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Consequences of Maternal Loss in a Long-lived Mammal, the Red Deer (Cervus elaphus)

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Consequences of Maternal Loss in a Long-lived Mammal, The Red Deer (*Cervus elaphus*)

by

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Abstract

In many mammals, mothers closely associate with offspring both before and after weaning. Social bonds during infancy and adulthood have consequences for offspring fitness and sociality, and this has been the subject of some research, especially in the field of primatology. However, few studies have assessed whether mothers influence offspring fitness after the point of weaning. When it comes to sociality, even fewer studies have assessed the role mothers play in influencing offspring social ties and social stability. In this thesis, I investigate these questions using long-term data from a population of red deer (*Cervus elaphus*). Specifically, I show that in both sexes orphaning reduces prospects of survival even when it occurs after weaning. I further show that orphaning prior to weaning reduces male antler growth but does not affect female primiparity at age 3 years. Finally, I find no evidence that mothers affect offspring sociality in infancy and adolescence.

Declaration

This thesis is entirely composed of original research that I have conducted. I wrote all of the chapters and carried out the analyses independently. Chapters 2 is formatted as a manuscript, and each of the co-authors provided valuable insight on the topics covered, and feedback provided by the co-authors was incorporated into these chapters. Katie Stopher wrote the code for calculating the harmonic mean of the maternal spatial locations, and Katie provided me with this data. I did not collect the field data used in this research, as this was collected under the direction of Tim Clutton-Brock, Loeske Kruuk, and Josephine Pemberton.

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Chapter 1: General Introduction

1.1 Overview

The data chapters in this thesis ask whether social bonds (between mothers and offspring) have value or not, I do not specifically explore the mechanisms involved in producing the benefits. In this general introduction, I give an overview of the potential value of social bonds with emphasis on mechanisms. I also review how social bonds are formed, and which factors can affect their maintenance. The aim of this introduction is to allow the reader to understand why social bonds might exist. This serves to introduce the data chapters (Chapter 2 and 3) that follow, both of which add new perspectives and conclusions regarding the value of social bonds.

1.2 Sociality and Social Bonds

Behavioural interactions among individuals are the basis of animal sociality. The degree and complexity of social behaviour varies widely across animal taxa (Whitehead 2008). Individuals may come together and interact to form large aggregations, and individual relationships may be largely random (Whitehead 2008). In other cases individuals with particular characteristics (based on sex, size, age, dominance, or relatedness for example) may be more likely to form ties: the associations are preferential and non-random (Whitehead 2008). The existence of these associations can have fitness consequences, ranging from the simple (e.g., reduced predation risk [group size in ungulates (Hebblewhite and Pletscher 2002)], and enhanced energy conservation [(huddling in flying squirrels [*Glaucomys volans*] (Merritt et al. 2001)]), to the more complex (e.g., coalitionary support (Fairbanks 2000). The benefits of social ties between two individuals can be affected by social stability (Berghänel et al. 2011). As a result of this, stable associations have presumably

evolved because they enhance fitness to a greater extent than ephemeral associations would. Associations of this type have been referred to as *social bonds*. Though rarely defined explicitly, the term bond suggests a temporal component (Whitehead 2008). Due to the rarity of operational definitions (Silk 2002), I adopt the very general definition offered by Berghänel et al. (2011): bonds consist of "lasting partner preferences in affiliative interactions." These mutual partner preferences are inherently individual-specific, meaning that the characteristics on which attractions are based are exclusive to a single individual. I use a less restrictive term, *social tie*, to describe social behaviour between two individuals that may *or* may not be individual-specific. These ties can involve bonded individuals, but social ties can also involve simple aggregation with no attraction or attraction based on characteristics not exclusive to particular individuals. Examples of the latter include attraction based on sex or age.

1.3 The Value of Social Bonds

1.3.1 ***Social Benefits Across Individuals and Time:*** Social bonds can take on many forms. Bonds can form between kin and non-kin as well as between members of the same or opposite sex (Silk 2007a). In addition, social bonds may last a lifetime, or they may terminate abruptly. Such is the case for social bonds between mothers and young in many mammalian species with sex-biased dispersal. Mothers often continue lifelong associations with their philopatric daughters and social ties are terminated with sons at the point of dispersal (van Noordwijk 2012). In both cases, most would assert that social bonds exist. Although social bonds are often defined based on a component of temporal stability, the above examples show that bonds can also vary across time. Hence, temporal stability in and of itself cannot be used to define the value of a bond. Indeed, for many species that form social bonds, the value of bonds likely varies across time. For instance, in Barbary macaques (*Macaca sylvanus*) unrelated males support each other in conflict during the *breeding*

season, and this coalitionary support is attributed to bonds that are forged and maintained during the *non-breeding season* (Berghänel et al. 2011).

1.3.2 Agonistic Support: Agonistic support appears to be a major benefit of social bonds. In many primates, rank acquisition is related to coalitionary support from kin (see Maestripieri 2009). In particular, mothers often interfere in conflicts involving their offspring, with the result that offspring acquire a dominance rank immediately below their mother's (Fairbanks 2000, Maestripieri 2009). The social benefits of this support can also be time-dependent due to age effects. In many Old World Monkeys, mothers preferentially interfere in conflicts of their youngest offspring. As offspring age and acquire younger siblings the disparity between their rank and their mother's increases (Fairbanks 2000). Other examples of conflict support include male-male alliances found in bottlenose dolphins (*Tursiops* spp.) (Krützen et al. 2003), benefits of maternal presence to resource access in ungulates (Holand et al. 2012), defense of females from male attacks in male-female bonded olive baboons (*Papio hamadryas anubis*) (Lemasson et al. 2008), and conflict interventions by bonded spotted hyenas (*Crocuta crocuta*) (Engh et al. 2000).

1.3.3 Predator Avoidance: In addition to protection from conspecifics, social bonds can also enhance predator avoidance. For instance, in some artiodactyls snorting (a loud expulsion of air through the nostrils) serves to communicate danger to conspecifics (Caro et al. 2004). In species where females form kin groups, females alarm call more than males. This suggests that social bonds may play a role in information sharing (see Caro et al. 2004). Similar observations come from other mammalian taxa as well (e.g. Belding ground squirrels, *Urocitellus beldingi*, Sherman 1977). In at least one species social bonding is specifically linked to cooperative attempts in thwarting predator attacks (Micheletta et al. 2012): In a study of crested macaques (*Macaca nigra*), Micheletta et al.

(2012) conducted field experiments with audio playbacks to ascertain whether socially bonded individuals were more likely to respond to each other's "python related alarm calls". The acoustic profiles of alarm calls differed between individuals, and closely bonded pairs were more likely to attend to each other's calls. In the future, similar studies may demonstrate these benefits to be more widespread.

1.3.4 Information Sharing: Social bonds may enhance information availability and sharing that extends beyond alerting conspecifics to danger. African elephants (*Loxodonta* spp.) provide an illustrative example of how social bonds can enhance transfer of accurate information and increase fitness as well. Elephants live in matrilineally structured female groups characterized by bonded sub-clusters and frequent group fissions and fusions (Moss and Lee 2011). From a distance, groups identify each other as bond-mates, acquaintances, and strangers based on the characteristic vocalizations of other herd members. In this species, group-mates respond to the calls of less familiar individuals (potential hostiles) by organizing into defensive formations. Groups led by older matriarchs are less likely to bunch in response to unfamiliar calls, which may indicate that such groups are more powerful. More interesting though is that groups led by older matriarchs are less likely to misidentify other groups as acquaintances when they are strangers, and vice versa. Thus, social bonds with old matriarchs may reduce possible risks from inter-group conflict and accidental avoidance of friendly groups. As evidence for this, McComb et al. (2001) found that families led by older matriarchs also had greater family-based reproductive success even after family size was controlled for. These observations suggest that, at least in African elephants, social bonds benefit information transfer and this provides fitness benefits as well.

