What Defines Us:
An Analysis of Grieving Behavior in Non-Human Primates as a Potential Evolutionary Adaptation

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May 2013

Abstract

Grief is one of the most fundamental human emotions and one of the least studied. One of the ways we discover more about humanity is by studying the rest of our order: the primates. Studying grief in other primates can help us understand our own grief better, and thus help those suffering from it. This thesis compiles accounts of primate grief (death of an infant, death of a parent, and death of a conspecific); compares those accounts to human grief, and analyzes whether grief could be an adaptive trait. It was found that primate grief is fundamentally no different than human grief. While there is not enough data to conclude whether grief is an adaptive trait, it does function in a beneficial way in most primates. The discoveries that grief can be found across our order and that grief is more beneficial if allowed to progress naturally has repercussions for how grieving humans are treated. Humans, like primates in the wild, should be allowed to grieve in their own time and way to ensure their health and survival.

Acknowledgements

I would like to thank my primary thesis advisor, Dr. Herbert Covert, for his incredible patience and encouragement throughout the process of writing this thesis. His insight into primate behavior and his willingness to look beyond straightforward behaviors were invaluable to me during this process. I would also like to thank my committee members, Dr. Michelle Sauther and Dr. Michael Breed for their support. My semester taking their classes is where I truly began work on this project.

I would also like to thank Dr. Douglas Bamforth, the students of the honors thesis seminar, Carol Fiore, and the Anthropology Club for dealing with my stress and letting me talk about grief in primates for months on end.

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Introduction

Of all the human emotions grief may be the most difficult to describe. This difficulty has been the inspiration for many writings on grief, from song lyrics to stories by the world's greatest authors. Given that grief is a universal emotion experienced among humans, should we not expect to see it in non-human primates as well? This thesis will focus on the many accounts of grief in non-human primates. It will seek to establish a hypothesis that the emotion of grief is deeply felt in primates and functions in a beneficial way.

Accounts of primate grief date back as far as 1879, when a naturalist described a "certain degree of genuine grief" in a captive male chimpanzee (Brown, 1879). The male chimpanzee had been housed with a female for many years at the Philadelphia Zoological Garden. In the absence of other chimpanzees, the two became predictably attached to each other. When the female died, the male first attempted to rouse her. When he was unable to wake his only friend, he proceeded to scream and tear at his hair. He tried unsuccessfully to prevent the removal of her body, and then spent the rest of that day and the next moaning and crying. The male was heard to utter a never before heard sound that the naturalist posited was "specialized as a note of grief" (Brown, 1879). The naturalist did not know how commonplace this grief reaction was.

Today we have more formal studies of primates, both in labs and in the wild. This thesis will discuss many similar accounts of responses to death; be that the death of an infant, a mother, or a conspecific. The grief response is widespread among non-human primates, from lemurs to chimpanzees. It will be established that in many cases grief serves a vital function in helping the animal adjust to its new environment without the deceased. Any discussion of grief must first begin with an attempt to characterize and define this intricate emotion.

Defining Grief

In the field of psychology there are two types of grief. The most common is referred to as “normal grief” and follows any kind of real or perceived loss or separation; from a person, an object, a pet, or an abstract need (Cowles and Rodgers, 1991). The second type of grief is referred to as “complicated grief” and occurs in approximately 10% of people (Shear, 2009). Complicated grief is a maladaptive mental disorder that differs from normal grief in length and severity. Those with complicated grief are unable to accept their loss and move on, so their symptoms persist (Glass, 2005). These people often refuse to accept the reality of their loss, which can lead to parapsychotic grief: hallucinations that their loved one is still with them (Corrigan, 1997). The distinction between normal grief and complicated grief is an important one. As with many normal and adaptive behaviors, grief can be taken to maladaptive extremes, which is what we are seeing in complicated grief. These extreme examples do not mean that grief lacks survival value.

Normal Grief

The concept of normal grief has historically been vague and ambiguous and has changed very little over the last several decades (Cowles and Rodgers, 1991). Grief remains just as difficult to identify, and just as painful to talk about, as it has for most of human history. It has been defined as both a syndrome and an adaptational response to death. Though it is often described as a universal emotion, grief remains difficult to define. Cowles and Rodgers are some of the few who have tried; their framework for understanding grief is one of the best and most comprehensive. Using concept analysis to examine the existing literature on grief, they compiled a comprehensive and holistic definition of grief. Grief is distress over a loss and is characterized by Cowles and Rodgers as “a dynamic, pervasive, highly individualized process with a strong normative component” (1991). This long definition requires some breaking down to build an understandable framework.

Their first attribute of grief is that it is “dynamic.” Grief is a process, but it is not linear. There are no stages or phases to grief; the emotions and thoughts that accompany grief are chaotic and do not occur in any kind of order (Cowles and Rodgers, 1991). These emotions occur in waves, which differs from major depressive disorder where sadness is constant (Shear, 2009). Similar to the waves of sadness, grief has clusters of activities and is not a state of being.

Grief is individualized. It is accompanied by a wide variety of symptoms and responses (Cowles and Rodgers, 1991). The characterization of grief as “pervasive” means that it invades multiple parts of a person’s life. It is not only an emotional response, it can also be physical, social, cognitive, affective, behavioral, and spiritual (Cowls and Rodgers, 1991). Responses in all these categories, except spiritual, can be observed in non-human primates. The last component of grief is that it is “normative.” This means that there is such a thing as normal grief. Beyond some point of time and severity, the response becomes pathological (Glass, 2005).

Symptoms of Grief

Given the pervasive and individualized nature of grief, it can be difficult to identify using a list of defining characteristics. However, in order to identify the grief response in primates—who cannot, for the most part, tell us that they are grieving—a general picture of what grief looks like must be constructed.

The general characteristics of grief are: shock, disbelief, painful experiences of loss and sadness, loss of interest in normal activities, and finally recovery (Glass, 2005). The symptoms of grief can be group into two general categories: physiological symptoms and psychological symptoms (Kowalski and Bondmass, 2008). These general symptoms can resonate throughout many behaviors and processes.

Anyone who has experienced grief knows that it can often feel like physical pain. Common ways for people to characterize the feelings that accompany grief are in reference to physical pain. This pain can be very real. In humans it has been shown that grief increases the incidence of physical illness (Kowalski and Bondmass, 2008). The actual physical effects of grief include general pain, gastrointestinal problems, medical or surgical conditions, sleep disturbances, and neurological problems (Kowalski and Bondmass, 2008). Many obscure medical conditions, such as Irritable Bowel Syndrome, are often thought to be caused by emotional distress including grief (WebMD). The psychological symptoms of grief are sweeping and can include depression, anxiety, loneliness, crying, sadness, stress, hopelessness, and worry (Kowalski and Bondmass, 2008). These symptoms may be shown together, in stages, or not at all (Shear, 2009).

These symptoms are numerous and can point to other problems besides grief, but the presence of one or more following a death or loss is a good reason to suspect grief. Charles Darwin did extensive work on grief in his book *The Expression of the Emotions in Man and Animals* (1890). He sought to characterize expressive grief. According to Darwin, immediate grief led to violent frantic movements, while prolonged grief led to motionlessness and passivity. In particular he described those suffering long term grief as motionless, but “rocking to and fro.” Darwin also sought to characterize the facial expressions that accompany grief and found certain ones in all cultures and “races:” a wrinkled forehead, eyebrows raised in the middles, the corners of the mouth drawn down, and the eyes dull and lacking in expression. Darwin labeled the forehead muscles the “grief muscles” as he believed they were only used to express this emotion (Darwin, 1890). Darwin’s characterizations of grief may actually be easier to see in non-human primates.

The Work of Grief

The “work of grief” was a phrase originally coined by Erich Lindemann in 1944 and describes a process requiring emotional and physical expenditure in order to recover (Cowles and Rodgers, 1991). This is a useful concept for thinking about grief as having survival value. When the work of grief is finished—if it is done properly as in normal grief—the person ends up with a new reality established and a new identity developed. This new identity, formed after grief is confronted, is better suited to the individual’s new environment; that is, the environment without the person or thing that was lost (Cowles and Rodgers, 1991). If this new identity helps the individual to survive following the grief, then the process of grief can be considered an adaptive trait, since it increased survival and therefore fitness (Strier, 2011).

Stages of Grief

A discussion of grief would not be complete without an examination of Elizabeth Kübler-Ross’s “5 stages of grief.” These stages of grief are well known: denial, anger, bargaining, depression, and acceptance (Kübler-Ross, 2005). Originally put down in her book *On Death and Dying* Kübler-Ross later clarified in *On Grief and Grieving* that she was too eager in branding them as stages (Kübler-Ross, 2005). Unfortunately, many psychologists continue to see the stages as a set progression that grief should follow—and anything off this path is abnormal. However, the highly individual and dynamic nature of grief makes classification into stages impossible. Viewing Kübler-Ross's five stages not as a linear timeline of grief but as responses to loss can be very useful in creating a general portrait of grief.

Denial is disbelief over the death. This is the stage where complicated grief generally becomes stuck (Shear and Shair, 2005). This is not denial about the actual death, but denial about how life must change after it. In normal grief this stage is temporary and helps the individual survive by pacing the emotions and only allowing in what can be handled immediately (Kübler-Ross, 2005). Anger, another stage, can be expressed toward the deceased, toward the self, or toward the world. Anger helps the individual avoid the loss temporarily; it is an emotion more easily managed than hopelessness and sadness (Kübler-Ross, 2005).

Bargaining, a third stage, is associated with preoccupation with what could have happened or been done to avoid the loss. Bargaining is sometimes called a transition stage. Depression is a stage characterized by withdrawal from life and activities and a lack of energy. This stage gives the individual time to think over their life and how it must now change, allowing them to begin to form that new reality that is so important in the work of grief. The final work of grief happens in the last stage of acceptance. This is where the new reality is accepted and a new identity shaped to fit the new environment (Kübler-Ross, 2005).

Though these stages are general, they can also be very visible. Therefore, the stages of grief as common responses can be useful in understanding what we are seeing when we observe grieving primates.

Complicated Grief

Complicated grief, as a pathology that can obscure the adaptive nature of normal grief, is also important to define so that it can clearly be separated from normal grief. The distinction between normal grief and complicated grief goes back to Sigmund Freud, who viewed normal grief as a normal and necessary process (Glass, 2005). Complicated grief is a long term functional impairment, which results in a failure to incorporate the reality of the loss or death into the individual’s life (Shear and Shair, 2005).

Complicated grief is occasionally treated like post-traumatic stress disorder (Prigerson et al., 1995). Most of the symptoms displayed by those with complicated grief are the same as those displayed during normal grief, just for a much longer duration and to a much greater extent. Sufferers from complicated grief may also display preoccupation with the death, distrust of others, avoidance of all reminders of the person lost, a feeling that life is empty, hallucinations, survivor guilt, bitterness, and a failure to return to a normal routine. These people cannot overcome disbelief concerning the loss, thus this condition is considered maladaptive (Prigerson et al., 1995).

Since the distinction between complicated grief and normal grief exists in humans, it is possible that it exists in other primates as well. This is important when considering extreme cases of primate grief, such as that of Gombe chimpanzee Flint, whom Jane Goodall described as having “died of grief” (Masson and McCarthy, 1995). Such cases of death due to the process of grief do not necessarily mean that grief lacks survival value, but instead could be examples of complicated grief.

Distinctions: What Grief is Not

It is important to distinguish grief from closely related emotions in order to diagnose and treat humans. In considering grief in non-human primates it is important to know whether the observed behavior was attributable to grief when assessing its survival value. Grief is part of a set of emotions; including sadness, depression, guilt, and grief (Nesse, 2000). However, grief is distinctive from these emotions.

