Statistical Time Series Analysis of a Howler Monkey Population

by

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B. A. (Yale University) 1993
M. A. (University of California, Berkeley) 1999

A thesis submitted in partial satisfaction of the requirements for the degree of
Master of Arts

in

Statistics

in the

GRADUATE DIVISION
of the
UNIVERSITY OF CALIFORNIA, BERKELEY

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Spring 2003
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Abstract

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This paper presents a data analysis of measurements of the howler monkey population of Barro Colorado Island, Republic of Panama, in order to ascertain whether this population is changing over time in terms of its size, age distribution, adult sex ratio, or fertility indicators. While the analysis does find changes in some population parameters from year to year and across seasons, for other parameters it was not always possible to separate long-term from seasonal variation. Overall, population size and characteristics seem to fluctuate around a long-term central tendency. This supports the hypothesis that this population is at an equilibrium size and structure, raising the possibility that a density-dependent mechanism may be preventing population growth. Given the picture of a long-term equilibrium found in the statistical analysis, observed age distributions are compared with those from a theoretical stationary population. The comparison suggests that the mortality schedule for howler monkeys is very severe, with a maximum of 14% of infants reaching adulthood, and with a large portion of mortality concentrated at the time of transition from infant to juvenile. It is possible that the mortality estimates arising from the analysis are faulty, however, if age and sex identification of some monkeys suffers from consistent errors.
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Acknowledgments

Many thanks to Professor Katharine Milton for the data and countless hours spent discussing it. Many thanks also to my departments, both Demography and Statistics, and especially to Professors Ronald Lee, David Brillinger and Ken Wachter, for all of their help and support. Thanks also to WJD for sticking by me and making me smile while I struggled through this work.
Chapter 1

Introduction

1.1 Motivation

Effective stewardship of endangered animal populations involves monitoring species’ population sizes and other characteristics essential for the species to survive. Knowing whether animal populations are growing or declining in particular regions lets activists and officials know whether new conservation programs are needed, or whether existing conservation programs are meeting their objectives or not. In addition, having accurate information about population changes over both the short and long term allows for further study to infer the causes of those changes. In addition to measuring population size and growth rate, measuring demographic characteristics such as age structure, fertility, and mortality are also important in conservation efforts and in the development of evolutionary models of reproductive and survival strategies. Given this need for measuring aspects of animal populations, conservationists and scientists have gathered vast amounts of data about animal populations and the environments in which they live. It is possible, however, that the data that have been gathered cannot answer all of the questions we have for it.

One location of intensive animal, as well as environmental, monitoring has been Barro Colorado Island in the Republic of Panama. Barro Colorado Island (BCI) is the home of the mantled howler monkey, *Alouatta palliata*, included as a species threatened with extinction in the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES, 2002). This paper attempts to exploit some of the data available about mantled howler monkeys on BCI, in order to examine basic parameters of the population over time. Through this attempt, we expect to gain a greater understanding of this
particular animal population. More importantly, perhaps, it also allows us to evaluate the extent to which the data as they have been gathered are up to the task and discuss ways in which data quality could be improved.

1.2 Thesis Goals and Outline

The main goal of the statistical analysis is to infer some basic facts about the howler monkey population, such as its current size, age composition, adult sex ratio, and fertility, and whether these parameters are stable or have been changing. Some of these questions have been posed before and investigated, based on data through 1993 (Milton, 1982; Milton, 1996). The analysis here takes advantage of data representing additional observations of howler monkey troops through 2001.\(^1\)

The second goal of the analysis is to use some simplified demographic models to see whether or not the conclusions from the statistical analysis create an internally consistent picture of the population. Of course, many problems that plague animal population monitoring in other locations should be minimized in this setting, as Barro Colorado Island’s geographic isolation and status as a protected park mean that there is relatively little human interference with the animals and their environment. This should help to decrease the number of unobserved factors that may interfere with proper modeling and observation. However, statistical analyses could still give inaccurate conclusions for reasons such as model invalidity, measurement error, or simply by chance, albeit a small chance.\(^2\) Thus, the demographic analysis is helpful in providing a first attempt at validation of the results of the statistical analyses. The demographic analysis is also helpful in providing a framework in which information we can observe in the data – the age distribution – can be used to estimate parameters that we cannot observe – mortality.

The subsequent chapters introduce the ecological context and the data, discuss some appropriate statistical analysis methods and report the results of those methods. More specifically, Chapter 2 sets the stage for the analysis with background information on the habitat of BCI and the population in question. The animal data is introduced with a

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\(^1\)The “troop” is a basic unit of howler monkey social organization. Troops travel together, occupy and defend food trees together, and mating occurs between troop members (Collias and Southwick, 1952).

\(^2\)This refers to Type I error, the chance that observations provide evidence of systematic change, but in fact only arose by chance. Formally, Type I error is the chance of rejecting the null hypothesis when it is true.
background on howler monkey ecology, a detailed description of the data collection method and descriptive statistics and charts that provide an orientation to the data. Attention is given to both seasonal and long-term variation. Following the data described in Chapter 2, Chapter 3 details the analysis methods that are appropriate both to the data that are available and to the specific research questions. The discussion of methods also includes discussion of the methods’ underlying assumptions. Analyses are carried out and results reported and discussed in Chapter 4. Finally, conclusions and implications are presented in Chapter 5, including a demographic analysis based on the statistical results. All figures and tables appear in appendices.
Chapter 2

Background and Introduction to the Data

2.1 Background on Barro Colorado Island

Barro Colorado Island (BCI) is a 15.5 km$^2$ nature reserve in the Republic of Panama, situated at 9°9’N latitude, 79°51’W longitude. It was created in 1914 when, as part of the construction of the Panama Canal, an area was flooded creating Gatun Lake which surrounds BCI (see Figure A.1). BCI was declared a nature preserve in 1923, after which human habitation of the island was severely limited, restricted mainly to scientists and workers manning the Smithsonian Institution’s Tropical Research Institute. The forest on BCI combines old and new growth areas, as portions of the forest were cut before it became a protected area. The newer growth areas, however, are completely re-forested and undisturbed for at least 70 years (Smithsonian Tropical Research Institute, 2000). Thus, plant and animal populations on BCI are far less affected by human intervention than populations in most other areas.

Sitting relatively close to the equator, BCI’s temperature does not vary much during the year (Paton, 2001), nor does the amount of daylight. The island’s main annual climatic variation is its distinct wet and dry seasons. The wet season features short periods of heavy rain, mostly in the early afternoon. Data tracking amounts of rainfall on the Island has been kept since 1929, and monthly distributions of rainfall show the wet and dry seasons clearly, as in Figure A.2. Each month is shown with a box bounded by the upper quartile
and lower quartile, with the median shown as a line in the box. The notches represent a 95% confidence interval around the median. The "whiskers" go out to the extreme values, excepting outliers defined as being more than 1.5 times the inter-quartile range away from the median. Any outliers are shown as lines above or below the whiskers. The distributions for January through April are much lower than the median monthly value and overlap very little with the distributions for the other months. Rainfall increases in May and stays at roughly the same level through September. The distribution increases again in October and is roughly the same in November, albeit with somewhat greater variability indicated by the wider spread between the top and bottom quartiles, compared to the other months. Rain then begins to fall in December, but the December rainfall amounts also show a great deal of spread. At a finer level of detail, researchers examining daily rainfall amounts have concluded that the daily rains usually begin at the end of April and end in late December (Leigh, 1982).

As there seems to be some degree of predictability in rainfall patterns throughout the year, it is reasonable to expect animal and plant survival and reproductive strategies that take this variability into account. Furthermore, many researchers connect the period of highest rains with higher animal mortality (Milton, 1990; Wright et al., 1999). This points to the potential existence of seasonal patterns in howler population parameters, such as the population being lower in the rainy season due to increased mortality from infections during this time. The age distribution could also be somewhat different during the rainy season if higher mortality from infections is concentrated among the very young and very old. In order to investigate seasonal changes in the howler monkey data, three seasons will be defined as the dry season from January through April, the early rainy season from May through August, and the late rainy season from September through December. Time series and distribution data for these three rainfall seasons are shown in Figure A.3, and howler monkey population data will be investigated by these seasons as well.

While the rainfall seasons are quite dependable over each twelve months, other aspects of rainfall change from year to year. Large swings in the amount of annual rainfall over time are evident in the annual time series plot in Figure A.4. The El Niño Southern Oscillation is thought to contribute to a two year cycle in rainfall, with dry years often followed by wet years. As intra-annual variation is less predictable than seasonal variation, researchers tend to focus on the potential indirect effects of annual rainfall fluctuations on animal populations rather than direct timing strategies on the part of the animals. The
paths of indirect effects include rainfall affecting fruit production, which may affect animal populations (Wright et al., 1999), and rainfall affecting parasite populations that may also affect animal populations (Milton, 1996). Thus, there is reason to expect variation in animal populations from year to year, which may have long-term effects, or may have effects that disappear the following year.

2.2 Howler Monkey Data

2.2.1 Introduction

With that brief orientation to howler habitat on BCI, we now turn attention to the howler monkeys of BCI themselves. Howler monkeys have a geographical range from southern Mexico to northern Argentina and there are many species of Howler. The focus here is on the mantled howler monkeys of BCI (Alouatta palliata), see Figure A.5. They are vegetarians, supplementing a diet of new leaves with fruits and flowers. While they spend most of their time eating leaves, fruits are thought to be very important dietary supplements, providing the additional nutritional energy necessary for reproduction and fighting off disease (Milton, 1982). The basic unit of howler monkey social organization is the troop. All evidence on howler troop organization finds that troops tend to have a small number of adult males, a larger number of adult females, and several juveniles and infants (Chapman and Balcomb, 1998). Some specific developmental aspects of A. palliata make it possible to gather reliable data on age (within broad categories) and adult sex by sight. Specifically, mothers carry their infants under themselves almost constantly until the infants are approximately two months old. For the next four to six months of the infant’s life, the mother will often carry it on her back, making these age classes more readily identifiable (Milton, personal communication). Once the carrying ends, infants stay close to the mother for another six to eight months, after which the juvenile stage begins and young monkeys become largely independent of their mothers. The sex and reproductive status of adults can be discerned by sight, as there is considerable difference in adult body size between males and females and males reaching adulthood have a white scrotal area (Crockett and Eisenberg, 1986; Milton, 1998). Most adult males weigh somewhere in the range of 10 to 20 pounds, with a body length between 20 to 27 inches. Females will generally be several pounds lighter and a few inches smaller through the body. Tail length varies from 20 to
25 inches (Rowe, 1996). The biggest potential problem in the classification of monkeys by age and sex is that older male juveniles can be classified as adult females. Juvenile males' testes descend only at puberty, but in the period before the testes are visible, an older male juvenile can be as large as an adult female and thus can be misclassified.