Information signaling and sharing occurs in many taxa ranging from domestic chickens (*Gallus gallus domesticus*) (Marler et al. 1986a), to artiodactyls (Charo et al. 2004), macaques (*Macaca* spp.) (Micheletta and Waller 2011), chimps (*Pan troglodytes*) (Slocombe and Zuberbühler 2006) and humans. In domestic chickens, a species with comparatively low cognitive capacity, cockerels emit calls that communicate the presence and quality of food items (Marler et al. 1986a). These calls are infrequent when cockerels are alone or with other males (competitors). However, they become significantly more frequent in the presence of familiar and unfamiliar hens (Marler et al. 1986b). It is no surprise then that more cognitively able species can convey similar information. In chimpanzees, for instance, grunts of various tones convey information about food quality as well (Slocombe and Zuberbühler 2006). In some ungulates offspring copy the foraging habits and food selection of their mothers (Mirza and Provenza 1992, Oostindjer et al. 2011). Given the widespread occurrence of information sharing and use, it is surprising how little research has sought to understand whether social bonds influence the likelihood of information transfer. Of particular importance is how the presence and strength of social bonds might influence the qualities of information signals: are more closely bonded individuals more likely to share information, and is this information more reliable (reduced chance of being deceitful)? If so, how does this influence the responses of individuals to information signals from conspecifics? This is certainly an area of research where major developments can be expected.

1.3.5 Food Sharing and Tolerance: In many primates, carnivores, and at least one cetacean species, food sharing occurs between bond-mates (e.g. Hoelzel 1991, Mitani and Watts 2001, Jaeggi et al. 2008, Holekamp and Smale 2010). Often this is involved with parental care. Frequently food is provisioned from parent to offspring (e.g. Jaeggi et al. 2008, Holekamp and Smale 2010), but

sharing can also occur between bonded parents, as it does in Corvids (see Goodwin 1986, Bugnyar et al. 2001). Though food sharing is most common in the context of parental care, it also occurs in other social contexts. For instance, in chimpanzees, male hunters occasionally share their kill with other males, but this occurs with great variability. Some pairs share very often while others never appear to do so. In this population, males form close bonds, meat sharing is often reciprocal, and those dyads that share more often are also more likely to support each other in conflict (Mitani and Watts 2001).

Beyond actual transfer of food items, social bonds can also facilitate enhanced resource access through tolerance. In baboons (*Papio cynocephalus*) there is increased tolerance between bond mates, particularly in respect to resting and feeding in proximity to one another (Silk et al. 2006). Similar kin-biased tolerance is observed in red deer: In this species females are permitted to remain in their natal group throughout their mother's lifespan, and aggression at feeding sites is reduced between relatives (Clutton-Brock et al. 1982).

1.3.6 Effects on Third Party Relationships: Social bonds can also affect third party relationships. Under some circumstances, the presence of social bonds with one individual can facilitate associations with other individuals. In these cases, removal of particular bond-mates is expected to result in the loss of other social ties as well (see Chapter 2). This appears to be the case in some mammals living in matrilineal societies. In rhesus macaques (*Macaca mulatta*) matrilines sometimes split following the death of an adult female (Chepko-Sade and Sade 1979). Groups splintered in such a way that the dead mother's descendants dissociated from her non-descendant kin. The death of certain matrilineal relatives is associated with similar effects in African elephants

as well (Moss and Lee 2011). This topic has rarely been investigated, and further developments are needed (see Chapter 3).

1.4 The Loss of Social Bonds: Responses and Fitness Consequences

Positive social interactions between individuals cause neurochemical changes that instate and serve to maintain social bonds (Young and Wang 2004). Neurochemical mechanisms of bonding appear conserved across bond types, and the mother-infant bond appears to be the original architect of this system (Curley and Keverne 2005). The parts of the brain that promote mate pair-bonding, and likely other pair bonds, involve the same circuits that process rewards. Rewarding tactile stimulation (e.g. from grooming or sex) causes the release of certain chemicals within the brain (e.g. beta-endorphin, oxytocin, vasopressin) (Young and Wang 2004, Curley and Keverne 2005, Crockford et al. 2013). The partner offering the reward also provides stimuli that are unique to him or herself (e.g. scent or visual profile). The result is that individuals learn to associate particular social partners with a reward (Young and Wang 2004). Individuals then seek the reward through continued contact with that social partner, and this leads to the formation of a bond. The reward system that social bonds are based upon overlap with that on which drug addictions operate (see Kelley and Berridge 2002, Young and Wang 2004), and it would appear that individuals develop a dependency on the chemical rewards that follow positive contact with bond-mates. This apparent dependency results in marked behavioural changes following the loss of social bonds.

In relation to social bonds, the changes that follow the removal of the social rewards are likely adaptive. For instance, infants separated from their mothers emit distress vocalizations, increase their movement, reduce foraging activity (Haley et al. 2005) and show intermittent spells of inactivity (Newberry and Swanson 2008). As with most responses to social deprivation, an adaptive value can be attributed to them. In the case above, the vocalizations and movement likely

serve to reunite mother and offspring, which has led to the term, “reinstatement behaviour” (Newberry and Swanson 2008). The *potential* benefit of reinstatement behaviours comes at a cost: increased energy expenditure occurs while energy intake declines and vocalizations may attract the attention of predators. When maternal bonds are forever lost, as is the case if the mother has died, then reinstatement behaviours bear only costs.

The permanent removal of social bonds, as described above, is one of the more extreme forms of social disruption, and recent research on the topic has highlighted the important effects of bond loss. In humans, where most research has occurred, the loss of family members elicits a stress response (e.g. Dietz et al. 2012), and this can be followed by reduced immune function and an increased hazard of death (see Engh et al. 2006, Boyle et al. 2011, Dietz et al. 2012 and references therein). Research on non-human mammals is scarcer, but recent work has demonstrated similar stress responses. For instance, Engh et al. (2006) used a population of chacma baboons (*P. hamadryas ursinus*) to investigate whether the loss of close kin resulted in behavioural and hormonal changes. They found that females who lost a close relative due to predation experienced a physiological stress response. The death of a family member also increased the frequency of grooming interactions among kin, and so it appears that females attempt to compensate for the lost bond by strengthening bonds with other family members. Such compensation attempts are expected based on the way in which positive social contact works on the reward system of the brain (see above discussion, and Engh et al. 2006). Increased grooming following the death of an associate may further benefit females because it counteracts the stress response: in females, positive social stimulation is followed by oxytocin release, and oxytocin is an antagonist of stress hormones like cortisol (see Engh et al. 2006). In reviewing the importance of social bonds in primates, Silk (2007b) and Fairbanks (2000) highlight similar changes in social affiliations following the loss of a

social bonds. A recent analysis of social patterns in red deer suggests that such adjustments are not limited to primates (Ruckstuhl et al. 2013, submitted).