Grief is not Depression

Though many people use grief interchangeably with depression, the two are distinguishable. Temporary depression may be a symptom of grief, but long term depression is a pathology that differs fundamentally from grief. Dr. Kay Jamison has experienced both grief from a loss and depression in the form of bipolar disorder. She characterizes depression as a madness, but grief as a healing process (Levin, 2010). In depression the sadness and hopelessness are constant and unchanging; in grief sadness comes in waves and can be accompanied by nostalgia or anger. In depression the accompanying thoughts ruminate unhelpfully, but with grief the thoughts help process the loss and assist in healing. Jamison states that depression is a destructive disease. Grief, conversely, provides a path to healing and is a necessary process to “preserve the self” (Levin, 2010).

The main symptom of grief that is not present in depression is yearning (Shear, 2009). Grieving people feel a longing for the thing they lost, but depressed people are often simply hopeless—they want nothing. Grieving people also retain the ability to experience positive emotions; they may even have moments of happiness while recalling good times spent with the deceased person. Those suffering from depression lose most of their ability to feel any positive emotions at all for long periods (Shear, 2009). This distinction makes it difficult to identity grief if the observations are fleeting, since it comes and goes rather than being constant like depression.

Grief versus Mourning and Bereavement

Mourning and bereavement are closely linked with grief. Mourning is defined as the rituals and activities accompanying a loss. It is associated with public displays of grief and can be considered the cultural aspect of the grief response (Parkes, 1985). The cultural and ritualized aspects of mourning make its usefulness limited in studies of non-human primates. Some have referred to nonhuman primates as in "mourning," but what they are usually describing in these cases is the grief response (Hanlon, 2009). Mourning behaviors do not necessarily mean someone is going through the grief response. Some people later convicted of murder have been seen mourning at the funeral of the person they killed, but they are usually not grieving for that person.

Bereavement is even more closely related to grief. Bereavement can be considered the emotional state of having experienced a death (Demi and Miles, 1986). Therefore bereavement can include any number of responses other than the grief response (e.g. joy at the death of an enemy or abuser). Bereavement, as a state of being not requiring any specific behaviors, is difficult to visualize. It is grief that is the emotions we so often think of as associated with bereavement.

These distinctions are important when reviewing literature on primates. Bereavement is fairly easy to establish given any long term study of the animal in question, while mourning is probably impossible. Although many people use these terms interchangeably with grief it is incorrect to do so.

Do Non-Human Primates Grieve?

The question of animal emotions is one of the most fiercely debated topics in animal behavior. For most of the 20th century behaviorists and ethologists considered emotions unimportant in studying behavior (Panksepp, 2011). That view has changed in recent decades. Some scientists, like Jane Goodall, had few qualms about naming their study subjects and attributing to them emotions and personalities. Others refuse to do either, using only numbers and stalwartly refusing to see emotions even when they are obvious. Perhaps the question should not be whether primates feel grief, but rather why anyone would ever think that so basic an emotion would not be felt by intelligent creatures, some of whom are even capable of using sign language.

Some scientists maintain that the existence of emotions can only be detected through verbal reports (Panksepp, 2011). However, few humans can express grief in words. But if it is communication that is needed Koko the gorilla provided it upon the death of her kitten All Ball, Koko told her trainer in sign language "cry, sad, frown" (Patterson, 1985). In three words Koko confirmed that, given the correct vector, animals can communicate their emotions to us nearly as well as humans.

The following is a brief argument for grief in primates, since it is only with the knowledge that primates grieve that an argument for the survival value of grief can be presented.

Funktionslust

One of the best, and most scientific, arguments for animal emotions stems from the idea of *funktionslust*. This term refers to the pleasure an individual, or animal, takes in what they are good at doing (Masson and McCarthy, 1995). This idea fits into evolutionary biology which holds that anything—be it a trait or a behavior—that enhances survival will be selected for (Strier, 2011). Combining this fact with the idea of *funktionslust* it follows that if an animal is good at something, and that behavior is important to survival, it would be adaptive for the animal to enjoy doing it (Masson and McCarthy, 1995). A cheetah who hates running will not survive very long. But if animals enjoy doing these behaviors, they could increase their survival and fitness.

It is difficult to assess whether it is a behavior that is selected for, or the underlying emotion. However, if an animal is observed performing the enjoyable and adaptive behavior in a situation where it has no survival advantage, it may mean that it is being driven by an emotion (Masson and McCarthy, 1995). If this premise is accepted the issue of animal emotions is resolved. What pet owner has not seen their dog howling, digging, or running for the pure pleasure of it? These wolf behaviors hold no survival value in singly kept pet dogs, but still our loving pets perform them day after day with apparent relish. Another good example is birdsong. In the wild birdsong is adaptive in that it helps to find a mate and defend territory. In captivity, and in the absence of other birds, most birds will still sing (Masson and McCarthy, 1995).

The behaviors of grief will never be demonstrated without the stimulus of grief, given their nature. But if behaviors like happiness and pleasure can be demonstrated in animals it seems obvious that grief can be as well.

Grief in the Brain

The neuroanatomy of grief has recently been studied in humans to determine the physiological basis of this emotion. Interestingly, the identified brain area is present in other primates and offers further evidence that primates grieve.

The concept of the emotional brain that is still dominant is Paul MacLean's triune brain (Dalgleish, 2004). MacLean proposed that the brain is made up of three parts; the most evolutionarily ancient part (the reptilian brain) houses the primitive emotions, the old mammalian brain houses the social emotions, and the new mammalian brain (the neocortex) connects emotions to cognition. One of the integral parts of the reptilian brain is the cingulate cortex (Dalgleish, 2004). In a study in which grieving women were shown pictures of their lost loved ones and listened to words describing them to elicit grief it was found that three primary brain regions activated; the cerebellum, the superior frontal gyrus, and the cingulate cortex (Gündel et al., 2003). These findings suggest that grief is housed, at least partly, in the most ancient part of the brain. This part of the brain is present not only in mammals, but also in birds and reptiles. This shows, at the very least, that primates have the brain structures that make them capable of grieving.

Given that grief (and emotions in general) are housed in a more ancient part of the brain than higher brain functions, looking at those who have and do not have higher brain functions is an indication of who has emotions (Panksepp, 2011). Primates do have higher brain function. We have shown that apes can learn language, monkeys can solve puzzles, and lemurs can count. Why then, would they not be able to grieve? Humans who have lost higher brain function, through accidents or through deteriorating mental conditions, retain their ability to feel emotions and to grieve (Panksepp, 2011).

Recent studies using localized brain stimulation have identified seven major emotional systems (Panksepp, 2011). One of those systems is referred to as the PANIC/GRIEF system. It is posited that this system may be the primal foundation for social attachments, which we know that primates are capable of. The PANIC/GRIEF system was aroused when young animals were socially separated from others, and was also found to lie partly in the cingulate cortex (Panksepp, 2011). The PANIC/GRIEF system was found to be evolutionarily related to the physical pain circuits and to play a role in human loneliness, sadness, depression, and grief. The researchers involved posited that this system helps an animal survive by causing them pain if they are separated from their social support or caregiver, and relieving them of that pain when social bonds are formed (Panksepp, 2011). Social bonds are incredibly important for primate survival, as well as for grooming and defense. A system that prevented them from losing that support system would be adaptive and therefore would be selected for.

The Primates Themselves

Perhaps the most revealing evidence of grief in primates comes from the animals themselves. Flint who "died of grief" and Koko who expressed her grief in words are just two examples. Washoe the signing chimpanzee who lost her infant Sequoyah is a third. The primary difference between grief and other emotions like depression and sadness is a yearning for the lost loved one. Can primates yearn for their lost loved one? Can they hope that they will return to them? After Washoe lost her baby the researchers in charge of her decided to find her a replacement, an infant she could adopt. When researchers told her they had a baby for her Washoe immediately perked up, repeatedly signed "baby" to them, hooted and swaggered, and showed general excitement. She signed to them "my baby." When the researchers placed the strange infant into her enclosure, Washoe immediately lost all her vivacity. She refused to touch the new infant, all the while signing "baby" (Masson and McCarthy, 1995). This clearly shows a devastated mother's hope that her lost infant was about to be returned to her.

Could Grief be an Adaptation?

Everyone suffering grief has likely asked themselves at some point: why do we grieve? This thesis will be concerned primarily with why non-human primates grieve. Biological anthropologists study non-human primates, not only because they are interesting in and of themselves, but also in order to learn something about human nature. Learning why our closest living relatives grieve may help in understanding grieving humans.

There is a school of thought among evolutionary biologists known as adaptationism that holds that all aspects of an organism are adaptive and have been selected for by natural selection (Stanford et al., 2009). Though it is imprudent to assume that all behaviors and traits are adaptive, it is not unreasonable to think that a behavior seen across so many primate taxa could have some survival value. Karen Strier cautions against assuming any behavior is adaptive. She points to five types of evidence needed: long term field studies to show that the behavior happens naturally, individual variation in the behavior, comparisons of the behavior across species, observations of the behavior in individual animals, and a demonstration of phenotypic plasticity—showing that the behavior is displayed under conditions that make it valuable (Strier, 2011). For primates, all of these lines of evidence exist.

What is a Behavioral Adaptation?

Karen Strier defines an adaptive behavior as one that increases the individual's survival, and therefore reproductive success (2011). A behavioral adaptation is both a feature of an organism and an evolutionary process. As an evolutionary process, it is sensitive to the influence of the environment. Behaviors, like physical traits, have a genotype (the genetics underlying the behavior) and a phenotype (the behavior displayed). The phenotype of the behavior is a strategy that has been shaped by natural selection for its survival advantages. Much behavior shows phenotypic plasticity; the behavior may show variability, which allows it to be adaptive in different environments (Strier, 2011). To determine whether grief is an adaptation, an assessment of the survival advantage to the organism must be made. However, not all aspects of an adaptation need to be used or be adaptive by themselves. An adaptation is not necessarily optimum; it is the best that natural selection had to work with (Bock, 1980). Therefore, components of the behavior can be maladaptive, but when they come in a set like the behaviors associated with the grief response we need only establish that the set of behaviors overall has survival value.

Grief as a Behavioral Adaptation

The majority of this thesis is dedicated to accounts of grief, with commentary on the survival value of the response in each situation. However, it has already been shown that certain depressive states similar to the grief response do confer survival value.

One defense of grief as an adaptation is the nature of grief itself. The depression that accompanies grief does not act like a disease or disorder. Grief is not rare and it is displayed in its highest frequency during the age at highest reproduction, which is very rare for a disease (Nesse, 2000). A defect is never useful, but a defense that has evolved through natural selection is associated with a situation in which it is useful. Grief is only found in the specific situation of loss, so if it is useful in this situation it cannot be a defect. It is posited that the function of an emotion is to create a special state in the organism that allows it to cope with a challenge or situation (Nesse, 2000). Thus, the question is; in what situations is grief seen, and does it help the animal survive that situation? For instance, in infant animals the depressive state brought on by grief after the loss of a parent can help the animal conserve its resources for as long as possible (Thierry et al., 1984). This gives the animal time to be adopted by another caretaker. This is rare, but it does happen (Fothergill and Linfield, 2012).

The remainder of this thesis consists of the many accounts of primate grief and commentary on why they are seen. Many of these accounts are labeled anecdotal. Many scientists refuse to pay any attention to anecdotes on the grounds that the situations they occur in cannot be controlled and that you cannot run statistics on them (Masson and McCarthy, 1995). Life cannot be controlled, and you can very rarely run statistics on it. Grief is a rare emotion that cannot be ethically brought on, controlled, measured, or easily categorized. In order to study it, anecdotes must be accepted as carefully documented examples of this rare but important behavior.

Jane Goodall is a proponent of using anecdotes as evidence. They are, in her words, “just terribly terribly important” (Masson and McCarthy, 1995).

Response to Death of an Infant

In the wild, infant animals die with shocking frequency compared to humans. Often, the researchers watching do not know why the infant died, as was often the case at Gombe (Goodall, 1990). Due to its frequency, responses to infant mortality are some of the most visible responses to death that can be seen. Not all of the responses can be called grief, but many can.