A troop is loyal to a specific home range area and a new troop cannot generally be established in another troop's home range. Troop home ranges do overlap at times considerably (Mittermeier, 1973; Milton, 1998). Members of a troop spend almost all of their time together in fairly close proximity. Several different attempts to take a census of all the troops on the island have been made in the last thirty years and indicate that monkeys exist in every part of the island and that the total number of troops has been fairly stable over time (Milton, 1982). Thus, while troops sometimes split into two smaller troops, or disappear altogether, it is a working assumption throughout the rest of this paper that the island is covered with monkey troops and their home ranges and the number of troops is roughly constant. Beyond the troop census efforts, there are other reasons to support the theory of a roughly stable numbers of troops on the island. If the number of troops was growing over time, there would be much more fighting between troops as fixed home-range sizes increasingly overlapped, and such has not been observed (Milton, personal communication). The idea that the number of troops might be decreasing over time is not supported either, as there have been no significant changes in the island's environment which would degrade the quality of the habitat, nor were any new diseases noted in the monkey population, over the time of data collection. Working with the assumption that the population of troops is approximately constant, population dynamics for the population of monkeys can be described by describing changes in the averages and variation of troops.

A few other points must be established to support the proposition that howler population dynamics can be fruitfully examined at the troop level. These points involve the possibility that there is a significant population of monkeys living outside of troops. While there is evidence that some young male howler monkeys leave their troops around the age of sexual maturity, they will most likely attempt to become members of another troop. This process often results in the death of the young male,\(^1\) less often results in his successful integration with a new troop. Either way, the young males do not become loners.

\(^1\)Deaths rarely occur due to direct conflict with other males, but more often are involved with the increased stress of conflict with the new troop that makes the animal more vulnerable to parasites, infections and other health threats.
living away from any troop. Another potential extra-troop population dynamic would be monkeys moving onto or off of the island. Here again, the evidence does not support such a proposition. Over a two decade period, there were only a few reports of howler monkeys swimming (Milton, 1982) and they did not swim away from the island but rather near it. In addition, preliminary analyses of genetic information on this population shows a very high degree of relatedness among members (Milton, personal communication), arguing against the idea that there are howler monkeys emigrating to BCI from the mainland or other islands.

As there does not seem to be much immigration or emigration in the population, fertility and mortality will be the main intermediate determinants of population dynamics, with the ultimate determinants being whatever forces shape fertility and mortality in both the short and long term. In understanding howler monkey mortality on BCI, the specific circumstances of the island help narrow down the number of factors that must be considered. Large predators are absent (Leigh and Wright, 1990) and animal poaching, once rare, is now non-existent (Glanz, 1990).2 Evidence indicates that ectoparasites play an important role in causing howler monkey deaths. Specifically, howler monkeys on BCI are often infected with bot flies (Alouattamyia baeri). Bot fly larvae penetrate the host’s skin, feed on the host as they develop, then emerge through the skin in order to drop to the ground and pupate. Bot flies can cause howler deaths by indirect means, creating wounds that can become infected, but evidence points to a more common direct effect as bot fly larvae draw down an animal’s energy reserves during times of scarce food availability (Milton, 1996). Other reported sources of mortality are old age, falls from trees (by infants not able to cling to the mother or by older monkeys during fights or when weakened by old age or illness), and parasites other than bot flies (Milton, 1982). There was also a reported population crash in the 1950s caused by yellow fever (Collias and Southwick, 1952) but no reports of yellow fever have occurred since then.

Turning to fertility, Milton reports an average inter-birth interval for howlers on BCI of 18 months, based on long-term study of a particular troop (1982). This interval consists of the time it takes a receptive mature female to become pregnant, gestate and give birth, followed by the time it takes her to begin to cycle again (becoming susceptible to pregnancy). This period of post-birth insusceptibility is likely caused by the action of

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2Even when poaching was occurring, howlers were never a target (Milton, personal communication)
nursing the infant and will last roughly until the infant is weaned or dies. As Milton finds no evidence that female reproductive capacity goes unused (i.e., no females are shut out of reproduction by other females and adults do not seem to exhibit efforts at preventing or postponing copulation when a female is in estrus), and the gestation period is fairly constant, variability in the inter-birth interval is determined more by infant mortality than by changing fertility. Thus, any changes in the number of infants in the population will be determined by the infant mortality conditions of the present (determining chances of observing a recently born infant) and the near past (determining how many infants were recently born). More information on inter-birth intervals is available for other populations of the same species. For a population in Costa Rica, researchers observed intervals of 18 to 24 months, with the average interval when the infant survived of 22 months. In the same study, they found that only 55% of infants survived past one year, with survivorship heavily skewed towards females to survive (Clarke and Glander, 1984). The Costa Rican habitat is quite different, however, in its ecology and the fact that it is not bounded, as BCI is by water, so there may be significant differences in the two populations. While there was no evidence of birth seasonality in some populations of Costa Rican howlers (Clarke and Glander, 1984), other populations did show a pattern, with fewer births in the rainy season (Di Bitetti and Janson, 2000).

### 2.2.2 Data Collection Methods

The data analyzed in this paper come from the howler monkey troop counts recorded by Dr. Katharine Milton of the University of California at Berkeley. She began her troop counts in 1974 with a few howler troops and has counted a different number of troops at various time intervals since then. Every calendar year in between is represented, with the exception of 1984. Table B.1 indicates the numbers of troops observed in each month from 1974 through 2001. There is a great deal of variability in the dataset in terms of time intervals and number of troops observed. Following Dr. Milton’s ability to be away from the University, more observations were made during the summer months and near the winter break than between those times, and some periods have many troops observed, while others have just one. Many of the months featuring one troop observation are for one specific troop that Dr. Milton was studying very closely, henceforth referred to as Troop V. This will be important to keep in mind for the data analysis, as it means that observations
from one period to the next cannot all be thought of as independent from each other or as time series random samples. In subsequent analyses, results will be reported sometimes including and sometimes excluding Troop V.\textsuperscript{3} Table B.1 also has columns summing months into the three rainfall seasons discussed previously. January through April is designated as the “Dry” season, May through August is the “Early Rainy” season, and September through December is the “Late Rainy” season.

During the months with several troop observations, Dr. Milton walked some part of the trail system of BCI (whether or not this constitutes a “random sample” will be discussed in subsequent sections). After encountering a troop, she attempted to count all troop members and to note their ages within the broad categories of infant (from 0 to 12 months), juvenile (from 12 months to 5 years) and adult (more than 5 years).\textsuperscript{4} The age ranges for each stage are approximate, as rates of physical development may vary. Among adults, sex was noted as well. As mentioned, many of those samples are known to contain one specific troop, Troop V. It is likely that other troops were observed at multiple time points as well.

\textbf{2.2.3 Descriptive Charts and Statistics}

In this section, exploratory data analysis techniques are used to examine data on the size, age composition, adult sex ratio and fertility of howler monkey troops. As our main interest is change over time, these aspects will be examined for long-term and seasonal variation, but also pooled together as one distribution without regard to year or season.

We begin with a graph of observed troop sizes over time, shown in Figure A.6. As there were occasionally multiple troops of the same size observed at a given month, the size of the point plotted is in proportion to the number of observations represented at any time and size combination. Troop V is marked with a different character (“\texttimes”) to distinguish it from the other observations. A solid line follows the median observed troop size at each month during which an observation was made. Examination of this graph leads to several observations. No obvious time trend emerges; the median observation at each time point

\textsuperscript{3}Descriptive statistics will be for Troop V and the sample ex-Troop V. Some statistical models will be more logically fit to the dataset excluding Troop V, as will be discussed in the next chapter.

\textsuperscript{4}Sub-categories within juvenile and infant were noted as well, although they are less reliable than the broader categories. One exception to this is the sub-category of “Infant I,” 0-2 months, which will be used to examine troop fertility. As the infants switch from being carried under the mother to being carried on top of the mother at about two months, this sub-category is fairly reliable.
seems to stay fairly close to the overall median of 19. There may still be a time trend, but it is not clearly visible on this simple graph. There is a great deal of overlap in the distribution of troop sizes observed from year to year and even from decade to decade. The observations of Troop V size do not stray from the range of the other troops, although they do occupy the lower range of the distribution fairly consistently after 1989. Finally, the three observations of troop sizes greater than 40 (in 1982 and 1987) look to be out of the range of the rest of the observations. A verification of Dr. Milton’s original field notes on these large troops does support the accuracy of the count. The square root transformation is helpful in stabilizing the variance of observations and the transformed data are presented in Figure A.7. This graph is also simpler as Troop V and non-Troop V observations are not differentiated and plot points are not sized relative to the number of observations. As in the previous figure, no overall increasing or decreasing time trend is visible.

Seasonal variation, or rather the lack of it, can be seen in Figure A.8, showing box plots of troop observations by season, both for the Troop V observations and for the other troops. Because each season has a different number of observations and not all years have data for all seasons, the 95% confidence interval notches around the season median values are helpful for comparing across seasons. For both the ex-Troop V and Troop V observations, all of the confidence intervals overlap so there is no significant difference found in troop size from season to season. We may note, however, that none of the very large troops are observed in the late rainy season, although this may be related to the fact that fewer troops were observed in this season than in the others.

Given the lack of obvious trend in the graphs over time and season, it does not seem unreasonable to examine the data as representing one distribution without regard to year or season, as in the summary statistics in Table B.2 and the histograms in Figure A.9. The ex-Troop V histogram shows a prominent right-hand tail caused by the three observations of over 40 animals. There seems to be a strong tendency for BCI troops to be in the range of 17 to 20 monkeys.