As discussed above, social bonds offer certain social benefits, and their loss is associated with costly reinstatement behaviours and stress responses. Given this, the loss of social bonds, such as family bonds, should also result in reduced fitness (reduced survival and/or reproductive success). In considering the literature on survival, few studies have been successful in demonstrating an effect of bond loss. For instance, in a review of maternal benefits in Old World primates, Fairbanks (2000) notes an absence of survival consequences following post-weaning maternal loss. A recent study of reindeer (*Rangifer tarandus*) showed that the presence of mothers enhanced resource access for offspring, yet over-winter survival appeared unaffected by maternal loss (Holand et al. 2012). As the above examples illustrate, most research on survival benefits of strong bonds have focused on the mother-offspring bond. Although most studies fail to show a benefit of mothers to offspring after weaning, a few have (see Fairbanks 2000). In mammals, the fitness benefit of maternal presence before weaning is obvious; therefore benefits at this developmental stage will not be discussed further. The survival benefit of post-weaning maternal bonds have been demonstrated in two cases, neither of which involve primates. This was first shown in North American wood rats (*Neotoma cinerea*), a species where daughters remain in their mother's home range after weaning. In this species the presence of mothers improves offspring survival at high population densities (Moses and Millar 1994). In orca whales (*Orcinus orca*), a species where both males and females remain in their natal group throughout life, it was shown that the presence of mothers enhances the survival of both sons and daughters even later into adulthood (Foster et al. 2012). Additional studies on the benefits of mothers after weaning are needed (see Chapter 2).

More research has been done on the reproductive benefits of mothers after weaning, but most of this work comes from primates. In vervet monkeys (*Chlorocebus pygerythrus*), adult females with mothers still alive produce more offspring and have higher infant survival rates (Fairbanks and McGuire 1986), and these patterns have been confirmed through experimental manipulations (Fairbanks 2000). In Japanese macaques (*Macaca fuscata*), daughters reproduced at an earlier age and had offspring with higher survival rates when their mother was still alive (Pavelka et al. 2002). Instances where grandmothers directly support their grand-offspring appear relatively common among some Old World monkeys (Fairbanks 2000). Further reproductive benefits from kin social bonds are provided in Silk (2007a). Few studies of non-primates have looked at the benefit of mothers to offspring reproduction. However, such benefits do occur in wood rats (Moses and Millar 1994) and may occur in many other non-primates where females are socially philopatric.

In the primate literature, a great focus has been placed on the benefits of mothers to their daughters (see Fairbanks 2000), and this reflects the sex differences in philopatry and dispersal. Since females are typically the philopatric sex in most mammals, mothers have an extended opportunity to affect the fitness of their daughters than their sons. However, even when males disperse, they tend to do so some time after weaning. Therefore, the value of mothers to their sons after weaning should also be considered.

1.5 Evaluating the Benefits of Social Bonds

From the discussion in the preceding section, one important question arises. Why is there such a lack of studies demonstrating fitness benefits of social bonds, especially those occurring with mothers after weaning? This might be explained by the difficulty involved in answering this

question. To do so one requires individual life history data, and longitudinal studies of this kind are relatively rare. Further, to demonstrate such benefits, the performance of individuals with intact bonds must be compared to individuals not possessing these bonds. In studying the mother-offspring bond, this can be accomplished through experimental removal of mothers, but many long-term life history studies typically avoid such potentially disruptive manipulations. The alternative is to rely on mothers dying of natural causes. The rate at which such data accumulate is proportional to the lifespan of the species. Hence, most studies on long-lived species are too short to make use of natural orphaning data. These reasons make it clear why maternal benefits after weaning are so rarely demonstrated. Few studies have attempted to determine whether mothers benefit offspring after weaning, and of those that have, the sample size limitations likely precluded a powerful test of the hypothesis (see Fairbanks 2000 and references therein). In addition, the correct statistical methods for such longitudinal data have not been widely available until recently, and this applies especially to the analysis of survival.

In this thesis I evaluate the benefits of maternal presence to *both* males and females in a population of red deer from the Isle of Rum, Scotland. Individual life-history data have been collected from this population since 1974, and this has resulted in the accumulation of sufficient natural orphaning events to make practical the analyses that follow. In Chapter 2, I use the latest statistical methods to investigate whether red deer mothers affect the fitness of their offspring before and after weaning. In Chapter 3, I go on to investigate the potential role that mothers play in shaping their offspring's social environment. In its entirety this thesis serves to fill a large gap in our knowledge regarding the value of mother-offspring social bonds. Importantly, my work focuses on these benefits in a non-primate mammal, which is a group that has been neglected in this area of research.

Chapter 2: Sex differences in the consequences of maternal loss in a long-lived mammal, the red deer (*Cervus elaphus*)

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2.1 Abstract

In several primates, the presence of mothers affects the growth, survival and reproduction of their offspring, but similar effects have not yet been demonstrated in ungulates. Here, we investigate the effects of the mother's presence in a population of red deer (Cervus elaphus) on the Isle of Rum, Scotland, which is the subject of a long-term, individual-based study. We compared measures of performance including antler growth in young males and age at first reproduction in females and survival of deer with mothers still alive against those that have lost their mothers (orphans). We show that orphaning both before and after weaning increases the risk of a natural death for both sexes. For males, no maternal benefit was detectable past 24 months of age while, for females, post-weaning benefits continued throughout life. Orphaning resulted in compromised male physical condition as measured by a reduced probability of growing antlers by 16 months of age while no evidence for compromised reproduction was found in females. These results support assertions that post-weaning maternal associations affect the development and survival of offspring.

Keywords: maternal care, sex differences, orphaning, philopatry, emigration, red deer, *Cervus elaphus*

2.2 Introduction

In many long-lived mammals where females are philopatric and live in groups, mothers have the opportunity to affect the fitness of their daughters throughout the maternal lifespan (Clutton-Brock 1991; Fairbanks 2000). Mothers also typically associate with offspring of the dispersing sex for at least some time after weaning (Green et al. 1989; van Noordwijk 2012). Therefore, maternal care towards dispersing young can continue up to the time of emigration (van Noordwijk 2012).

Although benefits of home-range familiarity and the costs of dispersal could favour philopatry and delayed dispersal after weaning (Fairbanks 2000), preferential association between mothers and weaned offspring suggest a role for social factors as well (Clutton-Brock 1991; Fairbanks 2000). Such associations are widely observed in group-living mammals such as red deer (Clutton-Brock 1991). In many mammals, mothers defend their offspring against predators (see Nowak et al. 2000; Grovenburg et al. 2009) and aggression from conspecifics (Cervus elaphus, et al. 1982; Bison bison, Brookshier and Fairbanks 2003). Maternal social support can allow offspring to maintain more central group positions (Cervus elaphus, Clutton-Brock et al. 1982; Bison bison, Green et al. 1989; Brookshier and Fairbanks 2003). Therefore, in the absence of their mothers, juvenile offspring may suffer higher predation, reduced foraging efficiency (due to increased need for vigilance) and lower access to resources (Brookshier and Fairbanks 2003). Juveniles may also continue to benefit from their mothers due to conflict support (Silk 2007a, b), and in bonobos (Pan paniscus) mothers affect their sons' reproductive success by assisting them during male–male mate competition (Surbeck et al. 2011). Other maternal benefits include food sharing (Jaeggi et al. 2008; Holekamp and Smale 2010), copying of foraging habits (Oostindjer et al. 2011) and food selection (Mirza and Provenza 1992; Sanga et al. 2011). For some species, juveniles also appear to learn traditional patterns of habitat use and movement from their mothers (Clutton-Brocket al. 1982;

Nelson 1998; Murray et al. 2008).

Although both males and females can gain from maternal care after weaning, sex differences in the extent to which they benefit are expected. The sexes often differ in body size and their tendencies toward philopatry. In sexually dimorphic species, in which adult males are larger than females, male juveniles typically have greater metabolic requirements and growth rates than females (Clutton-Brock1994). This life- history trait comes at a cost of higher sensitivity to resource shortage for males (Clutton-Brocket al. 1982; Clutton-Brock1994), and this has been put forth as a reason why, in species in which males are larger, mothers sometimes appear to invest more heavily in their sons (Reiter et al. 1978; Clutton-Brocket al. 1981). For most polygynous group-living species, however, males typically disperse while mothers continue lifelong associations with their philopatric daughters (Clutton-Brocket al. 1982; Kaminski et al. 2005). Such is the case in red deer (Clutton-Brocket al. 1982; Clutton-Brock1994). Therefore, later in the offspring's life, the mother's presence has the potential to benefit her daughters but not her sons.