The individual most likely to show a response to the death of an infant is the mother, since she is the sole caregiver in most primate species. Other group members, mainly females and juveniles, also respond to the death. The most observable response of the mother is continued carrying of the infant after death, which is seen in a large number of species. Mothers may also display other responses. Among group members other than the mother, infant carrying can sometimes be seen, but it is considered to be secondary to responses of curiosity and stress.

Infant Carrying by Mothers

Infant carrying is the phenomenon where the mother of the infant continues to carry the corpse after death has occurred. This can continue anywhere from a few hours to months. It is a well recorded event in many haplorrhine species. Infant carrying is rarely seen in strepsirrhine primates, but this may not be due to lack of trying.

Strepsirrhine mothers show many affective behaviors toward the corpses of their infants before eventually abandoning them. Infant carrying may be limited due to arboreality in many strepsirrhines, like pottos (*Perodicticus potto*). Arboreality combined with their small size makes it difficult for these animals to support a corpse while travelling through the trees (Anderson, 2011).

Strepsirrhines may also lack the dexterity and strength to properly handle the corpse, as is apparently the case among ring-tailed lemurs (*Lemur catta*). Ring-tailed lemur mothers have been seen attempting to carry their dead infants; one mother at the Berenty Reserve in Madagascar succeeded in carrying her infant for 15 minutes (Nakamichi et al., 1996). This mother only abandoned her infant when she needed to climb into the trees and was unable to do so encumbered by the tiny body. All of the mothers who lost infants at the reserve were observed remaining near the body, as though unwilling to abandon it (Nakamichi et al., 1996). This would seem to suggest that if they were able, ring-tailed lemurs might display infant carrying. Observations of this type have not been made in other strepsirrhine species; they could be helpful in determining just how widespread unwillingness to abandon a dead infant is within the primate order.

Hypotheses for Infant Carrying

Li et al. (2012) review three main hypotheses for why mothers continue to carry the bodies of their infants long after death and none state that the mother may be grieving and needs time to accept the loss of her infant.

The first of the hypotheses is the post-parturient condition hypothesis. This states that infant carrying is caused by hormones in the mother. Specifically, the mother still has the hormonal drive telling her to carry and groom her infant, so she keeps doing it. The second hypothesis is the slow decomposition hypothesis. This hypothesis states that infant carrying is only seen in hot and dry or cold and dry conditions where the climate slows decomposition of the body. Under these conditions, the mother will continue to carry the body until she is assured of death by clues other than inactivity of the infant, such as odor cues. The third hypothesis (and possibly the weakest) is the unawareness of death hypothesis. This hypothesis posits that primates are unable to understand that death has taken place, and so the mothers continue to carry their infants because they believe them to be still alive. This hypothesis fails to explain why the mothers would *ever* stop carrying their infants.

These three hypotheses give reasons for infant carrying that do not include an emotional or grief response. Though refuting these three hypotheses will not prove that infant carrying is a grief response, it will require a new hypothesis to be formed. This hypothesis could and should include the grief response.

Infant Carrying in Japanese Macaques, Chimpanzees and Gelada Baboons: Refutation of the Post-Parturient Condition Hypothesis

The best case studies to refute the post-parturient condition hypothesis come from Japanese macaques (*Macaca fuscata*), chimpanzees (*Pan troglodytes*), and gelada baboons (*Theropithecus gelada*).

At Takasakiyama in southern Japan infant carrying has been studied for over 24 years (Sugiyama et al., 2009). 157 cases of infant carrying have been observed there to date, showing just how common this phenomenon is for Japanese macaques. There was no difference in the rate of infant carrying between older and younger mothers. It was found that infants that died between one and thirty days after birth were carried significantly more often (28.7% of the time) than infants that died between 31 days and 253 days (15%). The researchers posited that this was due to the weight of older infants and the difficulty carrying them (Sugiyama et al., 2009). It could also be due to mothers carrying younger infants more often while they are alive.

Of interest to refuting the post-parturient condition hypothesis, 91% of infants were abandoned within a week of their death (Sugiyama et al., 2009). Mothers do not resume cycling this quickly. At this point in time their hormones would still be driving them to care for the infant, but they have abandoned them. The highest rate of infant carrying is seen when the infant dies at an age when it should be clinging to the mother (Sugiyama et al., 2009). Therefore, mothers who carry their infants at this age are showing a behavior contrary to normal infant rearing.

At the Chimfushi Wildlife Orphanage Trust in Northwestern Zambia chimpanzees are kept in large natural enclosures that allow researchers to observe them in mostly natural conditions. An instance of infant carrying was seen when a chimpanzee mother named Masya lost her infant to an unknown cause of death (Cronin et al., 2011). In this case the researchers were able to observe the whole period of infant carrying from death to abandonment, and there was a transition from constant contact and protection of the infant to letting go. Two days after the death of the infant, Masya set the body down for the first time. Other group members showed curiosity towards it, but Masya charged them each time she thought they would hurt the body (she did not charge if no overt aggression was displayed). She repeatedly checked her dead infant’s face. The following day Masya was seen without her infant (Cronin et al., 2011). This represents a case of a mother who was still affected by post-parturient hormones when she abandoned her infant. The post-parturient hypothesis suggests that the mother abandons her infant when her hormones no longer tell her to carry and care for it. But Masya and some of the Japanese macaque mothers only carried their infants for a couple days; their hormones were still present when abandonment occurred (they had not yet resumed cycling).

The best evidence to refute the post-parturient condition hypothesis comes from gelada baboons. At Gaussa, Ethiopia between January 2007 and September 2010, 14 cases of infant carrying were seen in wild gelada mothers (Fashing et al., 2011). Time of infant carrying varied from one hour to more than 48 days. Most mothers carried their infants from one to four days; three carried them for longer (13, 16, and 48 days). During their time carrying their infants the mothers continued to groom the infants. Of most consequence here, the mother who carried her infant for 48 days continued to carry it for two weeks after she had resumed cycling (Fashing et al., 2011). This case is remarkable. When cycling resumes all hormones associated with pregnancy and infant care are gone; the fact that the mother continued carrying her infant means that she was not doing it for hormonal reasons.

The last evidence to refute the post-parturient condition hypothesis comes from neurological studies of mother-infant bonds. These studies have shown that in primates the hormones of pregnancy, parturition, and lactation are not necessary for maternal care (Broad et al., 2006). Any adoptive human mother could tell you that. Primates can also adopt infants and show them maternal care. Jane Goodall saw adoption of infants by siblings—who had not started cycling—at least four times (Goodall, 1990). In primates there are attachment systems for maternal care and mother-infant bonding that are independent of hormones (Nelson and Panksepp, 1998). Primates need not have hormones present to care for an infant, so it cannot be assumed that *only* these hormones cause persistence of the bond after death.

Infant Carrying in Japanese Macaques, Yunnan Snub-Nosed Monkeys, Gorillas, and Chimpanzees: Refutation of the Slow Decomposition Hypothesis

The slow decomposition hypothesis asserts that infant carrying is only seen in hot and dry or cold and dry environments where decomposition is slowed and the mother is waiting for definite confirmation of death, usually odor cues (Li et al., 2012). There are cases from many species that refute this hypothesis. Much of the evidence that challenges this hypothesis also refutes the unawareness of death hypothesis.

In the case described above of the Japanese macaques, Sugiyama et al. (2009) noted that 145 of the 157 cases of infant carrying were seen between the months of June and September. In this environment June to September is the hottest and wettest part of the year and is the time when decomposition would have been fastest and most visible. The mean carrying time of infants was 3.3 days, which would have been long enough for decomposition to set in (Sugiyama et al., 2009). Most of the mothers would have had odor clues long before they abandoned the bodies, particularly the mothers who carried their infants for over a week (the longest bout of carrying was 17 days).

At the Baimaxueshan Nature Reserve in Yunnan, China Li et al. (2012) review three cases of infant carrying that have been observed in wild Yunnan snub-nosed monkeys (*Rhinopithecus bieti*). Two of these cases are entirely contrary to the predictions of the slow decomposition hypothesis. In one instance an infant died of disease and was carried and groomed by its mother for four days. During those four days she protected the infant and did not interact socially with other group members. After four days, the researchers removed the body. The mother searched for it, vocalizing the whole time—probably indicating that she would have carried it longer had it not been removed. This infant died in the summer and was already decomposing when the researchers removed it. This contradicts the slow decomposition hypothesis in the same way mentioned above.

Another contradictory case comes from Yunnan snub-nosed monkeys; a mother had a stillborn infant and carried it for one day. She behaved toward it much like the previous mother—grooming the body and avoiding grooming with group members. This mother abandoned her infant after one day. This infant died in the winter and at the time it was abandoned it showed no evidence of decomposition (Li et al., 2012). The mother had no clues other than inactivity that the infant was dead, but she abandoned it anyway. These two cases from Yunnan snub-nosed monkeys both contradict the predictions of the slow decomposition hypothesis.

At the Karisoke Research Center in Rwanda four adult female gorillas (*Gorilla gorilla*) were observed carrying the corpses of two infants for 15-24 days (Warren and Williamson, 2004). Two of the females carrying infants in this case were not the mothers of those infants. The researchers hypothesized that the females were attempting to practice mothering using the dead infants (Warren and Williamson, 2004). The fact that infant carrying is seen at all at Karisoke refutes the slow decomposition hypothesis. The environment around Karisoke is cold and wet—conditions not conducive to slow decomposition and not the conditions specified in the hypothesis as likely ones for infant carrying. Dian Fossey made reference many times to the general dampness of the area (Fossey, 1983).

Another, very strong, case for contention of the slow decomposition hypothesis is the wild population of chimpanzees at Bossou, Guinea where three infants were carried for 19, 27, and 68 days (Biro et al., 2010). The condition of the infant carried for 19 days (Figure 1), which is the shortest carrying episode, is enough to refute the slow decomposition hypothesis.

Figure 1: Remains of infant chimpanzee at Bossou, Guinea after being carried by its mother for 19 days postmortem. Image by Claudia Sousa (Biro et al., 2010).

The bodies of all three infants were mummified beyond recognition and mostly hairless (Biro et al., 2010). Decomposition in this case was extremely advanced. Every possible death cue was present long before abandonment occurred. This case, and the accompanying image, also soundly refutes the unawareness of death hypothesis.

Infant Carrying in Japanese Macaques, Yunnan Snub-Nosed Monkeys, Gelada Baboons, and Chimpanzees: Refutation of the Unawareness of Death Hypothesis

The unawareness of death hypothesis proposes that primates do not understand death has taken place, so they continue to carry the infant as though it were living (Li et al., 2012). If this hypothesis is accurate we would expect to see the mothers carrying dead infants and treating them as though they were still alive. They do not.

Again the highest rate of infant carrying in Japanese macaques occurs when the infants are at an age when they should be clinging to the mother (Sugiyama et al., 2009). If the mother was unaware of the infant's death she would expect it to cling; she would not carry it. Clearly, she is at least aware that it cannot cling.

In Yunnan snub-nosed monkeys the behavior of the mother changed when the infant died (Li et al., 2012). Grooming of the infant was observed at a higher frequency in the dead infants than the live infants. The mother held the body while she fed (Figure 2), which she did not do with the live infant.

Figure 2: Mother Yunnan snub-nosed monkey clutching her dead infant while she feeds (Li et al., 2012).

The mother also avoided social contact when she had the dead infant (Li et al., 2012). These are altered behaviors that accompany the death of the infant, indicating the mother knows that something has changed.

Yunnan snub-nosed monkeys, gelada baboons, and chimpanzees all change the way they carry their infants after death (Li et al., 2012; Fashing et al., 2011; Biro et al., 2010). Dead infants were carried by Yunnan snub-nosed monkeys with one hand (Li et al. 2012). The geladas carried them with their mouth or with one hand (Fashing et al., 2011). The chimpanzee mothers also ceased trying to carry their infants ventrally and instead grasped one limb (Biro et al., 2010). This is not the way live infants are carried in any of these species and mothers have never been seen to carry live infants in this manner, additionally it is very difficult for them to move around carrying them like this (Figure 3). The mothers change in carrying style further illustrates her knowledge that something has happened to her infant and that she must handle it differently.