Having looked at the data on troop size, we move within the troop to examine the age distribution among the broad categories of adults, juveniles and infants. Using the

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5For the rainfall box plots in Figure A.2, each month represents the same number of observations because each month was observed in each year, so that comparing month to month distributions is an “apples to apples” comparison. For the troop observations, however, the seasons with more observations have a greater chance of coming up with values at the extremes, even though the population distributions may be exactly the same. Therefore, the 95% confidence interval notches in Figure A.8 are necessary for comparison as they take the number of observations into account when computing the interval.
square root transformation again, Figure A.10 shows the square root of age group counts over time. There is no obvious time trend in the medians of the age group sizes, nor does the distribution of age group sizes appear to have changed noticeably over time. All of the points and the median line seem to bounce around the overall median for each age group. Age group observations are grouped by season in Figure A.11. The distribution of adults in a troop looks lower in the late rainy season for adults in the ex-Troop V group, but not for Troop V.  

There seems to be much more that is similar in the distributions of age group at each season, however, than there is to differentiate them. We will hold off looking at the pooled age group distributions for a moment.

The adult sex ratio (number of adult females per adult male in a troop) is another important aspect of troop organization. Graphs showing this ratio for each troop, over time and grouped into seasonal box plots, appear in Figure A.12. Again, the time series plot seems to show values bouncing around the median line with no overall trend or even extended period where the monthly median is above or below the overall median. Thus, there seems to be a strong tendency for the adult sex ratio to be from one to four females per male. As the sex ratio of howlers at birth is roughly one to one (Glander, 1980), this highly skewed adult sex ratio suggests a much higher male mortality in early life compared to females (Milton, 1982). Looking at the seasonal distributions of sex ratio in Figure A.12, visual inspection does not produce much to differentiate one seasonal distribution from another and the confidence intervals around the median ratios all overlap, indicating no significant difference across seasons.

While we cannot observe fertility directly in these data, we use the ratio of infants in age class I (less than two months of age) to adult females and the ratio of all infants to adult females as indicators of fertility.  

Graphs of the number of infant I’s and the ratios

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6. The non-overlapping notches between ex-Troop V adults in late rainy season, compared to the dry and early rainy seasons, indicate a significant difference in the location of distributions at the 5% level. However, the box plot analysis of seasons could be misleading. The reason is that not all years have observations for all seasons and not all seasons are observed in all years. Thus, the box plots risks mistaking seasonal differences for annual ones. A multivariate model with year and season included as variables is better able to distinguish effects, or indicate when effects are not able to be partitioned into year and season. Such a model will be discussed and estimated in subsequent chapters. One other issue with drawing conclusions from the notches in box plots is that the 95% confidence level is only valid for two-way comparison. Multiple comparisons will have a lower than 95% confidence level.

7. As discussed earlier the number of infant I’s and infants observed is determined by mortality as well as fertility, and there is no data for this population estimating how many infants die at birth or within the first two months. The ratio of infants to adults or immatures (infants and juveniles) is often used in observational studies to indicate approximate replacement rates, rather than fertility. (Zucker and Clarke 2003; Chapman and Balcomb, 1998)
of infant I’s and all infants to adult females are shown in Figures A.13 and A.14. Looking at these graphs, it seems as though many troops are observed with no newborn monkeys and that, comparing median lines for the count of infant I’s and the ratio, they look almost the same, indicating little change in the number of adult females relative to the number of infant I’s. The only pair of non-overlapping confidence notches in Figure A.14 is in the ratio of all infants to adult females, ex-Troop V. The median for the dry season looks significantly lower than the median for the late rainy season.

Figures A.15 and A.16 show histograms for the age and sex group sizes, as well as the sex ratio and the crude fertility indicator ratios, allowing examination of the distribution without regard to year or season. The age group distributions support previous researchers’ conclusions that troops are organized with a large number of adults, a smaller number of infants, and only a few juveniles (Crockett and Eisenberg, 1986; Chapman and Balcomb, 1998). In fact, the modal category of juveniles for the ex-Troop V group is zero. The distributions all appear somewhat skewed. Observed distributions are described numerically in Table B.2.

Finally, Figure A.17 shows the relationships among troop size and the age and sex groups that contribute to it. A local regression line is fit to each plot, to show the general trend but to allow that trend to be nonlinear if the data so dictate. Most of the relationships with troop size seem fairly linear, if showing differing degrees of dispersion around the regression line. An exception is the infant I group, where there is a suggestion that a high number of infant I’s is associated with the middle of the troop range distribution, and more clearly with the middle of the range of potential mothers, rather than with larger troops or more mothers. Caution is warranted, however, as this association is based on a small number of high-leverage observations with more than three infant I’s. For the older infants, however, we see more of the expected relationship, along the lines of “more moms, more infants.” In general, though, all of these relatively linear relationships suggest that the age and sex distribution within troops is fairly constant, no matter the size of the troop. This proposition will be examined further in the statistical analyses.

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8The lines are fit using the S-plus function loess() with a span of 0.5 (Venables and Ripley, 1999). This graph does show the observations of Troop V, and may have other replicated troops over short time periods, so there may be more uncertainty about these lines than under the strict independence assumption.
2.3 Summary

Exploratory techniques have given general impressions about the size and organization of howler monkey troops on Barro Colorado Island. Specifically, average troop size and composition (by age and sex) seem fairly stable, albeit with some variability around a central tendency, both over time and by season. This fairly stable age and sex composition also implies fairly stable rates of fertility and mortality, at least over the long term. Thus, if any systematic variation is to be supported, we will need to ask more specific questions of these data than the general ones we can ask of a visual inspection of a graph. Using statistical principles, we can add quantities to the graphs that indicate uncertainties. Through these estimates of uncertainty we can then draw formal inferences about the parameters of interest.
Chapter 3

Some Theory for the Analyses

3.1 Introduction

There are many ways to study animal populations and many different techniques to gather data about them. Ideally, the study should begin with a specific research question, and the data collection is then designed with that specific question in mind (National Research Council, 1981; Williams et al., 2002). This might involve a pre-sample, a small-scale observational study so that some understanding of the population can be gained, which would then allow the researcher to decide on a sampling or study technique. There are many possible techniques. Transect censuses, where a researcher records all of the animals sighted along a transect through a habitat, are used for some studies, as are capture-recapture samples, catch-effort methods, quadrat censuses, and long-term study of specific groups. For studies in which the research question is one of change over time, one method would be selected and repeated at regular intervals, so that the data could be treated as a regular time series. Time series techniques could then be used to estimate seasonality and trend.

The ideal time series study, however, is often not practical with animal populations where data must be gathered by a highly skilled observer in the field, and the field in question is a remote animal habitat. Such is the case with the data in question here. This data set represents an irregular time series, as observations were made when they could be made and for as long as they could be made, so time intervals are not regular. Beyond the issue of the regular time intervals, many time series techniques are very data-intensive, requiring many data points. This is often impractical for animal populations when data must be collected by individual researchers.
Designing a sampling procedure is also quite a challenge in many animal studies. While the set of troops observed in a given month constitute a sample of all troops on the island at that time, there was no formal randomizing mechanism in place for each of those samples. The issue of sample size at each month is complicated as well. While Dr. Milton attempted to observe at least five troops in each sample, the observation process is very complex and time did not always permit the observation of five troops. Thus, the nature of the data prevents us from taking a design-based approach to analysis. Instead, a model-based approach can be used, but will require defending more assumptions that we would otherwise wish to make.

One assumption was already discussed in Chapter 2 – that the number of troops on the island was relatively stable, making it reasonable to study population parameters by modeling them at the troop level. In this chapter, troop-level models for the parameters in question will be presented, along with how to fit those models to the data, and what assumptions underly the ability to interpret the fitted results. The questions we want to ask about these data are about change over time, so each model will describe some aspect of the population as it varies over time.

### 3.2 A Poisson Model of Troop Size

We saw in Chapter 2 that, over time, median troop sizes tended to bounce around the overall median of 19. The question we want to ask is whether or not troop sizes ever strayed in any material way from this central tendency. At the same time, while seasonal variation is not our main concern, we need to include it in the model because it may cause short-term variation that must be separated from the long-term variation of interest. In other words, as we have reason to believe that troop sizes may be larger in some seasons on a regular basis, we want to account for this source of variation before estimating the change

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1 Discussing certain limitations of the data brings to mind the question of what the “perfect” study would be. Imagining a sampling procedure to address the question of whether population parameters are changing within and across years, one would want to draw a sample with some randomizing mechanism, such as dividing the island into equal-sized areas and sending observers to a random draw of areas. This process would be repeated at regular time intervals in each year in each season. If estimating seasonality was not important to the study, observations could just be made at the same time every year, instead of year and season. The number of troop observations necessary to achieve a certain level of statistical power could be calculated and, although sending observers to a particular area would not guarantee a troop observation at each area, some estimate of how many areas would have to be sampled to guarantee a certain number of troop observations could be made. Such a study, however, would be require extensive time and resources, as well as many trained observers.
in troop size from year to year. This amounts to a model in which both season and year are “predictors” of the “outcome” of troop size.

One of the most commonly used models connecting predictor variables with an outcome is the normal regression model. This model assumes that the outcome variable is continuous and normally distributed and that the variance of the outcome is constant relative to the predictors (homoskedasticity). Count data such as troop size is not continuous or normally distributed, although a transformation could help it to appear more normal. A larger issue with employing the normal model is the assumption of homoskedasticity. With the troop size data, one can imagine that an impact increasing average troop size might also increase the variance as well.\(^2\) Such a relationship seems to exist in Figure A.18, a plot of mean versus variance for the troop sizes observed at each year-season combination.

As a more appropriate alternative to the normal model, then, we can model the troop size data as coming from a Poisson distribution and use a generalized linear model to relate the predictors to the outcome. Following McCullagh and Nelder’s specification (1989), the generalized linear model has three parts. The random component specifies the distribution of the outcome. The systematic component specifies a linear model of predictors. Finally a link function connects the random outcome component to the systematic predictor component.

For the Poisson version, the random component posits troop sizes as being Poisson distributed. The probability density function for the Poisson distribution, giving the probability that a random variable \(Y\) with parameter \(\lambda\) takes the values \(y = 0, 1, 2, \ldots\), is as follows:

\[
f_{Po}(y; \lambda) = \frac{e^{-\lambda} \lambda^y}{y!}
\]

for \(\lambda > 0\). The mean and variance of this distribution are

\[
E\{Y\} = \text{var}\{Y\} = \lambda.
\]

Thus, any factor that affects the mean will also affect the variance.\(^3\)

\(^2\)One reason this might occur was mentioned in the previous chapter. Differing numbers of troops were drawn in different years and seasons. Thus, time periods with more observations will have a higher chance of having larger troops that increase both the mean and variance of observed troop sizes for that time period.