Despite the great interest in post-weaning maternal associations, relatively few studies have quantified its effect on offspring fitness. A few exceptions are provided by studies of primates where dominance positions influence reproductive success and mothers provide assistance in conflict (Fairbanks 2000; Silk 2007a, b). In these cases, maternal presence appears to enhance offspring fitness (Fairbanks and McGuire 1986; Fairbanks 2000; Pavelka et al. 2002; Surbeck et al. 2011), and it appears that sex differences in philopatry affect the duration of these effects (van Noordwijk 2012). Similar contrasts have not been performed in other mammals. Although there is growing evidence that mothers influence offspring reproduction after weaning, the idea that mothers also influence survival has rarely been subjected to tests (but see Foster et al. 2012). Here, we use an extensive long-term dataset on red deer to investigate to what degree orphaning (both natural and

human caused) affects juvenile survival of both sexes, what effect the absence of mothers has on the fitness of their offspring and which sex is more affected by the absence of a mother.

In this study, we assess the general hypothesis that post-weaning maternal associations are a form of maternal care. In doing so, we test the following hypotheses and predictions:

H1: Maternal presence affects offspring survival.

1. Offspring losing their mothers (orphans) will experience an elevated risk of death compared to non-orphans.

H2: Sex and age at orphaning interact to affect the consequences of maternal loss.

2. For both sexes, orphaning will reduce survival, but female philopatry means that maternal loss later in life affects females but not males.

H3: Survival of males and females is affected differently by maternal care prior to weaning.

3. Orphaning prior to weaning (13 months of age) increases the risk of death more for males than females.

H4: Maternal presence affects correlates of reproductive success.

4. Maternal loss prior to 13 months of age inhibits male antler growth.

5. Maternal loss prior to 28 months of age reduces the probability of calving at 3 years of age for females.

2.3 Methods

2.3.1 Study Area and Animals

All data used in this study were collected in the North Block on the Isle of Rum, Scotland (57^{o} 01' N, 06^{o} 17' W, NM-402996). A detailed description of the study site is found in Clutton-Brocket al. (1982). Study years spanned from 1973 to 2011. Since 1972, all individuals in the 12-km2 North Block of the island have been individually recognisable based on identification collars or natural markings, and since 1974 formal monthly censuses have been routinely conducted (Clutton-Brocket al. 1982). The behaviour and physical appearance of females was used to identify postparturient mothers, and their calves were located, captured, sexed and marked with unique ear tags and/or collars. Their survival was monitored through monthly censuses (minimum of five per month) and intensive mortality searches in the spring. Death timing for individual deer was indicated by visible reductions in body condition and restricted movement, the discovery of their carcass on the hill, larder records and/or the disappearance of the animal (Clutton-Brocket al. 1982).

As typical seasonal breeders, red deer on the island display synchrony in conception, with 70 % of conceptions occurring during a 2-week period in mid-October leading the (singleton) calves to be born primarily in late May and June (Clutton-Brocket al. 1982). In the harsh climate of Rum, females do not conceive as yearlings, and the earliest age at first calving is 3 years. For deer born in June, this corresponds to a first possible conception age of approximately 28 months. Red deer mothers and daughters frequently maintain life-long associations, and associations with sons continue up to the point of dispersal (Guinness et al. 1979; Clutton-Brocket al. 1982). Male dispersal is most common between 2 and 5 years of age (Clutton-Brocket al. 2002), but maternal associations typically decline prior to dispersal and become infrequent by age 24 months (<25 % association) (Guinness et al. 1979). The age at which males grow their first set of calcified antlers

also varies. On the island, most males complete their first antler growth at 16 months of age, but for some this can be delayed to 28 months of age. Malnutrition is the primary cause of mortality for deer on the island, and this occurs principally during winter and early spring (Clutton-Brocket al. 1982). Other proximate causes of death include accidents, intraspecific conflict (e.g. rutting injuries), rare cases of eagle predation on young calves, and shooting (Clutton-Brocket al. 1982). Reproduction, survival and development vary greatly across cohorts, and this is related to large between-year variation in climatic conditions (Guinness et al. 1987). In the North Block, professional deerstalkers culled deer until 1972, at which point culls terminated. Controlled recreational hunting and culling continues to regulate population levels outside of the study area. Deer born within the North Block which range outside it risk being shot; since males are the dispersing sex, the probability of males being shot over their lifetimes is higher than for females.

2.3.2 Data and Analysis

Cox survival analysis (predictions 1-3):

Survival time was analysed with Cox regression using SAS® PROC PHREG and the Efron approximation to handle tied event times. All models accounted for non- independence between death times of siblings by including mother identity as a clustering variable. In these models, regression parameters are estimated by maximising partial enhances offspring performance) and incorporating it into the analysis, we considered all deer to be weaned at 1 year of age. This helps to partially buffer against some cases where calves continue suckling beyond 7 months of age. Each age at orphaning class was included as a separate time-dependent factor with two levels (orphan, non-orphan). Our analysis spans across all ages of orphaning considered. For both males and females, the earliest orphaning events observed occurred at 3 months of age, and the latest events

occurred at 187 and 150 months for females and males, respectively. On Rum, most females die before 18 and males before 15 years of age (Kruuk et al. 2002; Nussey et al. 2006).

The following additional variables were used in the modelling of deer survival

Maternal age category – As per the methods of Guinness et al. (1978), deer were classified as being born to young (3–6 years old), middle (7–10 years old), and old-aged (≥11 years old) mothers, where age represents the age of the mother at the time of calving.

Residual capture weight – The residual of capture weight from a general linear model incorporating capture age (hours—extending from 0 to 312 h) and sex. Capture weight was included in the models at the cost of some data loss (not all deer in the study were weighed at birth). This was justified given the finding that both male and female orphans tended to be heavier at capture than non-orphans (see Appendix A).

Birth year (cohort) – Categorically defined as the year of birth (1973 through to 2011 inclusive).

Birth month – Categorically defined as the month of birth (May, June, July, August, September).

Home range area – The North Block of the island is divided into five discrete areas to which we assigned deer mothers based on the harmonic mean of their spatial locations (see Dixon and Chapman 1980). The harmonic mean was calculated using census observations from January to May of each year. Similar methods have already been applied to assess and control for spatial differences in habitat quality on the Isle of Rum (see Nussey et al. 2007). To avoid confounding between habitat quality and orphaning status, deer were assigned to one of these five regions based on the spatial locations occupied by their mother in their year of birth. Of the deer eligible for analysis, 6 % (n = 172/2,714) could not be assigned to a region due to insufficient data on their mother's region in the year of her offspring's birth. In these cases, we still assigned a region if this

information was available in the year preceding or following a deer's birth. The latter was selected when both were available. Using the above methods, a total of 2,602 individuals were assigned regions, and 96 % of these involved the mother's home range in the year of each focal calf's birth.

Cause of death – Deaths were categorised as natural [starvation, accidents, died at birth, died while giving birth (birthing complications) and unknown (missing and never observed again)] and shot. In modelling survival, female and male offspring were analysed separately. Survival plots were constructed for maternal age category, birth month and home range area in order to visually assess the proportional hazards assumption (i.e. that the relative difference in risk between categories remains constant over time). Survival plots for home range area showed frequent crossing of survival curves, which strongly indicated a case of non-proportional hazards. Therefore, we stratified all further analyses on home-range area, which allowed for different baseline hazards across the various subdivisions of the study area (i.e. allowed for unspecified interactions between the survival effect of home range area and time).

