

USING VOCALIZATIONS TO DETERMINE
THE CAPACITY FOR FUTURE COGNITION
IN THE COMMON RAVEN (*CORVUS CORAX*)

by

Caitlyn E. Roehmholdt

A Thesis
Submitted in partial fulfillment
of the requirements for the degree
Master of Environmental Studies
The Evergreen State College
June 2019

©2019 by Caitlyn E. Roehmholdt. All rights reserved.

This Thesis for the Master of Environmental Studies Degree

by

Caitlyn E. Roehmholdt

has been approved for

The Evergreen State College

by

John Withey, PhD
Member of the Faculty

Date

ABSTRACT

Using vocalizations to determine the capacity for future cognition in the common raven (*Corvus corax*)

Caitlyn E. Roehmholdt

Common ravens (*Corvus corax*) are known to be highly intelligent birds and have been the subjects of many behavioral studies. However, not many natural experiments that examine the ability of ravens to understand time and predict events have been conducted. The population of wild ravens at Wolf Haven, a nonprofit sanctuary for abandoned and displaced wolves, provides a unique opportunity to study both the behaviors of ravens that have been exposed to a regular schedule of events (for example, scheduled feeding of the wolves, regular sanctuary visitors, and non-food enrichment activities for the wolves) and their ability to predict when food will be available. Here, recordings were taken of raven vocalizations over 16 weeks on scheduled feeding days, fasting days, and two instances where the feeding and fasting days were reversed. The recordings were analyzed for presence of “haa” calls, a food associated call in ravens. The number of haa calls observed on feeding days versus on fasting days was compared using a paired t-test under the assumption that the anticipation of food would lead to more food related vocalizations. The number of haa calls on days when feeding was expected to occur but was not observed was also analyzed. Though there was not a statistically significant difference between the number of calls observed on feeding days versus fasting days, this study poses many questions and suggests possibilities for future research into the use of audio recording to investigate the behavior and cognitive abilities of ravens.

Table of Contents

List of Figures	v
List of Tables	vi
Acknowledgements	7
Chapter 1: Introduction	1
Chapter 2: Literature Review	8
Avian Intelligence	9
Corvids	11
Ravens and Myth	12
Ravens and Wolves	14
Raven Cognition	16
Raven Vocalization	18
New Frontiers	19
Chapter 3: Methods	21
Site Selection	21
Observation Schedule and Recording	22
Analysis	24
Chapter 4: Results	27
Chapter 5: Conclusion and Discussion	30
Bibliography	35
Appendices	43

List of Figures

Figure 1 Diagram of Wolf Haven study site	23
Figure 2. Haa call spectrogram	24
Figure 3. Two examples of non-haa raven calls	24

List of Tables

Table 1. Average number of haa calls on feeding and fasting days	27
Table 2. Haa calls on observed feeding days	28
Table 3 Haa calls per hour on scheduled feeding days	28
Table 4 Summary of data used for ANOVA	29

Acknowledgements

I would like to thank my advisor John Withey for his guidance, reassurance, sharing of knowledge, and curiosity in and support of my work; my fiancé Aaron for his unending support and belief in me and my abilities; my parents and family members for raising me to believe that anything is possible; and my friends and cohort members for their much needed emotional support. I would also like to thank the staff of Wolf Haven International for allowing me to use their fantastic facility as my research site.

CHAPTER 1: INTRODUCTION

The *Corvidae* family of birds is a highly intelligent group that includes crows, ravens, rooks, jackdaws, jays, magpies, and nutcrackers. Members of this family group, known collectively as *corvids*, have exhibited the ability to use tools, follow human gazes and remember interactions with humans, communicate the presence of food and its status (protected, available, etc.) to conspecifics, and live in highly social groups. Their problem-solving ability is similar to that of great apes. Birds of any species have not always been recognized for their intelligence, especially those abilities that indicate higher level cognitive processes. Perhaps only the parrot, with its great ability to mimic, has regularly been thought of as intelligent by the average layperson. However, as advances in behavioral studies and neurological imaging allow for more in-depth study of animal brains and abilities, the days of birds being regarded as unintelligent are slowly becoming a relic of the past.

All birds have a brain that is very different from the mammalian brain. For many years, it was assumed that due to this difference in structure birds were incapable of producing complex, flexible, intelligent behavior (Emery, 2006). For instance, whereas mammals have a neocortex, birds have a structure called a pallium; however, the pallium has been found to have analogous functions to the neocortex, proving that the brain's structure and anatomy does not necessarily determine the intelligence and abilities of a species (Nomura & Izawa, 2017).

In addition to assumptions about structural differences, it was long thought that the intelligence of an animal corresponded to the size and structure of an animal's brain, but recent studies have begun to change that notion: it is the ratio of the size of the animal's brain to its body (called encephalization) that seems to correlate with intelligence and cognitive ability, not just physical brain size or the presence of a human-like neocortex (Emery, 2006). Emery and Clayton (2004) theorize that the brains of corvids evolved such similar processes and capabilities to the brains of apes despite the structural differences due to the two groups facing many of the same socioecological challenges, using the understanding of complex social dynamics and the ability to cache and retrieve food as examples. Indeed, although the brains of corvids and parrots are large in comparison to their body size and have a similar encephalization to that of monkeys and apes, they are still small, with the average raven's brain weighing in at around 15 grams (Iwaniuk & Nelson, 2002). Despite this, the corvid brain is packed with neurons; ravens not only have a large amount of neurons, their neurons are very tightly packed, which allows their brains to contain as many or more neurons than that of the much larger brains of monkeys (Fitch et al., 2016).

These neuron-dense brains also enable corvids to use and manufacture tools, something once thought to be an ability exclusive to primates but now understood to be present in many animal species (Anderson, 2002). The most prolific and best studied corvid tool maker is the New Caledonian crow (*Corvus moneduloides*), which is the only non-human species known to manufacture tools in the wild other than chimpanzees (Emery & Clayton, 2009). Although only the two aforementioned non-human species

have been found to manufacture tools, many more species have been found to use tools, and even species that do not use tools in the wild can be prolific tool users under novel conditions in a lab setting (Emery & Clayton, 2009).

Although ravens do not manufacture tools like their New Caledonian relatives, they have other abilities that place them in league with primates. Captive ravens exhibit bartering abilities exceeding those of both the great apes, as well as an average 4-year-old human (Kabadayi and Osvath 2017). Recent experiments have shown that ravens exhibit flexible behavior and even imagination: when presented with a novel situation requiring problem solving to find the only solution—in this case, a piece of meat hanging from a long string attached to a perch—the hand-raised ravens participating in the study were able to solve the puzzle by repeatedly pulling on the string, holding it with their foot, and pulling again, some of them solving the problem on their first attempt (Emery & Clayton, 2004).

High sociality and communication ability are also raven traits. Through experimentation, Schwab and colleagues (2008) found that raven sibling pairs tended to sit together both more frequently and for a longer duration than non-sibling pairs, pointing to the highly social and family-oriented nature of the species. Furthermore, the study showed that social learning in ravens is influenced by the interrelationships of the birds, not just by the birds being in a similar age range. Fraser and Bugnyar (2010) confirmed that raven siblings have more meaningful relationships than non-siblings, furthering the comparison between the sociality of ravens and that of great apes.

Ravens are also known for being scavengers in the habit of caching their food, a behavior that requires them to remember where they place their caches for extended periods of time for the purpose of later retrieval. Ravens are able to distinguish whether other ravens have observed their caching, and retrieve food from caches observed by other ravens sooner than from unobserved caches (Bugnyar and Heinrich 2005). A similar earlier study determined that raven that cache and ravens that observe employ “countertactics” to gain the upper hand in securing food (Bugnyar & Kotrschal, 2002). It has also been shown that ravens observe other ravens both inside and outside of their social group more than other species (Scheid et al., 2007), which is possibly linked to their tendency for social learning. This type of behavior implies that ravens can take their observations, commit them to memory, and use them to plan for future events.

Ravens have also been shown to engage in, and possibly understand, social behavior and cues from humans. Bugnyar, Stöwe, and Heinrich (2004) conducted an experiment, the first of its kind on birds, to determine whether ravens were able to follow a human experimenter’s gaze around a barrier. They found that ravens of different ages succeeded at this task during around 80% of the trials. However, the experimenters do caution that while the results of the experiment do point to the possibility that ravens are able to understand the visual activities of others, there is still a question as to whether or not ravens understand or attribute any mental significance to the gaze of others (Bugnyar et al., 2004).

The robust social lives of ravens are also tied to their memories, both for other ravens and for humans. It has been found that ravens can remember which human experimenter in a food exchange experiment trial gives “fair” exchanges and which is “unfair” after single events and act accordingly in future trials, preferring to trade with the “fair” experimenter for up to a month after the observation of the experiment (Muller et al., 2017). Their memories are not just related to the humans that they may interact with: Ravens are able to remember the individual calls of past group mates for up to 3 years (Taylor, 2014).

Vocalizations aren’t just used for group and individual identification. As a highly social species, ravens use vocalizations to communicate with each other. One of the most commonly communicated topics amongst ravens is food: whether it is available or unavailable, its location, and even the quality of the food (Bugnyar et al., 2001). Food calls also carry information about the caller: it has been found that ravens can distinguish between individuals based upon the characteristics of their food calls (Szipl et al., 2015). Ravens are also known to call conspecifics to feeding sites, with resident ravens tending to produce food calls more frequently than vagrant birds, supporting the idea that raven social groups are strongly based on population dynamics that change over time as individual animals enter and leave the group (Szipl & Bugnyar, 2014).

The specific call type that ravens use to “talk about” food is referred to in the literature as either the “haa” call or the food yell or scream (Bugnyar et al., 2001). These calls, which are speculated to have developed from the begging calls of young ravens,

have been found to be practiced and modified throughout a raven's early years and may even be used by raven parents to locate individual young (Boeckle et al., 2012). Haa calls are used all throughout a raven's life; Although the call varies slightly based on a caller's age, the core characteristics are the same (Boeckle et al., 2012; Boeckle et al., 2018) and the call can be identified relatively easily using audio spectrogram analysis.

All of these traits combine to paint a picture of an extremely intelligent and social animal not too unlike humans. However, the study of foresight, future cognition, and planning in animals in general is still in the early stages due to the difficulties inherent in studying the minds of species we cannot directly communicate with to ask about their experiences. Many opportunities exist for studies in this realm, especially as our understanding of animal neuroscience continues to advance. For example, Zentall (2005) and associates have shown through experimentation the different ways that pigeons and mice may experience both episodic and semantic memory, and how they can be trained to report their experience by pressing different colored keys. Studies with corvids have helped to illuminate their intelligence: Corvids have demonstrated a superior ability to understand the relationships between items, being able to make pairwise comparisons and correctly order a given set of objects (Emery & Clayton, 2004). Crows are able to recognize specific, individual human faces of those humans that have been deemed dangerous for at least 3 years after the initial encounter (Marzulff et al., 2010). Ravens recruit others from roosts outside of their own to feeding bonanza, many times from miles away (Heinrich, 1994).

These studies and many more beg the question: If corvids can learn things such as facial recognition and tool use, couldn't they learn the schedule of a guaranteed food source appearing?

The goal of this study is to answer the aforementioned question by attempting to determine whether wild ravens can predict and anticipate scheduled feeding events at a wolf sanctuary. At the time of this writing, to the author's knowledge no natural experiments that examine the ability of ravens to understand time and predict events have been conducted, although experimental studies examining the reaction of wild ravens to the feeding of game park animals at various game parks around the world have been conducted (Bugnyar & Kotrschal, 2001; Bugnyar & Kotrschal, 2002; Bugnyar et al., 2001; Loretto et al., 2016).

CHAPTER 2: LITERATURE REVIEW

Long before animals were considered to have thoughts, feelings, and emotions, humans were interested in the thoughts of their own kind. Since the time of the ancient Greek philosophers, human thought and the human condition in general has been pondered at great length, with human beings held in high esteem and seen as being of higher status and, in fact, as higher beings not related to animals at all (Adamson & Edwards, 2018). This idea that animals are unintelligent, “soulless” automatons is an idea that was solidified by Rene Descartes’s assertion that animals are no more than mere machines (Gould, 2004). However, during the past century, attitudes towards animals have changed and more and more studies of animal cognition have taken place. Although scientists and many non-scientists alike now recognize that humans are animals and are content to group mankind in with the rest of the primates, this concept is far from being internalized in the majority of the population (Boddice, 2011).

The human brain is similar to the brain of other mammals, and is similar enough that other animal brains are used as models for uncovering the mysteries of the brain; for example, dye can be injected into the brain of a mouse to trace the neural networks and reactions of the brain to stimuli (Allen, 2006). The concept that different areas of the brain are linked to different abilities is not a new one. In the mid eighteenth century, the pseudoscience of phrenology was extremely popular. Thought at the time to be fact based science, phrenology was based on the belief that the physical characteristics of the skull—lumps, bumps, protrusions, and the like—were determined by the shape of the brain underneath, and subsequently that areas of the brain that were assumed “larger” due

to the shape of the skull imparted increased aptitude or enhanced abilities in the assigned corresponding “character trait” (Parssmen, 1974). Although phrenology has long been debunked and relegated to the realm of pseudoscience, it has helped steer the scientific community into the more modern field of cognitive neuroscience (Voros & Markic, 2014). For example, it is currently understood that different regions of the brain do serve different functions: there is a region for processing sensory stimuli, one for managing and coordinating movement, one for memory, decision making, language processing, and so on (Stegmann, 2013).

Beginning in the early 1900s, the study of what we would refer to today as animal cognition began in earnest. The terms “animal intelligence” and “animal mind” were used by Thorndike and Washburn, respectively, around the turn of the century to theorize on the psychological underpinnings of behavior in animals, whereas in the 1920s and 30s the more well-known Pavlov and Skinner were examining the behavior of animals through the lens of conditioning and reinforcement (Church, 2001). According to Church, “At least four major intellectual movements in the 20th century have provided challenges to the field of animal cognition: cognitive psychology, animal rights, ethology, and molecular biology” (2001).

AVIAN INTELLIGENCE

While there have been numerous studies and paradigm shifts in the general populous since the time of Descartes that have begun to undo the stereotype of the

unintelligent animal, until quite recently birds were thought to be some of the most unintelligent in the animal kingdom. Phrases like “bird brain” commonly used by the general public to refer to someone who is unintelligent and small minded support this stereotype as a cultural mainstay. However, the truth is that many birds are very intelligent.

Avian intelligence, though informally recognized through myth and religion for thousands of years, has not been formally studied until the late twentieth century. It was Darwin’s theory of evolution that first gave scientific respectability to the idea that humans are not separate from or somehow above other animals, and it was Darwin’s theory that subsequently introduced the study of animal behavior into the realm of mainstream science (Mackintosh, 1994). However, studying the behavior of animals is not the same as recognizing them as cognizant, sentient beings. Donald R. Griffin, a pioneer of cognitive ethology and one of the first scientists to convincingly prove the existence of echolocation in bats, caused a paradigm shift when he suggested that animals have consciousness in his book “The Question of Animal Awareness,” first published in 1977. In it, he suggested that although it was unlikely that animals think exactly in the same way that humans do, it would benefit the scientific community to consider the possibility that animals have their own cognitive abilities: essentially, the idea that animals think like animals (Griffin, 1977).

The physical structure of the avian brain has been one of the major causes of dismissing the possibility of intelligence in birds. Bird brains do not have an elaborate

cerebral cortex, the part of the brain responsible for higher level cognitive abilities in mammals. Due to this, any attempts to “train” birds—usually pigeons or parrots—using standard psychological techniques that failed were blamed on the fact that birds seemed to lack an area of the brain critical to higher thought processes and learning abilities (Pepperberg, 2010). This idea was challenged by neuroscientist Stanley Cobb, who in the 1960s discovered that although avian brains are vastly different from mammalian brains, they are complicated systems containing structures that are analogous to those in the mammalian brain and are capable of complex cognitive feats (Cohen & Stemmer, 2007).

Birds belonging to the corvid (*Corvidae*) and parrot (*Psittacinae*) families have forebrains that are comparatively large and relatively the same size as that of the great apes, live in complex social groups sometimes including extended family ties, and have young that have a long developmental period before becoming independent from their parents (Emery, 2006).

The corvid family—crows, ravens, jays, nutcrackers, and magpies—is regarded as one of the most intelligent bird families, perhaps rivalling the intelligence and problem-solving ability of the great apes (Kabadayi et al., 2017).