\(^3\)The random component of the model also involves an assumption that the observations are independent. For the whole dataset, we already know of one violation of the assumption: the consistent inclusion of Troop V in the sample. To avoid this problem, we will fit the model using the ex-Troop V data. There is still some pseudo-replication in the data if the same troops are counted at repeated times, but removing Troop V removes at least the problem that is known.
The systematic component is an unbalanced two-way layout that addresses the annual variation question. The model is expressed as

$$\eta_{ij} = \mu + \alpha_i + \beta_j$$

where $i$ indexes season and $j$ indexes year.\(^4\) The $\mu$ parameter represents the central tendency for troop size, while the $\alpha_i$ and $\beta_j$ are (fixed) main effects for season and year, respectively. We include no interactions between year and season in the model because we posit the seasonal effects as purely additive, and any systematic variation beyond the seasonal main effect will be considered part of the yearly variation. This model can be read as hypothesizing an underlying central tendency for troop size ($\mu$), with some variation from season to season (the $\alpha$'s) and some variation from year to year (the $\beta$'s). To obtain parameters that are meaningful in this way, we apply constraints to the estimation of the parameters. As is common with fixed effects analysis of variance models, we use the constraints that $\sum_{i=1}^{3} \alpha_i = 0$ and $\sum_{j=1974}^{2001} \beta_j = 0$.

Finally, the link function connecting the outcome and predictors is the logarithm:

$$\log \lambda_{ij} = \eta_{ij}$$

Taking these three parts together amounts to modeling the logarithm of the mean as a linear function of year and seasonal effects. While additive in $\eta$, the effects will be multiplicative in $\lambda$, so for example the average troop size in season $i$ is expected to be larger than the overall mean by a factor of $e^{\alpha_i}$.

Parameters are estimated using the maximum likelihood criterion which involves finding parameters that maximize the computed likelihood of observing what you observed in the data. Assuming independence of observations, the likelihood function $L(\lambda_{ij})$ is the product of probabilities, given by the Poisson probability density function, of the observed outcomes: $L(\lambda_{ij}) = \prod_{ijk} f_{Po}(y_{ijk}; \lambda_{ij})$.\(^5\) In practice, the log likelihood is the object of maximization and in the Poisson case, this reduces to $\log L(\lambda_{ij}) = \sum_{ijk}(y_{ijk}, \log \lambda_{ij} - \lambda_{ij})$ (McCullagh and Nelder, 1989). The values of $\mu$, $\alpha_i$ and the $\beta_j$ are found that maximize this function. This is done numerically using the method of iteratively reweighted least squares (Venables and Ripley, 1999).

\(^4\) $i = \{1, 2, 3\}, j = \{1974, 1975, 1977, ..., 1983, 1985, ..., 2001\}$. There are no observations for 1976 or 1984 in the ex-Troop V dataset that will be used to fit the model.

\(^5\) $k$ indexes the $k$-th troop observed in season $i$ in year $j$, $k = \{1, ..., R_{ij}\}$ where $R_{ij}$ is the number of troops observed in season $i$, year $j$. 


The importance of the model will be whether any of the year effects are significantly different from zero and whether or not the model written as above is a significantly better fit than a reduced model without the year parameters. The ability to judge a significant difference or not in the year or seasonal effects comes from the distributions of the parameters implied by the model. Under the model, the estimated parameters are asymptotically normally distributed with a variance estimated after the model is fit. Thus, for each parameter we can calculate the asymptotic p-value: the probability of observing the estimated parameter if it came from a normal distribution with mean zero and the estimated variance. If the p-value is small, we infer that the true parameter is not zero. If the probability is large, the data offer little evidence to support a claim that the year or season in question is different from the overall mean. The ability to judge whether the whole model, or a whole set of coefficients, provides a significantly better fit to the data than a simpler model comes through an analysis of deviance (ANODEV). In an ANODEV, we examine how much twice the log likelihood, or the deviance, changes from model to model. If the null model containing just the mean value has deviance $2\log L(\lambda_0)$ and a more complex model with $p$ additional parameters has deviance $2\log L(\lambda)$, then under the null hypothesis that the additional coefficients in the more complex model are all really zero, the difference $D = 2\log L(\lambda_0) - 2\log L(\lambda)$ is approximately $\chi^2$ distributed with $p$ degrees of freedom.\(^6\) Given that any additional parameters will reduce deviance or at least not increase it, the idea behind the analysis of deviance is to test whether the reduction of deviance from the addition of a group of parameters is “sufficiently large” (Stone, 1996). Sufficiently large reductions in deviance are unlikely to have occurred by chance under the reduced model. The procedure is the same for any set of nested models, thus the same idea applies in evaluating the addition of groups of terms as in evaluating the whole model against the null model.

This process can be done sequentially, analyzing the deviance reduced by just the seasonal coefficients, or just the year coefficients, although the nature of the data offer some problems in separating the difference between year and season effects. As we do not have a complete factorial design with respect to year and season, the deviance reduction of year or season effects will depend on the order in which the test is performed. A conservative approach in terms of estimating year effects would be to fit the seasonal effects first, and leave any remaining variation to be explained by the year.\(^7\) That will be the main approach

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\(^6\)This is asymptotically true for large samples.

\(^7\)This is conservative with respect to year in that it sets the bar higher for year effects to be significant
here, although any differences in conclusions with respect to sequence will be discussed.

3.3 Binomial Models of Troop Age and Sex Composition

To model troop composition, as defined by the proportion of the troop in three age groups (infants, juveniles, and adults) and the proportion of adults in a troop that is male or female, we will use binomial models. These models are similar to the troop size model in that they posit a central tendency that may vary systematically across seasons and from year to year. Also, while Figure A.17 suggests little variation of these proportions by troop size, we will include troop size in the model to examine more closely whether there is any association between troop size and composition.

To review the binomial case, if independent draws are taken \( n \) times from a population with a probability of success \( \pi \) on each trial, \( 0 \leq \pi \leq 1 \), the number of successes \( Y \) is a random variable with the binomial distribution with parameters \( \pi \) and \( n \). This relates to the monkey population age distribution case if we think of the proportion of a particular group on the island as \( \pi \). We treat each sample with \( n \) monkeys in it as being made up of \( n \) independent draws having \( y \) members of the group of interest. Each troop’s proportion may be viewed as an estimate of the island’s proportion at a given time. We want to know if the proportion is varying significantly over time, while controlling for the fact that it may vary with troop size as well. The same idea applies to the adult sex ratio if we think of draws from the adult population only. We want to estimate the effect of year and season on the group proportion, just as we wanted to estimate it with respect to troop size, including a variable for troop size to investigate any possible relationships.

Using McCullagh and Nelder’s (1989) generalized linear model specification once again, the random component for the binomial models is the binomial distribution of the group in question, with probability density function

\[
 f_B(y; \pi) = \binom{n}{y} \pi^y (1 - \pi)^{n-y}.
\]

The systematic component is a linear model similar to that described for the troop size

in the inference procedures. It attributes to season any reduction of deviance for which it is not entirely clear whether the change is a seasonal or yearly one, and leaves as the year portion only that reduction of deviance that can be unambiguously attributed to year.
model, but with the addition of a linear and quadratic term for troop size:

\[ \theta_{ijk} = \mu + \alpha_i + \beta_j + \gamma y_{ijk} + \eta y_{ijk}^2 \]

where \( i \) indexes season, \( j \) indexes year and \( k \) indexes the \( k \)-th troop observed in season \( i \) in year \( j \).\(^8\) The parameters \( \mu, \alpha_i, \beta_j \) are again central tendency, season main (fixed) effects and year main (fixed) effects, \( \gamma \) is a linear coefficient of troop size on troop composition and \( \eta \) is a quadratic coefficient of troop size on troop composition. The reason for including the quadratic term as well as a linear term is to allow for the possibility of a curvilinear relationship between troop composition and troop size.\(^9\) Finally, the link between the random and systematic components is the logit function:

\[ \pi_{ijk} = \frac{e^{\theta_{ijk}}}{1 + e^{\theta_{ijk}}} \]

Here again, parameters satisfying the maximum likelihood criterion are found using the iteratively reweighted least squares algorithm.\(^10\) As with the troop size model, the estimated coefficients are asymptotically normally distributed and the changes in deviance are asymptotically chi-square distributed. The interpretation of the coefficients here is somewhat different than for the Poisson model. The exponentiated coefficients are still a multiplicative factor, but they multiply the odds of a random draw selecting a member of the group in question. This is roughly analogous to a multiplicative factor on group proportion. The questions we wish to ask about the effects and the inferential techniques we can use to address them are the same as for the troop size model.

### 3.4 A Binomial Model of Fertility

As our crude fertility indicator is a ratio, Infant I’s per adult females, we can use the binomial model again, only the population is now adult females and we consider the

\[ y_{ijk} \]

\[ R_{ij} \]

\( R_{ij} \) is the number of troops observed in season \( i \), year \( j \).

\(^8\) This could occur with the proportion infants if troops could be too large or too small to sustain a large number of infants. Smaller troops might not be able to command enough prime fruit trees to provide optimal nutrition for reproduction. Very large troops, on the other hand, might experience relatively more conflict among adults, which could mean higher infant mortality if nursing females are in conflict.

\(^9\) Assuming independence, the likelihood of observing the \( y_{ijk} \) that we observed is the product of all the

\[ f_B(y_{ijk}; \theta_{ijk}) : L(\pi) = \prod_{ijk} f_B(y_{ijk}; \pi_{ijk}) \]
“draw” from the population a success if the adult female has an infant in age class I. All of the model estimation procedures and hypothesis testing procedures we use are the same as those described in the previous section, as the questions we have are the same: controlling for seasonal and troop size effects, is there evidence that the fertility indicator changes from year to year at all?

We have some outside indications of what central tendency to expect for this ratio. Previous research has estimated the average interbirth interval in this monkey population to be approximately 18 months. As the infant I stage is approximately two months, we expect to see the proportion of adult females in a troop with an infant I of roughly $2/18 = .111$, if there is an even or random time distribution of births. Higher infant mortality than usual should increase the observed proportion as the interbirth interval shrinks.\textsuperscript{11} In fact, we do see a mean of 0.12 and median of 0.11 in the descriptive statistics in Table B.2. Fitting the binomial model allows us to investigate whether or not this central tendency changes from year to year, having made some assumptions.