A list of candidate models were constructed which included all combinations of maternal age category, capture weight, birth year, birth month, and the interaction between birth month and year. For models with the interaction term, both birth month and birth year main effects terms were included as well. The aforementioned orphaning factors were included in all of the candidate models. Models were ranked according to their AIC values and the top model was selected for assessing the orphaning effect hypothesis. This method allowed us to select among potential confounding factors, account for their influence on the risk of death and finally conduct a formal hypothesis test of the orphaning effects at various ages (e.g. make comparisons among both significant and non-significant terms). Using the approach of dividing orphaning effects into separate age at orphaning categories, the estimated effect of age at orphaning on the risk of death

represents an averaged effect over the post-orphaning period (Allison 2010); the possibility that the risk of death declines as time since orphaning increases is not directly assessed. The approach taken facilitates the direct comparison of hazard estimates between the various ages at orphaning (as opposed to comparing slopes, for instance) (Allison 2010).

The saturated model is shown below (as per Allison 2010; Foster et al 2012):

$$h_i(t, Z(t)|Z_1,\ldots Z_5) = h_0(t)exp[\beta_{BC}Z_{iBC}+\beta_{WT}Z_{iWT}+\beta_{BY}Z_{iBY}+\beta_{BM}Z_{iBM}+\beta_{BMBY}Z_{iBYBM}+\beta_{OR1}Z_{OR1}(t)+\beta_{OR2}Z_{OR2}(t)+\beta_{OR3}Z_{OR3}(t)+\beta_{OR4}Z_{OR4}(t)]$$

where:
h is the hazard of death (the rate at which death occurs)
$Z(t)$ indicates the full set of predictors at time t
Z_i.. indicates the covariate value/factor level for individual i
t_{OR} = deer age (in months) when mother died
β_{BC} = maternal age category
β_{WT} = residual capture weight
β_{BY}= birth year
β_{BM} = birth month
β_{BMBY} = interaction between birth year and birth month
t_{OR} = deer age (in months) when mother died
β_{OR1} = 1 if the mother is dead at time t and if $t_{OR} \leq$ 12 mo, otherwise 0.
β_{OR2} = 1 if the mother is dead at time t and if 12 mo $< t_{OR} \leq$ 24 mo, otherwise 0.
β_{OR3} = 1 if the mother is dead at time t and if 24 mo $< t_{OR} \leq$ 36 mo, otherwise 0.
β_{OR4} = 1 if the mother is dead at time t and if 37 mo $\leq t_{OR}$, otherwise 0.
$Z_1,\ldots Z_5$ indicate the 5 strata for home-range area.

The structure of the above model is such that each time an event occurs (death of a deer) the orphaning status value is determined for all individuals that had an opportunity to die at that time. Therefore, the relative hazard is calculated based on the distribution of the covariate (orphaned or not) in relation to event times (Williams 2008). This time-dependent modelling avoids issues encountered prior to the development of this method. Namely, individuals who experience a treatment (e.g. orphaning, organ transplant, heart attack etc.) must have survived long enough to

experience this event. Due to this fact their survival may already be longer than the group not experiencing the event (e.g. non- orphans), and the treatment effect would consequently be biased toward a positive effect on survival.

We assessed the possibility that orphaning influenced the risk of the offspring's death differently depending on the cause of the offspring's death (natural versus shot). Hence, they were modelled as competing risks. In these analyses, we ran separate models for each risk type of interest (death by natural causes for instance) and all other event types were considered censored (i.e. deer dying of a factor not of interest contribute to the risk set for the time they are known to be alive and are considered as missing data thenceforth). For example, death by shooting obviously removes an individual from being at risk of a natural death, but if this event had not occurred, then natural causes would eventually kill the animal. Therefore, we ran separate models for natural (not caused by humans) and hunting deaths, and in each model animals still alive at the end of the study were censored. As before, these analyses were stratified on home-range area.

To test if males are more sensitive to orphaning, we compared the hazard of natural death from orphaning between males and females orphaned prior to 1 year of age. The Wald chi-square test statistic with 1 degree of freedom was calculated as:

$$\frac{(b_1 - b_2)^2}{[(s.e._1)^2 + (s.e._2)^2]}$$

where b1 and b2 are the sex-specific estimated coefficients for orphaning, and s.e.1 and s.e.2 are their respective standard errors (Allison 2010).

Antler spike growth (prediction 4): The presence or absence of antler spikes at age 16 months was visually assessed in the field. We used these data to investigate the likelihood of deer carrying antlers (spikes) as yearlings and whether this is related to orphaning prior to age 13 months. This

effect is conditional on deer surviving through to their second summer; therefore, these surviving orphans likely represent individuals on the upper end of a physical health spectrum. Thus, the analysis is assumed to provide a conservative estimate of the degree to which orphaning causes physical condition to deteriorate.

The data used for this analysis include all individuals for which yearling antler measures were available. We aimed to compare antler growth of orphans and non-orphans within cohorts (birth years). Given that there are many cohorts (strata), each with few observations, ordinary maximum likelihood estimates may be invalid; in such cases, a conditional likelihood is preferred (Stokes 1999). Therefore, we performed a conditional logistic regression in the SAS® system using PROC PHREG and stratified the analysis by birth year. This analysis models the relative risk of not growing spike antlers given an individual's orphaning status; therefore, results are presented as hazard ratios. A total of 16 orphans, 198 non-orphans and 11 cohorts contributed to this analysis. Cohorts where both orphans and non-orphans experienced the same outcome (e.g. did not grow antlers) did not contribute to the analysis, nor did cohorts that included only deer of a single orphaning status (e.g. all non-orphans). We refer to these as non-informative strata with the converse being informative.

As a check for a mix-up in our interpretation of cause and effect from the previous analysis (herein referred to as confounding), we performed the same analysis using a different subset of the data. This subset of data excludes deer orphaned prior to 15 months of age and instead classifies individuals as orphans if their mother died between 16 and 24 months of age. By this time, the first opportunity to grow hardened antlers has already passed, and if an orphaning effect were observed it would indicate that growing antlers predicts orphaning (instead of orphaning predicting antler growth, as we wish to test). A total of 16 orphans, 202 non-orphans and 12 cohorts contributed to

this analysis. In doing so, we found no significant difference between orphans and non-orphans in the probability of growing antlers [hazard ratio=1.208 (0.321, 4.544 95 % CI), Wald $\chi 21_{df=}$ 0.078, P=0.78]. Therefore, we accordingly reduce our concern over whether the focal analysis on the effect of orphaning prior to 13 months is confounded.

Female reproduction at 3 years of age (prediction 5): We modelled the probability of reproductive failure at age 3 using conditional logistic regression. To be included in this analysis, females had to survive until August of their third year of life. Females dying after having given birth in their third year were also included. As with the antler growth analysis, this reproductive analysis provides a conservative test of whether orphaning affects female physical condition. Here, we performed two analyses using different criteria to define orphans. In the first analysis, deer were considered orphaned if they lost their mothers prior to 28 months of age. For deer born close to peak calving time (May or June), this corresponds to maternal loss shortly before the average date of first possible conception. In the second analysis, we defined orphans as those deer that lost their mothers prior to age 13 months. To remove cohort effects and reduce possible confounding, individuals that gave birth at age 3 and those that did not give birth were matched on birth year. A total of 43 orphans, 207 non-orphans and 17 strata were utilised in this analysis.