CORVIDS

Birds in the corvid family have been shown to have many abilities indicative of higher intelligence such as problem solving, familial/social associations, long juvenile period, tool use, and learning and idea transmission. New Caledonian crows are able to

not only use but to craft tools to complete novel tasks (Hunt & Gray, 2004), and American crows and magpies can distinguish between human faces and can even distinguish between the faces of friendly humans and foes (Marzluff et al., 2010; Lee et al., 2011). Further examples of corvid intelligence is seen in the ability of Clark's nutcrackers to remember the location of their seed caches over 280 days after caching (Balda & Kamil, 1992), and the ability of scrub jays, who can preferentially cache food in "private" locations as opposed to locations that other birds have seen them use, thereby deterring thieves (Grodzinski & Clayton, 2010).

The common raven (*Corvus corax*) is the largest bird in the passerine group. Ravens can measure over 2 feet long and have an average weight of one and a half to three and a half pounds (Boarman & Heinrich, 1999). They are larger than their more commonly seen crow 'cousins', and have a more robust beak, a chevron shaped tail (as opposed to a crow's fan shaped tail) and distinctive long throat feathers called hackles; ravens are also more solitary than crows, found in pairs much more than in the large extended social groups that crows are known for (Boarman & Heinrich, 1999). Ravens are the largest of all passerine birds. Passerines, sometimes referred to as "songbirds" or "perching birds," are defined by two key features: three toes facing forward and two toes facing back, and their ability to sing (Unwin, 2011). Ravens form monogamous life-long breeding pairs, are omnivorous although they seem to prefer carrion, and are known for being very vocal and having a large call repertoire (Driver, 1999).

RAVENS AND MYTH

Ravens have always shared an interesting relationship with humans. Sometimes seen as gods or helpful tricksters and sometimes reviled, ravens have been a part of humans' lives since time immemorial. Tales of ravens and their exploits and abilities have been told since ancient times in many cultures around the globe. Native American mythology varies from tribe to tribe, but many tribes have stories featuring Raven (which is capitalized as a formal name in these tales). In the northwestern North American and Siberian lore, Raven primarily plays the role of the trickster. In this trickster role, Raven often acts both altruistically and selfishly, making him paradoxical (Carroll, 1984).

Heinrich hypothesizes that tales of ravens aren't just interesting stories, but that the myths and legends surrounding the bird can give clues towards understanding their distribution and even their food sharing and foraging behaviors (1989).

In other cultures, ravens have held various places in mythology from being a messenger of the sun (Greek) or a gatherer of news for a god (Norse), predicting disasters at sea (Alaskan Native) and epidemics (Dene), and even locating game animals for human hunters (Blackfoot, Cheyenne, Koyukon, Dene, and Apache tribes; Driver, 1999). Ravens are also thought to have brought light to the world and even to have created the world in the beliefs of some North American native peoples (Plec, 2012). Ravens (and other corvids) have also been discovered with some frequency in Iron Age and Roman Britain burial sites, though the meaning of their inclusion in these burials is still up for debate (Serjeantson & Morris, 2011). Similarly, the skeletal remains of ravens have also

been found in Paleoindian burial sites over 10,000 years old with evidence suggesting that humans buried the remains intentionally (Driver, 1999).

Humans have had close relationships with ravens since time immemorial. In fact, there have been studies confirming that ravens associate with human hunters. Ravens are scavenging birds and have been seen at the gut piles left from carcasses of animals killed by human hunters (White, 2005). This seems counterintuitive as gunshots signal danger and disturbance, both of which are typically avoided by animals—especially scavenger animals that have a history of being shot at (White, 2005). White hypothesizes that due to the long lifespan of ravens it's unlikely that they have evolved an affinity for gunshot sounds in so few generations, and instead suggests that ravens have learned to associate gunshot sounds with food as a foraging strategy (2005). This behavior is hypothesized to have replaced the relationship between wolves and ravens in an environment that has become distinctly lacking in wolves due to human involvement.

RAVENS AND WOLVES

Ravens have been known to associate closely with wolves. It is thought that this association with wolves is a survival strategy on the raven's end, as ravens primarily feed on carrion which can be difficult to locate in winter; associating with wolves almost guarantees them a year-round food source (Vucetich et al., 2004). However, this is not the only time during which ravens can be seen with wolves. It has been found that ravens associate with wolves not only when they are feeding on kills but when they rest, travel,

and hunt prey, and that a similar association does not occur between ravens and other animals (Stahler et al., 2002).

Ravens have been observed to be cautious of new food sources, going so far as to avoid approaching a food source until other animals begin feeding (Boarman & Heinrich, 1999). However, when ravens associating with wolves were studied for this innate reaction it was found that ravens did not exhibit this fear response towards carcasses when wolves were present (Stahler et al., 2002), possibly indicating that ravens connect wolves feeding with the safety to eat carrion. It has also been observed that ravens are attracted to the distress calls of dying animals, suggesting that auditory cues may be one way that they are able to locate wolf kill sites to scavenge from (Frame, 2010).

Wolves and ravens make a great hunting team. If a flock of ravens happens upon a carcass of an animal that has died of natural causes or has frozen to death in the winter, their beaks are not strong enough to access the meat; if a predator such as a wolf kills an animal, ravens can take advantage of the situation and scavenge some of the meat for themselves with greater ease (Plec, 2012). Between eating and caching, an individual raven can consume or stash away up to 2 kg of food per day from large prey animal carcasses, and it is estimated that for every one wolf that participates in a kill, between 2 to 4 kg of meat are lost to scavenging ravens (Vucetich et al., 2004). Although it is easy to imagine that ravens may associate with wolves when food is involved, ravens also associate with wolves for other reasons not yet entirely understood by humans. Heinrich also observed that ravens at Yellowstone preferentially associated with wolves, even

when there was no meat in the immediate vicinity (1999). Although wolves hunt for themselves and their packmates and not for ravens, wolves have been found to be remarkably tolerant of the birds. Ravens have been observed to exhibit exceptionally brave, play-like behaviors around wolves, diving at wolves and even nipping at their tails, even after being snapped at (Heinrich, 1989).

Even the population dynamics of the two species are intertwined: it was found that when grey wolves were reintroduced to Yellowstone National Park in the late 1990s, the ravens in the park began to depend less on anthropogenic food sources, began to associate preferentially with wolves, and experienced population stabilization (Walker et al., 2018). Associating with wolves benefits ravens in other ways as well: the number of eggs laid by ravens annually has been found to correlate with the availability of carrion (Newton et al., 1982), with more carrion leading to more eggs. In this way, wolves positively impact the yearly growth of raven populations.

RAVEN COGNITION

Historical accounts, myths, and observations like these have led towards the formal scientific study of ravens as intelligent animals capable of many complex mental abilities. Memory, and the ability to act based upon memory, is one such complex mental ability. Episodic memory, the ability to remember events that an individual personally experienced, allows for contextual information for memory retrieval; this provides for a more rich and complete retrieval of memory (Kelley et al., 2018). The ability of scrub jays in the wild to locate their caches accurately even after months was stated to be the

first conclusive evidence of behavior indicating episodic memory in animals other than humans by Clayton and Dickinson (as cited in Salwiczek et al., 2010). Ravens, like their scrub jay cousins, have also shown to have strong memory-related abilities.

Like scrub jays, ravens cache food; they are also similar to scrub jays in that they both raid other ravens' caches and anticipate that their own caches may be raided if they are not careful to cache out of view of any potential competitors (Bugnyar & Kotrschal, 2002). However, the ability of ravens to remember is not restricted to food related events. Kabadayi and Osvath found that ravens who were trained to exchange tokens for food from the researchers would, when they knew trading would happen the next day, collect and store tokens as soon as the opportunity to take the tokens was presented to them (as cited in Boeckle & Clayton, 2017). When ravens participate in experiments with human experimenters, they remember which experimenters are fair and which are unfair and can remember this for up to a month; they then also show preference to those experimenters that they remember for their fairness (Muller et al., 2017).

Ravens also form strong bonds and memories for other birds in their social circle. They are able to remember former group members by their calls after spending up to three years separated from them (Boeckle & Bugnyar, 2012). Ravens also have strong relationships with their siblings - stronger than their relationships with other unrelated birds (Fraser & Bugnyar, 2010). Additionally, they receive more benefit from social learning experiences with the other bird or birds involved are their siblings (Schwab et al., 2008).

RAVEN VOCALIZATION

As social birds, ravens communicate in a variety of ways. Perhaps the most noticeable way they communicate is through their vocalizations.

Avian vocalization is fairly unique amongst animal communication in that birds, unlike the great majority of animals, are able to learn from the vocalizations of others. Although there have been anecdotes about other animals—humpback whales, porpoises, orca, harbor seals, bats, and elephants—being able to imitate vocal sounds, the best and most well documented examples come from birds (Nottebohm & Liu, 2010).

Birds are very creative and able in their vocal abilities. They are able to learn the calls and songs of their own species in the wild, and under laboratory conditions many species of songbird are also able to learn the songs of “tutors” of a different species (Nottebohm & Liu, 2010). Some species of birds, such as parrots and mynahs, are extremely skilled at mimicking and making a variety of sounds and are also able to form associations between a particular auditory stimulus and a specific response in a seemingly unconstrained manner (Seyfarth & Cheney, 2010). A high level of complexity and sophistication in avian communication has been found from field research in recent decades, a complexity that may rival the communication abilities of non-human primates (Suzuki, 2016).

Ravens, with their large brains, are especially skilled at communication. As reviewed in Reber et al. (2016), ravens are able to distinguish between the calls of ravens that are familiar and those that are unfamiliar, or even ravens that were former associates; they can also recognize in group or out group membership of other ravens based on vocalizations. Societal changes can also be detected by ravens through vocalizations. When recorded raven calls are played back over loudspeaker to the same group of ravens that the recording was taken from, the ravens are able to recognize the calls as coming from a bird that they are familiar with and pay attention to the social rank of the birds they are hearing; when researchers altered the recording to make dominant individuals sound as if they had become submissive, the listening ravens would stop what they were doing and show signs of distress (De Waal, 2016). This shows the importance of vocalizations in developing and maintaining the social ties between ravens.

Ravens also yell at food sources both to communicate their status in the group and to attract others to the food (Heinrich & Marzluff, 1991). Social status is also an important factor in group feeding behavior. At a food source, ravens are more likely to respond to the food-related haa calls of other ravens that are familiar to them, especially those of their same social status, effectively choosing their dining groups based on vocally transmitted information (Szipl et al., 2015).

NEW FRONTIERS

The body of work on avian cognition grows larger as research in new areas expands to include more facets of animal intelligence yet to be explored. Like the

aforementioned study by Kabadayi and Osvath, this study explores another hypothesis related to a raven's ability to plan for the future and behave accordingly: the hypothesis that wild ravens can anticipate the occurrence of scheduled feedings in a sanctuary setting independently of behavioral cues from the captive wolves that reside there.

CHAPTER 3: METHODS

Although wild ravens are typically territorial animals living together in pair bonds upon reaching breeding age, they do form bonds with other ravens that they remember for years (Braun & Bugnyar, 2012) and tend to gather at sources of food whether led there by vocal or behavioral cues from conspecifics, especially as unpaired young adults (Bugnyar & Kotrschal, 2001). However, in situations where food is readily available on a regular basis such as at a garbage dump, camp site, or game park, ravens may form more permanent flocks (Loretto, 2016). The latter is the case at Wolf Haven International (“Wolf Haven”). Wolf Haven is a not for profit animal sanctuary located in the city of Tenino in Washington State, taking in displaced and formerly captive grey wolves (*Canis lupus*) and becoming a permanent home for them. They also participate in species recovery for the endangered Mexican grey wolf (*Canis lupus baileyi*) and red wolf (*Canis rufus*). At any given time, Wolf Haven is home to approximately 60 wolves, though numbers fluctuate with births, deaths, and new arrivals from outside. Wolf Haven is also home to large population of wild ravens that live on the sanctuary premises year-round.

SITE SELECTION

Wolf Haven was selected as the site for this study due to both its large resident raven population and the manner in which the animal care workers feed the resident wolves. In the wild, wolves are only successful at bringing down prey about 10% of the time (Mech et al., 2015); To mimic the natural feeding habits of wolves as much as is possible in captivity, the wolves are not fed every day. Instead, the wolves are fed 3 to 4 times per week with Saturday always being a scheduled feeding day and Sunday always

being a scheduled fasting day with very few, very infrequent exceptions (Erik Wilber of Wolf Haven International, personal communication, August 1, 2018).

On feeding days, wolves are fed a diet of chicken, fish, and beef, as well as deer carcasses as they are available. Food is typically given to the wolves around noon unless there is an emergency at the sanctuary. On fasting days wolves are typically supplied with enrichment items, which are usually not food items; however, on hot days they may be supplied with “popsicles” made of frozen tuna juice or blood.

OBSERVATION SCHEDULE AND RECORDING

No regular sanctuary activities were disrupted by data collection. Observations took place every Saturday and Sunday from September 15, 2018 to February 3, 2019, beginning at 11:00 a.m. and lasting for at least one hour but for no more than two hours. The first two days of recording—September 15 and 16—no haa calls were recorded and no feeding was observed. Scheduling adjustments were made with Wolf Haven staff to ensure that, barring any unforeseen emergency circumstances, feeding would be observed on all subsequent observation days. On two days—December 22 and January 12—technical issues with the recording equipment caused recordings to be only 46 and 39 minutes in duration, respectively. Recording on January 13 was also cut short due to poor weather. This observation window was selected in order to allow for observation of ravens prior to the scheduled wolf feeding time, which under normal circumstances occurs around noon on feeding days. A total of just over 58 hours of recording was completed for this study.

Audio recordings were taken using a ZOOM H4N Pro handheld recording device. Observations took place at the same stationary location near the center of the public visitor route (a loop of 6 wolf enclosures). The recording device was attached to a small “tabletop” tripod with a shock mount, a sound buffer was placed over the microphone, and the device was then placed directly onto the ground. The recorder was oriented towards the south for every recording session. Written notes were taken from a chair placed approximately 1 to 3 feet away from the recorder (Figure 1).

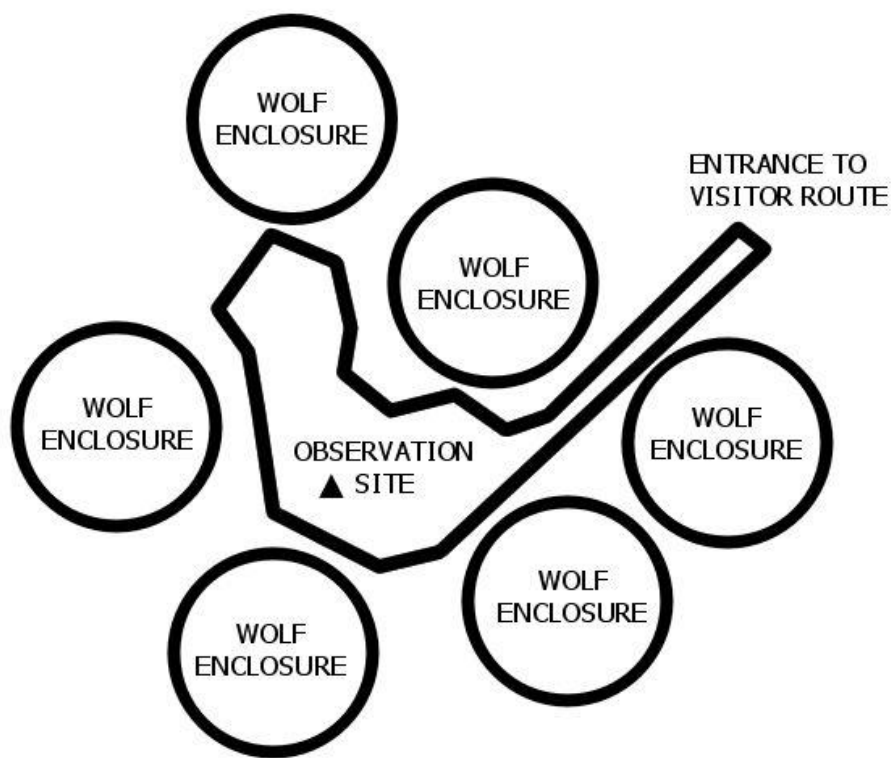


Figure 1 Diagram of Wolf Haven study site

ANALYSIS

Recordings were imported into Cornell Lab’s “Raven” bioacoustic software for spectrogram analysis. Captured sound files were displayed as spectrograms in 30 second intervals at a time and manually searched for the signature of the haa call (Figure 2). The haa call was selected as the focus of the data collection for this study because it has reliably been shown to be associated with food (Szipl et al., 2015; Bugnyar et al., 2001; Conner, 1985).