\textsuperscript{11}If the increased infant mortality occurs after the infant is out of the infant I stage, i.e. in the infant II or III stage, the effect will be unambiguous. If the increased infant mortality is in the infant I stage, however, the proportion could decrease or increase.
Chapter 4

Results

4.1 Troop Size

The results of analysis of deviance for the fitted two-way layout Poisson model for troop size\(^1\) are given in Table B.3 and shown in Figure A.19. The picture of the fitted model versus the observations in the top of Figure A.19 shows some variation in troop size from year to year. Furthermore, the effects of season and year estimated by the model show some variability as well. Before interpreting the effects, however, we need to use inferential techniques to determine if the effects are worth discussing. This is a question of whether or not the variation (by seasons and years) is large enough to indicate that the average troop size on the island has probably changed, versus the alternative (null) hypothesis that the observed variation may have arisen due to the random chance of observing a group of relatively larger or smaller troops when the overall average size has not really changed at all. Analysis of deviance helps discern between these two alternatives.

The first test in Table B.3 is whether the reduction in deviance from the null model (where average troop size is modeled to be the same as the observed overall mean for all seasons and all years) to the model with year and seasonal effects is large enough to reject the null model. As mentioned, if the model assumptions of independence and Poisson distribution are valid, the reduction in deviance is asymptotically chi-square distributed. The p-value for the reduction in deviance under the null model is virtually zero,\(^2\) so we

\(^1\)Fitting was performed in S-plus using the function \texttt{glm()}, for the Poisson family with link log (Venables and Ripley, 1999).

\(^2\)This indicates that the probability of observing the changes in average troop size across year and season that we observed due only to random variability and not systematic effects is very, very small.
can reject the null model in which all of the year and seasonal effects are really zero. The next two tests in Table B.3 test whether the reduction in deviance from adding a group of effects is sufficiently large to argue for their inclusion in the model. More specifically, the null hypothesis tested in these tables is that a whole set of coefficients (all the $\alpha$’s or all the $\beta$’s) are equal to zero, versus the alternative hypothesis that at least one coefficient in the set is not zero. As discussed in the previous chapter, because of the design matrix of the model, the results will be different depending on which group of coefficients is fit first, so both possibilities are shown. In both sequences, the tests for both sets of coefficients produce p-values lower than the 5% significance level. In the hypothesis testing framework, then, the null hypothesis is rejected and we conclude that there is evidence of a seasonal effect in troop size and of variation in mean troop size from year to year.

With evidence from the inferential techniques that the effects probably did not arise by chance, we can take a look at the estimated effects in the bottom graphs in Figure A.19. All estimated effects are shown exponentiated (i.e. $e^\alpha$ and $e^\beta$ are graphed), with confidence bands to indicate uncertainty. These exponentiated effects can be interpreted as multiplicative factors, relative to the overall mean value, for that season or year. The seasonal effects are graphed in boxes, where the middle is the estimated effect and the top and bottom of the box are plus or minus two standard errors. Given that the effects are asymptotically normally distributed under the model, this corresponds roughly to a 95% confidence band around the effects. Thus, the model indicates that troop sizes tend to be somewhat lower in the late rainy season. This is consistent with other data showing highest mortality in the late rainy season (Milton, 1996).\footnote{Higher mortality in the late rainy season is connected with higher rates of infections and, more importantly, with the lack of fruit during this season. Lacking the higher quality nutrition from fruit, animals are more susceptible to parasites and other threats to their health (Milton, 1982; Milton, 1996).}

Interestingly, this contrasts with the lack of seasonal difference shown in the box plots in Figure A.8. Thus, the multivariate model with year and season detects an effect not clear from the bivariate comparison of season and troop size. Moving to the plot of year effects, the same approximate 95% confidence interval that was represented by boxes for seasons is now represented by dotted lines above and below the solid line following the estimated effects for each year. Looking at the years in which the confidence band does not include 1.0, it seems as though there are peaks in 1977, 1982, 1987 and 1994.\footnote{The band around the peak in 2000 is just barely crossing the 1.0 level.} The only significant trough, where the confidence band lies below the 1.0 line, is in 1990. Generally, the estimated effects give an impression of a population...
that grows up to 10-20 percent above the long-term average, then decreases back down to 10-20 percent below the long-term average. While the 1977 to 1987 period shows two five-year cycles, the period between successive peaks changes after that. The return to central tendency suggests that there might be some density-dependent mechanism operating on the population.

In order to support these conclusions, we must be reasonably sure that the model’s assumptions are not violated, mainly that troop size has a Poisson distribution. The top left plot in Figure A.20 shows a quantile-quantile plot of the quantiles of the troop size data versus quantiles of the Poisson distribution with the same mean as the troop size data. Three comparison plots are shown, in which the y-axis quantiles are computed from pseudo-random draws from the Poisson distribution with the same mean as the troop data. The closer the points line up on the 45 degree lines, the closer the data match the theoretical Poisson distribution. The assumption of the Poisson distribution is not very strong at the high end, with the few large troops contributing to the lack of fit. Furthermore, we can observe in the summary statistics that the overall variance in troop observations is larger than the mean. This is referred to as over-dispersion. Further changes to the model could address this issue, however for modest amounts of over dispersion the effect should not be very large (McCullagh and Nelder, 1989). While there may be an issue with the distribution, the model residuals (observed minus fitted values) do not pose any problems, beyond the large residuals contributed by the three troops observed with over 40 animals. Figure A.21 shows residuals versus observed values and then grouped by season and year. There does not seem to be much patterning of the amount of variation in the residuals relative to the fitted values or the predictors.

4.2 Age and Sex Composition

The set of hypotheses and tests we are interested in for the age and sex composition models are the same as for troop size: do all of the coefficients, or some subset of coefficients provide a significantly better fit to the observed data than a simpler model of the mean value alone, and which if any of the individual year or season coefficients significantly different from zero? The analyses of deviance are shown for the adult, juvenile and infant models in Tables B.4, B.5 and B.6, respectively. The estimated effects and their confidence bands are
shown in Figures A.22, A.24 and A.26, respectively.\(^5\)

To begin with the model for troop proportion adult, while the likelihood ratio test rejects the null model when compared to the full model (with season, year, troop size and troop size squared), not all of the groups of terms are judged to reduce deviance enough to conclude that the coefficients are significantly different from zero. Looking at the sequential ANODEV, the addition of the group of seasonal coefficients is found to reduce deviance significantly, but adding the year coefficients after the seasonal ones is not judged to reduce deviance significantly. The coefficient of the troop size term, added after season and year, is judged to be significantly different from zero, but the quadratic term is not.\(^6\) As discussed in the previous chapter, the ANODEV analysis is sequential, attributing different amounts of deviance reduction to groups of coefficients depending upon what order they are assessed in. Although the tests are not reported here, the significant result for the linear troop size term is robust to changes in the sequence. Such is not the case for the year and seasonal effects. While the ANODEV shown in Table B.4 shows the seasonal effects to be reducing deviance significantly, if the year coefficients are evaluated first, they are found to reduce deviance significantly while the season effects are not. (This is true regardless of where the troop size effects are in the sequence.) Thus, for the effect on proportion adult, it is not possible to have much confidence in the data’s ability to distinguish between changes due to year versus season. There is not enough data and the effects themselves are too small. The fact that the chi-square distribution assumption is only approximate could also be contributing to a lack of power in distinguishing year and seasonal effects. Observing the fitted model and estimated effects graphed in Figure A.22, it seems that only the slight negative relationship between proportion adult and troop size comes through as a more or less reliable finding. Checking the residuals with plots in Figure A.23, there does not appear to be any pattern in variance with respect to the fitted values. With respect to the predictors, neither year nor season show a pattern, but there is some decrease in the variance of residuals as troop size increases.

The model for proportion juvenile finds the addition of the year effects reduces

\(^5\)Fitting was performed in S-plus using the function \texttt{glm()}, for the Binomial family with link logit (Venables and Ripley, 1999).

\(^6\)In fact, as long as it is added after the troop size linear term, the troop size quadratic term is never found to reduce deviance significantly for any of the age group models. This result is robust to changing the sequence in which the year or season groups of coefficients are added. Therefore, this term will not be discussed for any of the subsequent models and the graphs of estimated effects will only include the linear term for troop size.
deviance by a significant amount. No other groups of coefficients reduces deviance enough to allow us to reject a simpler model without them. This result is robust to changes in the sequence. The graphs of the fitted model in Figure A.24 show a steady upward trend of year effects since about 1987, although only that for 1999 has a 95% confidence band that does not contain 1.0. The residual plots in Figure A.25 show some patterns, such as less variation for small and large fitted values than those in the middle. Variation in residuals seems to decrease with troop size as well. These patterns may indicate that the model is not appropriate because of the small number of juveniles in most troops.

In the model for proportion infant, the sequential ANODEV in Table B.6 shows that both season effects and year effects are judged to reduce deviance significantly, as is the effect of troop size. Changing the sequence in which variables are entered into the model does not change this result for troop size, but for the season and year sets of coefficients, however, that is not the case. In any permutation other than the one shown in Table B.6, the set of coefficients entered first is judged significant, while the other is not. Thus, as was the case for the proportion adult model, there is not enough data nor are the effects large enough to distinguish between annual effects and recurring seasonal effects. The graphs of the fitted model in Figure A.26 show the year and seasonal effects mostly overlapping with the 1.0 level and show the increasing effect of troop size on proportion infant. The residuals in Figure A.27 look similar to those for the proportion adult model, with some decrease in the variance of residuals with respect to troop size, but no other patterns.

Finally, for the model for proportion female of the adults, the full model likelihood ratio test shown in Table B.7 is unable to reject the null hypothesis that a mean value model would be a better fit than a model with season, year and troop size effects. The sequential ANODEV results do find a significant positive relationship between adult proportion female and troop size, however, robust to changes in the sequence of the analysis. Residual analyses in Figure A.29 have some patterning with respect to troop size.

Taking all four of these models together, we get a general impression that average troop composition does change from year to year and season to season, but we do not have enough data to distinguish those effects precisely. There is also not enough data at this point to say whether there is a long-term trend for change in troop composition. Troop size does seem to effect troop composition somewhat as well, with the reason for larger troops being more juveniles and infants produced by the larger female to male ratio in bigger troops.
4.3 Fertility

The same season, year and troop size (linear and quadratic effect) model is fit to the ratio data of infant I per adult female, with fit shown graphically in Figure A.30. The tests are reported in Table B.8. Both the seasonal and year effects are judged to decrease deviance significantly, and this result is the same for all permutations of the order in which parameters are entered into the model. The fertility ratio is highest in the late rainy season, lowest in the dry season. The ratio was somewhat higher than average in 1977, 1983, 1988 and 1990 and lower than average in 1982, 1987, and 1995.