Figure 3: Adult female gelada carrying the corpse of her infant which she carried for 48 days after its death, showing how hard it is for the animals to carry these corpses (Fashing et al., 2011).

In all three species there is no evidence that the mother continued to try and feed her infant after it was dead (Li et al., 2012; Fashing et al., 2011; Biro et al., 2010). The pungent odor of decay coming off infants that have been dead for 48 days and 68 days is evident to all group members (Fashing et al., 2011; Biro et al., 2010). It is very unlikely that the mothers would not notice this smell and realize that something was wrong with their unresponsive infants.

Is Infant Carrying an Example of the Grief Response?

None of the current three hypotheses for infant carrying have proven sufficient to explain all, or even most, of the cases of observed infant carrying. Maternal behavior is independent of hormones and a mother that resumed cycling and mating while still carrying her dead infant shows that hormones alone cannot explain this event. Infants that have been carried long past decomposition or abandoned before it sets in have shown that the mother isn't simply waiting for confirmation of death. Pathetically mummified infants and behavioral changes in their mothers have shown that primate mothers are aware that their infants are dead. These hypotheses do not provide an explanation for infant carrying. Another hypothesis is needed. Could infant carrying be an example of the grief response?

In all primates that carry their dead infants grooming continues to occur (and often occurs at a higher frequency than while the infant was alive); grooming is an affective behavior. It has already been established that the mothers know the infants are dead; therefore they do not need to be kept free of parasites for their health. In some cases the mothers were so tenacious in their grooming and chasing away flies that the corpses mummified (Biro et al., 2010). The persistence of affective behavior toward the infant could be evidence that the mother still feels connected to the infant. Other possible affective behaviors are seen as well, such as inspecting the face of the deceased infant (Figure 4) (Cronin et al., 2011).

Figure 4: Chimpanzee mother inspecting the face of her dead infant (Cronin et al., 2011).

These behaviors suggest some type of enduring emotional connection to the now inanimate body.

When separated from the bodies of their infants many mothers showed a stress response. The snub-nosed monkey that had the body of her infant removed by researchers searched for it, vocalizing the whole time (Li et al., 2012). Stress was also seen in gorillas when they were temporarily separated from the bodies of their infants, but this stress was not seen if the mother was allowed to abandon her infant on her own (Warren and Williamson, 2004). That the mother does not display stress if she is allowed to abandon the body when ready suggests that she has completed some period of grief and can now move on.

Further evidence for grief can be seen while the mother is carrying the infant. In snub-nosed monkeys in particular the mother who carried her dead infant withdrew from normal social life, neither interacting with groups nor grooming for the period she carried the body (Li et al., 2012). This withdrawal from normal activities is similar to the depression and withdrawal that are symptomatic of grief in humans (Glass, 2005).

Due to these behaviors in the mothers, and the inadequacy of the three current hypotheses for infant carrying, it seems possible that infant carrying is a demonstration of grief in primate mothers who have lost their infants.

Is Infant Carrying an Adaptive Grief Response?

The obvious answer to the question of whether infant carrying is an adaptive response is no. The mothers are burdened and slowed by the body they must carry. They are also more likely to attract predators to them due to the smell of the body (Fashing et al., 2011). But infant carrying is not the grief response itself, it is only the evidence of the grief response; and this grief response may be functional. One of the purposes of grief is to process the loss so that the individual can move on and reintegrate into normal life. This is what infant carrying may be accomplishing.

As described above, the Yunnan snub-nosed monkey mother who lost her infant and was forcibly separated from it by researchers showed a large amount of stress. She searched for the body and vocalized (Li et al., 2012). The same stress response was seen in gorilla mothers who were forcibly separated from their infants (Warren and Williamson, 2004). This extreme level of stress was not seen in mothers who were allowed to abandon their infants on their own (Li et al., 2012; Warren and Williamson, 2004). Warren and Williamson (2004) posited that the gorilla mothers needed time to accept their loss. Two of the snub-nosed monkey mothers were confirmed to have isolated themselves during their infant carrying episode. They received no grooming from group members and groomed no one but their dead infant. They avoided all group situations (Li et al., 2012). If allowed to abandon their infants naturally, the mothers do not call for it and search for it, but rejoin their group and reintegrate smoothly.

One of the purposes of grief is to allow the individual to accept the loss and move on with their life—infant carrying seems to be serving this function for the primate mothers. When allowed to complete their grief they do not show stress on reentering their group, but instead resume their normal activities smoothly. In this way infant carrying is serving an important function. The case of the chimpanzee mother Masya who was observed for her whole period of infant carrying shows a gradual transformation from constant contact with and protection of the body to being able to let it go (Cronin et al., 2011). This gradual change in behavior is how the mother is able to separate herself from her infant and move on. This transition period is needed for the mothers to rejoin their groups and lives. Carrying the body of their infant gives the mothers something to hold on to during this transition, the same way grieving humans may carry a photo or possession of their lost loved one until they are ready to let go of the person. For non-human primates this grief response is functional and important.

Other Responses to Death of an Infant

There are many other responses to the death of an infant, both by group members and by mothers. Common responses by mothers include depression, withdrawal, strengthening social bonds, helping daughters with their infants, and compensating by babying older children. Responses by group members, who generally did not know the baby all that well and therefore do not show a strong stress response, include curiosity and sometimes infant carrying.

Ring-tailed lemur mothers show typical reactions to infant death, though to a lesser extent than monkeys and apes. Upon the death of their infant they will vocalize strongly, lick and touch the infant, and show an unwillingness to abandon it (Nakamichi et al., 1996). This is one of the only strepsirrhine species whose reaction to loss has been observed. The terrestrial nature of ring-tailed lemurs makes them easier to observe.

Depressive States in Mothers

There are numerous cases of primate mothers who lose an infant showing some level of depression and withdrawal. A captive mother chimpanzee at the Arnhem Zoo, oddly named Gorilla, lost several infants during her life. After each death she would withdraw from her group and her normal routine and sit huddled in a corner, refusing social contact. At random intervals she would suddenly begin vocalizing loudly (Masson and McCarthy, 1995).

A similar depressive state can be seen in wild chimpanzees. Goodall (1971) described an example of a Gombe chimpanzee named Olly who lost her month old infant to sickness. Olly's behavior changed immediately. She carried the body of her infant for two days. During this time she carried the infant by one arm and tucked it into her leg while feeding. Olly ignored her group members and showed a marked listlessness and decrease in activity. Olly showed stress when her other child tried to play with the body and snatched it away, only to release it again.

Depression, and also panic, can be seen in the Gombe chimpanzee mothers whose infants were the victims of a series of brutal cannibalistic attacks by females Passion and Pom, as described by Goodall (1990). Over a period of four years this mother and daughter pair killed and ate several infants born into their own group. One chimpanzee named Gilka lost two infants in these violent attacks. In both instances Gilka tried to defend her baby, also trying to recover the body of her infant even after it was obvious it was dead. Though she was harmed, she ran after the killers and fought to reclaim the corpse. After these attacks Gilka never really recovered, physically or emotionally. She showed withdrawal from her group members and was often seen alone. When she did seek companionship it was almost always from the brother who had helped raise her. Gilka never had another child and died a short time after the last attack.

In all of these cases the mothers show a marked withdrawal and depressive state after the death of their infants. Depression and withdrawal are some of the main symptoms of grief (Kowalski and Bondmass, 2008). In the cases of Gorilla and Olly the work of grief was successfully completed. Gorilla did reintegrate into her group each time and, happily, eventually became a successful mother (Masson and McCarthy, 1995). Olly did the same. For these chimpanzees their depression and withdrawal was successful in helping them cope, as their reintegration into their group and routine demonstrates. In their cases, grief functioned in a long-term beneficial way.

Gilka, though she recovered from the first attack and had another baby, was unable to recover from the second (Goodall, 1990). Part of this inability to recover was physical as she was severely wounded in the second attack, but part of it may also have been mental. It is possible that Gilka suffered from complicated grief. The distinctive circumstances under which she lost her infants, and her position as a relative loner, may have led her to grieve for an abnormally long time or with extreme severity. These distinctive conditions cannot be replicated, so we may never know what prevented Gilka from completing the work of grief.

Strengthening of Social Bonds by Mother

Following the death of an infant some female gorillas will show an unusual response that at first glance looks nothing like grief, but may function in the same way that grief does.

After the death of their infants, mother gorillas Bravado and Pantsy showed increased sociality and play behavior, particularly with younger individuals. This is a frequent response shown by gorilla mothers after losing an infant (Fossey, 1983). This distinctive response may be doing the work of grief. This increased sociality and play is helping the mother to strengthen bonds with her group and may be a necessary step towards healing after the trauma of infant loss (Fossey, 1983). It could also be compared to humans who immediately buy expensive things or party after the death of a loved one; perhaps they are just trying to feel better. It is possible that the mother gorillas are trying to be “cheered up.”

Helping Daughters with Their Infants, Seeking Mother’s Comfort

When a female loses an infant her relationship to her mother or daughter can change. Since a daughter or mother is probably the individual closest to her, this is not surprising.

A response of mothers to infant death is to help daughters with their infants, since they no longer have one of their own to care for. It could be a way of compensating for their loss. A gorilla mother named Marchessa lost an infant shortly after her daughter Pantsy had given birth to an infant. After she lost her own infant Marchessa sought contact with Pantsy’s infant for the first time. She helped care for it and protect it during antagonistic encounters with other groups (Fossey, 1983).

A response of younger females to infant loss is to seek proximity to their mother again. When Gombe chimpanzee Pom lost her infant she became sick, lethargic, and sought out her mother’s company. Their relationship became very close; Pom rarely sought anyone else’s company in her depressed state (Goodall, 1990). Pom may have been seeking comfort from her mother, or just companionship.

These reactions are expected. Most humans will seek out other loved ones after the death of someone close to them. This reaction is very functional, in humans and in primates. Marchessa and Pom found sociality and grooming from their loved ones after the deaths of their infants. Finding comfort is among many very functional ways to complete the work of grief.

Compensating for the Loss with an Older Child

In some cases if a mother loses an infant she will compensate for the loss by treating an older child as if it were an infant. The most famous case is that of Gombe chimpanzees Flint and Flo. Flint's response to Flo's death is famous, but Flo's response to the death of her last infant—Flame, is also interesting. Flint was over six years old when Flame died. But upon Flame's death Flo began treating Flint just like an infant. She shared food with him, let him sleep in her nest at night, groomed him more frequently, and even carried him on her back (Goodall, 1971). This very unusual babying behavior by Flo may have been her way of coping with the loss of Flame.

The same reaction has also been seen in gorillas. When Old Goat lost an infant she allowed her older son Tiger to act like one (Fossey, 1983). The bond between Tiger and Old Goat grew closer with Old Goat allowing Tiger to cling dorsally to her while travelling; she groomed him excessively, and even allowed him to suckle from her. Old Goat's obsession with treating Tiger as an infant even caused her to withdraw from her social group (Fossey, 1983). This case is even more drastic than that of Flint and Flo. For Old Goat, caring for Tiger seems to be how she dealt with losing her infant. This would be a logical response in humans as well.

Babying an older child is not only functional in that it allows the mother to heal, but it also may be adaptive. Most primates, especially great apes, can have very few pregnancies in their life compared to other animals of similar size, so the death of an infant can have more drastic effects on their lifetime fitness. After they lose an infant, it is beneficial to ensure that older juveniles are going to survive to reproduce. By taking extra care of these older children the mothers are increasing their chances of survival, and increasing their own fitness. This method backfired with Flint, who died shortly after Flo, but it seems to have worked in Tiger, who did survive. This response is not only logical and functional, but it could be adaptive in a very specific way.