2.4 Results

Of the deer included in the study, 28 % of males and 36 % of females lost their mothers at some point during their lifetime (Table 1). Of those that lost their mothers prior to 13 months of age, 71 % of males and 84 % of females were orphaned after 7 months of age (the average weaning age). Orphaning was associated with reductions in survival, but it influenced the risk of death by specific causes (natural versus shot) differently. The consequences of orphaning also differed between the sexes and across the age at orphaning categories.

Table 1. Sample sizes for number of orphans included in the analyses of survival. Age Class represents the age (months) interval that deer were orphaned in. The Total column includes the total number of orphans and the percentage of those that remained alive throughout the duration of the study. Percent of population indicates the proportion of deer used in our analyses that were orphaned. Natural and Shot columns indicate the number of orphans dying of natural and shooting related deaths, respectively.

		Sample Sizes			
Sex	**Age Class**	**Total, % Censored**	**Percent of Population**	**Natural**	**Shot**
Male	0 to 12	74, (3%)	7.5%	65	7
	13 to 24	41, (7%)	4.2%	18	20
	25 to 36	20, (10%)	2.0%	7	11
	37 +	131, (8%)	13.3%	82	39
Female	0 to 12	55, (4%)	5.8%	41	12
	13 to 24	25, (12%)	2.6%	13	9
	25 to 36	44 (5%)	4.6%	26	16
	37 +	203 (15%)	21.4%	133	40

2.4.1 Orphaning and Survival:

The estimated effects of orphaning presented below are taken from the top-ranking model for each analysis (Table 2). Effects of orphaning at various age categories are summarised in Table 3.

Males - When modelling death by any cause, orphaning was associated with an increased risk of death for male deer orphaned between 0 and 12 months, 13 to 24 months, but not for deer orphaned from 25 to 36 months or greater than 36 months of age (Figure 1a, Males). When modelling only natural death, the same general pattern emerged (Figure 1b, Males). Orphaning was not associated with any change in the risk of being shot within a given month (Figure 1c, Males).

Females - When death by any cause was modelled, orphaning in all age classes was associated with an increased risk of death (Figure 1a, Females). In a separate analysis modelling the effect of orphaning on natural death, orphaning increased the risk of death for deer orphaned at 0–12 months, 25 to 36 months, but not for those orphaned at 13 to 24 months or after 36 months of age (Figure 1b, Females). Orphaning was associated with an increased risk of being shot for deer orphaned between 13 and 24 months, 25 to 36 months, but not for those orphaned at 0–12 months or older than 36 months (Figure 1c, Females).

Males vs. females - The effect of orphaning between 0 and 12 months of age on natural death was significantly greater for males than for females (Wald $\chi 21_{df=9.27,}$ P=0.002).

Table 2. Top ranked Cox survival models for male and female red deer. All models include hypothesised effects of orphaning (orphaned at age: 0-12 months; 13-24 months; 25-36 months; > 36 months). Parameters abbreviated as: *MA* mother's age at parturition; *WT* residual capture weight; *BY* birth year; *BM* birth month.

Death Type Modeled	**Parameters, Males**	**Parameters, Females**
All death types	WT + BY + BM	MA + WT + BY + BM
Natural death	WT + BY + BM	MA + WT + BY + BM
Shot	-	BY

Table 3. Effects of orphaning on survival of red deer orphaned at various age categories. Death types abbreviated as *N* natural death, *S* shot.

		Males		Females	
Age Orphaned	**Death Type Modeled**	**Hazard Ratio**	**P-value**	**Hazard Ratio**	**P-value**
0-12 mo	N + S	2.61	<0.0001	1.52	0.03
	N	3.41	<0.0001	1.67	0.02
	S	0.52	0.56	1.63	0.22
13-24 mo	N + S	1.55	0.04	1.63	0.04
	N	2.63	<0.001	0.99	0.88
	S	0.90	0.67	2.80	0.01
25-36 mo	N + S	1.22	0.45	2.52	<0.001
	N	1.52	0.41	1.78	0.04
	S	1.01	0.96	2.77	<0.01
37 mo +	N + S	1.34	0.55	1.56	0.01
	N	1.49	0.12	1.21	0.34
	S	0.98	0.91	1.38	0.27

2.4.2 Antler Spike Growth and Orphaning:

Compared to non-orphans, deer that were orphaned prior to 13 months of age were 3.27 times less likely to carry antlers in their second autumn [hazard ratio = 3.272 (1.111, 9.633 95 % CI), Wald $\chi 21_{df} = 4.63$, P=0.032, n=16 orphans/198 non-orphans, 11 informative strata/years].