In addition, the result of troop size being judged not significant holds true regardless of parameter order. This is an interesting contrast to the outcome of the model of troop proportion infant, where “bigger troops, relatively more infants” was the only detectable relationship. This suggests that mortality may be performing a regulatory function in troops, turning sets of newborns of variable size into more consistently proportional sets of infants. In other words, a relatively small troop with many newborns may experience more die-off of those newborns in the later infant stages. At the same time, a relatively large troop with few newborns may be able to do a better job at making sure those newborns make it through the later infant stages. This interpretation is highly speculative, however, given that an examination of the residual plots in Figure A.31. That variance in residuals increases with the fitted values while it decreases with troop size indicates that the model may not be appropriate to this type of data, and thus the results may be misleading.
Chapter 5

Discussion and Conclusions

5.1 Conclusions from the Statistical Analysis

The model fitting results are summarized in Table B.9. The troop size model found evidence of changes in average troop size over year and season. Seasonally, there seems to be a population decrease in the late rainy season, on the order of ten percent below the overall mean.\footnote{We may also be seeing the age composition shift to the younger ages in the late rainy season as well, although the evidence is weak. While it seems that the shift should be in the opposite direction with harder weather conditions picking off the young and weak members of the troop, perhaps it is not so due to bot fly parasitism. Bot fly prevalence is highest in the rainy season, but is lower for infants than adults (Milton, 1996), so the larger parasite loads of older individuals may bring them down in relatively larger numbers.} Over the years, average troop sizes seem to have increased from 10-15% above the long-term average and then fallen to 10-15% below it, but with varying periods between peaks and troughs. There are three pairs of peaks separated by five year intervals: 1977 to 1982, 1982 to 1987, and 1994 to 1999. Certainly, there seems to be a strong tendency for the average size not to stray too far from 19 monkeys per troop, suggesting the possibility of some density-dependent mechanism regulating population size. Effects on the order of 10-15% do not seem like very large swings in population, though, when you consider that for the average-sized troop of 19 animals, the change amounts to two or three additional animals when population is very high and two or three fewer when population is very low.

While analysis of age and sex ratio shifts from year to year and season to season are largely inconclusive, there are some relationships between troop composition and size that seem fairly consistent. Larger troops tend to have relatively more infants and an adult sex ratio weighted more toward females than troops of average size. Taken together with
the results of the troop size analysis, one hypothesis of troop change over time is that when one or two additional females reach adulthood in a troop and then give birth to one or two additional infants, troop size reaches an untenable size and higher mortality will then bring the troop back down roughly 19 animals. Of course, this is a very broad generalization based on averages, and it is possible that variation in troop sizes is more important in overall population dynamics.

Discussion of the fertility indicator analysis results is probably not warranted, as the model used here may not be appropriate. More data following individual females and tracking individual births will probably be necessary to model the process precisely.

Overall, while the population does increase and decrease over time, over the long term it seems to have a stable size and composition. There may be temporary fluctuations from the equilibrium, but there is not evidence for something existing that pushes troops away from the central tendency for very long.

5.2 Implications of Stable Population Theory

It is possible to take the statistical results discussed above and combine them with demographic models, thus generating more hypotheses about the population. Supposing that average troop statistics are good indicators of overall population statistics, the results of the analysis here suggest that the population parameters of size, age composition, sex ratio and fertility have had a strong central tendency over the period of observation. From 1974 to 2001, those 27 years represent more than five generations, given generation lengths of four to five years. The demographic theory of stable age structures and stationary populations makes some very strong predictions about populations whose size and age composition remain unchanged over the long term. Of course, the howler population is not truly stable or stationary in exact mathematical terms, but looking at stable theory gives us a way to connect population parameters we can observe, such as age composition, to others that we cannot (mortality).

Under the stationary population model, developed by several mathematicians and explained in detail in Keyfitz (1985) and Wachter (1998), the crude birth rate (CBR) must equal the inverse of the average life expectancy from birth \((e_0)\). This is the fact behind the intuition that, for population to remain fixed, if deaths occur once every \(e_0\) years on

\(^2\)Stationary meaning a population with long-term growth rate \(r = 0\).
average, then a birth must occur every $e_0$ years as well. We have some information that can be used to estimate the crude birth rate in the howler population. First of all, we have researcher estimates of the BCI population’s interbirth interval of 18 months (Milton 1982), or one birth every 1.5 years for each adult female. Secondly, using the long-term averages of 61% adults in the population and 2.83 females per male adult sex ratio, we can estimate the proportion of the population that is adult females: $(0.61) \left( \frac{2.83}{1+2.83} \right) = 0.45$. Combining these two estimates gives estimates $CBR$ and $e_0$:

$$CBR = \left( \frac{1}{1.5} \right) \text{ births per year per adult female} \times (0.45 \text{ adult females per monkey})$$

$$= 0.3 \text{ births per year per monkey}$$

$$e_0 = \frac{1}{0.3}$$

$$= 3.33 \text{ years}$$

In a stationary population, this life expectancy can be divided up by the observed age group proportions to represent the average number of person-years, or monkey-years in this case, lived in each age group. If the howler population is at a long-run equilibrium size and structure, albeit with fluctuations around that equilibrium, overall age distributions should be roughly consistent with this model. Using the statistics shown in Table B.2, we take the overall mean troop group proportions as estimates of the stable age distribution (26% infant, 13% juvenile, 61% adults) and calculate the average number of monkey-years lived in each stage by an individual:

<table>
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<td>Infant Monkey-Years</td>
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<tr>
<td></td>
<td>= 0.87</td>
</tr>
<tr>
<td>Juvenile Monkey-Years</td>
<td>(0.13)(3.33)</td>
</tr>
<tr>
<td></td>
<td>= 0.43</td>
</tr>
<tr>
<td>Adult Monkey-Years</td>
<td>(0.61)(3.33)</td>
</tr>
<tr>
<td></td>
<td>= 2.03</td>
</tr>
</tbody>
</table>

Considering that the infant stage lasts approximately one year and the juvenile stage approximately three years, the years lived calculation implies substantial mortality, especially for juveniles.

We can analyze this mortality further by breaking the number of monkey-years
lived in each stage into two parts. First, to define a few variables:

\[ i = \{I, J, A\} \] indexing the age stages of infant, juvenile and adult
\[ n_i = \text{number of years in stage } i \]
\[ L_i = \text{average number of monkey-years lived in stage } i \]
\[ a_i = \text{average number of monkey-years lived in stage } i \]
\[ d_i = \text{probability of dying in stage } i \]
\[ l_i = \text{probability of surviving through stage } i \]
\[ \omega = \text{maximum possible age at death}. \]

Next, the equation dividing average number of monkey-years lived into parts:

\[ L_i = (n_i)(l_i) + (a_i)(d_i). \]

This equation breaks \( L_i \) into the contribution of those who survive \( (l_i) \) and those who die \( (d_i) \). Filling in this equation for each of the three stages with the values we know, we get the following three equations:

\[ 0.87 = (1)(l_I) + (a_I)(d_I) \]
\[ 0.43 = (3)(l_J) + (a_J)(d_J) \]
\[ 2.03 = (\omega)(0) + (a_A)(d_A). \]

We can also substitute survival probabilities for the death probabilities to reduce the number of variables:

\[ 0.87 = (1)(l_I) + (a_I)(1 - l_I) \]
\[ 0.43 = (3)(l_J) + (a_J)(l_I - l_J) \]
\[ 2.03 = (a_A)(l_J). \]

While this system of three equations with five unknowns is not solvable, it allow us to generate some graphs to explore how the system works. The first equation describes \( l_I \) as a function of \( a_I \), the next relates \( l_J \) and \( l_J \), given some level of \( a_J \), and the last relates \( a_A \) and \( l_J \). These three equations are shown graphically in Figure A.32 and they give several maximum and minimum bounds to aspects of the howler monkey mortality schedule. (The
A strange configuration of graphs is to facilitate comparisons from the infant to juveniles graphs, where the x-axes are the same, and from the juvenile to adult graphs, where the y-axes are the same.) The maximum survival probability through the infant stage would occur if all those who died did so right at birth, so that \( a_I = 0 \) and thus \( l_I = 0.87 \). Similarly, maximum survival through the juvenile stage would occur if all those who died in that stage did so at the moment they entered it, so that \( a_J = 0 \) and \( l_J = 0.43/3 = 0.14 \). This is a very high mortality level. This high mortality level likewise implies that those who do manage to make it to the adult stage are likely to survive a very long time after that. With maximum survival through the juvenile stage, we see that the minimum (average) monkey-years an adult can expect to live is \( a_A(\text{max}) = 2.03/0.14 = 14.2 \) years.

These “back of the envelope” calculations were done assuming that both sexes have the same mortality schedule, which is certainly not appropriate, shown by the fact that the sex ratio at birth is fairly even but is highly skewed toward females by the end of life. The implication, then, is that male mortality must be much higher than the population average of only 14.3% reaching adulthood. Taking the average proportion adult female of 0.74, this implies that approximately 21% of female babies reach the adult stage, while only 8% of males do.\(^4\)

Beyond establishing bounds on parameters, what might be a reasonable guess for the parameters? Taking the estimate of 55% of infants dying within the first year from a Costa Rican howler monkey population (Clarke and Glander, 1984), this gives an average age at death of infants dying in the stage of \((0.87 - 0.45)/(0.55) = 0.76 \) years. While this is possible, it contrasts a great deal with the human case. Mortality rates for humans are the highest right after birth and decrease rapidly thereafter. Thus, human infants dying in the first year usually do not survive more than one month (Human Mortality Database, 2003). If the same is true for howler monkeys, then an implication of this use of the stationary population model may be that the observed age distribution is not accurate. The lack of juveniles in the age distribution, and the average number of years lived in that stage being so much smaller than the three year length of the stage suggest that there may be

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\(^3\)We can also deduce a minimum possible infant survival from the maximum juvenile survivorship scenario. Maximum juvenile survivorship occurs if all those dying upon reaching the juvenile stage do so right at the instant of transition to the juvenile stage. Under this scenario, survivorship through infancy is equal to the survivorship through the juvenile stage. Thus, the maximum survivorship through the juvenile stage sets the minimum bound for survival through the infant stage.