Responses by Group Members

The mother is not the only individual who responds to an infant's death. Infants are not usually social with anyone but their mothers, so group members don't know them well and don't usually grieve over them. However, it is useful to mention their reactions, some of which may be grief.

The strongest reaction is curiosity. The reactions of chimpanzee Masya's group to the death of her infant are typical (Cronin et al., 2011). Group members inspect the face of the infant and often touch or prod it and sniff their hands afterward. This reaction, often seen in juveniles, is probably a way of learning about death. Some group members, often siblings, will show affective behaviors like grooming toward the body (Cronin et al., 2011). Olly's daughter Gilka showed a lot of curiosity, and affective behaviors, to her dead sibling (Goodall, 1971). In the case of individuals that show affective behaviors, specifically siblings, the individuals may well be grieving for the lost infant.

Approaching the infant and inspecting or grooming it may also be a way of sharing the mother's grief. In gelada baboons the group members do not avoid a mother who is carrying a dead infant, despite the smell (Fashing et al., 2011). They will groom the mother and the baby.

This may be a way of seeking comfort for the group's loss; it may also be a way of comforting the mother.

Group members may also be seen carrying the corpse of the infant, or trying to steal the body. This can be seen in gorillas, where the mother will actively try to recover the body of her infant (Warren and Williamson, 2004). This reaction is probably not grief. It is most likely a way for young females to practice handling an infant. They are not allowed to handle the live infants of other females (Warren and Williamson, 2004). The unwillingness of the mothers to surrender the bodies is grief, and further evidence that they are in a transition phase of learning to let go.

Not all reactions by group members to dead infants can be called grief. Since the group members barely knew the baby it is not surprising that they are not grieving over it to any large extent. The affective behaviors seen in siblings and some group members could be grief and are likely functioning to help them accept their loss. Behaviors like grooming the mother may be a way for group members to share the mother's grief and help her work through it, even if the individuals themselves are not grieving over the infant. The idea that group members may share in a mother's grief is profound. Though there is not enough evidence at this time to say anything definitively, this could be evidence of empathy.

Response of Infants and Juveniles to Death/Separation

Infants grieve upon the loss of a parent. Grief in a juvenile was recently made famous on Earth Day 2012 when audiences across the country flocked to theaters to watch Disney's *Chimpanzee*. The movie tracked the story of Oscar, a juvenile chimpanzee who lost his mother and was subsequently adopted by an adult male, a very unusual occurrence. Oscar's grief responses—searching, vocalizing, and decreasing activity levels—were typical under the conditions of losing a parent (Fothergill and Linfield, 2012).

Infants exhibit the same general response to death and to separation. It is possible that, like human children, they cannot really tell the difference. The most important thing in an infant primate's life is its mother. Therefore, most grief responses in infants and juveniles are in response to the death of its mother. The majority of this section focuses on loss or separation from a mother, with a short section on infant-infant separation. Responses of adult primates to the loss of their mother are discussed in the next section.

In the case of death or separation from a mother there are both observations of wild primates and controlled captive studies. The responses in the two situations are similar. The experiments of psychologist Henry Harlow on infant rhesus monkeys (*Macaca mulatta*) are the most well-known separation studies (Masson and McCarthy, 1995). These experiments, though unnecessarily cruel, give a general picture of infant grief after losing a parent and can be compared to wild observations. In both wild and captive cases, infants generally show two stages of response. Oscar showed the two stages quite well for audiences all over the country; a period of searching and vocalizing, followed by a period of depression and inactivity (Fothergill and Linfield, 2012). This general response is widespread, though it can vary and be accompanied by other responses. These two responses are very adaptive and give the infant the best chance of either finding its missing parent or being adopted by another group member. Vocalizing and searching (the first stage) are also seen in primates separated from their mothers for very short periods, as well as if their mother gets too far away from them while travelling (Goodall, 1990). A primate infant that is still dependent on its mother's milk will usually not survive long; therefore, most of the primates described are old enough to at least have a chance of survival.

Forced Temporary Separation from Mother

The experiments performed by Henry Harlow were only some in a series of forced separation studies performed on monkeys (mainly rhesus monkeys). These studies represent some of the only accounts of the grief response seen under controlled conditions. Temporary separation from mothers invokes the same reaction in infants as the death of the mother does. Forced temporary separations can also be seen in the wild during weaning. Again, the same general response is displayed.

Forced Separation in Labs

Observations of human children separated from their mothers showed that they went through three general phases: protest, despair, and sometimes detachment. Studies on primates aimed to determine whether they also went through these stages. Studies discovered that primates went through the first two, but not the third (Kaufman and Rosenblum, 1967). The protest stage is characterized in primates by increased activity, mainly the infant searching for its parent and vocalizing. The despair stage is characterized by inactivity and a depressed state (Thierry et al., 1984).

In a study by Charles Kaufman and Leonard Rosenblum four pigtail monkeys (*Macaca nemestrina*) were raised in laboratory pens and then forcibly separated from their mothers for four weeks, when the infants were four to six months old (1967). Upon initial separation the infants screamed, paced, and searched for their mothers (Figure 5).

Figure 5: Infant pigtail monkey in state of agitation after forced separation from mother (Kaufman and Rosenblum, 1967).

They displayed only erratic play behavior and would alternate cooing with screeching. They did not sleep the first day their mother was gone and continued to search and vocalize for 24 to 36 hours. After the first 24 to 36 hours, the infant ceased most activity. It would sit hunched over with its head down. The researchers noted facial sagging and an appearance of dejection on its face (Figure 6) (Kaufman and Rosenblum, 1967).

Figure 6: Pigtail infant showing typical depression and inactivity after forced separation from its mother (Kaufman and Rosenblum, 1967).

The sagging face described by the researchers is reminiscent of Darwin’s description of the expressionless face, sagging mouth, and wrinkled forehead characteristic of using the grief muscles. Darwin also noted that prolonged grief would lead to motionlessness and passivity, with a tendency to rock to and fro (Darwin, 1890). All of these symptoms were observed in the pigtail infants.

The depressed state was also characterized by little social interaction (Kaufman and Rosenblum, 1967). After a further five to six days separated from their mother, the infants showed increased movement and exploration and some social interaction and play behavior (but nowhere near pre-separation levels). They noted that periods of depression alternated with periods of play and exploration. These alternating periods are characteristic of the “dynamic” aspect of grief (Cowles and Rodgers, 1991). By the third or fourth week after separation, the infants showed play and movement levels that were closer to normal, though still not their normal behavior and routine (Kaufman and Rosenblum, 1967). Behaviors that were common throughout the month, but are generally not seen normally, were digit sucking, self orality, genital self-stimulation (including genital self orality), and an increase in inanimate object exploration (Figure 7).

Figure 7: Infant pigtail monkey tentatively exploring its bedding; a behavior shown in infants forcibly separated from their mothers (Kaufman and Rosenblum, 1967).

Forced separation from the mother is a threat to an infant's survival. Under the conditions of a threat two responses are generally possible. The first is the familiar flight or fight response, which uses energy. The other is the conservation-withdrawal response, which conserves energy and is used if the threat cannot be fought or escaped, or if all energy will be used up before the problem can be solved (Thierry et al., 1984). The protest-despair response can be framed in terms of conservation-withdrawal. In this way, protest and despair can be viewed as stages of a single response, which Thierry et al. termed the searching-waiting strategy.

In the searching-waiting strategy the infant first attempts to locate its mother (essentially searching for a solution to its problem). If this fails the infant reverts to inactivity to conserve resources as long as possible (waiting for a solution). These two extremes of activity and inactivity are often seen in the grief response, either one or the other or in combination (Thierry et al., 1984). The period of inactivity can also be viewed as a conservation-withdrawal system that is deployed automatically when a helpless individual, like an infant, loses their caretaker. The conservation-withdrawal system is implemented when the fight or flight system fails and is a way to conserve resources (Kaufman and Rosenblum, 1967). The conservation-withdrawal model is essentially the same as the searching-waiting strategy. Both models suggest that the infant will first attempt to find its mother and, when unsuccessful, will become inactive to ensure survival for as long as possible.

The benefit of searching for the mother first is that she may, in fact, be located. This often happens in the wild when mother and infant are separated accidentally. By searching for her initially, the infant is increasing its chances that she is found (Thierry et al., 1984). Vocalization would, in the wild, bring the mother back if she could hear it (Kaufman and Rosenblum, 1967). After some initial amount of searching it is beneficial to stop searching and wait, since it will conserve resources for as long as possible (Thierry et al., 1984). The depressive state will also minimize the infant's obviousness to predators and aggressive conspecifics and could encourage allomothering (Kaufman and Rosenblum, 1967). These stages of behavior are very clearly designed to increase the infant's chance of survival. The depressive state is adaptive in that it allows the infant to stay alive for the maximum amount of time possible, which increases its chances of either being found by its mother or being adopted by a group member (Thierry et al., 1984). Adoption—thought to be rare—may happen more than previously thought, as seen with Oscar in *Chimpanzee* and numerous other cases from Gombe (Fothergill and Linfield, 2012; Goodall, 1990).

Modifications to the searching-waiting strategy may be seen depending on the conditions of separation. If the infant is the one removed to a new location it will show more searching than if the mother is removed. This is adaptive since searching for the home range will increase the infant's probability of success more than waiting for the mother in a strange area she may never venture into (Thierry et al., 1984). Alternatively, if the mother is removed and the infant is left in the same location it will display less searching. This is also adaptive: if the infant is left in the home range, it is more beneficial to wait, since the mother is often in that area and there is a good chance that she may return (Thierry et al., 1984). This is a good example of the cost benefit analysis employed in an attempt to adapt to a new environment (without mother). This response system clearly has selective advantage (Kaufman and Rosenblum, 1984).

There are many studies of this sort that examined infant responses to separation. Since each study showed basically the same result, there is no need to discuss all of these experiments.

Forced Separation in the Wild: Separation by Researchers and Separation during Weaning

Both experiments in the wild where infants were separated from their mothers, and the natural separation of weaning, generally confirm the grief responses seen in the lab experiments.

In a wild experiment by Mewa Singh four rhesus monkey mothers were drugged and removed from their group and their infants (1975). The mothers and infants were separated for three days. The infants showed overall decreases in play and sociality and avoided other infants. On the first day they exhibited numerous distress calls and increases in locomotion. After that, they showed increases in sitting behavior. These results are generally seen in lab tests. These natural studies confirm that the same behaviors will be observed in a natural setting.

Weaning is a natural state that is comparable to forced mother infant separation. Weaning separation (generally when the mother starts mating again) is the mother’s choice, so for the infant it is a form of forced separation. Infants in this stage will show many of the same behaviors seen in infants forcibly separated from their mothers. Many times Jane Goodall described the tantrums and whimpering that accompanied weaning in young chimpanzees (Goodall, 1990). Weaning depression was systematically studied in free-ranging rhesus monkeys in Puerto Rico by Berman et al. (1994). There are differences between this situation and forced separation: separation is not complete and the time of separation is shorter. However, it is still useful to compare responses to natural separation to the lab studies.

In rhesus monkeys when the mother resumes mating she increases separation from the infant. The infants responded by showing agitation and sometimes depression. Ignored infants often throw tantrums characterized by emitting constant distress calls. These are the same calls the infant emits when it loses its mother entirely. In this situation, the increase in distress calls was not associated with increased contact. The distress calls may be a general response to separation that is adaptive when the mother is actually lost, but not when she is choosing to ignore her infant. Other aspects of tantrums, such as running and clutching at the mother, were associated with more contact. Some infants displayed less play behavior overall during their period of separation, much as the infants in the labs did. During this stage more passive and depressive behavior was also seen and inactivity increased. A full-blown despair stage was not seen, likely due to the short and incomplete nature of the separation periods (Berman et al., 1994).

This natural type of separation shows the infants displaying many of the same behaviors as when they are completely separated from their mothers. Decreases in play, decreases in activity, depressive states, and increases in distress calls are all seen. This natural type of separation is positive confirmation that these responses are natural responses to any type of separation. These studies confirm the validity of the lab tests and indicate that the grief response seen in the labs is not a product of artificial conditions.