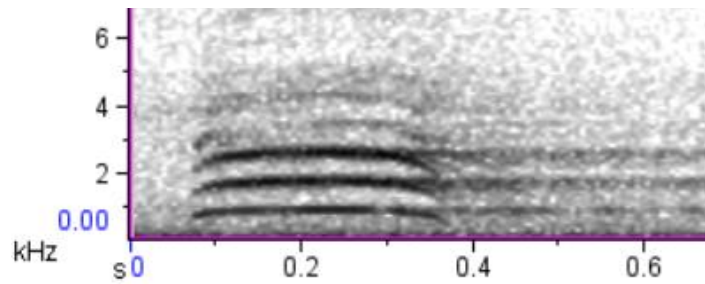


Figure 2. Haa call spectrogram (recorded October 27, 2018 at Wolf Haven International)

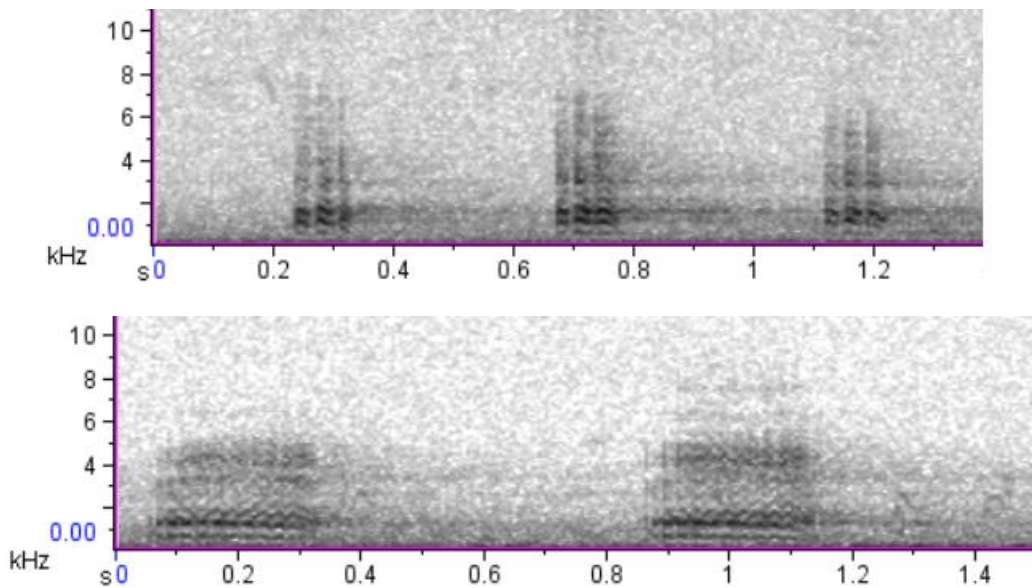


Figure 3. Two examples of non-haa raven calls (recorded January 12, 2019 at Wolf Haven International)

Calls that were ambiguous or overlapping with other calls were not included in the final call count. Additionally, days during which an unusual event causing more raven vocalizations than normal (e.g. the feeding of an entire deer carcass to one wolf enclosure) were noted as outliers and not included in the final data tables. The accepted haa calls were then sorted by start time. The accepted calls were then reviewed a second time for accuracy. On days when wolf feeding was scheduled, the feeding time was noted. It was also noted when a feeding was scheduled but not observed, and when scheduled feeding days and fasting days were swapped by Wolf Haven animal care staff for the benefit of this study. Other disturbances, such as train whistles or noise from airplanes, were also recorded, as well as any wolf behaviors suggesting that the wolves were anticipating being fed soon.

A paired t-test for two sample means was used to determine whether the difference in the average number of haa calls per hour on feeding days and on fasting days was statistically significant. A paired two sample t-test for means on observed feeding days comparing the number of haa calls before and after feeding was also conducted. Additionally, a two-sample t-test assuming unequal variances was conducted to compare the average number of haa calls per hour on feeding days when feeding went as planned to scheduled feeding days where feeding was not observed. This analysis did not include weekends where feeding and fasting days were switched by Wolf Haven staff, nor one Sunday on a weekend during which the wolves were fed on both Saturday and Sunday but the feeding was unobserved. A more fine-grained analysis was also employed via a one-way ANOVA to examine the number of calls in the 30 minutes

before and after feedings, and before and after the average feeding time of noon on non-feeding days and on days during which feeding was not observed. Finally, for the two weekends during which Wolf Haven staff switched the feeding and fasting days, the average number of calls per hour on the “switched feeding day,” the Sunday in both cases, was compared to a typical feeding day and the average number of calls per hour on the “switched fasting day” (the Saturday) was compared to a typical fasting day.

The haa call frequency from each recording day was also plotted as a scatterplot and a generalized additive model (“GAM”) was employed to visually detect patterns in the recorded vocalizations and the time of observed feeding, if applicable, was marked (Appendix B).

CHAPTER 4: RESULTS

The paired two sample t-test for means comparing the average number of haa calls per hour on feeding days (including days upon which feeding was scheduled to occur but was not observed) to the average number of haa calls per hour on fasting days yielded the following results: the mean number of haa calls on feeding days (15 ± 2 SE) was similar to the mean number of calls on fasting days (13 ± 3 SE; paired $t_{16} = 0.60$, $p = 0.56$).

Table 1. Average number of haa calls on feeding and fasting days

WEEKEND	FEEDING DAY AVERAGE	FASTING DAY AVERAGE
9/29 & 9/30	7.98	1.04
10/6 & 10/7	22.51	15.02
10/13 & 10/14	8.03	35.37
10/20 & 10/21	22.24	11.54
10/27 & 10/28	4.02	11.18
11/3 & 11/4	12.59	3.04
11/10 & 11/11	10.78	2.15
11/17 & 11/18	25.15	41.71
12/1 & 12/2	9.39	7.12
12/8 & 12/9	14.10	31.02
12/15 & 12/16	11.60	15.38
12/22 & 12/23	12.89	6.28
1/5 & 1/6	26.08	13.42
1/12 & 1/13	15.47	6.15
1/19 & 1/20	2.37	9.32
1/26 & 1/27	21.54	10.89
2/2 & 2/3	28.43	1.03

For the paired two sample t-test for means on observed feeding days comparing the number of haa calls before and after feeding, the mean number of haa calls before feeding (13.9 ± 4.4 SE) was similar to the mean number of haa calls after feeding (11.5 ± 3.4 SE; paired $t_{11} = 0.36$, $p = 0.73$).

Table 2. Haa calls on observed feeding days

DATE	HAA CALLS BEFORE FEEDING	HAA CALLS AFTER FEEDING
9/29/2018	10	5
10/6/2018	46	1
10/13/2018	1	15
10/27/2018	7	1
11/3/2018	7	19
11/10/2018	13	8
11/17/2018	42	8
12/1/2018	11	7
12/22/2018	10	0
1/6/2019	0	33
1/27/2019	20	7
2/2/2019	0	34

The results of the two-sample t-test assuming unequal variances comparing the average number of haa calls per hour on feeding days when feeding went as planned (14.81 ± 2.61 SE) to scheduled feeding days where feeding was not observed (13.16 ± 3.22 SE) resulted in $t = 0.25$ and $p = 0.81$.

Table 3 Haa calls per hour on scheduled feeding days

DATE	FEEDING AS SCHEDULED	DATE	FEEDING UNOBSERVED
9/29	7.98	10/20	22.24
10/6	22.51	12/8	14.10
10/13	8.03	12/15	11.60
10/27	4.02	1/13	15.47
11/3	12.59	1/19	2.37
11/10	10.78		
11/17	25.15		
12/1	9.39		
12/22	12.89		
2/2	28.43		

The mean number of calls divided into three groups: A) 60 minutes surrounding observed feedings (30 minutes before and 30 minutes after), B) 60 minutes surrounding

the average feeding time of noon on non-feeding days (from 11:30 a.m. to 12:30 p.m.), and C) 60 minutes surrounding noon on days during which feeding was scheduled but not observed, were statistically similar ($F_{2, 29} = 0.29, p = 0.75$). On observed feeding days, the average number of haa calls was 12.33 ± 2.43 SE. On non-feeding days the average was 12.29 ± 4.17 SE, and on days when feeding was scheduled but not observed, the average was 8.16 ± 3.10 SE.

Table 4 Summary of data used for ANOVA

<i>Groups</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>
Feeding days	12	148	12.33	70.97
Scheduled but unobserved feeding days	6	49	8.17	57.77
Non feeding days	14	172	12.29	243.30

Regardless of the specific comparison, the differences in haa call frequencies in all described scenarios were not statistically significant. Additionally, review of the scatterplots with added GAM analysis did not yield any detectable pattern in frequency of haa calls.

CHAPTER 5: CONCLUSION AND DISCUSSION

As shown in the previous section, both the difference in number of haa calls between feeding days and fasting days and the difference between the number of haa calls when feeding went on as scheduled versus when feeding was schedule but not observed were not statistically significant. Additionally, no obvious pattern was apparent when examining plots of the data. This result could be for a number of reasons.

As has been established, ravens are extremely intelligent birds that exhibit insight and complex thought processes, as well as the ability to remember other birds, people, and events. As described by White, ravens have been observed as being capable of learning to associate certain auditory cues with food; in the case of White's study, ravens associated the sound of a hunting rifle with the opportunity to feed on fresh carcasses (2005). As White points out, due to the longevity of ravens and their relative slowness to reproduce when compared to some other animals, it is not possible for ravens to have evolved to be attracted to the sounds of gunshots, so some other mechanism must be at play. He hypothesizes that due to the fact that ravens already associate certain sounds, such as the calls of other ravens and possibly that of wolf howls, with an accessible food source, ravens have also simply learned that the sound of a hunting rifle firing also is associated with food. According to studies of raven foraging styles, once ravens are alerted to the presence of food – such as they might be by a gunshot – they often times return to their roosting location to alert other ravens of the presence of a food source (Dall & Wright, 2009). Due to Wolf Haven's relatively small area and the ease of accessing food for resident ravens treating the grounds as a roost, it is possible that due to

the plentiful food and lack of motivation to travel the behavior of resident ravens has changed due to learning and becoming adapted to their living situation, just like ravens living near hunters become accustomed to their gunshots signaling food.

Just like the multifaced role of Raven in myth – a trickster, a knowledge bringer, and even a god – ravens in the natural world are also multifaceted and can be difficult for humans to understand and are easy for us to misread (Munday, 2013). There is a widespread belief in many cultures that, due to their vocal nature and association with humans, ravens bring news to or alert people of future events (Drive, 1999). Ravens in all of their ranges have been noted to be extremely vocal and endowed with a large vocabulary, as well as exhibiting regional “dialects;” that is, certain calls that are only present in discreet populations (Conner, 1985). It is possible that the population of ravens at Wolf Haven has been stationary for long enough to form their own dialect, leading to the potential for misunderstandings of their vocalizations. However, more studies of this specific group and their vocalizations would need to occur before any claims to the validity of this theory could be made.

The choice of Wolf Haven as the site for the study also brought about challenges. Although the feeding of the wolves took place on a regular schedule on weekends, sometimes the feeding days during the week were more variable and did not occur in regular intervals. This could impact the ability of the ravens to internalize a feeding schedule and their ability to “know” when the weekend was coming or tell Saturday feeding days apart from Sunday fasting days. Additionally, as touched upon earlier, even

on the weekend some unexpected, unscheduled events occurred that likely interfered with data collection. These included two occasions upon which an entire deer carcass was fed to a group of wolves, increasing the number of haa calls, and days during which feeding was scheduled but did not occur during the observation period, which had an unknown or undetectable effect on the number of haa calls.

In addition to unplanned scheduling abnormalities, there were environmental factors that may have impacted the calling habits and call frequency of the ravens. For example, the food for the wolves was delivered via an older pickup truck that had a distinctive noise both when it was first started and upon driving. This sound was audible from the observation point in the sanctuary. The wolves, with their superior sense of hearing, visibly reacted to the sound of the food truck by assuming a physically alert posture and in some occasions whimpering. The ravens could easily observe the wolves and it is possible that their behavior was influenced by that of the wolves. Enrichment for the wolves also posed an unexpected challenge, as when enrichment was delivered the food truck was used to transport the enrichment items from the main office to the wolf enclosures. This triggered the same reaction in the wolves as food delivery, which in turn could have altered the behavior of the ravens.

Finally, the behavior of the ravens themselves could have posed a problem with the study design. Ravens, like all corvids, are known to cache food, observe others caching food, and raid the caches of others (Bugnyar & Kotrschal, 2002). Due to the advanced ages of many of the wolves at Wolf Haven, some are slow eaters, leaving

ample time for ravens to steal away food for eating or for caching. Additionally, some of the oldest wolves have smaller appetites and thus leave leftovers, allowing the ravens even more chances to eat or cache what the wolves leave behind. These circumstances allow for food to be available to ravens even on fasting days, which could cause the ravens to make calls signaling food or hunger less than they typically would in a situation where food, both to eat and to cache, was less available.

The study design outlined here may yield more conclusive results when conducted under laboratory settings. The controlled conditions of a laboratory would eliminate any external environmental factors that could have had an effect on the behavior of the ravens such as the aforementioned scheduling issues, unusual occurrences, environmental “clues,” and copious opportunities for storing food. Under a laboratory setting, a strictly adhered to feeding schedule could be implemented, and any haa calls made by the ravens in the study would be uninfluenced by the myriad of external factors encountered at Wolf Haven.

However, a laboratory setting cannot mimic natural behavior in the wild. Although a wolf sanctuary also cannot perfectly mimic conditions unimpacted by human schedules and feedings, it does allow for wild ravens to react to novel situations and can give insights into their natural problem solving and social behaviors. Additional studies, such as those examining the relationship between wolves and ravens more closely, would benefit from a setting such as Wolf Haven. Although this study did not find a significant difference between the number of haa calls on feeding days versus those on fasting days,

perhaps with an altered study design or a longer length of time for data collection there would be a different outcome. Another possible avenue of investigation is to apply this study design to other sanctuary or zoo settings that have a local wild raven population, ideally a raven population that interacts with wolves residing at said sanctuary or zoo.

Additional research into the scavenging behavior of wild ravens interacting with animals in captivity could be leveraged into applications such as preventing food loss at zoological parks and lessening or eliminating undesirable behaviors of wild ravens that are in close contact with humans. As human populations continue to grow, contact with wild animals that are usually reclusive will continue to increase. Further studies of such animals, like ravens, may contribute to a more cooperative human-animal relationship with increased understanding of the animal cousins that we share the planet with.

Bibliography

- Adamson, P., & Edwards, G. (Eds.). (2018). *Animals: A history*. Oxford: Oxford University Press.
- Allen, J. (2009). *The lives of the brain : Human evolution and the organ of mind*. Cambridge, Mass.: Belknap Press of Harvard University Press.
- Anderson, J. R. (2002). Gone fishing: tool use in animals. *Biologist*, 49(1), 15–18.
- Balda, R. P., & Kamil, A. C. (1992). Long-term spatial memory in clark's nutcracker *nucifraga columbiana*. *Animal Behaviour*, 44(4), 761-769.
- Boarman, W. I. and B. Heinrich (1999). Common Raven (*Corvus corax*), version 2.0. In *The Birds of North America* (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA.
- Boddice, R. (2011). *Anthropocentrism : Humans, Animals, Environments*. Leiden: BRILL.
- Boeckle, M., & Bugnyar, T. (2012). Long-term memory for affiliates in ravens. *Current Biology: CB*, 22(9), 801–806.
- Boeckle, M., & Clayton, N. (2017). A raven's memories are for the future. *Science* (New York, N.Y.), 357(6347), 126-127.
- Boeckle, M., Szipl, G., & Bugnyar, T. (2012). Who wants food? Individual characteristics in raven yells. *Animal Behaviour*, 84, 1123–1130.
- Boeckle, M., Szipl, G., & Bugnyar, T. (2018). Raven food calls indicate sender's age and sex. *Frontiers in Zoology*, 15(1), 1–10.
- Braun, A., & Bugnyar, T. (2012). Social bonds and rank acquisition in raven nonbreeder aggregations. *Animal Behaviour*, 84(6), 1507–1515.

