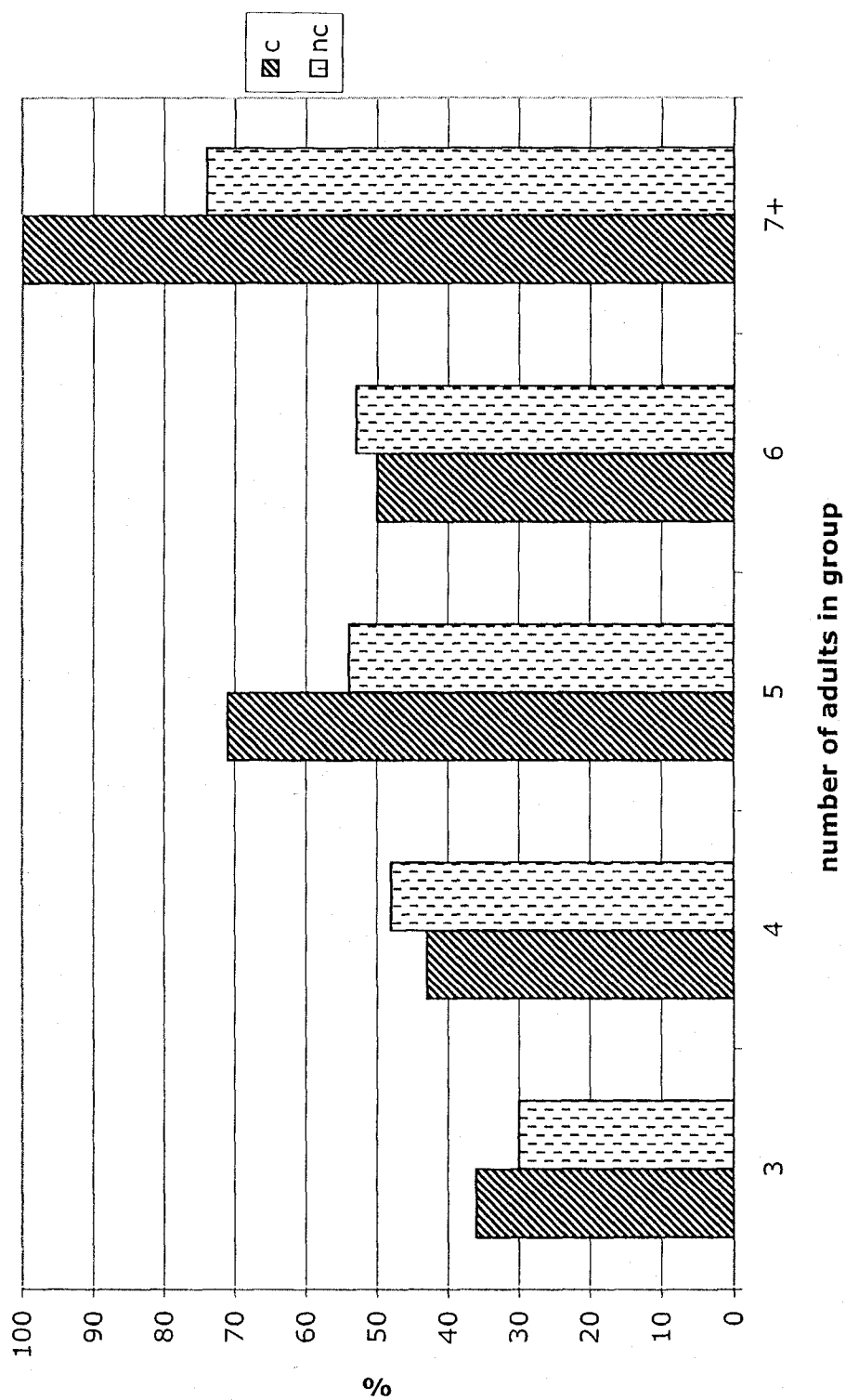
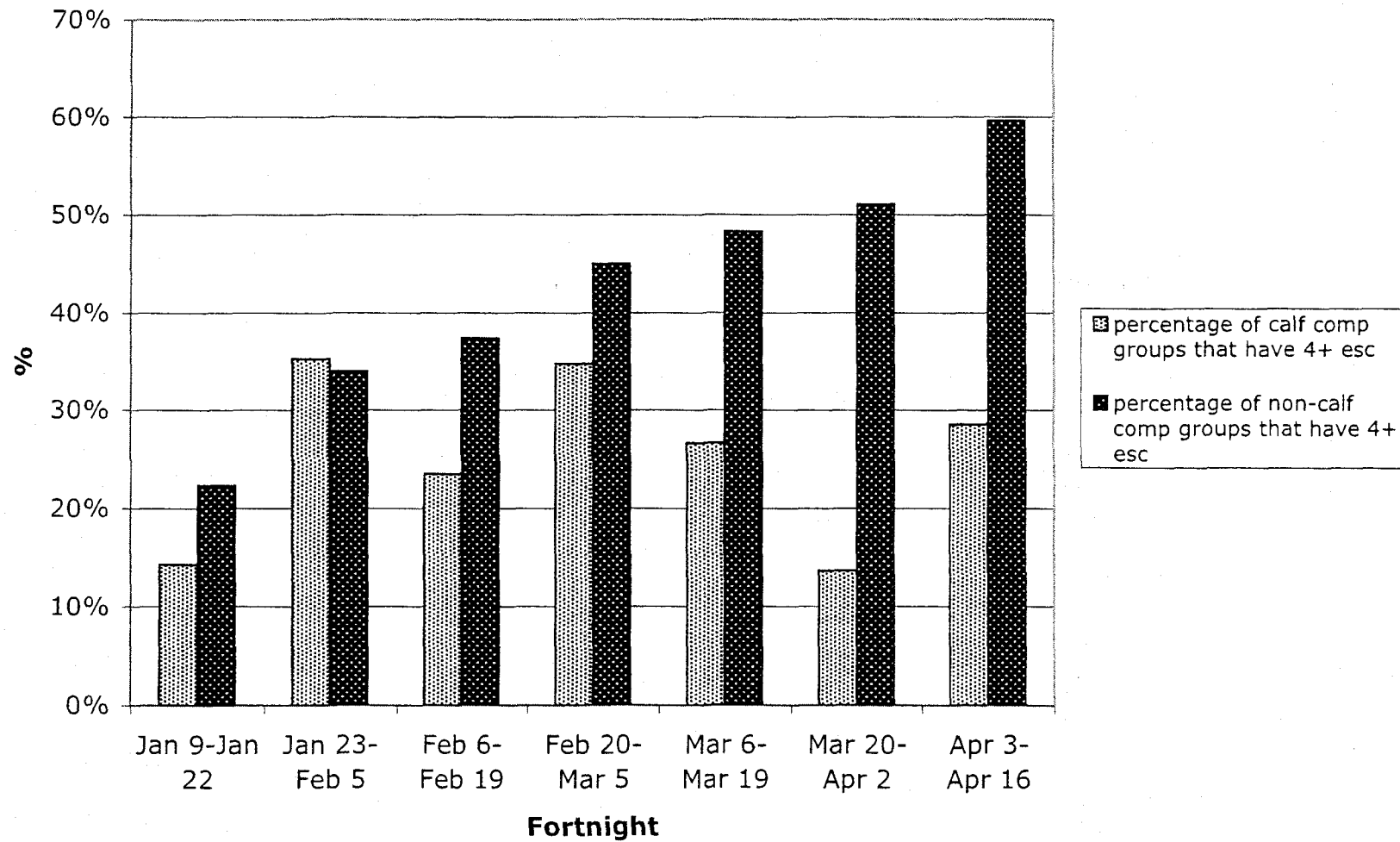# Figure 11: Percent of competitive groups that have 4+ escorts

Legend:
- ▣ percentage of calf comp groups that have 4+ esc
- ■ percentage of non-calf comp groups that have 4+ esc

X-axis (Fortnight): Jan 9-Jan 22, Jan 23-Feb 5, Feb 6-Feb 19, Feb 20-Mar 5, Mar 6-Mar 19, Mar 20-Apr 2, Apr 3-Apr 16

Y-axis (%): 0% to 70%

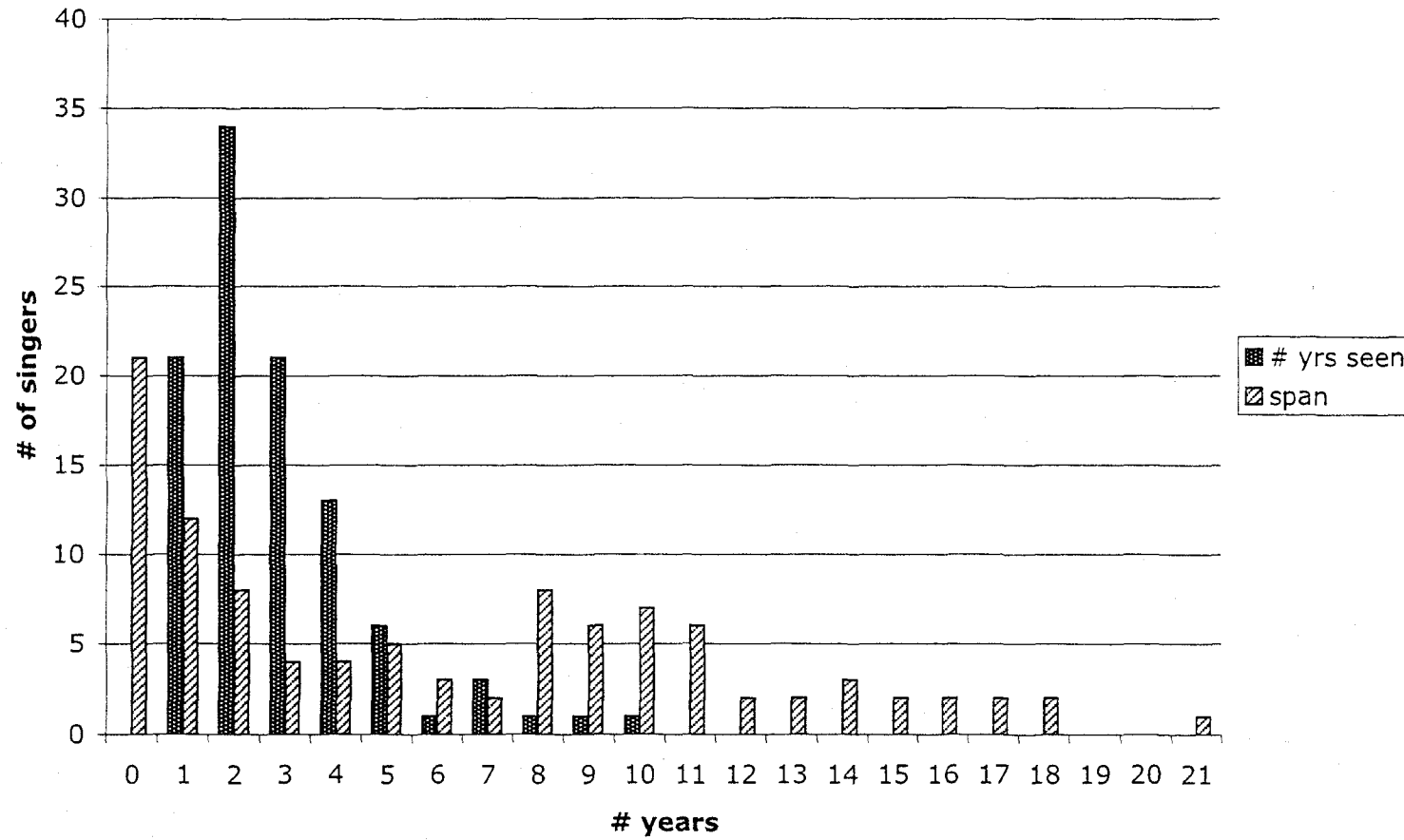Figure 12: Singers- # years seen and span of sighting history
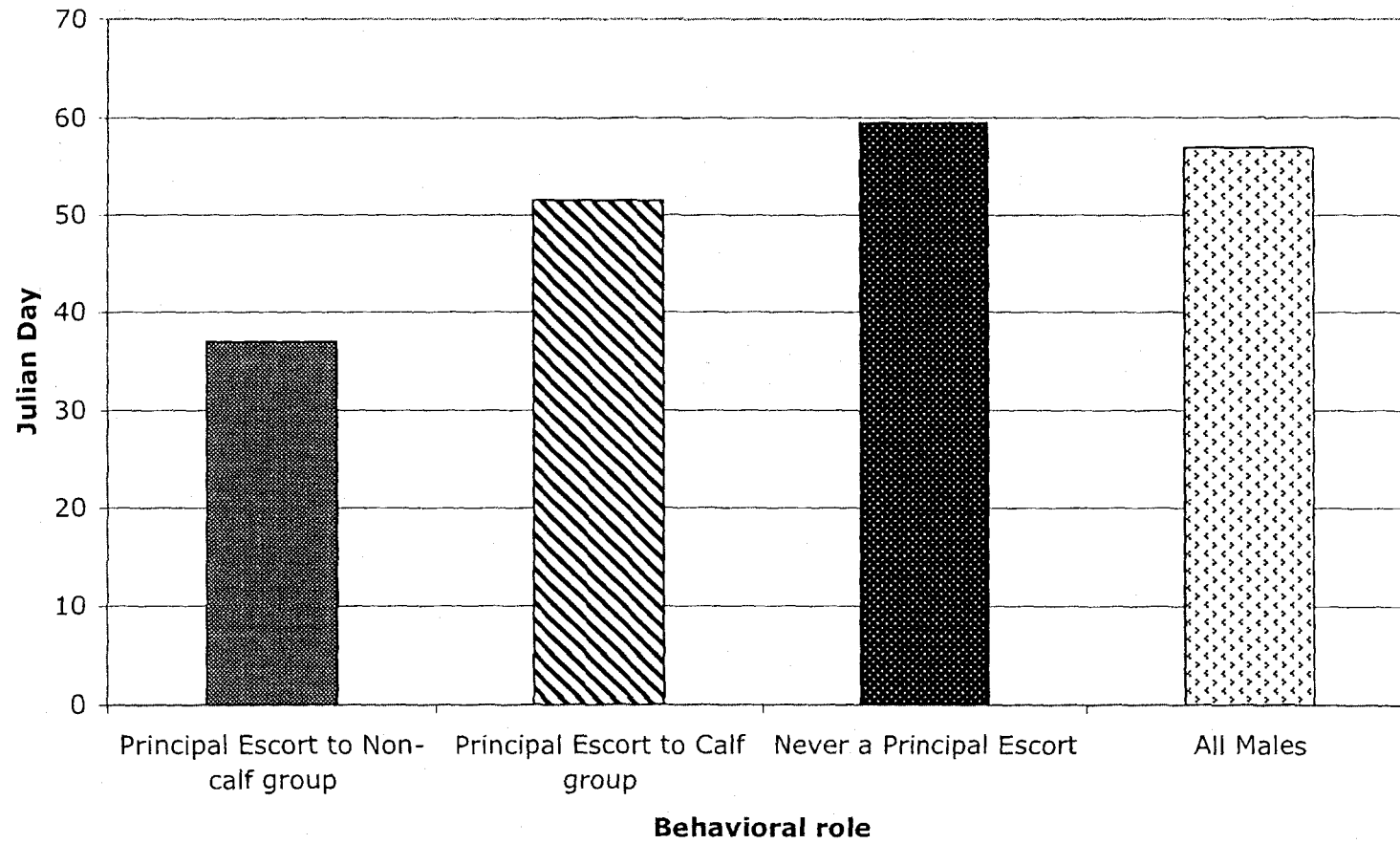
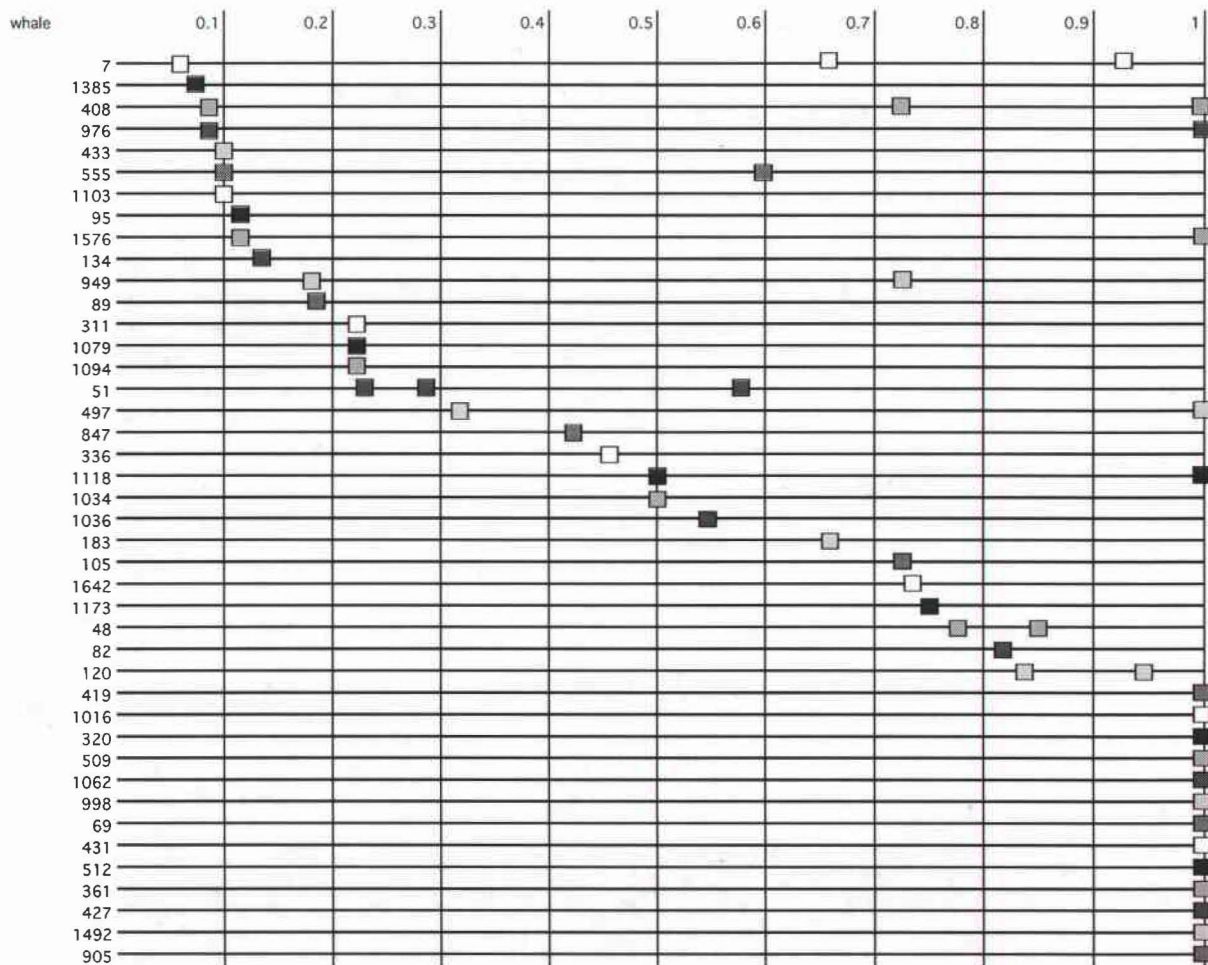## Figure 13: Median day of first sighting

Figure 14: Singer Index Scores:
Occurrence of singing in whales' life histories

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