Permanent Separation from Mother

Responses of infants to permanent separation from their mother are seen when the mother dies. Sometimes, as in Oscar’s case, the infant doesn’t see the body and may not realize that its mother is dead. Whether an infant understands death, even when it does see the body, is debatable. Since killing mothers would be incredibly cruel and unethical, response to a mother’s death is only seen in wild studies. Infants who survive their mother’s death (restricted to older infants and juveniles that are no longer reliant on their mother’s milk) generally do so because they are adopted by either a family member or an unrelated individual (much rarer). The most data on this subject comes from observations at Gombe, perhaps due to the extended nature of the study or to Jane Goodall's willingness to describe emotions.

Infants Who Were Adopted by Siblings and Survived

From Gombe there are a number of examples of infants who lost their mothers and were adopted by siblings. Infant grief is often evident, as is desperation.

One infant chimpanzee adopted by an older sister, whose survival is unfortunately unknown, was Beatle (Goodall, 1971). Beatle was about three years old when she lost her mother. But her older sister was a competent foster mother. Beatle showed common signs of depression among orphans in the wild. She played less and became lethargic and emaciated. Happily, Beatle's condition did improve and by age six she was acting much like any juvenile of her age, though she was entirely dependent on her older sister. If her sister moved only a few yards away, Beatle would show extreme distress, vocalize, and run after her—much like an infant forcibly separated from its mother. The pair stopped visiting the research center and it is unknown whether Beatle lived or not (Goodall, 1971). The unusual dependence on her older sister that Beatle displayed may be evidence of fear of abandonment. This is seen often in humans, if abandoned, an individual is more likely to fear it happening again.

Jane Goodall (1990) provided a number of other interesting examples of infant chimpanzees adopted by siblings. Pax was four years old when his mother—Passion—died. He actually observed the body. The two older children—Pom and Prof—only stared at their mother's body, but Pax approached it repeatedly and even tried to suckle. When Passion did not respond Pax began screaming and tugging at his mother's body. His older siblings inspected it and returned to it many times throughout the day. This may be evidence that the young Pax did not understand that she was dead, while his older siblings did. The three siblings stayed near the body the whole day. Pax became more and more depressed and his screams turned to whimpers. For the next several weeks, Pax showed a marked depression and decrease in play behavior. He had two older siblings to care for him and he recovered fairly quickly. However, Pax refused to ride on his siblings back's—screaming if they tried to make him—despite his difficulty in keeping up and their continual offers. There could be a number of reasons for this refusal, but it is possible he was unwilling to fully treat another female as his mother, which is often seen in adopted children. Pax also refused to share his siblings' night nests, possibly for the same reason.

When Pax's sister migrated to another community he was fully adopted by his brother, Prof. Pax showed the same desperate dependence on Prof that Beatle showed toward her older sister. If they were even out of sight of each other Pax would become extremely agitated; at six years old he should have been more independent. During one incident in which Pax and Prof were separated for almost a day Pax showed many of the same behaviors as infants forcibly separated from their mothers in labs or in the wild. Pax first whimpered and cried and when Prof didn't appear, he began searching for him—climbing trees and crying louder and louder. When he could not locate Prof, he built a nest next to another male and whimpered throughout the night. Fortunately, the two were reunited the next day. Pax displayed the beginnings of the searching-waiting strategy seen so often in the lab.

Gimble was eight when his mother died, and he was also adopted by his brother. Gimble showed the same depression and listlessness most infants show when they lose their mother. Gimble, like the others, sought comfort with his siblings, in this case his brother Goblin. Goblin took over most of the responsibilities of a mother for Gimble. Seeking comfort after a death was also seen in mothers who lost infants, and is often seen in humans. It is a very common part of the grief response.

The infant chimpanzee Wolfi who was adopted by his older sister Wunda shows the most extreme example of adoption. The two were close before the death of their mother; afterwards Wunda became a new mother for the three year old Wolfi. Incredibly, Wolfi began suckling from Wunda every couple of hours. It is unknown whether Wunda was actually producing milk (she was not sexually mature so that would be remarkable), but she was at least providing the same comfort to Wolfi as a mother would. This contrasts with the behaviors of Pax, who wouldn't even allow a surrogate mother to carry him or share a nest with him. Perhaps the younger Wolfi was desperate enough to allow it, or it could simply be that Wolfi and Wunda were close before the loss (or that there is some variation in these sorts of behaviors).

Infants Who Were Adopted by Unrelated Individuals and Survived

Infant chimpanzee Skosha had no siblings to adopt her when she lost her mother at five years old. Skosha became attached to Pallas, an adult female friend of her late mother. Pallas had recently lost an infant of her own. It is possible that Pallas was Skosha's aunt, though this was not determined conclusively (Goodall, 1990). Perhaps Pallas adopted Skosha as a way to compensate for the loss of her own infant. Pallas carried Skosha, shared food with her, waited for her during travel, and even put up with her extreme tantrums. When Pallas successfully gave birth to Kristal, Skosha behaved toward her much like an older sister would. When Pallas died Skosha essentially lost a second mother. Skosha became depressed and seemed unable to make decisions for her and Kristal, whom she was now caring for. Skosha wandered about the forest with Kristal, who became severely depressed. Despite Skosha's efforts Kristal did not survive the death of her mother as Skosha had (Goodall, 1990).

When infant chimpanzee Mel lost his mother his only surviving sibling had emigrated to a different group (Goodall, 1990). Mel, following the death of his mother, wandered from group member to group member growing increasingly lethargic. Surprisingly, he was adopted by Spindle, a completely unrelated adult male. Spindle himself had lost his mother to the same epidemic that claimed Mel's mother. Could it have been his loneliness that prompted him to adopt Mel? Spindle protected Mel, shared his nest, carried him, and even rushed to rescue him when Mel whimpered. When Mel became separated from Spindle for a time, Pax adopted him. Still thoroughly attached to Prof, Pax cared for Mel just as Spindle had, and Prof cared for them both. Mel was reunited with Spindle and a year after losing his mother he started to show signs of improvement. He became less depressed, less withdrawn, and even played a bit. Unlike many other adopted orphans, Mel's bond to Spindle eventually weakened (Goodall, 1990).

After Mel's bond with Spindle weakened he became attached to Gigi, a large sterile female (Goodall, 1990). Another orphan, Darbee, also travelled with them. The two infants chose to associate with Gigi, who did not show the care a mother would but did protect the two orphans and made decisions. Perhaps that is what the infants really needed, since they now had each other for play and affection. Though Mel and Darbee survived, they did not act like normal infants. They played less and showed less curiosity. They spent more time resting and grooming themselves. Jane Goodall observed that they acted more like adults, and posited that it was due to their trauma (1990). Many human children show the same tendency to grow up quickly after the loss of a parent.

The relationship between Mel and Spindle was very much like the relationship that developed between Oscar and adult male Freddy in *Chimpanzee* (Fothergill and Linfield, 2012). Upon the death of his mother by predation, Oscar spent days calling and searching for her. When he was unsuccessful, Oscar stopped playing and socializing and became weak. He was adopted by the highest ranking male, Freddy. Freddy acted like a mother toward Oscar; grooming him, carrying him during travel, and even sharing food with him (Fothergill and Linfield, 2012). Adult males do not generally care for infants, so the cases of both Mel and Oscar were unusual. It is unknown what might drive this relationship. It was thought that Spindle might have been lonely after losing his own mother. It is possible that Freddy, as a high ranking male who must constantly assert his position and be in charge, wanted to simply enjoy the company of another chimpanzee. Oscar posed no threat to his dominance, and he may have been an appealing companion.

Infants Who Did Not Survive the Death of Their Mother

Not all infants are lucky enough to survive the death of their mother. Some, like Merlin, are adopted but die anyway. Others, like Tussock, do not get adopted at all. While still others, like Flint, simply cannot get over their loss.

Chimpanzee Merlin was three years old and still suckling when he lost his mother; his inability to survive was no surprise (Goodall, 1971). When he was first seen after his mother's death, he was close to his older brother. In camp Merlin huddled against his brother and groomed his sister Miff only a little when she groomed him. As time went on Merlin's condition deteriorated, probably due to lack of milk. Despite his sister's attempts to act like a mother, Merlin displayed little play behavior and displayed inappropriate reactions to group situations (Goodall, 1971).

Merlin responded to a charging male as a younger infant would. This sort of age inappropriate behavior increased over time. Many infants upon losing their mother will display behavior more typical of adults (much as human children do). Merlin seems to have done this imperfectly. He became aggressive toward infants his age and only groomed adults, but was unable to response appropriately to adult situations such as a charging male. Interestingly, Merlin showed the same posturing as orphaned monkeys in labs. He would sit hunched over, rocking, grooming himself, and exploring objects near him (Goodall, 1971). This behavior is very characteristic of grief, as described by Darwin and others. Near the end of his life, Merlin started showing some recovery; he began playing again. But he was emaciated and unhealthy and died in a polio epidemic. Merlin’s problem may have been his sister’s young age. She acted as a companion, but not really as a mother. Merlin’s social insecurity may have contributed to his poor mental state. Though he began recovering from his grief near the end, as evidenced by increased play behavior, it was too late to salvage his physical state (Goodall, 1971).

Chimpanzee Sorema was just one year old when her mother died. Her age and dependence on milk made it inevitable that she would die, despite the care of her brother Sniff, who adopted her. Sniff was only seven years old when he adopted his sister. For two weeks, he carried her everywhere, grooming her and pressing her against his chest. When Sorema died Sniff carried her dead body (Goodall, 1971). Infant carrying is very rare in males. It may have been young Sniff’s own grief over his mother that prompted him to care for his young sister and continue to carry her after death.

Three year old chimpanzee Cindy was not adopted upon her mother's death. Cindy trailed after other group members and showed marked depression. She died two months after her mother (Goodall, 1971).

Infant gelada baboon Tussock, like Cindy, was also not adopted. When Tussock's mother was ill her group members helped carry Tussock. But upon her death Tussock was left alone on the cliffs where her mother died. Tussock spent a day on the cliffs vocalizing; she died beside her mother the next day (Fashing et al., 2011).

During Dian Fossey's research at Karisoke she rescued two gorilla orphans, Coco and Pucker, from poachers who were intending to sell them to zoos (1983). The trauma they underwent during their capture and incarceration makes it difficult to determine which behaviors are due to grief over their lost mothers and which are due to trauma, but they do show many of the same behaviors as other orphans. Even after recovering physically, Coco and Pucker showed marked depression and listlessness, with less play than is seen in the wild (Fossey, 1983). In the same way that some chimpanzees become desperately dependent on their adoptive mothers, Coco became dependent on Fossey. If Fossey did not pay attention to her or come when needed she would emit distress calls and throw tantrums. Pucker, conversely, showed a marked introversion and apprehension at physical contact with anyone. Like Mel and Darbee, Coco and Pucker became attached to each other and Pucker would scream when Coco was removed temporarily from the enclosure. Coco and Pucker were eventually transferred to the Cologne Zoo, where they died within a month of each other in 1978 (Fossey, 1983). Perhaps they never got over their grief combined with the trauma of their capture.

The most famous case of a juvenile chimpanzee who did not survive the loss of his mother is Flint. Flint was eight and a half years old when his mother—Flo—died (Goodall, 1990). He should have been able to survive and take care of himself, but he died shortly after his mother did. Flint was five years old when Flo gave birth to her last infant Flame. Flint showed extreme jealousy toward Flame and became depressed when Flo's attentions were diverted away from him. Flame died after Flo became sick, and Flint reverted to almost infantile behavior. Flo once again allowed Flint to ride on her back, shared food with him, and shared her nest with him (Goodall, 1971). It was, perhaps, this extreme dependence on Flo that resulted in Flint's death after Flo died. Flint sank into depression and lethargy without Flo. Though his older siblings attempted to care for him he sank deeper into depression. Several times Flint revisited night nests that he and Flo had shared, sitting huddled up and staring at them for long periods of time before moving off slowly. Flint lost the will to live. At the end, Flint travelled to the site where Flo had died. He sat staring at it for hours. He then moved a little further, curled up, and died (Goodall 1990).