- Bugnyar, T., & Heinrich, B. (2005). Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proceedings: Biological Sciences*, 272(1573), 1641–1646.
- Bugnyar, T., & Kotrschal, K. (2001). Movement coordination and signalling in ravens. *Acta Ethologica*, 3(2), 101–110.
- Bugnyar, T., & Kotrschal, K. (2002). Observational learning and the raiding of food caches in ravens, *Corvus corax*: Is it “tactical” deception? *Animal Behaviour*, 64(2), 185–195.
- Bugnyar, Kijne, & Kotrschal. (2001). Food calling in ravens: Are yells referential signals? *Animal Behaviour*, 61(5), 949-958.
- Bugnyar, T., Stöwe, M., & Heinrich, B. (2004). Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proceedings: Biological Sciences*, 271(1546), 1331–1336.
- Carroll, M. (1984). The Trickster as Selfish-Buffoon and Culture Hero. *Ethos*, 12(2), 105-131.
- Church, R. M. (2001). Animal cognition: 1900–2000. *Behavioural Processes*, 54(1-3), 53-63
- Cohen, H., & Stemmer, Brigitte. (2007). *Consciousness and cognition fragments of mind and brain*. London: Academic Press.
- Conner, R. N. (1985). Vocalizations of Common Ravens in. *The Condor*, 87(3), 379–388.
- Dall, S. R. X., & Wright, J. (2009). Rich pickings near large communal roosts favor “gang” foraging by juvenile common ravens, *corvus corax*. *PLoS ONE*, 4(2).

- De Waal, F. (2016). *Are we smart enough to know how smart animals are?* New York: W.W. Norton & Company.
- Driver, J. (1999). Raven Skeletons from Paleoindian Contexts, Charlie Lake Cave, British Columbia. *American Antiquity*, 64(2), 289-298.
- Emery, N. J. (2006). Cognitive ornithology: The evolution of avian intelligence. *Philosophical Transactions Biological Sciences*, 361(1465), 23–43.
- Emery, N. J., & Clayton, N. S. (2004). The Mentality of Crows: Convergent Evolution of Intelligence in Corvids and Apes. *Science*, 306(5703), 1903-1907.
- Fitch, W. T., Porteš, M., Němec, P., Herculano-Houzel, S., Lučan, R. K., Kocourek, M., & Olkowicz, S. (2016). Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the National Academy of Sciences*, 113(26), 7255–7260.
- Frame, P. (2010). Observations of a Possible Foraging Tool used by Common Ravens. *The Wilson Journal of Ornithology*, 122(1), 181-182.
- Fraser, O. N., & Bugnyar, T. (2010). The quality of social relationships in ravens. *Animal Behaviour*, 79(4), 927–933.
- Gould, J. L. (2004). Animal cognition. *Current Biology*, 14(10), R372-R375
- Griffin, D. R. (1977). *The question of animal awareness: Evolutionary continuity of mental experience*. New York, NY: Rockefeller University Press.
- Grodzinski, U., & Clayton, N. S. (2010). Problems faced by food-caching corvids and the evolution of cognitive solutions. *Philosophical Transactions of the Royal Society B: Biological Sciences*.
- Heinrich, B. (1989). *Ravens in winter* (2014 print ed.). New York, NY: Simon & Schuster Paperbacks.

- Heinrich, B. (1994). Does the Early Common Raven Get (and Show) the Meat? *The Auk*, 111(3), 764-769.
- Heinrich, B. (1999). *Mind of the raven: An investigation into the mind of the raven*. New York: Cliff Street Books.
- Heinrich, B., & Marzluff, J. M. (1991). Do Common Ravens Yell because They Want to Attract Others ? *Behavioral Ecology and Sociobiology*, 28(1), 13–21.
- Hunt, G. R., & Gray, R. D. (2004). Direct observations of pandanus-tool manufacture and use by a new caledonian crow (*corvus moneduloides*). *Animal Cognition*, 7(2), 114-120.
- Iwaniuk, A. N., & Nelson, J. E. (2002). Can endocranial volume be used as an estimate of brain size in birds? *Canadian Journal of Zoology*, 80(1), 16–23.
- Kabadayi, C., & Osvath, M. (2017). Ravens parallel great apes in flexible planning for tool-use and bartering. *Science*.
- Kelley, T. D., Thomson, R., & Milton, J. R. (2018). Standard model of mind: Episodic Memory. *Procedia Computer Science*, 145, 717–723.
- Lee, W. Y., Lee, S., Choe, J. C., & Jablonski, P. G. (2011). Wild birds recognize individual humans: Experiments on magpies, *pica pica*. *Animal Cognition*, 14(6), 817-25.
- Loretto, M.-C., Reimann, S., Schuster, R., Graulich, D. M., & Bugnyar, T. (2016). Shared space, individually used: spatial behaviour of non-breeding ravens (*Corvus corax*) close to a permanent anthropogenic food source. *Journal of Ornithology*, 157, 439–450.

- Mackintosh, N. (1994). *Animal learning and cognition* (Handbook of perception and cognition (2nd ed.)). San Diego: Academic Press.
- Marzluff, J. M., Walls, J., Cornell, H. N., Withey, J. C., & Craig, D. P. (2010). Lasting recognition of threatening people by wild American crows. *Animal Behaviour*, 79(3),
- Müller, J. J. A., Massen, J. J. M., Bugnyar, T., & Osvath, M. (2017). Ravens remember the nature of a single reciprocal interaction sequence over 2 days and even after a month. *Animal Behaviour*, 128, 69–78.
- Munday, P. (2013). Thinking through ravens: Human hunters, wolf-birds and embodied communication. *Perspectives on Human-Animal Communication: Internatural Communication*, 207–225.
- Newton, I., Davis, P. E., & Davis, J. E. (1982). Ravens and Buzzards in Relation to Sheep Farming and Forestry in Wales. *Journal of Applied Ecology*, 19(3), 681–706.
- Nomura, T., & Izawa, E. I. (2017). Avian brains: Insights from development, behaviors and evolution. *Development Growth and Differentiation*, 59(4), 244–257.
- Nottebohm, F., & Liu, W. C. (2010). The origins of vocal learning: New sounds, new circuits, new cells. *Brain and Language*, 115(1), 3–17.
- Parssmen, T. M. (1974). Popular Science and Society: The Phrenology Movement in Early Victorian Britain. *Journal of Social History*, 8(1).
- Pepperberg, I. M. (2010). Alex: A Study in Avian Cognition. *Encyclopedia of Animal Behavior*, 44–49.

- Plec, E. (2013). *Perspectives on human-animal communication : Internatural communication* (Routledge studies in rhetoric and communication ; 12). New York: Routledge.
- Reber, S. A., Boeckle, M., Szipl, G., Janisch, J., Bugnyar, T., & Fitch, W. T. (2016). Territorial raven pairs are sensitive to structural changes in simulated acoustic displays of conspecifics. *Animal Behaviour*, *116*, 153–162.
- Salwiczek, L. H., Watanabe, A., & Clayton, N. S. (2010). Ten years of research into avian models of episodic-like memory and its implications for developmental and comparative cognition. *Behavioural Brain Research*, *215*(2), 221-234.
- Scheid, C., Range, F., & Bugnyar, T. (2007). When, What, and Whom to Watch? Quantifying Attention in Ravens (*Corvus corax*) and Jackdaws (*Corvus monedula*). *Journal of Comparative Psychology*, *121*(4), 380–386.
- Schwab, C., Bugnyar, T., Schloegl, C., & Kotrschal, K. (2008). Enhanced social learning between siblings in common ravens, *Corvus corax*. *Animal Behaviour*, *75*(2), 501–508.
- Serjeantson, D., & Morris, J. (2011). Ravens and Crows in Iron Age and Roman Britain. *Oxford Journal of Archaeology*, *30*(1), 85–107.
- Seyfarth, R. M., & Cheney, D. L. (2010). Production, usage, and comprehension in animal vocalizations. *Brain and Language*, *115*(1), 92–100.
- Stahler, D., Heinrich, B., & Smith, D. (2002). Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. *Animal Behaviour*, *64*(2), 283-290.

- Stegmann, U. (2013). *Animal Communication Theory : Information and Influence*. New York: Cambridge University Press.
- Suzuki, T. N. (2016). Semantic communication in birds: evidence from field research over the past two decades. *Ecological Research*, 31(3), 307–319.
- Szipl, G., & Bugnyar, T. (2014). Craving Ravens: Individual ‘haa’ Call Rates at Feeding Sites as Cues to Personality and Levels of Fission-Fusion Dynamics? *Animal Behavior and Cognition*, 1(3), 265.
- Szipl, G., Boeckle, M., Wascher, C. A. F., Spreafico, M., & Bugnyar, T. (2015). With whom to dine? Ravens’ responses to food-associated calls depend on individual characteristics of the caller. *Animal Behaviour*, 99, 33–42.
- Taylor, A. H. (2014). Corvid cognition. *Wiley Interdisciplinary Reviews: Cognitive Science*, 5(3), 361–372.
- Unwin, M. (2011). *The Atlas of Birds : Diversity, Behavior, and Conservation*. Princeton: Princeton University Press.
- Voros, S., & Markic, O. (2014). Photograph of the Soul: Towards a Critical Neuroscience. *Teorija in Praksa*, 51(5), 811–831.
- Vucetich, J. A., Peterson, R. O., & Waite, T. A. (2004). Raven scavenging favours group foraging in wolves. *Animal Behaviour*, 67(6), 1117-1126.
- Walker, L. E., Marzluff, J. M., Metz, M. C., Wirsing, A. J., Moskal, L. M., Stahler, D. R., & Smith, D. W. (2018). Population responses of common ravens to reintroduced gray wolves. *Ecology and Evolution*, 8(22), 11158–11168.
- White, C. (2005). Hunters Ring Dinner Bell For Ravens: Experimental Evidence Of A Unique Foraging Strategy. *Ecology*, 86(4), 1057-1060.

Zentall, T. R. (2005). Animals may not be stuck in time. *Learning and Motivation*, 36, 208–225.

Appendices

Appendix A

DAY	RECORDING START TIME	FEEDING TIME	FEEDING IN MINTUES AND SECONDS
9/15 Saturday ¹	11:01	Not observed	n/a
9/16 Sunday ²	11:10	Not observed	n/a
9/29 Saturday	11:11:45	12:31:45	1 hr 20 min / 80 min / 4800 sec
9/30 Sunday	11:01:32	n/a	n/a
10/06 Saturday ³	10:54:54	12:32:15	1 hr 37 min 21 sec / 97 min / 5841 sec
10/07 Sunday	10:57:32	n/a	n/a
10/13 Saturday	10:56:56	12:16	1 hr 19 min 4 sec / 79 min / 4744 sec
10/14 Sunday	10:00:00	n/a	n/a
10/20 Saturday ⁴	10:57:03	Not observed	n/a
10/21 Sunday	11:00:26	n/a	n/a
10/27 Saturday	10:55	12:38	1 h4 43 min / 103 min / 6180 sec
10/28 Sunday	11:01:51	n/a	n/a
11/03 Saturday	11:00	11:32	32 min / 1920 sec
11/04 Sunday	11:04:37	n/a	n/a
11/10 Saturday	11:06	12:35	1 hr 29 min / 89 min / 5340 sec
11/11 Sunday ⁵	11:09	n/a*	n/a
11/17 Saturday	10:58	12:39	1 hr 41 min / 101 min / 6060 sec
11/18 Sunday	11:06	n/a	n/a
12/01 Saturday ⁶	11:03	12:31	1 hr 28 min / 88 min / 5280
12/02 Sunday	11:10	n/a	n/a
12/08 Saturday	11:07	Not observed	n/a
12/09 Sunday	11:07	n/a	n/a
12/15 Saturday ⁷	11:04	Not observed	n/a
12/16 Sunday ⁸	11:05	Not observed	n/a
12/22 Saturday	11:08	12:29	1 hr 21 min / 81 min / 4860
12/23 Sunday	11:04	n/a	n/a
01/05 Saturday	11:00	Food switch week	n/a
01/06 Sunday	11:11	11:53	42 min / 2520 sec
01/12 Saturday	11:04	Not observed	n/a
01/13 Sunday	11:05	n/a	n/a
01/19 Saturday	11:04	Not observed	n/a
01/20 Sunday	11:04	n/a	n/a
01/26 Saturday	11:03	Food switch week	n/a
01/27 Sunday	11:07	11:51	44 min / 2640 sec

02/02 Saturday	11:08	11:08	0
02/03 Sunday	11:10	n/a	n/a

1, 2: No haa calls were observed on 9/15 or 9/16

3: Full deer carcass given to wolf group outside of observation area

4: Animal care emergency delayed feeding of wolves

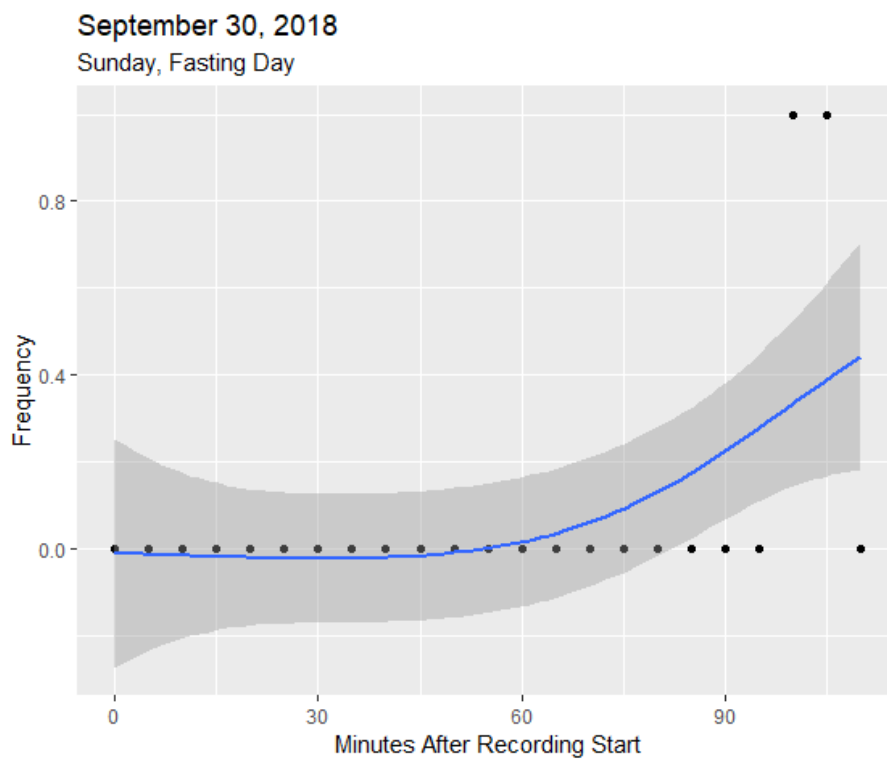
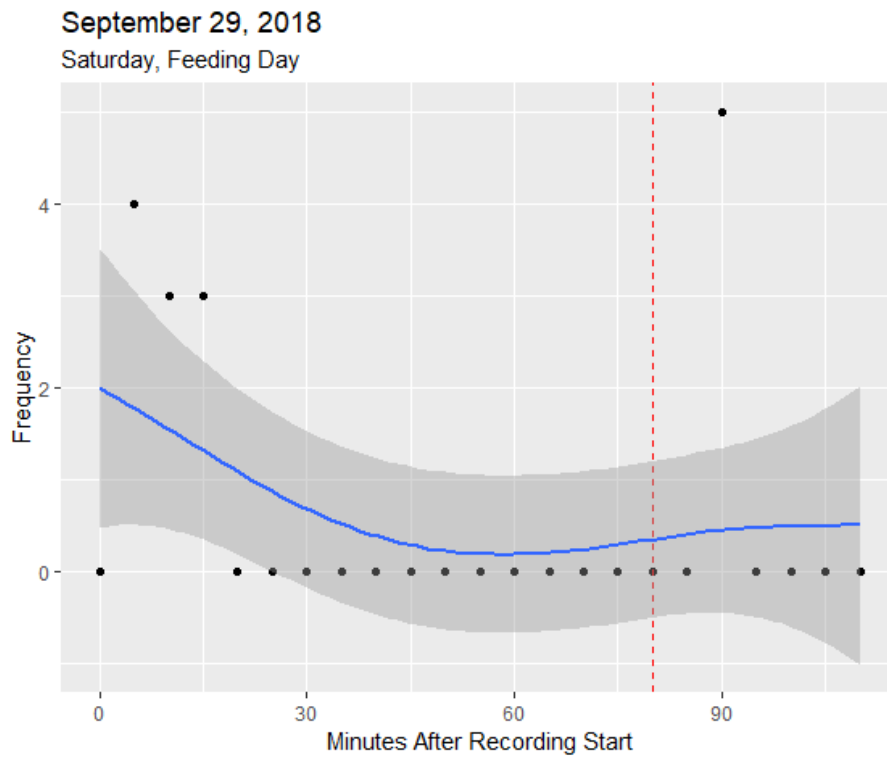
5: Wolves given food-based enrichment