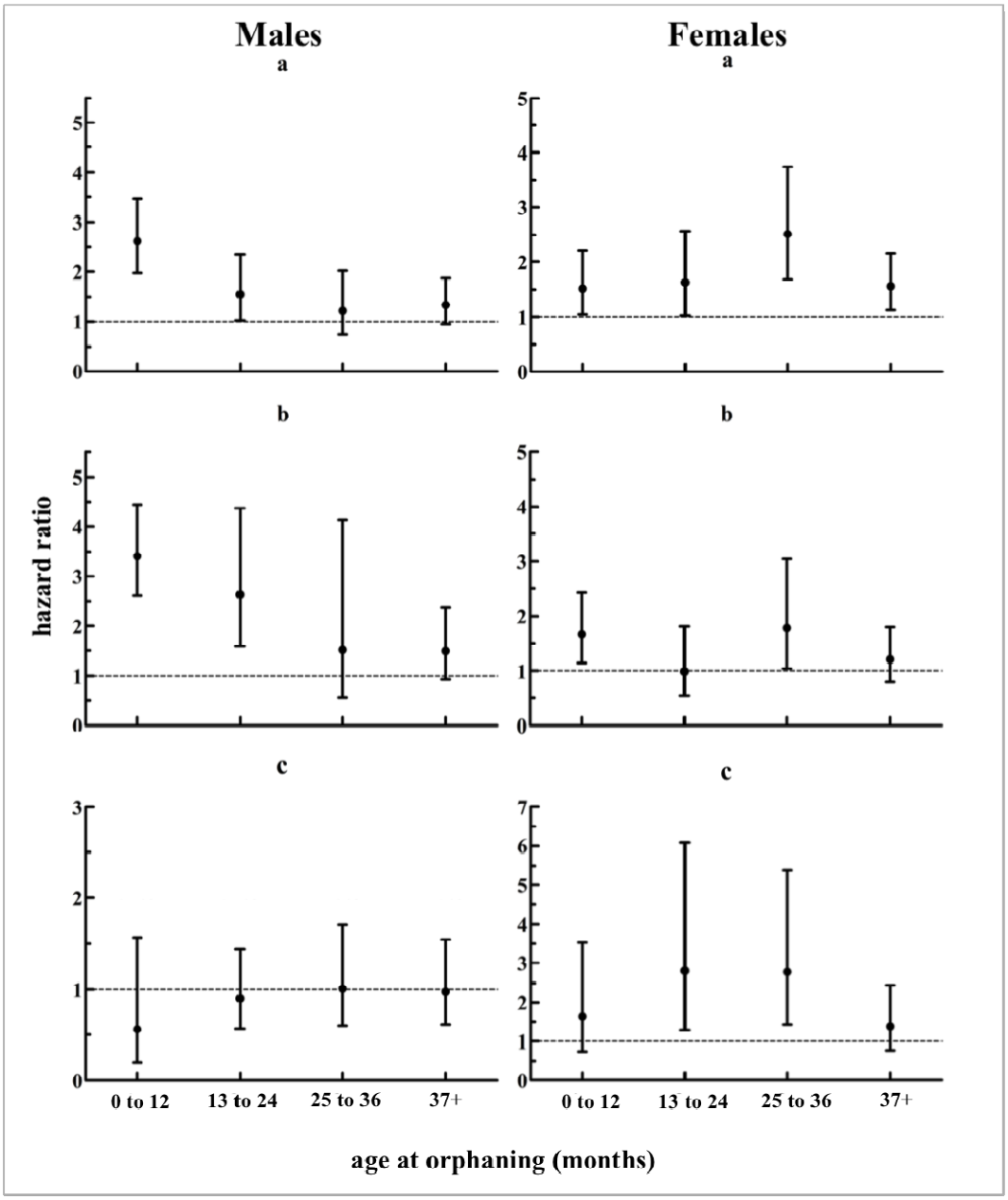

Figure 1. Hazard ratios for death and 95% confidence intervals for orphan relative to non-orphan red deer. Ages at orphaning are divided into age categories: 0-12 months; 13-24 months; 25-36 months; 36+ months. The effect of orphaning on the risk of death by different causes are indicated: a) natural and shooting caused death; b) natural death; c) shooting caused death.

2.4.3 Orphaning and Female Reproduction:

There was no significant difference in the likelihood of reproduction at age 3 between deer orphaned prior to 28 months of age and those not orphaned [HR = 1.219 (0.51, 2.91 95 % CI), Wald $\chi 21_{df}$ =0.20, P=0.65, n=43 orphans, 207 non-orphans, 17 informative strata]. We still found no difference when we considered deer to be orphaned if they lost their mothers prior to 13 months of age [HR = 5.710 (0.735, 44.386 95 % CI), Wald $\chi 21_{df=2.77}$, P=0.10, n=22 orphans, 169 non-orphans, 13 informative strata].

2.5 Discussion

The extent of maternal care is a major determinant of fitness for both mothers and their offspring, yet few studies have assessed the duration of this care and its contribution to components of offspring fitness. A number of studies have evaluated its contribution to survival and/or growth at certain stages of development in various cervids (e.g. Jolicoeur and Crete 1988; Holzenbein and Marchinton 1992; Giuliano et al. 1999; Holand et al. 2012), and other studies of Old World primates and one cetacean species have contrasted its effects between the sexes (Fairbanks 2000; Foster et al. 2012).Yet surprisingly little work has sought to assess sex differences in later life maternal care, especially in non-primates.

As expected, there was an observed benefit of maternal presence prior to 13 months. A consequence of early orphaning is that access to milk may be prematurely cut off. The negative effects of premature weaning have previously been demonstrated in farmed red deer, and these effects appeared to be exacerbated when parasitism was common (Pollard et al. 2002). The effect of early weaning should be more pronounced in the wild; competition, exposure to the elements and

predation serve to challenge deer in the wild but their influence is kept to a minimum in farm settings. It is unlikely that the loss of a milk supply was the sole cause of depressed survival in deer orphaned before 13 months of age. Most of these deer were probably transitioning to a post-weaning phase, as the majority of these orphans lost their mothers after age 7 months. Though both sexes suffered from maternal loss prior to 13 months, orphaning influenced the risk of natural mortality more for males than females. This falls in line with theory that suggests males are more sensitive to resource limitation (Clutton-Brock1994).

Our results further demonstrate that the consequences of maternal loss extended beyond the simple removal of a milk supply. In this study, it appears that both male and female red deer benefit from their mothers before and after weaning. For males, we found an increased risk of death when mothers died prior to their sons reaching 24 months of age, and this trend remained when we accounted for deaths by human hunting. The point that maternal benefits cease coincides roughly with the age that sons dissociate from their mothers and eventually disperse (Clutton-Brocket al. 1982). In contrast, female survival was impaired across all ages of orphaning investigated, though the death of mothers influenced their daughters' cause-specific risk of mortality differently. Overall, the data support the idea that the extent of maternal care differs between the sexes. Increased receipt of intraspecific aggression when mothers are absent may explain the reduced survival performance of orphans. Such increases in aggression towards females in the absence of their mothers have been documented previously in red deer (Clutton-Brocket al. 1982) and bison (*Bison bison*) (Green et al. 1989), and such an effect was implied through a recent study of reindeer (*Rangifer tarandus*) (Holand et al. 2012). It is unknown why females aged 13 to 24 months appear unaffected by maternal loss, while those aged 24 to 36 months are. This could be related to the reduced sample sizes that were available for this analysis (see Table 1 for sample sizes). Future work on the age-

specific social repercussions of maternal loss might also shed light on the cause(s) of this pattern.

Although we failed to find evidence that female orphans paid a reproductive cost, we cannot discount an effect on female physical condition. The reproductive analysis required females to survive at least to reproductive age, and this leads to a conservative test. Because orphaning reduced survival, those females able to survive to reproductive age were likely at the upper end of a physical health spectrum. Despite the conservative nature of both the female reproduction and male antler growth analyses, we did find evidence that pre-weaning maternal loss negatively affected male antler development. Yearling antler growth is positively related to male body weight and size as a yearling, and the latter two correlate with adult antler size and reproductive success (Clutton-Brocket al. 1982). Therefore, even if male orphans manage to survive to maturity, they are unlikely to breed successfully or grow trophy class antlers. In populations managed for trophy hunting opportunities, the orphaning of young stags should be strongly avoided.

A surprise finding was the elevated risk of shooting among female but not male orphans. This could arise if orphaning has sex-specific effects on deer behaviour and/or makes females more conspicuous to deerstalkers. Deer- stalkers often target individuals in poor condition and selectively cull females to reduce population densities. Thus, orphaning could reduce both male and female physical condition, but increases in the risk of being shot would only occur for females. This can also explain why females orphaned between 13 and 36 months of age were the only age-at-orphaning groups at greater risk of being shot. Non-reproductive adult females, such as those 13 to 36 months old, often display a ‘yeld wander’, where they move around the study area more than at other times (Clutton-Brocket al. 1982). Deerstalkers likely encounter such females with greater frequency as they wander outside the North Block, and orphans in poor condition would be selectively culled.

Orphaning may also alter deer behaviour and leave females more vulnerable to deerstalkers. Differential behavioural responses to orphaning between the sexes are unknown for red deer, but the peripheral group positions and increased movement noted for female orphans in this population (Clutton-Brocket al. 1982) could have also increased their risk of being shot. Studies on other deer species have documented sex-based differences in ranging behaviour following orphaning. In an enclosed herd of white-tailed deer (*Odocoileus virginianus*), home-range shifts of female orphans exceeded those of male orphans (Woodson et al. 1980). Similarly, Holzenbein and Marchinton (1992) showed that the emigration rate for male white-tailed deer was lower among those orphaned prior to 11 months of age, while Etter et al. (1995) documented higher emigration rates and wandering behaviour among orphan as compared to non-orphan females. These results imply that mothers play some role in affecting their daughters' ability to remain on their natal range. If such sex differences apply to red deer as well, then they could produce sex-specific differences in the risk of being shot. Further work on red deer will need to determine if orphaning is followed by age and sex-specific changes in social and ranging behaviour.

This study took place on an island free of natural mammalian predators and large-scale seasonal migrations; however, it would be expected that under conditions of migration and natural predation, the benefits of maternal presence would be more pronounced. This study provides evidence that maternal associations before and after weaning affect the development and survival of offspring in a non-primate mammal.