\(^4\)If the sex ratio is 50/50 at birth and 74/26 in adulthood, with 14.3% overall survivorship, female mortality should be roughly \((0.143 \times 0.74)/0.5 = 0.21\) and male survivorship roughly \((0.143 \times 0.26)/0.5 = 0.08\).
some inaccuracy in counting juveniles. As mentioned in the introduction to the data, it is possible that juvenile males are being counted as adult females. Supporting this idea is the fact that the proportion juvenile for Troop V, a troop that Dr. Milton has monitored over the long-term and would thus be able to make a more accurate accounting of, is somewhat higher than that observed in the rest of the dataset. Fixing this inaccuracy would serve to increase the proportion juvenile and decrease both the proportion adult and the adult sex ratio (thus decreasing the calculated CBR).

Recalculating the system under the hypothesis of one misclassified juvenile male as an adult female, however, creates other problems. Under this scenario, the life expectancy rises from 3.33 years to 3.77 years and the monkey-years lived in each stage become 0.98, 0.69, and 2.10. This helps to increase the juvenile stage picture, but it also implies that either most infants survive or that any that die do so right at the end of infancy. It is possible that the transition from infancy to the juvenile stage is a time of great stress for the infant and thus very high mortality. Further study on the timing of mortality would be needed to confirm this hypothesis.

5.3 Further Research

Even though that data analyzed here suffer from various problems, they are consistent in indicating a return to central tendency over time for troop size and composition. Confirming whether there is any consistent time period of the fluctuations around the central tendency would require a longer period of monitoring on a more consistent time schedule. Whether the pattern around this central tendency might relate to other environmental factors is a matter for further study.

Further study also seems necessary to settle the question of whether the mortality schedule is in fact as severe as the age distribution suggests, or whether the age distribution as observed is inaccurate. Designed in advance, such a study could address major problems with the data as it is examined here. Collecting observations at regular time intervals throughout the year would produce data able to make definite statements about the existence and magnitude of seasonal variability and separate that variability from longer-run fluctuations. Finally, power calculations would indicate just how many observations needed to be gathered at each time interval in order to discern between systematic and random variation.
Bibliography


Appendix A

Figures
Figure A.1: The Republic of Panama and Barro Colorado Island

(Source: Smithsonian Tropical Research Institute, www.stri.org.)
Figure A.2: Monthly Rainfall on Barro Colorado Island, 1929-2001

Notes: All data from the Smithsonian Tropical Research Institute. The boxes for each month mark off the upper and lower quartiles of the distribution for that month, with the median monthly value marked as a line. The “whiskers” extend to the extreme values of the distribution, excluding outliers defined as values farther than 1.5 times the inter-quartile range from the median. Outliers are shown as lines above or below the whiskers. The box notches represent 95% confidence intervals, so if two notches do not overlap, this indicates a difference in location at the 5% significance level.
Seasonal Rainfall on Barro Colorado Island, 1929-2001

Notes: All data from the Smithsonian Tropical Research Institute. The dry season is January through April; early rain is May through August; later rain is September through December. See notes with Figure A.2 for seasonal box plot details.

Seasonal Rainfall Distribution

Seasonal Rainfall Over Time

Rain (mm)

0 500 1000 1500 2000

Dry

Early Rain

Late Rain

Rain (mm)

0 500 1000 1500 2000

Seasonal Median

1940

1960

2000

Figure A.3: Seasonal Rainfall on Barro Colorado Island, 1929-2001
Figure A.4: Annual Rainfall on Barro Colorado Island, 1929-2001

Notes: All data from the Smithsonian Tropical Research Institute.
Figure A.5: Mantled Howler Monkeys of BCI

Figure A.6: Observed Troop Sizes Over Time

Note: For “Other Observations,” size of plotted character is proportional to number of troops observed at that size in that month. Dotted line is overall median. Solid line is monthly median value.
Figure A.7: Observed Troop Size with Square Root Transformation

Notes: Data represent all observed troops (ex-Troop V and Troop X).
Figure A.8: Seasonal Troop Size Distributions

Notes: The dry season is January through April; early rain is May through August; later rain is September through December. See notes with Figure A.2 for box plot details.
Figure A.9: Histograms of Observed Troop Sizes

ex-Troop V (N=369)

Troop Size

Probability

0.0  0.05  0.10  0.15

10  20  30  40

Troop V (N=69)

Troop Size

Probability

0.0  0.05  0.10  0.15

10  20  30  40
Notes: Data represent all observed troops (ex-Troop V and Troop A).

Figure A.10: Square Root of Observed Age Group Sizes
Notes: The dry season is January through April; early rain is May through August; later rain is September through December. See notes with Figure A.2 for box plot details.
Figure A.12: Adult Sex Ratio (F/M) Over Time and Season

Notes: Data in time series plot represent all observed troops (ex-Troop V and Troop V). In the box plots, the dry season is January through April; early rain is May through August; later rain is September through December. See notes with Figure A.2 for box plot details.
Notes: Data represent all observed troops (ex-Troop V and Troop A).

Figure A.13: Fertility Indicators, Time Series Plots

Number of Infant I

Fertility Ratio I (Infant I's per Adult Female)

Fertility Ratio II (Infants per Adult Female)

Number of Infant I
Figure A.14: Fertility Indicators, Seasonal Distributions

Notes: The dry season is January through April; early rain is May through August; later rain is September.
Figure A.15: Pooled Distributions, ex-Troop V

- **Adults**
  - Adult Females
  - Adult Males

- **Juveniles**
  - Adult Sex Ratio (F/M)

- **Infants**
  - Infant I
  - Infant I per Ad. Fem.
  - Infants per Ad. Fem.
Figure A.16: Pooled Distributions, Troop V
Figure A.17: Paired plots of population groups by age and sex of 0.5 (Vemahes and Hyvärin, 1999).

Notes: Lines represent local regression model smoothed trend. Use `loess()` with a span of 0.5.
Figure A.18: Mean versus Variance of Troop Sizes in Each Year-Season

Notes: Points represent the mean and variance of troop sizes observed for the 44 year-season combinations observed in the ex-Troop V dataset.
Figure A.19: Troop Size Model, Fitted and Effects

Notes: Data and model fits represent the ex-Troop V information only. In the estimated seasonal effects graph, the boxes are an approximate 95% confidence band of \( e^2 \), with \( e \) marked as a line through the middle of the box. In the estimated year effects graph, the solid line represents \( e \), with an approximate 95% confidence band of \( e^2 \).
Figure A.20: Comparison of Troop Sizes to Poisson Distribution

Notes: The "Observed Data" graph compares the quantiles of observed troop size data (ex-Troop V only) with the quantiles of the theoretical Poisson distribution with mean equal to the mean of troop sizes. In other graphs, the quantiles of computer-generated pseudo-random samples from the same theoretical Poisson distribution are compared with the quantiles of earlier calculated data.

Randomly Generated Dataset Quantiles

Quantiles of Troop Size

Observed Data

Simulation 1

Simulation 2

Simulation 3
Figure A.21: Troop Size Model Residual Analyses

Fitted vs. Residual

Residuals by Season

Residuals by Year

Notes: Residuals are in original scale (one unit is one animal). All data and model fits based on ex-Troop V observations only. See notes with Figure A.2 for box plot details.
Figure A.22: Proportion Adult, Fitted and Effects

Notes: Data and model fits represent the ex-Troop V information only. In the estimated seasonal effect graph, the boxes are an approximate 95% confidence band of $e^{\hat{\beta}}$, with $\hat{\beta}$ marked as a line through the middle of the box. In the estimated year effects graph, the solid line represents $e^{\hat{\beta}}$, with $\hat{\beta}$ marked as a line through the graph. The boxes are an approximate 95% confidence band of $e^{\hat{\beta}}$, with $\hat{\beta}$ marked as a line through the graph.
Notes: Residuals are scaled to represent group proportion. All data and model fits based on ex-Troop V observations only. See notes with Figure A.2 for box plot details.
Figure A.24: Proportion Juvenile, Fitted and Effects

Notes: Data and model fits represent the ex-Troop V information only. In the estimated seasonal effects graph, the boxes are an approximate 95% confidence band of $e^{\hat{\sigma}^2}$, with $e^{\hat{\sigma}^2}$ marked as a line through the middle of the box. In the estimated year effects graph, the solid line represents $e^{\hat{\sigma}^2}$, with an approximate 95% confidence band denoted by dotted lines.
Notes: Residuals are scaled to represent group proportion. All data and model fits based on ex-Troop V observations only. See notes with Figure A.2 for box plot details.

Figure A.25: Proportion Juvenile Model Residual Analyses
Notes: Data and model fits represent the ex-Troop Y information only. In the estimated year effects graph, the solid line represents $e^\gamma$, with an approximate 95% confidence band denoted by dashed lines. In the estimated seasonal effect graph, the boxes are an approximate 95% confidence band of $e^\beta$, with $e^\beta$ marked as a line through the middle of the box. In the estimated troop size effects graph, the solid line represents $e^\delta$, with an approximate 95% confidence band of $e^\delta$ denoted by dashed lines.
observations only. See notes with Figure A.2 for box plot details.

Notes: Residuals are scaled to represent group proportion. All data and model fits are based on ex-Troop A.

Figure A.27: Proportion Infant Model Residual Analyses
Notes: Data and model fits represent the ex-Troop V information only. In the estimated seasonal effects graph, the boxes are an approximate 95% confidence band of $e^{\alpha_{i} + \beta_{i}x}$, with $e^{\alpha_{i}}$ marked as a line through the middle of the box. In the estimated year effects graph, the solid line represents $e^{\alpha}$, with an approximate 95% confidence band of $e^{\alpha + \beta_{i}x}$. In the estimated Troop Size effects graph, the dotted lines denote the estimated 95% confidence band of $e^{\alpha_{i} + \beta_{i}x}$, with $e^{\alpha_{i}}$ marked as a line through the middle of the box.

Figure A.28: Proportion Female (of Adults) Fitted and Effects
Observations only: see notes with Figure A.2 for box plot details.

Notes: Residuals are scaled to represent group proportion. All data and model fits based on ex-Troop A.