6: Full deer carcass given to wolf group outside of observation area

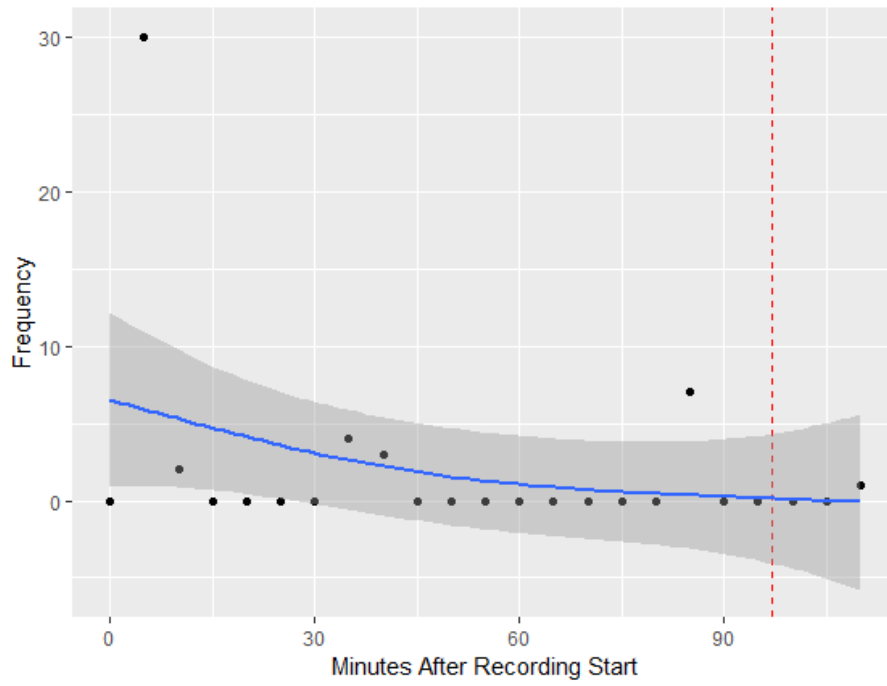
7, 8: Wolves fed on both Saturday and Sunday

* 12/29 and 12/30 recording skipped due to high wind warning

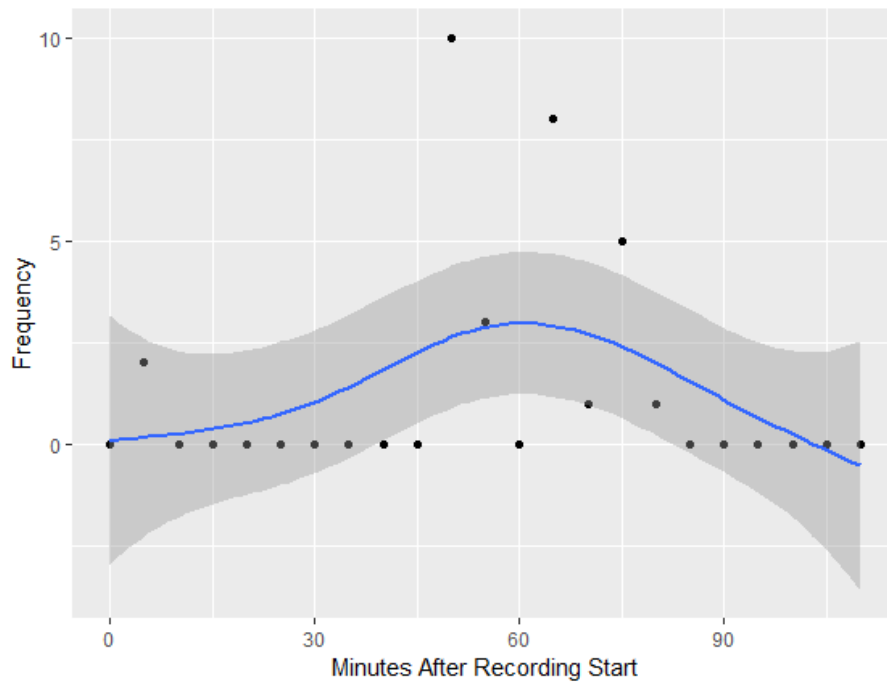
Appendix B



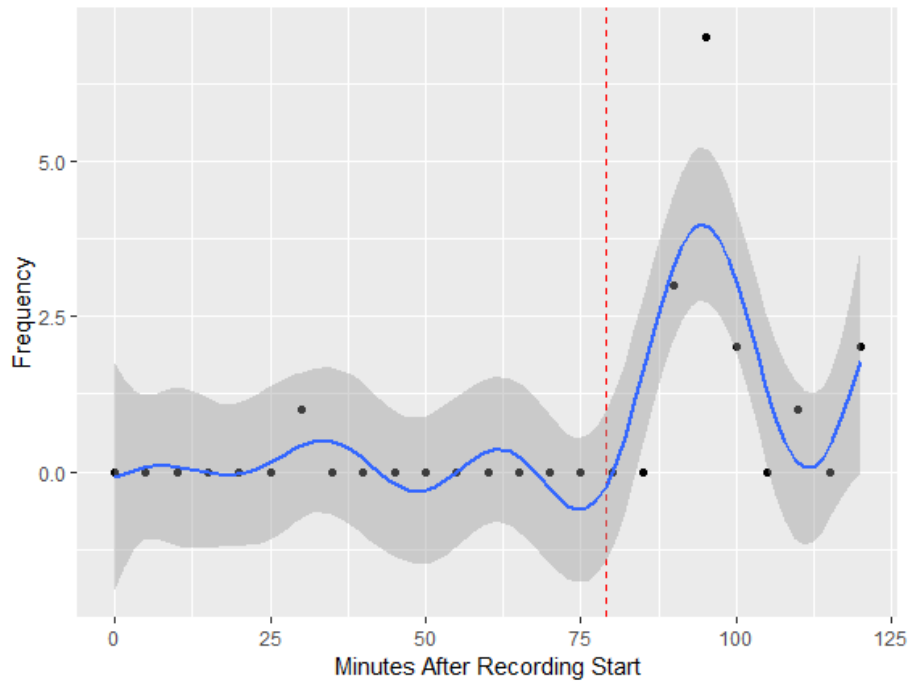
October 6, 2018
Saturday, Feeding Day



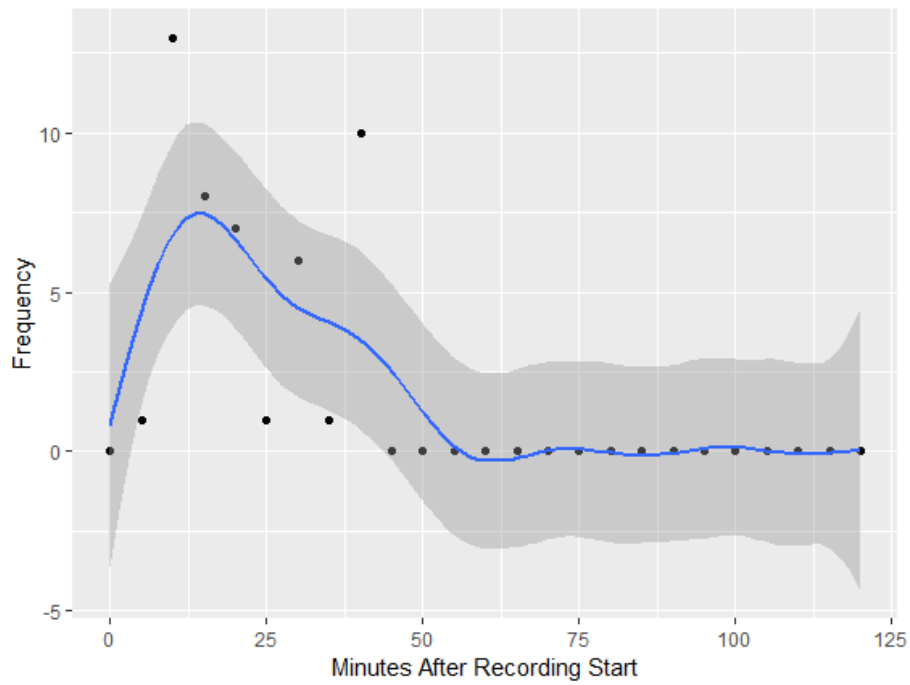
October 7, 2018
Sunday, Fasting Day



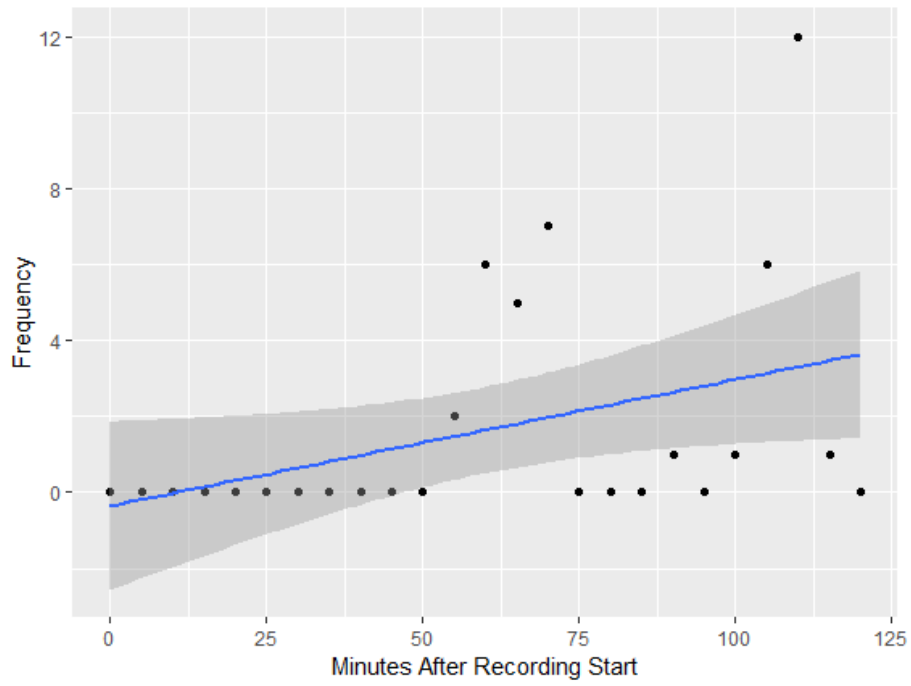
October 13, 2018
Saturday, Feeding Day



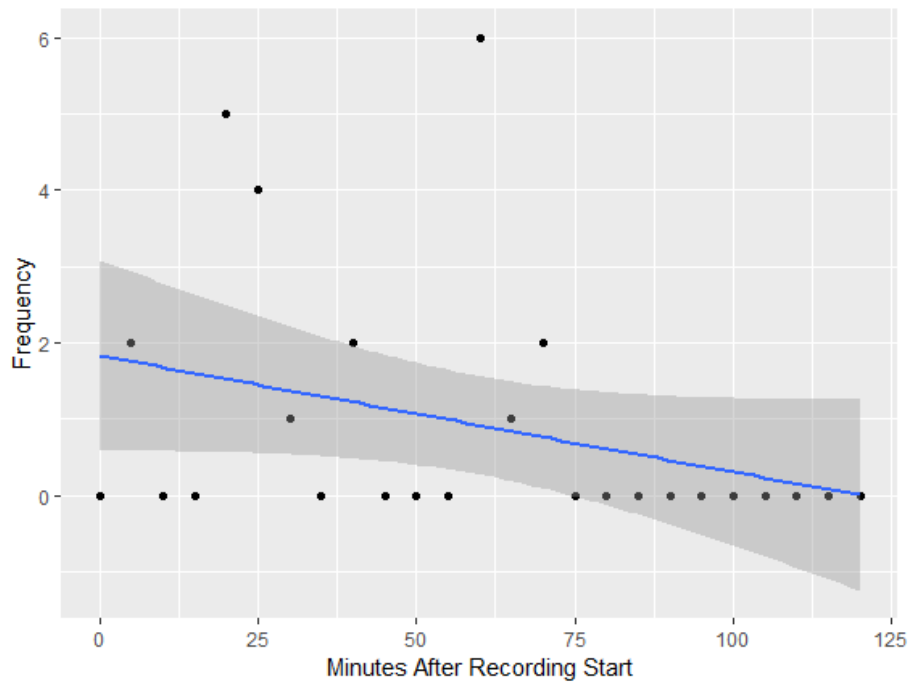
October 14, 2018
Sunday, Fasting Day



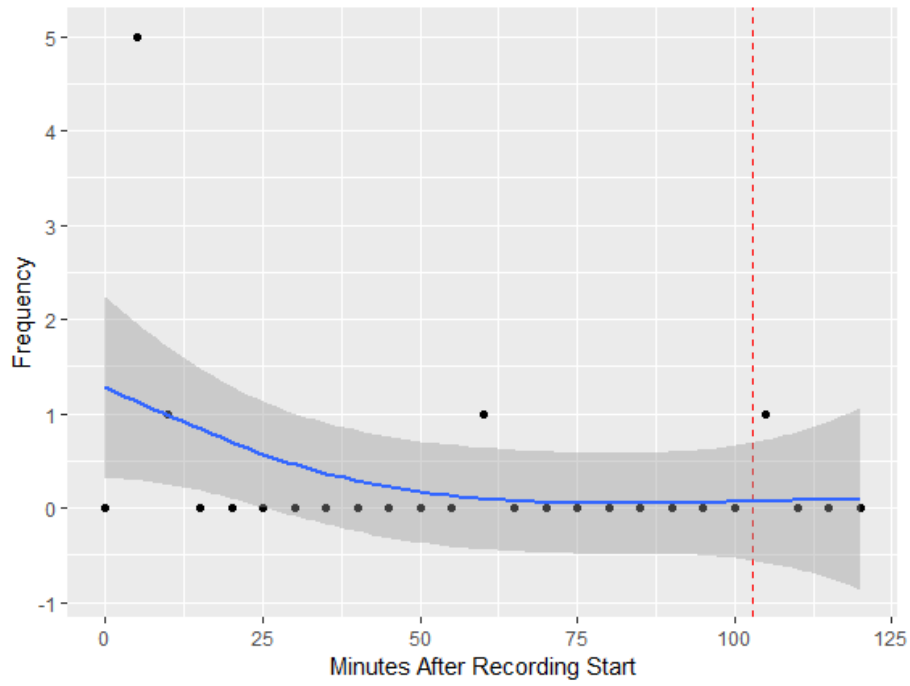
October 20, 2018
Saturday, Feeding Day (feeding not observed)