No clearer account of grief than Flint's exists. He was perfectly capable of caring for himself, but he didn't. This is not a case of dependence on milk or death from a depressed immune system. Flint is the primate who most clearly suffered from complicated grief. He took his depressive state to maladaptive extremes, likely because of the unusual relationship he had with his mother. In many other primates—and chimpanzees of Flint's own group like Pax—presentation of the symptoms of the searching-waiting strategy helped them get adopted and survive. Many adaptations can be maladaptive under certain circumstances; this is what happened with Flint. Like in many humans, a normal and healthy behavior—taken to extremes—can become deadly.

Infant-Infant Separation

A last type of separation that generates grief in infants is separation from other infants. In this case, researchers reared four infant rhesus monkeys together from birth without mothers. They then separated these infants to see if they would display the same reaction as when infants are separated from mothers (Suomi et al., 1970). This study is further evidence of the consistent nature of the grief response.

When the infants were separated from each other they showed the same response as the infants separated from their mothers—namely the protest and despair stages (Suomi et al., 1970). The separations were repeated a number of times, and it was shown that the monkeys did not adapt to separation, but showed the same response each time. In later separations the protest stage was found to be shorter and the despair stage longer, probably showing that the monkeys were learning that protest was pointless. Toward the end of the separation period the monkeys showed very little behavior of any kind. Multiple separations resulted in total arrest of development of social behaviors. Cumulative grief wore them down. These monkeys showed more infantile behavior when older (Suomi et al., 1970).

These unnecessarily cruel experiments show that the grief response is not something that one becomes used to. Each period of separation, each loss, results in the same behaviors. Repeated losses can result in very abnormal behavior. It also shows that the grief response is much the same for any loss, be it a mother or a friend.

Response to Death of a Conspecific

Some primates grieve over the death of an unrelated member of their group, not just over family members. Many responses associated with grief have been documented in these situations, even becoming famous in recent media. They have been presented as solid evidence of grief or a “period of quiet mourning” (Hanlon, 2009). Though the photos and stories made famous in the media are not irrefutable evidence of grief, they are still quite interesting. Primates have even been seen grieving over animals of different species. Koko the gorilla grieved over the loss of her cat.

There is a distinct difference between the responses of primates to violent death and to peaceful death, as seen in the wild and in captivity. In chimpanzees violent or sudden death results in screaming and frenzy, and no group member will approach the body for some time. When death is peaceful chimpanzees remain quiet and calm and will touch the body almost immediately (Anderson, 2011). Due to these differences violent and peaceful death will be considered separately. This section includes responses to death of unrelated individuals, individuals of a different species, and responses of mature individuals to the death of their mother.

Responses to Violent/Sudden Death

Many violent deaths in the wild are due to predation or poaching. Gombe chimpanzee Rix’s death, however, was accidental (Masson and McCarthy, 1995). Several groups of chimpanzees were gathered together when Rix accidentally fell down a gully and died. There was an instant frenzy in response, including vocalizing and charging. After the panic died down the chimpanzees remained near the body for hours. They studied the body in detail, but did not touch it. An adolescent male named Godi displayed the most severe grief. He continually stared at Rix’s face and moaned, becoming agitated when others approached the body too closely. Godi was the last to leave Rix’s body, and he gazed at him intently before abandoning him. The responses of the chimpanzees in this episode are characteristic of violent death for many primate species. The calls used are often heard when chimpanzees observe a corpse. They have been observed vocalizing at the corpses of other species, such as baboons (Masson and McCarthy, 1995).

Similar pandemonium was seen in gorillas at Karisoke when a juvenile was caught in a poacher’s snare. The juvenile did not die immediately, but the immediate result was chaos. The other members of her group began displaying and screaming around her (Fossey, 1983). It is possible they were expressing their helplessness. The juvenile did break free, but died sixty days later. During that whole period, her group traveled slower to accommodate her needs.

The frenzy that follows a violent death may function to help the remaining group members survive. If the death is due to predation wild displaying and vocalizing may help drive the predator away. In the case of violent death at or near a sleeping site, but not peaceful death, the sleeping site is often abandoned (Anderson, 2011). This would also be functional in assuring that the predator cannot find them again easily.

On Cayo Santiago Island in Puerto Rico a group of free ranging rhesus macaques were observed after the death of an adult male (Buhl et al., 2012). The male had been killed in an attack by high-ranking males of his own group. This unusual situation resulted in much aggression directed toward the body. Four of the highest-ranking males directed aggression toward the body, as well as one female. This female directed aggression toward the body three times, and followed the bouts by soliciting copulations from the highest-ranking male, who had participated in the attack. The responses of the other group members were less violent. One hundred individuals remained within six meters of the body; most of them looked at it continually. After 50 minutes, the attackers allowed them to approach the body. Most group members inspected the face and body and smelled the corpse. An adult female and a sub-adult male groomed the body. The group spent 90 minutes near the body before moving away (Buhl et al., 2012).

The responses of the other macaques toward each other are very characteristic of grief. There were a significantly greater number of pairs grooming after the death than baseline or after non-fatal fights. Those nearer to the body were more likely to groom. Group members also displayed stereotypic behaviors like brushing leaves and dirt (Buhl et al., 2012). These behaviors and the increase in grooming indicate the macaques were highly stressed. The increase in affective behaviors could be reassurance of or from group members.

The grief displayed by Koko the gorilla upon the loss of her cat All Ball is one of the clearest examples of documented grief. Koko herself selected the tailless cat that she named All Ball. In many ways, Koko treated her cat as she would an infant. Despite the cat’s sometimes aggressive behaviors, Koko frequently told researchers (in sign language) “Koko love Ball” and even painted pictures of the cat. Sadly, All Ball was hit by a car; the death was unexpected for Koko. On receiving the news, Koko emitted distress calls. When researchers showed her a picture of a cat that looked like All Ball she signed “Cry, sad, frown.” Koko remained withdrawn for weeks and only fully cheered up when she received a new cat (Patterson, 1985).

Few animals can tell us their emotions. Koko was able to put her grief into words and give us a unique insight into the nature and duration of primate grief. Her sadness at seeing pictures of her lost pet or talking about her is very similar to the sadness humans feel when reminded of their loss. Koko shows that primates can grieve away from the bodies of their companions and even understand death when they hear about it second-hand.

Response to Peaceful/Natural Death

Responses to peaceful or natural death are also quite similar across species. This type of death is characterized by much quieter and calmer responses. Possibly, since there is no danger, there is no value in frenzy. This grief response may also be very widespread. Pottos in captivity are known to respond to peaceful death in a similar way to chimpanzees. Just before a sick male died two group members groomed him. After his death his group members showed decreased appetite, and even seemed to leave uneaten food for the deceased individual (Anderson, 2011).

Chimpanzees in Captivity

The responses of captive chimpanzees to death are possibly the most famous in popular media. When captive chimpanzee Dorothy died at the Sanaga-Yong Chimpanzee Rescue Center in Cameroon, West Africa the striking response of her group members was caught on camera (Figure 8). This photo came with the headline “Chimps Mourn Death of Fellow Primate in

Figure 8: Chimpanzees in West Africa observe as the body of Dorothy is removed from the enclosure. Photo by Monica Szczupider (Hanlon, 2009).

Display of Grief" (Hanlon, 2009). The photo was presented as evidence that primates grieve. Dorothy's group members were described as "stricken by sorrow" and in a "period of quiet mourning." This photo is indeed both striking and touching, but on its own, it is not evidence of grief. All primates, and most animals, show curiosity at the dead of their own species. Discovering how group members died can help assess if there is any danger nearby. Curiosity alone is not enough to conclude grief. The behavior of Dorothy's group members is much better evidence of grief than the photo. After Dorothy's death by heart failure her group members were quiet and subdued (Hanlon, 2009). Less play and more grooming are both characteristic of grief in primates.

Another case of peaceful death in captivity is Pansy, a chimpanzee living at a Safari Park. Pansy was estimated to be over 50 years old when she died naturally (Anderson et al., 2010). Pansy's stunning case shows most clearly the "stages of grief" in her group members. Nearing death, Pansy was unable to make a nest on the platforms the group usually used, so her group members stayed on the ground with her and groomed her right up until her death. Pansy's daughter Rosie remained near her body all night and went to sleep 92 minutes later than her previous latest time. A male in the group displayed three times, each time ending with an attack on the corpse. The male's behavior is suggestive of the anger stage. Before the body was removed, Pansy's group members cleaned it, removing straw and other debris. The chimps were subdued in the days following Pansy's death and showed increased grooming. This continued for weeks, during which time they also ate less and avoided sleeping where Pansy had died (Anderson et al., 2010). Pansy's group members clearly showed some forms of anger and depression (two of the stages of grief) (Kübler-Ross, 2005). Their eventual recovery shows they must have gone through some form of acceptance as well. The display of these general responses to death by primates shows how deeply rooted these responses are.

Chimpanzees in the Wild

Natural death of chimpanzees in the wild was observed at Gombe. An adult male named McGregor was struck by polio, which resulted in paralysis of his legs. It took McGregor ten agonizing days to die (Goodall, 1971). During this time, most of McGregor's group members showed fear at his strange condition and avoided him. Another adult male named Humphrey who was probably McGregor's brother did not avoid him. Humphrey waited for McGregor when feeding and built his nests near him. Humphrey rarely went more than a few hundred yards from McGregor and returned often to check on him. When McGregor finally died researchers removed his body immediately. For almost six months, Humphrey returned continually to the place that McGregor had died. He would sit staring and waiting (Goodall, 1971). It is possible that at first Humphrey didn't realize McGregor was dead. However, after a few weeks it seems likely that he knew his friend was not coming back. Humphrey continued to look for McGregor and return to the last place he had seen him.

Adult chimpanzees show a marked response to the death of their mother, even though they are no longer dependent on her. When Flo died her sons Faben and Figen showed a change in their relationship to each other. Neither of the brothers saw their mother's body, so their grief was not immediate. As time went on the two grew closer. They began spending more time together and Faben began supporting Figan in his quest for dominance, which he had not done before. After Flo's death Faben displayed with his brother and supported him whenever he challenged another male. Both brothers had been close to Flo and had been comforted by her as adults. It is possible that the sudden absence of her comfort and safety caused the brothers, in their grief, to grow closer to make up for their loss (Goodall, 1990). This is a common response in human siblings.

The case of Madam Bee's death is an interesting one. Her death was a result of an attack by males of another community. But since Madam Bee died several days later with only her daughter for company, her death resembles a natural and gradual death more than it does a sudden and violent one. After she was attacked (her group members did not witness the attack) Madam Bee dragged herself into some vegetation to die. It took her several days. Throughout her gradual death her daughter remained by her. Her daughter groomed her and kept the flies from her wounds. Her daughter's presence was the only thing that calmed Madam Bee in those last days (Goodall, 1990). The daughter's actions during her mother's last days are quite similar to those shown by Pansy's daughter.

Gorillas in the Wild

Gorillas in the wild show many of the same behaviors that chimpanzees do when faced with the death of a group member. Many examples come from Dian Fossey's work with gorillas at Karisoke (1983). When adult female Idano grew ill and died her group slowed their pace to allow her to keep up. The adult male slept near her the night she died. Both of these behaviors have been observed in wild chimpanzees when a group member is dying.

The death of adult female Marchessa was natural, though somewhat sudden. She may have died of cysts in her spleen. As she lay dead, adult male Icarus showed some of the same behaviors seen in violent death. He subjected Marchessa's body to repeated attacks, pounding on her and even dragging her. The male in Pansy's group also showed some of these behaviors. Icarus continued his displays for three hours; they continued intermittently through the next day. Between Icarus's displays Marchessa's son Shinda attempted to reach his mother and suckle, much as Pax did when his mother died.