Figure A.29: Proportion Female (of Adults) Model Residual Analyses

Fitted vs. Residual

Residual by Year

Residuals by Season

Residual vs. Troop Size

Residual
Figure A.30: Fertility Ratio (Inf. I/Adult Female), Fitted and Effects

Notes: Data and model fits represent the ex-Troop V information only. In the estimated seasonal effects graph, the boxes are an approximate 95% confidence band of $e^{\beta x}$, with $e^x$ marked as a line through the middle of the box. In the estimated year effects graph, the solid line represents $e^{\beta y}$, with an approximate 95% confidence band of $e^{\beta y}$, with $e^y$ marked as a line through the middle of the box. In the estimated seasonal effects graph, the solid line represents $e^{\beta z}$, with an approximate 95% confidence band of $e^{\beta z}$, with $e^z$ marked as a line through the middle of the box.
Figure A.31: Fertility Ratio (Inf. I/Adult Female) Model Residual Analyses

Notes: Residuals are scaled to represent robust fits. All data and model fits based on exact troop observation dates only. See notes with Figure A.2 for box plot details.
Figure A.32: Stationary Population Model of Howler Mortality

Infants

Juveniles

Adults

% Surv. Through Infancy

% Surv. Through Juv.

% Surv. Through Infancy.
Appendix B

Tables
Table B.1: Numbers of Howler Monkey Troop Observations in Milton Dataset by Year, Month and Season

<table>
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<th>Year</th>
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Notes: Seasons are Dry (Jan-Apr), Early Rainy (Mar-Aug), and Late Rainy (Sep-Dec).
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Notes: Adult sex ratio is adult females per adult male in each troop. Fertility is measured by the ratio of infants in age class 1 (0-2 months) per adult female.
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<td>25</td>
<td>65.354</td>
<td>366</td>
<td>658.197</td>
<td>0.000</td>
</tr>
<tr>
<td>Season after Year</td>
<td>2</td>
<td>14.262</td>
<td>341</td>
<td>643.935</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Notes: Sequential ANODEV test results for troop size and troop size squared are robust to changes in sequence. For season and year, only the set of coefficients added first is judged significant, for all possible sequences.

### Table B.4: Proportion Adult Model Results

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Deviance</th>
<th>Residual Df</th>
<th>Residual Dev.</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full Model Likelihood Ratio Test:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Null</td>
<td>368</td>
<td>200.354</td>
<td></td>
<td></td>
<td>0.005</td>
</tr>
<tr>
<td>Model</td>
<td>29</td>
<td>52.116</td>
<td>339</td>
<td>148.238</td>
<td></td>
</tr>
<tr>
<td>Sequential ANODEV:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Null</td>
<td>368</td>
<td>200.354</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>2</td>
<td>8.597</td>
<td>366</td>
<td>191.757</td>
<td>0.014</td>
</tr>
<tr>
<td>Year</td>
<td>25</td>
<td>34.901</td>
<td>341</td>
<td>156.855</td>
<td>0.090</td>
</tr>
<tr>
<td>Trp. Size</td>
<td>1</td>
<td>8.299</td>
<td>340</td>
<td>148.556</td>
<td>0.004</td>
</tr>
<tr>
<td>Trp. Size²</td>
<td>1</td>
<td>0.318</td>
<td>339</td>
<td>148.238</td>
<td>0.573</td>
</tr>
</tbody>
</table>

Notes: Sequential ANODEV test results for troop size and troop size squared are robust to changes in sequence. For season and year, only the set of coefficients added first is judged significant, for all possible sequences.
Table B.5: Proportion Juvenile Model Results

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Deviance</th>
<th>Residual Df</th>
<th>Residual Dev.</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>368</td>
<td>300.123</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>29</td>
<td>48.077</td>
<td>339</td>
<td>252.046</td>
<td>0.014</td>
</tr>
</tbody>
</table>

Sequential ANODEV:

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Deviance</th>
<th>Residual Df</th>
<th>Residual Dev.</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>368</td>
<td>300.123</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>2</td>
<td>0.898</td>
<td>366</td>
<td>299.225</td>
<td>0.638</td>
</tr>
<tr>
<td>Year</td>
<td>25</td>
<td>46.359</td>
<td>341</td>
<td>252.866</td>
<td>0.006</td>
</tr>
<tr>
<td>Trp. Size</td>
<td>1</td>
<td>0.668</td>
<td>340</td>
<td>252.198</td>
<td>0.414</td>
</tr>
<tr>
<td>Trp. Size²</td>
<td>1</td>
<td>0.152</td>
<td>339</td>
<td>252.046</td>
<td>0.697</td>
</tr>
</tbody>
</table>

Notes: Sequential ANODEV test results for all sets of coefficients are robust to changes in sequence.

Table B.6: Proportion Infant Model Results

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Deviance</th>
<th>Residual Df</th>
<th>Residual Dev.</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>368</td>
<td>213.941</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>29</td>
<td>52.206</td>
<td>339</td>
<td>161.735</td>
<td>0.005</td>
</tr>
</tbody>
</table>

Sequential ANODEV:

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Deviance</th>
<th>Residual Df</th>
<th>Residual Dev.</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>368</td>
<td>213.941</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>2</td>
<td>6.585</td>
<td>366</td>
<td>207.356</td>
<td>0.037</td>
</tr>
<tr>
<td>Year</td>
<td>25</td>
<td>38.089</td>
<td>341</td>
<td>169.267</td>
<td>0.045</td>
</tr>
<tr>
<td>Trp. Size</td>
<td>1</td>
<td>6.639</td>
<td>340</td>
<td>162.628</td>
<td>0.010</td>
</tr>
<tr>
<td>Trp. Size²</td>
<td>1</td>
<td>0.893</td>
<td>339</td>
<td>161.735</td>
<td>0.345</td>
</tr>
</tbody>
</table>

Notes: Sequential ANODEV test results for troop size and troop size squared are robust to changes in sequence. For season and year, only the set of coefficients added first is judged significant, for all possible sequences excepting that shown above.

Table B.7: Proportion Female (of Adults) Model Results

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Deviance</th>
<th>Residual Df</th>
<th>Residual Dev.</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>368</td>
<td>120.102</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>29</td>
<td>25.071</td>
<td>339</td>
<td>95.031</td>
<td>0.675</td>
</tr>
</tbody>
</table>

Sequential ANODEV:

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Deviance</th>
<th>Residual Df</th>
<th>Residual Dev.</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>368</td>
<td>120.102</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>2</td>
<td>0.728</td>
<td>366</td>
<td>119.374</td>
<td>0.695</td>
</tr>
<tr>
<td>Year</td>
<td>25</td>
<td>16.138</td>
<td>341</td>
<td>103.236</td>
<td>0.911</td>
</tr>
<tr>
<td>Trp. Size</td>
<td>1</td>
<td>7.048</td>
<td>340</td>
<td>96.188</td>
<td>0.008</td>
</tr>
<tr>
<td>Trp. Size²</td>
<td>1</td>
<td>1.157</td>
<td>339</td>
<td>95.031</td>
<td>0.282</td>
</tr>
</tbody>
</table>

Notes: Sequential ANODEV test results for all sets of coefficients are robust to changes in sequence.
**Table B.8: Fertility Ratio (Inf. I/Adult Female) Model Results**

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Deviance</th>
<th>Residual Df</th>
<th>Residual Dev.</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Full Model Likelihood Ratio Test:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Null</td>
<td>368</td>
<td>472.559</td>
<td>339</td>
<td>379.216</td>
<td>0.000</td>
</tr>
<tr>
<td>Model</td>
<td>29</td>
<td>93.343</td>
<td>339</td>
<td>379.216</td>
<td>0.000</td>
</tr>
<tr>
<td><strong>Sequential ANODEV:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Null</td>
<td>368</td>
<td>472.559</td>
<td>339</td>
<td>379.216</td>
<td>0.000</td>
</tr>
<tr>
<td>Season</td>
<td>2</td>
<td>12.151</td>
<td>366</td>
<td>460.407</td>
<td>0.002</td>
</tr>
<tr>
<td>Year</td>
<td>25</td>
<td>79.750</td>
<td>341</td>
<td>380.657</td>
<td>0.000</td>
</tr>
<tr>
<td>Trp. Size</td>
<td>1</td>
<td>0.053</td>
<td>340</td>
<td>380.604</td>
<td>0.819</td>
</tr>
<tr>
<td>Trp. Size²</td>
<td>1</td>
<td>1.389</td>
<td>339</td>
<td>379.216</td>
<td>0.239</td>
</tr>
</tbody>
</table>

Notes: Sequential ANODEV test results for all sets of coefficients are robust to changes in sequence.

**Table B.9: Summary of Statistical Model Results**

<table>
<thead>
<tr>
<th>Model</th>
<th>Model v. Null</th>
<th>Season</th>
<th>Year</th>
<th>Troop Size</th>
<th>Model Concerns?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Troop Size</td>
<td>Reject</td>
<td>Lower in Peaks:77,82,87,94,99</td>
<td>na</td>
<td></td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td>Late Rain</td>
<td>Troughs:90,91</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Adult</td>
<td>Reject</td>
<td>Inconclusive</td>
<td>Bigger troops ~</td>
<td>Lower % Adult</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Juv.</td>
<td>Reject</td>
<td>Not Sig.</td>
<td>Peaks:99</td>
<td>Not Sig.</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td>Troughs:81,86</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Inf.</td>
<td>Reject</td>
<td>Inconclusive</td>
<td>Bigger troops ~</td>
<td>Higher % Inf.</td>
<td>No</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult % Fem.</td>
<td>Cannot</td>
<td>Bigger troops ~</td>
<td>Not Sig.</td>
<td>Higher % Fem.</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>Reject</td>
<td>Higher in Peaks:77,83,88,90</td>
<td>Not Sig.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fert.</td>
<td>Reject</td>
<td>Late Rain</td>
<td>Peaks:82,87,95</td>
<td>Not Sig.</td>
<td>Yes</td>
</tr>
</tbody>
</table>

Notes: All models include seasonal and year fixed main effects. Models other than troop size also include terms for troop size and troop size squared. The “Model v. Null” column represents the conclusion of the likelihood ratio test of the full model versus null model (with only mean value). The “Model Concerns?” column indicates whether or not the residual analysis suggested that the model might not be appropriate. Seasons are Dry (Jan-Apr), Early Rainy (Mar-Aug), and Late Rainy (Sep-Dec). The Fertility model is a model of the ratio of Infant I’s to Adult Females.