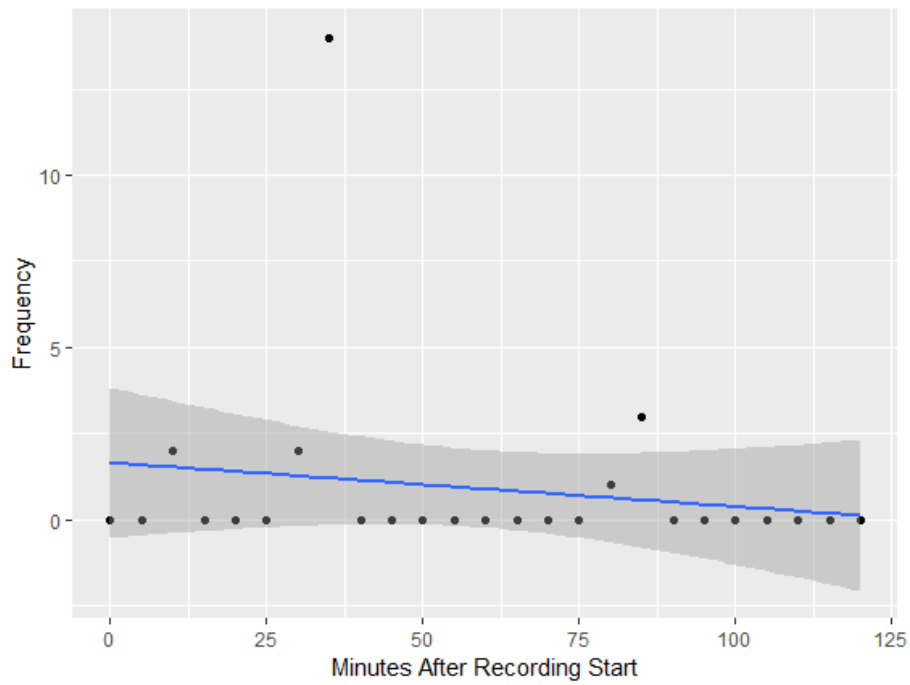
October 21, 2018
Sunday, Fasting Day



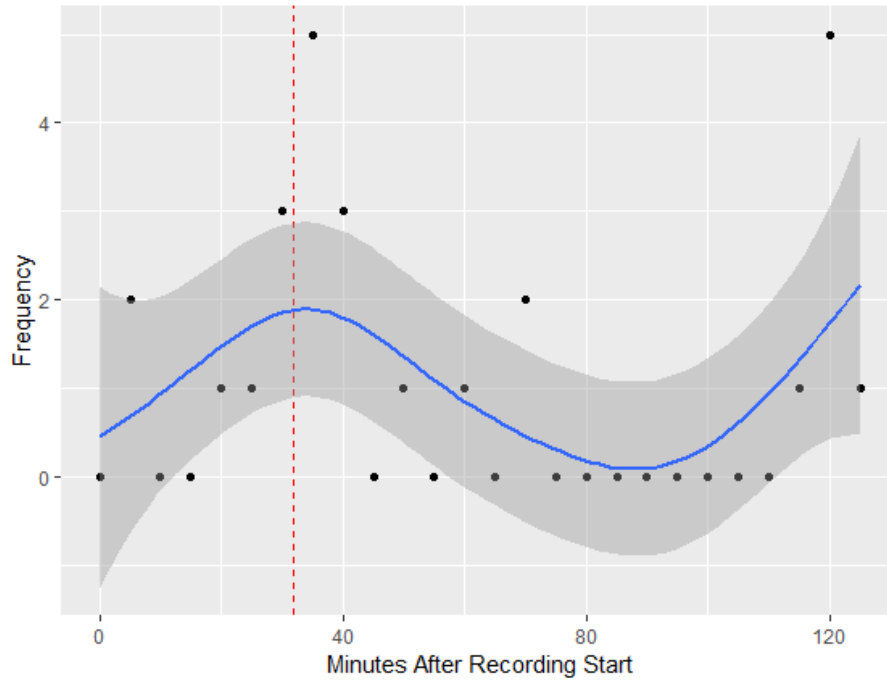
October 27, 2018
Saturday, Feeding Day



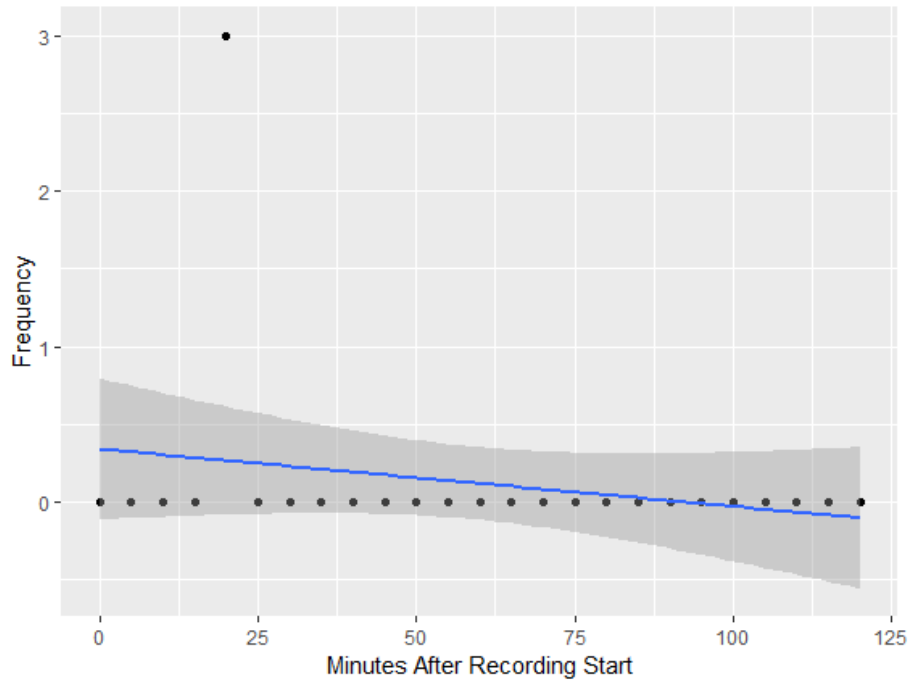
October 28, 2018
Sunday, Fasting Day



November 3, 2018
Saturday, Feeding Day

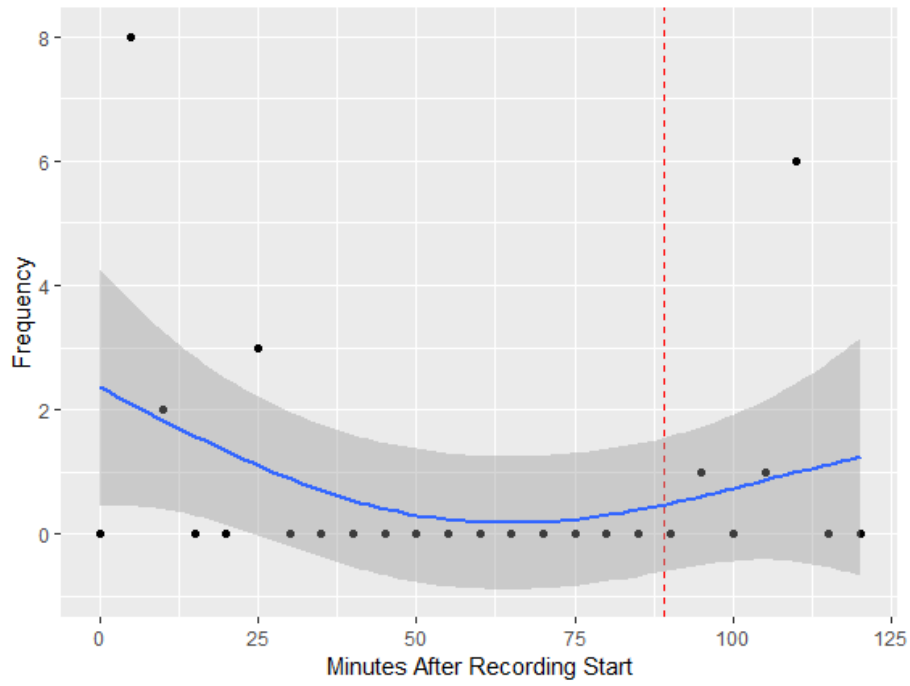


November 4, 2018
Sunday, Fasting Day



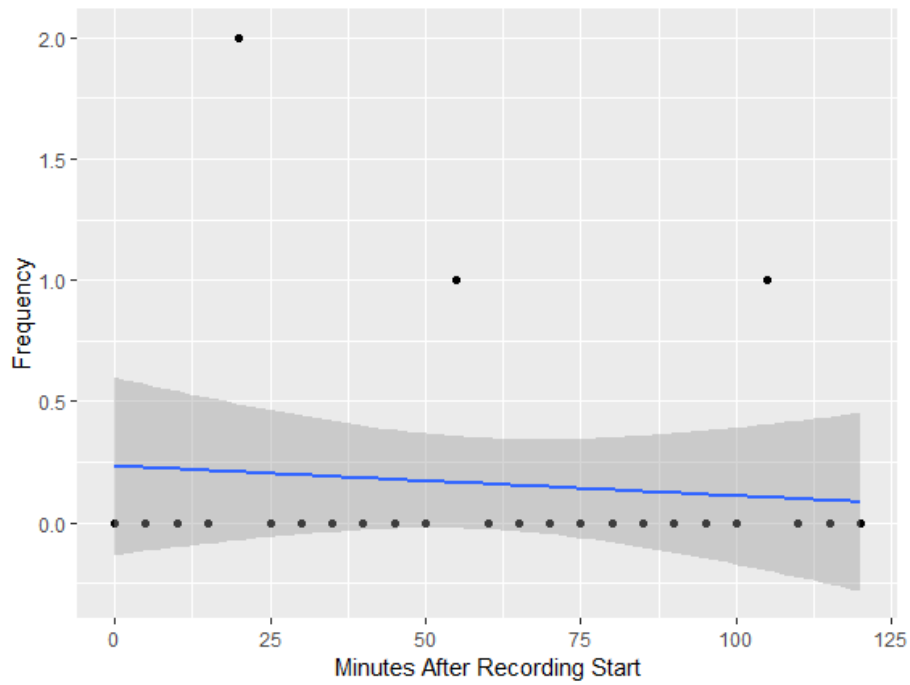
November 10, 2018

Saturday, Feeding Day



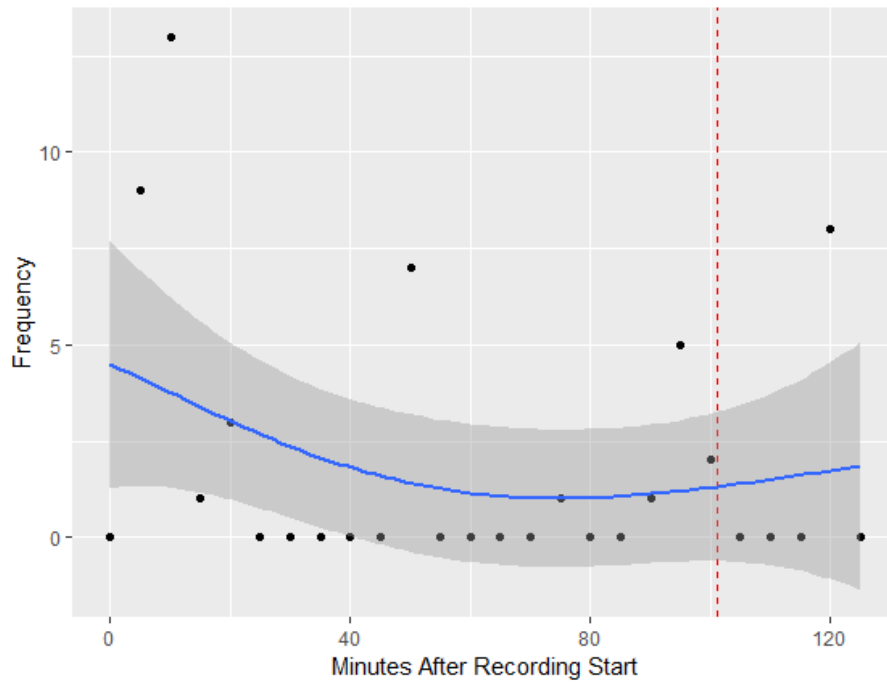
November 11, 2018

Sunday, Fasting Day



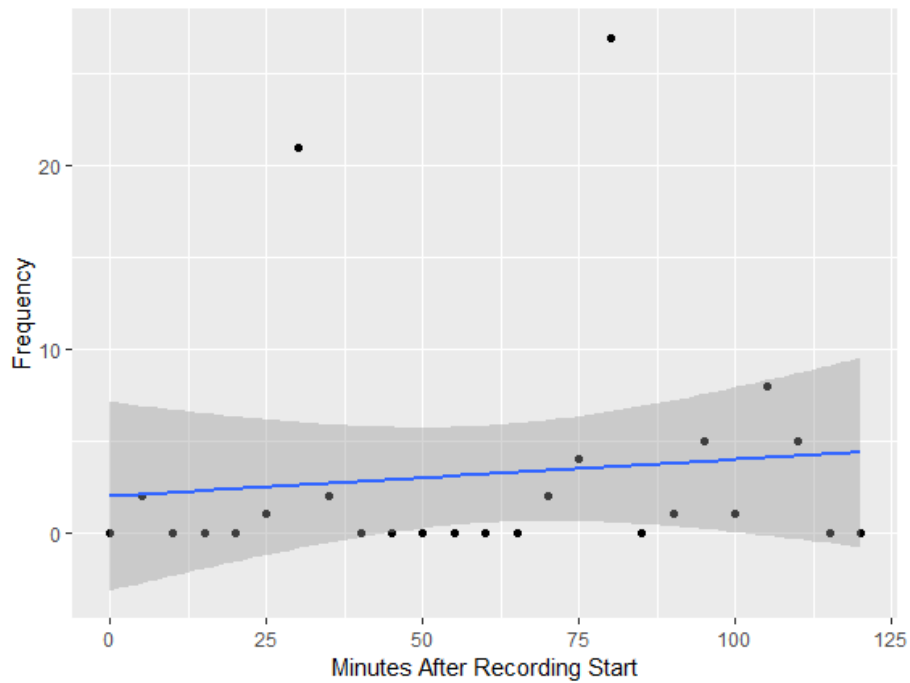
November 17, 2018

Saturday, Feeding Day

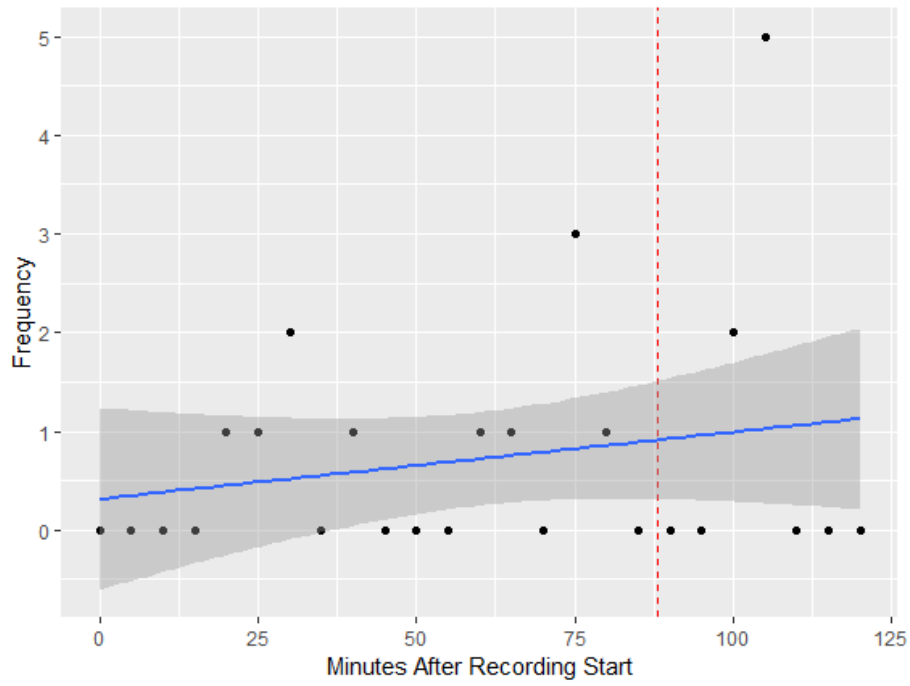


November 18, 2018

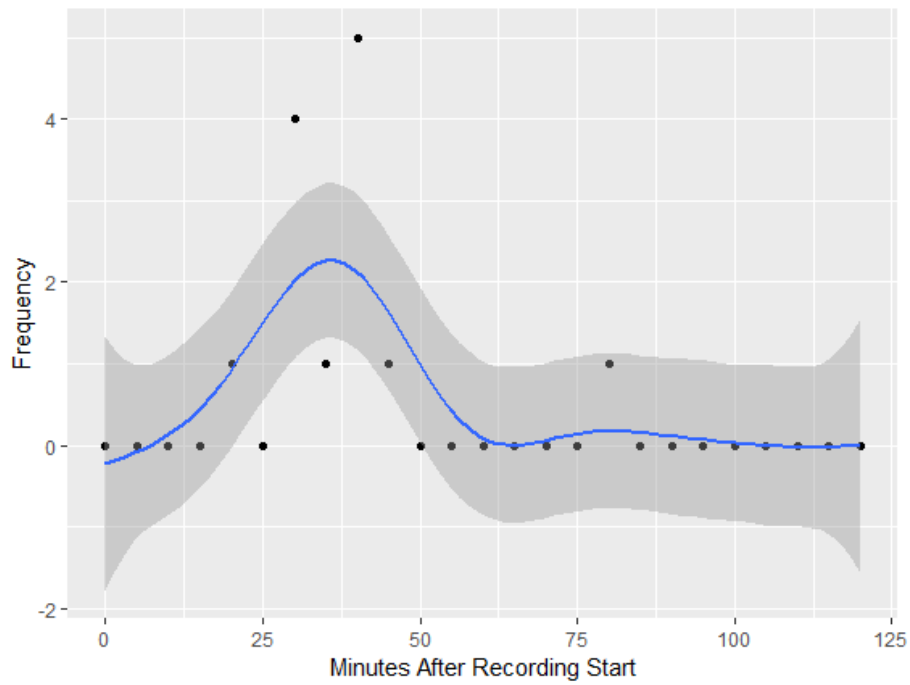
Sunday, Fasting Day



December 1, 2018