Other juveniles in the group investigated the corpse by smelling and prodding it. Marchessa's daughter also beat on the corpse while her granddaughter groomed her. All the responses shown after Marchessa's death are common. Since her death was sudden, some of the responses displayed are more akin to violent death than peaceful death. Most behaviors shown toward corpses seem designed to invoke some sort of response from the deceased. This may be an expression of frustration or anger over the death, or it may simply be desperate attempts to revive the deceased.

After adult female Quince's mother left her group, Quince became depressed. Perhaps her lowered immune system, resulting from depression, allowed her to contract the malaria that killed her. During her illness the head adult male slowed the group's pace to match hers and defended her from group members. As Quince became weaker other members of her group directed violence toward her. This is common. When a group member cannot respond appropriately the others get frustrated and angry and may show violence toward the sick group member. When Quince finally died her group members were seen circling her body from 150 feet away. This is yet another example of frustration and anger in primates when faced with a loss. Is it surprising that these emotions are so common? They are common in humans.

The death of young Kweli might be considered along with responses to death of an infant, but since both Kweli's parent had died, he was really a group member for the gorillas who mourned him. After poachers killed his parents, Kweli lost the will to live. Kweli himself suffered a gunshot wound and could not recover. He vocalized in distress if the group moved away from him. They continually returned to him and tried to comfort him, even attempting to help him sit up. The group spent the day near Kweli. As his death grew nearer each group member stared intently into his face before leaving him.

This fascination with the face of the dying is also seen in chimpanzees. It could be simple curiosity. It could also be an attempt to get one last look at someone who is part of life and who will be gone soon. Humans often speak of trying to memorize the face of their loved one before they are lost. Might not primates also try to ensure that they will remember the friend who was part of their life? Grief is about learning to live in a new world, a world without your loved one in it. This transition can be easier if one remembers the face of the lost one, perhaps returning to a place they used to go, as Humphrey did.

Conclusion

Grief is a universal human emotion. Its causes and symptoms have captivated and baffled us for hundreds of years. Writers from Anton Chekhov to Charles Darwin have explored the meaning of grief. While grief is expressed in a variety of ways across the primate order, it is infrequently reported in the literature. In humans, the grief response can be generated by many situations, not simply the loss of a loved one. A last emotion—one that is similar to grief—should be discussed for its implications in our treatment of primates. That emotion is despair.

Responses to the Loss of Oneself: Primates in Labs

It doesn't take much searching to find evidence of the horrific conditions that primates in labs are subjected to. Despite widespread outcry against it, biomedical research facilities continue to use primates and insist that their experiments are necessary for humans, even when the experiments require drilling into the brains of primates and inserting toxins. The people who run such labs insist that their standardized cage sizes and diets of monkey pellets provide everything the animals need to live (Randerson, 2008). But is merely existing enough?

On her visits to laboratories Jane Goodall described the conditions of the primates—both their physical environment and their emotional state (1990). No one involved in the testing will comment on their mental state, only that they have enough food to survive. In the name of controlled experiments primates are often kept in solitary cages with little natural materials or enrichment. In recent years facilities have attempted to add some enrichment. But this is tantamount to giving prisoners televisions; it doesn't change the fact that they are prisoners. Primates in laboratories do not display ordinary emotions. They hardly display any emotions at all. Goodall noted their vacant eyes and apathy (1990).

Primates in these labs are suffering from a sort of grief. What they have lost is themselves, and their ability to live a full life. This loss is perhaps more serious than any loss of a loved one. These creatures can learn to use language; they can tell us they are sad (Patterson, 1985). Even the potto understands when a friend is dying and can comfort him (Anderson, 2011). No creature that can feel and think at that level should be subjected to such cruelty.

Primates Grieve

The evidence from Koko the gorilla should be enough to establish that primates grieve; she told us herself how she was feeling (Patterson, 1985). But the wealth of other examples leaves no doubt. All the main symptoms and aspects of grief have been observed in numerous primate species.

The dynamic aspect of grief has been seen in the brief periods of recovery in chimpanzees like Flint who would briefly rouse themselves from their depression to play (Cowles and Rodgers, 1991; Goodall, 1990). The pervasiveness of grief was seen in snub-nosed monkey mothers who withdrew from all social activity after losing their infants (Cowles and Rodgers, 1991; Li et al., 2012). The highly individualized nature of grief was seen in the wildly different responses of infants to the loss of their mother, from Flint who died, to Pax who recovered and thrived. The normative component of grief was conspicuous in its absence, when Flint's case of complicated grief resulted in his death (Cowles and Rodgers, 1991; Goodall, 1990).

The various symptoms of grief have also been seen in primates. Darwin's characteristic facial sagging and passivity were seen in numerous infants in laboratories (Darwin, 1890). Evidence of anxiety was seen in macaques upon the violent death of their group member (Buhl et al., 2012). Loneliness, crying, sadness, and depression were all seen in orphaned infants like Oscar. Hopelessness is seen in primates in labs who have lost themselves (Goodall, 1990).

Every symptom and aspect of the grieving process that has been described in humans is seen in primates. There cannot be any further doubt: primates grieve.

Grief is Functional

The question of whether grief is adaptive is a complex one. To pronounce anything as complicated as grief indisputably adaptive would require more data than we currently have. The lack of systematic observations and experiments makes it impossible to say that grief is absolutely adaptive. However, we can say that grief is functioning in a beneficial way.

Most of the primates suffering grief that have been discussed have survived. Those that didn’t were either too young to survive on their own or were possibly suffering from the pathological condition of complicated grief. Primates like the snub-nosed mothers who lost their infants were able to reintegrate smoothly into their groups after completing the work of grief. Many small infants who lost mothers were able to cope and flourish under the care of siblings and unrelated individuals. These infants were able to reframe their behaviors and environment without their mother. Reframing life is what the work of grief is all about.

The process of grief may come with behaviors—like withdrawal and decreased activity—that do not seem advantageous. But the overall process of grief does serve a purpose; it allows primates, and humans, a time to adjust to their new environment. Therefore, for cases where this is successful and complicated grief is not seen, grief has a beneficial function.

Allowing for Grief

In the current Diagnostic and Statistical Manual of Mental Disorders (the DSM-IV) major depression can be diagnosed just two months after a loss (Shear, 2009). The manual is currently being revised. In the new DSM-V there is a push to remove the "grief exclusion" and say that major depression can be diagnosed before two months have passed (Moran, 2011). The ability to diagnose major depression in grieving people would come with all the ways depression is treated, including anti-depressant pills.

We have seen a case where a mother chimpanzee carried her infant for 68 days (Biro et al., 2010). This period of grief would be too long for the current DSM-IV, and yet there is a push to lower the amount of time people are allowed to grieve. If gelada baboons are capable of grieving, carrying their infants for up to 48 days, how can we possibly expect humans to grieve for less (Fashing et al., 2011)? Grief is a natural process in primates, from pottos to chimpanzees to us. We cannot put restrictions on how long someone can grieve. To rush the process—as researchers did when they removed a mother snub-nosed monkey's infant before she was done carrying it—can cause severe anxiety (Li et al., 2012). When primates are allowed to decide for themselves when to let go of their grief—as mother gorillas allowed to abandon their infants bodies in their own time were—stress is not seen and the transition back to life is smooth (Warren and Williamson, 2004).

Humans should be allowed the same opportunity as the gorilla mothers were; to decide themselves when they are ready to move on and go back to their life and routine. If we deny people that choice, we deny them the power of knowing that they survived the hardest time in their life. There can be no moving on until people feel strong enough to face their life without their loved one.

Grief is not major depression. If grief is diagnosed as major depression it will be treated as such, and most likely medicated away. Prescribing anti-depressants is not the right treatment for grief. Psychologists have pointed out that treatment with anti-depressants may block a person's ability to complete the work of grief (Shear, 2009). Personal accounts by people who have been given pills for grief confirm this. The pills don't help you complete the work of grief; they only help you avoid it. When you stop taking the pills, you have to start all over again (Fiore, 2008).

Anti-depressants like Xanax have been shown to cause sleep trouble and cognitive difficulties, symptoms that grieving people are already struggling with. Moreover, 20% of people prescribed anti-depressants for grief never stop taking them (Parker-Pope, 2007). By prescribing these addictive drugs we are robbing people of the ability to work through their emotions and forcing them instead to dull and avoid the pain, sometimes for the rest of their lives. Is it fair to subject grieving people to this simply because the rest of society wishes to avoid seeing their pain?

If medication is not the right course of action, what is? How can we help those suffering from grief? We can do what the group members of the gelada mothers did: they quietly shared the mother's pain by grooming her infant, and they didn't avoid her despite the unseemly smell of the corpse (Fashing et al., 2011). Instead of encouraging people to get over their grief and move on, we can quietly accept their pain and do what we can to comfort them, instead of avoiding their indecorous grief. Sometimes someone sitting quietly beside us, not pressuring us to be happy or get over our loss, is all that is needed.

Further Work

The amount of anecdotal evidence for grief is impressive, but the amount of systematic studies of grief is disappointing. Little has been done on strepsirrhines, with the exceptions of the potto and well-studied ring-tailed lemur. The only experiments done have been exercises in cruelty that revealed nothing that wasn't fairly intuitive.

Grief is difficult, if not impossible, to conduct experiments on, as most emotions are. What is needed is a greater willingness to systematically describe grief in wild primates and the conditions surrounding it. Most of the anecdotes we have are incomplete with respect to context and ultimate results. The fear of being called anthropomorphic has caused some researchers to ignore critical behaviors and emotions. Jane Goodall's willingness to describe emotions should have begun a revolution, yet some researchers still remain hesitant to describe emotions in primates. We need to make this practice acceptable and encourage it before work can really progress. Caution is needed, primates are not humans and may not capable of all the depths of emotions that we are (similarly, we are not them and may not be capable of their emotions). Nevertheless, such fundamental emotions as grief and joy must be described if we ever hope to understand them.

I would encourage researchers working with wild or captive primates to describe any cases of grief as systematically as they would any other behavior. The unpredictable nature of death makes it difficult to begin a study aimed only at grief. But if people are prepared to note it, then they can collect data on it when it happens. This would greatly contribute to our understanding of this behavior.

While further research concerning primates is important, further research with humans is essential. If we ever hope to help those suffering grief we need to understand them better. It is not enough to prescribe pills or therapy and then never follow up. Those suffering grief need to be monitored and interviewed at various stages. People who have been given pills and found them detrimental need to be heard and given a chance to share their experiences with experts. Grief shares many symptoms with major depression, but it is not major depression and we should not assume that the two can be treated in the same way. If we ever hope to help the grieving then we must talk to them; find out what helped them and what didn't and match our treatments accordingly.

Just Like Us

Anyone who has suffered grief has likely seen echoes of themselves in the accounts of the non-human primates discussed. What mother, after having lost a child, wouldn't sympathize with the desperate wailing of a mother snub-nosed monkey separated from her infant's body? What human being, after losing a best friend, wouldn't empathize with Humphrey's obsession with searching for his lost friend? What child, after losing a parent, would not see their own feelings in Flint's listless disinterest in life?

As humans we can lay sole claim to certain depths of emotions, but we cannot claim the emotions themselves. The discussed primates grieved, perhaps not as deeply as humans, but they definitely grieved. As more and more primate species are threatened with extinction, can we afford to let the nature of their emotions go unstudied? If chimpanzees vanish from the world what will be more valuable; data on what they ate, or the memory of how they loved and grieved? What would we want to be remembered for? We can no longer ignore the emotions of animals in the name of science or medical testing. It would be a tragedy to lose any creature without fully understanding its emotional life (the greater tragedy being the loss of the species).

It may be a chilling road to travel, given the human penchant for insisting that we are fundamentally different from other animals. As we discover more and more about our fellow primates we may discover that they are just like us.

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