Saturday, Feeding Day

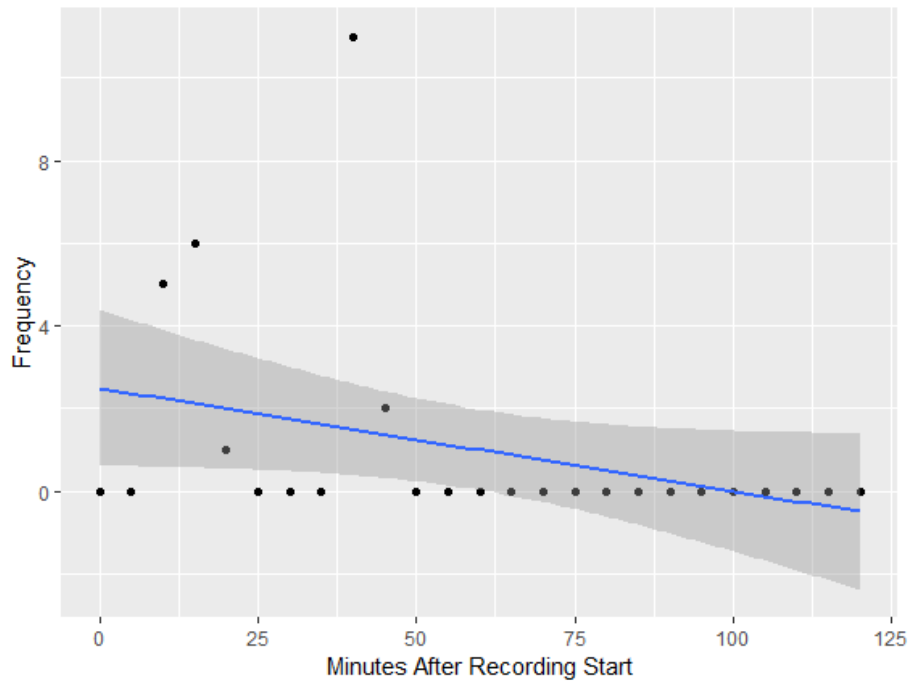


December 2, 2018
Sunday, Fasting Day



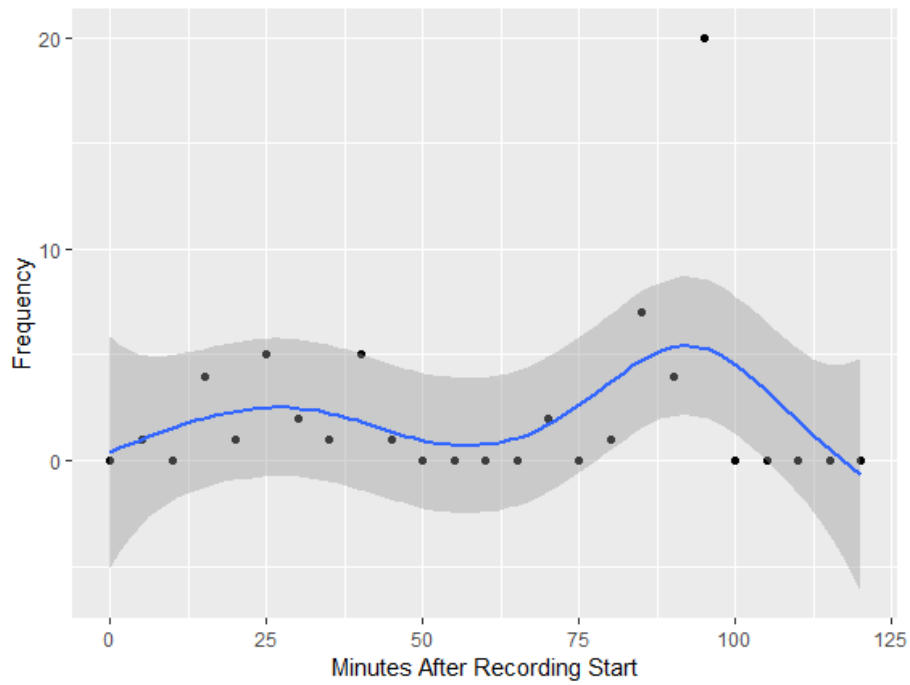
December 8, 2018

Saturday, Feeding Day (feeding not observed)



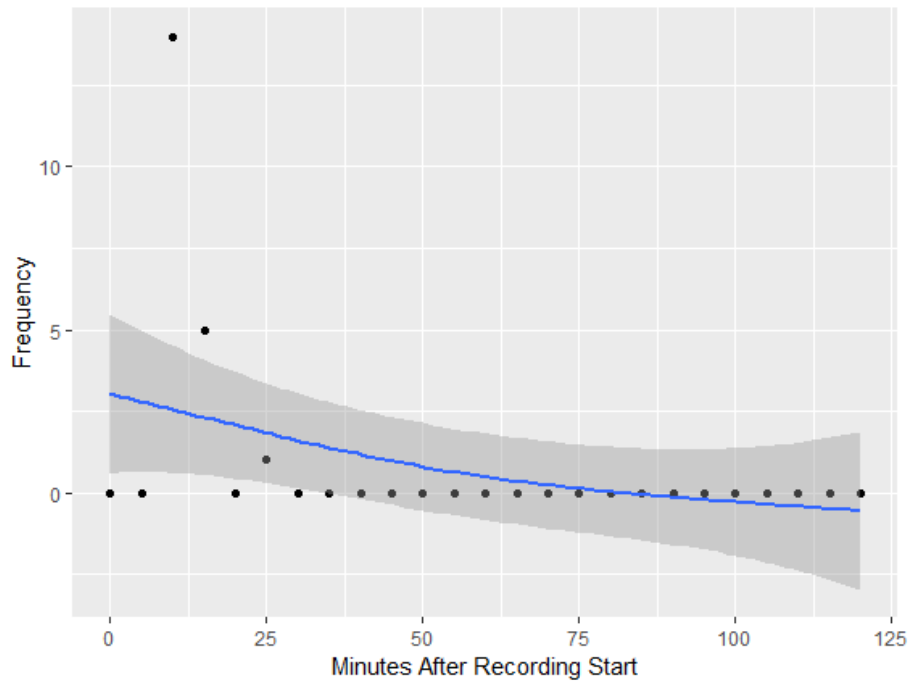
December 9, 2018

Sunday, Fasting Day



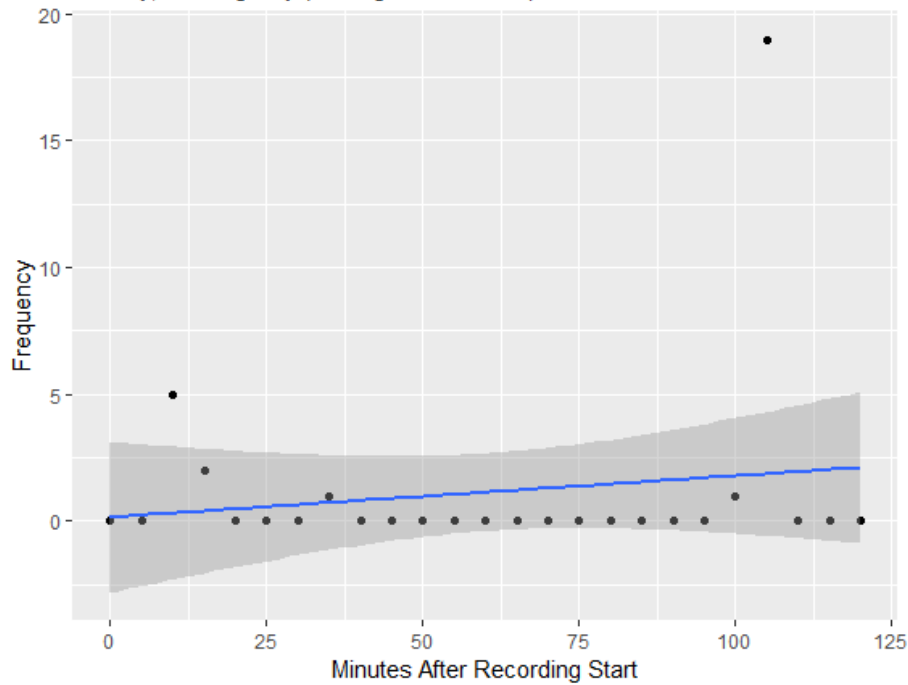
December 15, 2018

Saturday, Feeding Day (feeding not observed)



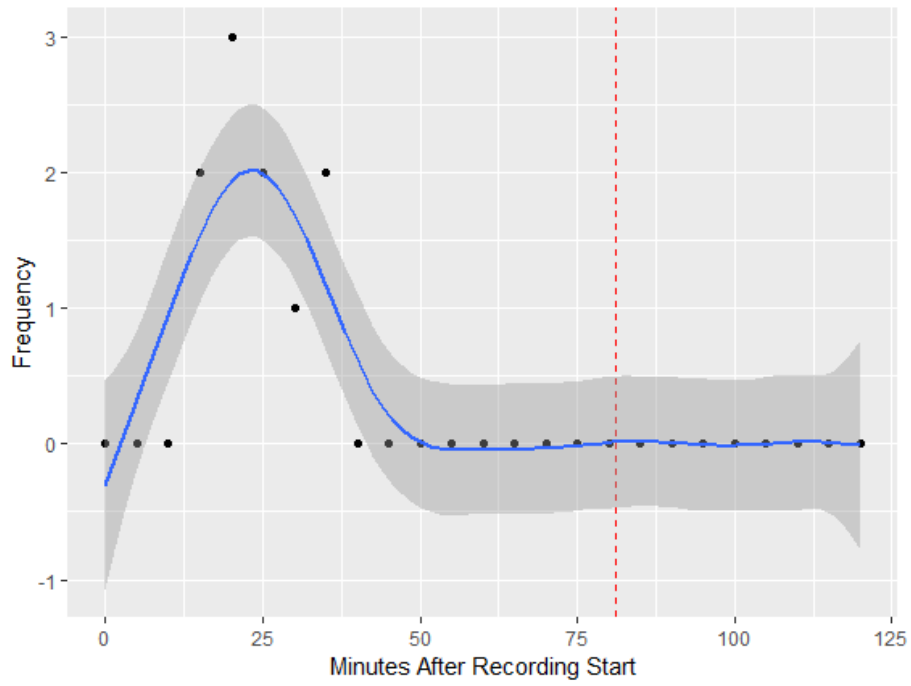
December 16, 2018

Sunday, Feeding Day (feeding not observed)



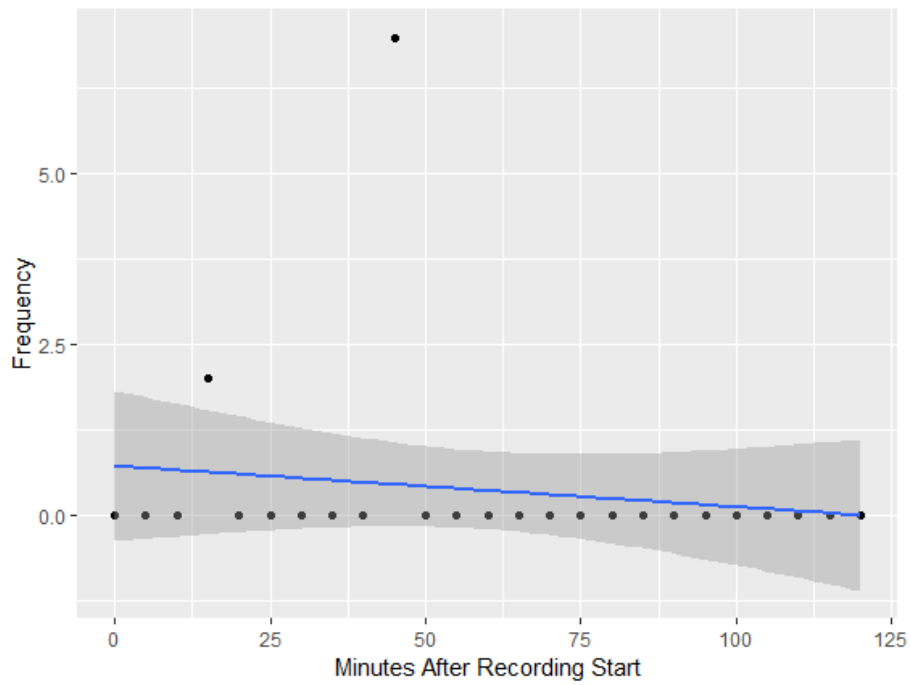
December 22, 2018

Saturday, Feeding Day



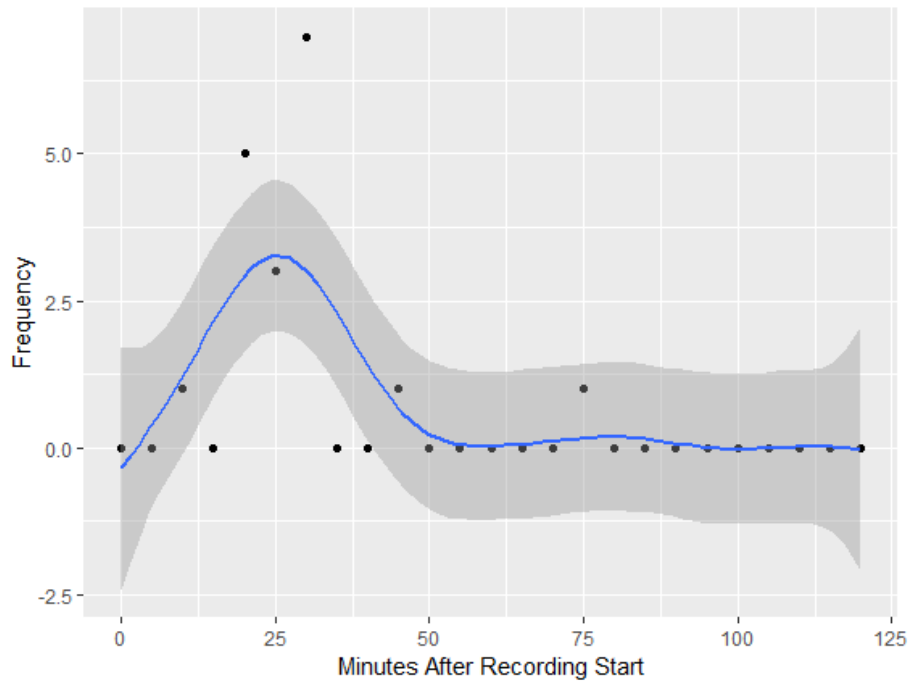
December 23, 2018

Sunday, Fasting Day



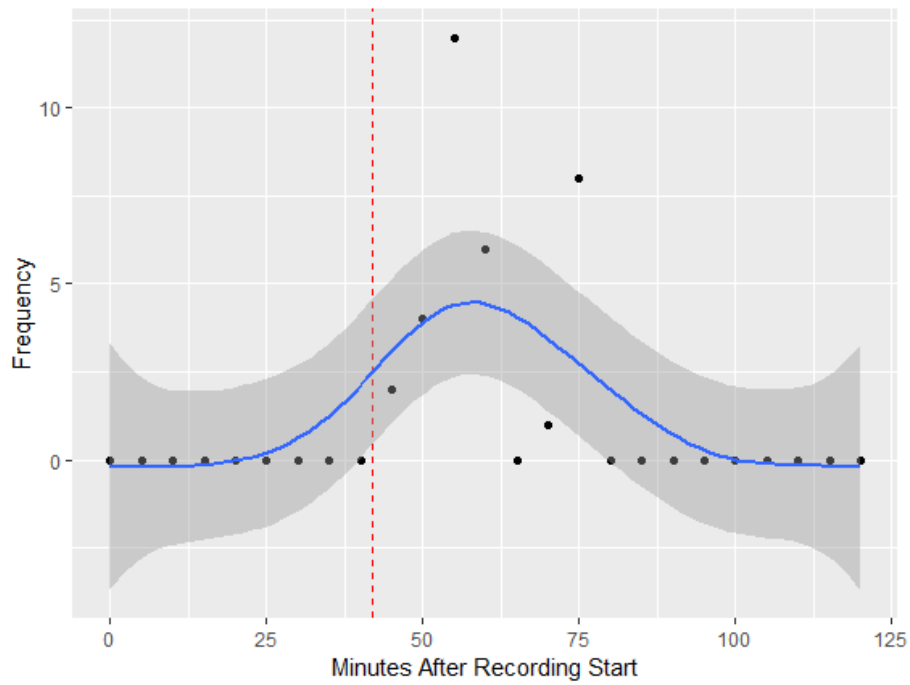
January 5, 2019

Saturday, Fasting Day (schedule switch week)



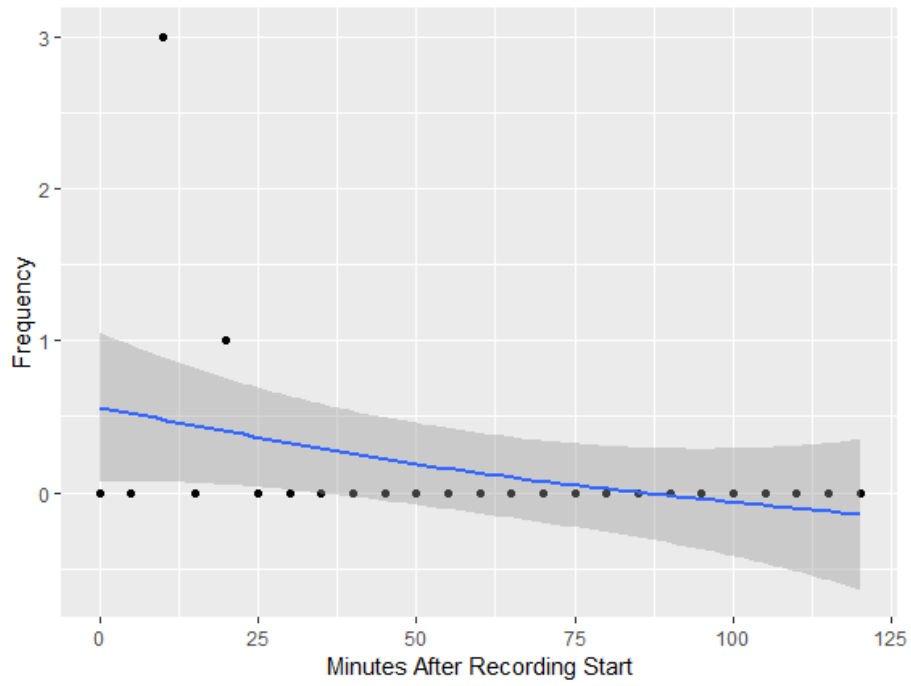
January 6, 2019

Sunday, Feeding Day (schedule switch week)



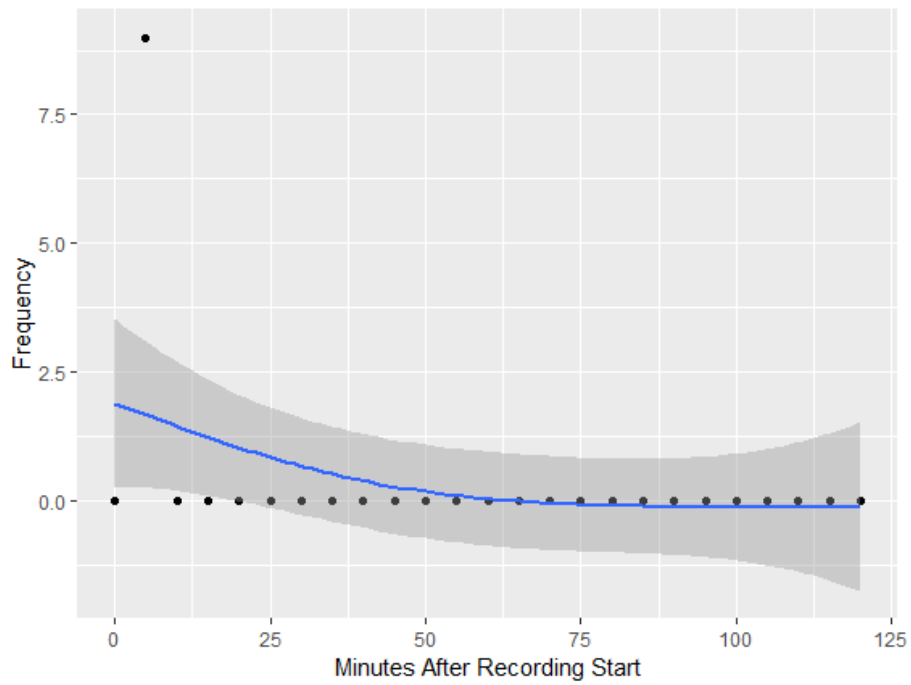
January 12, 2019

Saturday, Feeding Day (feeding not observed)



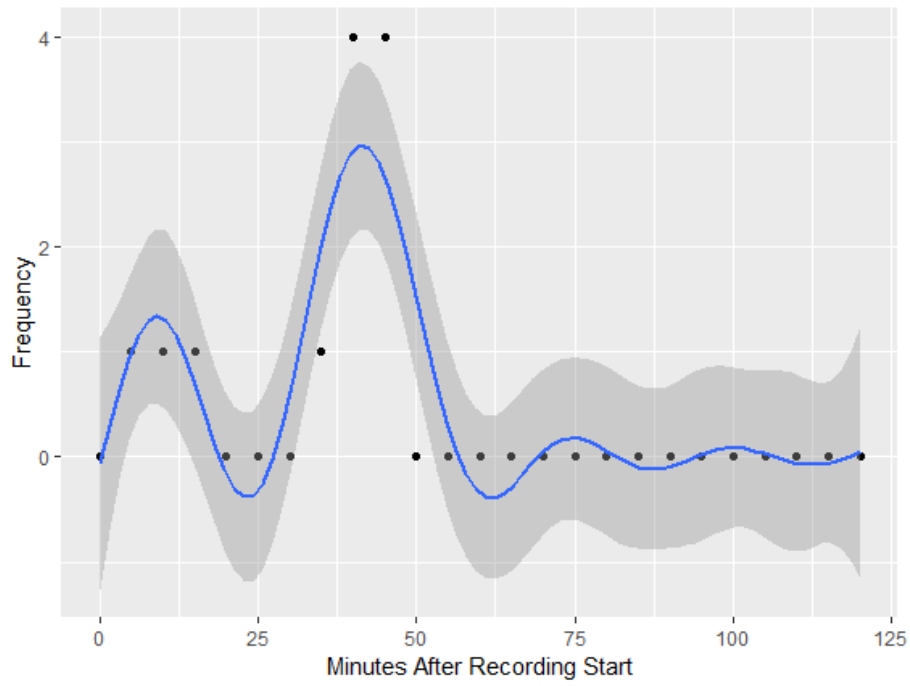
January 13, 2019

Sunday, Fasting Day



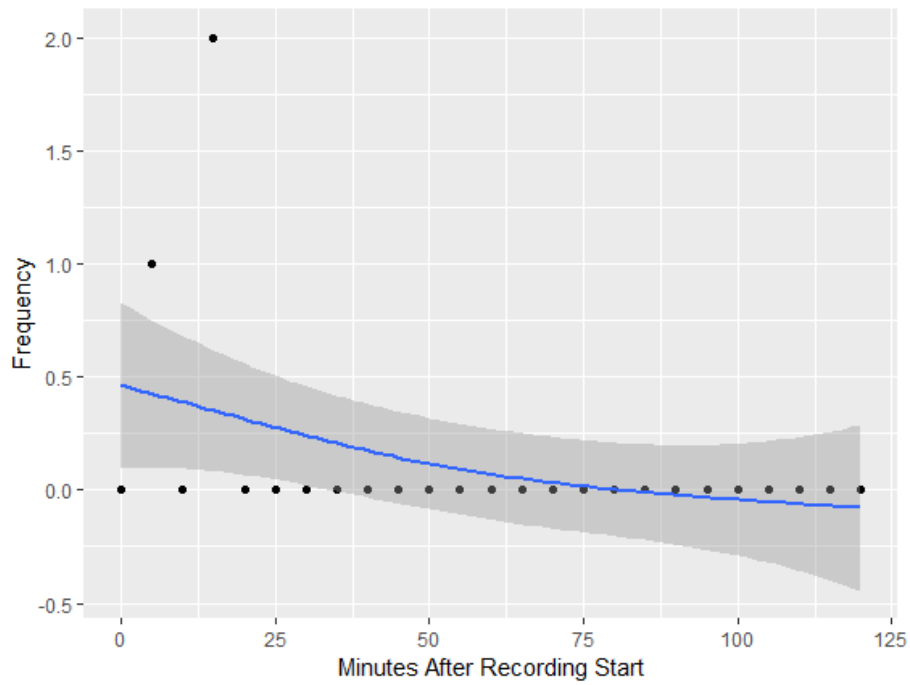
January 19, 2019

Saturday, Feeding Day (feeding not observed)



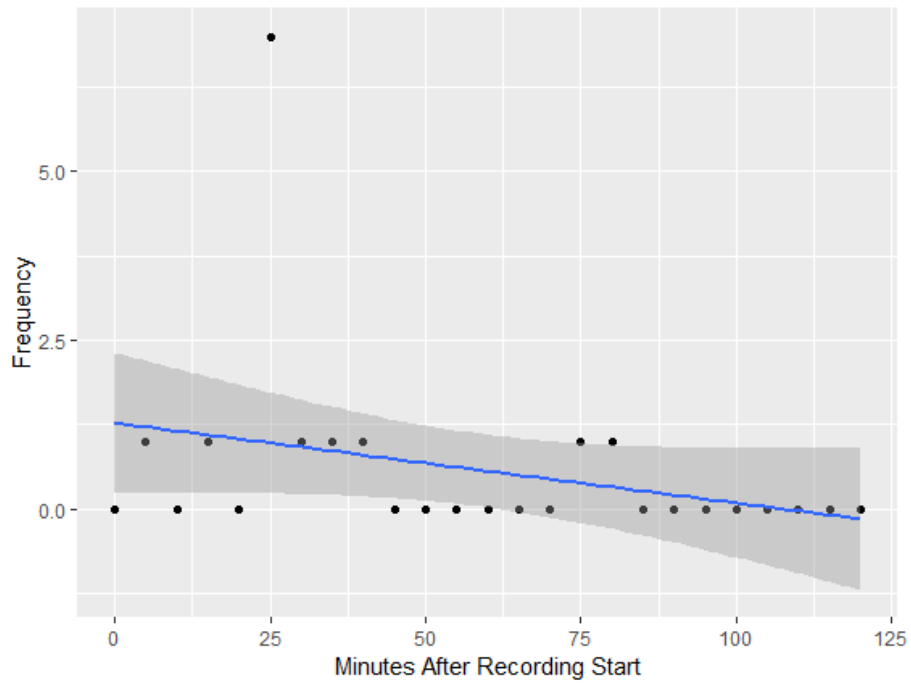
January 20, 2019

Sunday, Fasting Day



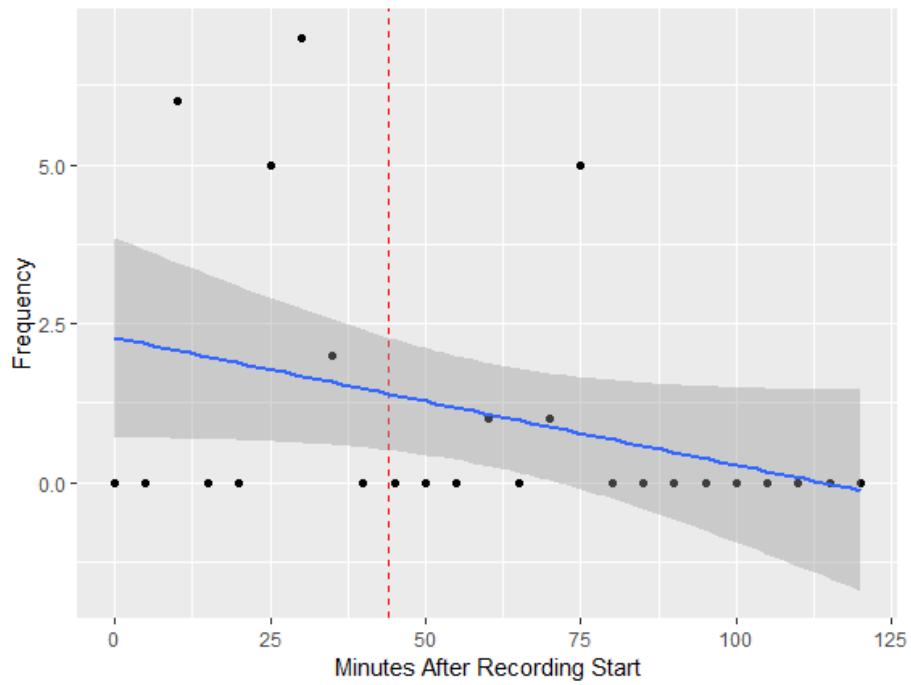
January 26, 2019

Saturday, Fasting Day (schedule switch week)

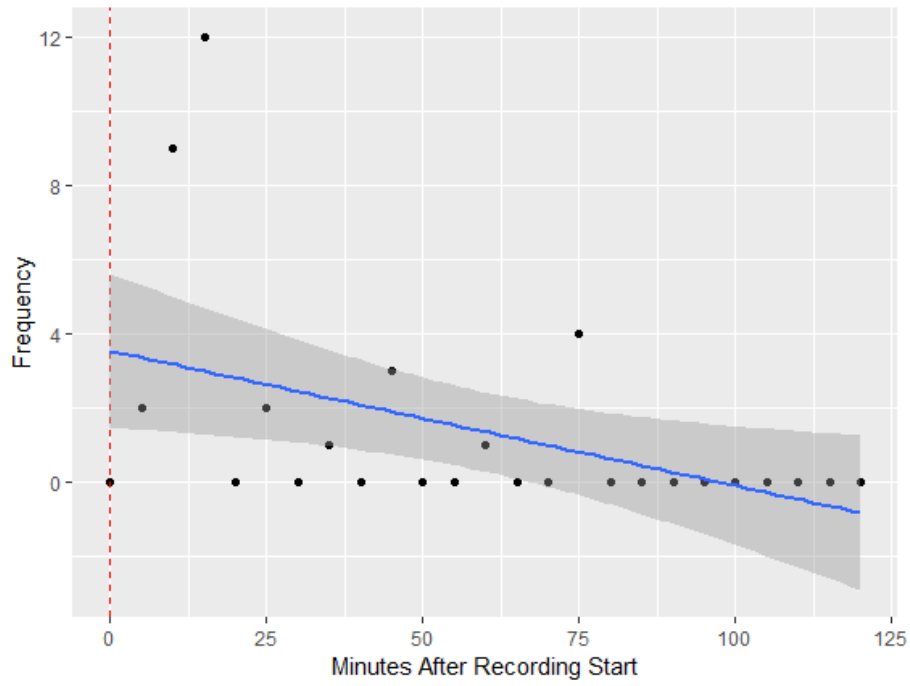


January 27, 2019

Sunday, Feeding Day (schedule switch week)



February 2, 2019
Saturday, Feeding Day



February 3, 2019
Sunday, Fasting Day