2.6 Acknowledgements

We would like to thank Scottish Natural Heritage for permission to work on the Isle of Rum, the UK National Environmental Research Council for funding the project and the many dedicated field personnel for collecting the detailed data necessary to perform this study, especially Sean and Ali Morris, Martyn Baker, and Fiona Guinness. We also thank Gillian Raab, professor emeritus at Napier University, for her helpful guidance with the survival analyses. This research was supported by the National Sciences and Engineering Research Council of Canada CGS and MSFSS scholarships awarded to D. Andres, and an NSERC DG to KER.

Addendum to Chapter 2:

The content below serves to answer select questions from my supervisory committee. These answers and clarifications are presented here, as the above chapter is a direct replicate of copyrighted material.

The code for implementing the Cox survival model in SAS® can be found in Appendix B.

I was asked why I tested for a maternal effect on female reproduction. This was done because age at first reproduction in ungulates is inversely related to fitness components (longevity, reproductive capacity, and offspring survival) (Moyes et al. 2009)

I was asked why I tested for a maternal effect on male antler growth. This is indicated later in the thesis: "Yearling antler growth is positively related to male body weight and size as a yearling, and the latter two correlate with adult antler size and reproductive success (Clutton-Brocket al. 1982)."

Clarification on age-at-orphaning classes:
I split age-at-orphaning into 4 groups – Age orphaned $\leq$ 12 months of age; 13 $\leq$ 24 months; 24 $\leq$ 36 months; > 36 months

Clarification on Cause of Death as a covariate:
Cause of Death refers to the cause of the focal deer's death, not the mother's.

Clarification on the term, 'Coefficient' – this refers to any number of Beta coefficients within a statistical model. In the paper, I refer to the coefficient for orphaning at $\leq$ 12 months of age. This is shown in the model expression as $\beta_{OR1.}$

A reviewer wondered why 28% of males and 36% of females were orphaned, and they commented that this seems to be low (i.e., more individuals should outlive their mothers). This pattern is caused by the high mortality rate observed in young animals. Few individuals actually make it to reproductive age, and once they do, their survival mortality risk declines. Another interesting pattern is the fact that males were more likely to become orphans compared to females. This was beyond the scope of this thesis, but this likely reflects the increased maternal investment that comes with raising sons.

There was a question regarding how well the survival models explained mortality patterns. Cox models do not produce a measure of fit that is comparable to those produced by certain other statistical methods (e.g., R^2 in linear regression). The quality of the models is indicated more by their relative AIC values. The final models all explained a significant amount of variation in survival. The models were penalized for each additional parameter included (via AIC-based model selection), so this was not a case of over-fitting.

In this chapter, I make frequent comparisons between red deer and primates. These comparisons are meant to apply mostly to cercopithecine primates, as post-weaning associations tend to be extended and sex-specific in this group of primates.

This paper does not discuss at length the natural eagle predation that occurs on the island. This is because eagle predation is focused on only very young calves that are still dependent on their mother's milk. Therefore, eagle predation does not influence our results relating to maternal presence and survival. Also, I make suggestions that the impact of natural predation is very minor in this population. In all ungulates, the probability of death by non-predator causes declines with age. Therefore, the population-level impact of removing a young animal via predation will be less than the impact of removing an older animal. Since most intact predator-prey systems include predation on adults, the numerical impact of predation in such natural systems will be much higher than it is on Rum (where eagles only take the young, which are unlikely to survive to reproduce anyways).

In the paper, I suggest that the impact of orphaning in populations with migration and predation will be greater than it is on Rum. This is because some ungulates may learn migratory routes from their mothers, and migration is a strategy that enhances fitness. Also, orphans are more likely to be found on the peripheries of groups, and peripheral positions make deer more vulnerable to predators. In intact predator-prey systems, orphans would be expected to experience a greater risk of predator-caused mortality.

I was asked: How do you know when an animal dies due to malnutrition?
First, in suggesting malnutrition as the cause of death, I refer to cases where the body is starved of nutrients. Therefore, malnutrition can be a result of social factors, range quality, disease, or a total absence of food, for instance. Malnutrition was inferred when individuals became visibly gaunt and were shortly thereafter discovered dead. Malnutrition involves eventual fat and protein catabolism, with the result being that the animal's skeletal frame becomes more distinct (e.g., protruding tuber coxae of the pelvis).

Clarification on terminology:

Maternal Care – any maternal behaviour likely to increase the fitness of offspring (Clutton-Brock 1991).

Conflict Support – occurs when one individual assists another during an agonistic interaction.

Maternal associations – any instance where social affiliation/interaction occurs between mother and offspring.

Chapter 3: Does the loss of mothers affect the social ties of their juvenile daughters? An assessment in a female philopatric species, the red deer (*Cervus elaphus*)

3.1 Abstract

In some mammals, mothers appear to shape the social behaviour of their offspring, however their role in affecting the number and stability of their offspring's social ties has rarely been explored. We used a population of red deer to investigate if maternal loss affects the number, strength, and stability of female social ties. We found no evidence that mothers affect offspring sociality. The change in number of social ties after orphaning did not differ from changes experienced by same-aged non-orphans. Further, mothers did not appear to affect the average strength of social ties held by their daughters, nor did they influence the stability of strong social affiliations early in life. Unlike some other social mammals, the social behaviour of red deer daughters appears to be relatively independent of the mother. We discuss the results in the context of what is known about maternal effects on sociality, and we present some conceptual models of how mothers may structure social groups in similar species.

Key words: social development, orphaning, red deer, *Cervus elaphus*, maternal effects

3.2 Introduction

In many group-living mammals, group membership and association patterns are organized and non-random, and individuals often maintain stable and close associative ties with conspecifics (see Archie 2011, Moss and Lee 2011). Sociality and bonding are thought to have evolved due to the survival and/or reproductive benefits that they offer (Fairbanks and McGuire 1986, Fairbanks 2000, Archie 2011), and these benefits are facilitated through a wide variety of social behaviours. For instance, long-term social relationships can promote the formation of alliances, in which individuals may cooperate to sequester and defend food resources or territories (Clutton-Brock 2009). In mammals, the survival of offspring depends on the transfer of milk from mother to offspring, and this has promoted the evolution of strong social bonds between mothers and their infants.

Though much interest surrounds the value of social bonds, their importance has primarily been demonstrated in some primates and a few other mammals (e.g. Carter and Wilkinson 2013; Foster et al. 2012; Stanton 2012). For example, in savannah baboons (*Papio cynocephalus*) the strength of social ties between females and other adults are positively related to offspring survival (Silk et al. 2003). The presence of long-term affiliative relationships can also affect alliance formation (Clutton-Brock 2009). In chimpanzees, a species where males are the philopatric sex, males that maintain strong bonds are more likely to engage in mutual grooming (Mitani 2009), and in vervet monkeys mutual grooming between dyads increases their responsiveness to cries for social support (Seyfarth and Cheney 1984).

Despite the suggested importance of social bonds, little work has sought to understand the factors affecting the development and stability of social bonds. If social stability and number of social ties affect fitness, then which factor(s) can affect these social parameters? One possible

factor involves the social ties themselves: it is likely that bonds with certain individuals can influence social opportunities with other individuals. Surprisingly, this topic rarely has been explored in much detail. When it has been studied, researchers have focused on an obvious and potentially influential bond: the bond between mothers and their young (see Maestripieri 2009). There appear to be three primary ways in which mothers can exert influence over offspring sociality. Mothers can affect their offspring's competitive abilities, serve as models of social behaviour and increase or restrict their offspring's social opportunities (Maestripieri 2009).

Mothers have the potential to influence offspring sociality when the ability to integrate into groups is affected by dominance rank. Behavioural transfer of dominance from mother to young is observed in some primates, such as macaques (*Macaca* spp.) (Chapais 2004), and in several ungulate species (e.g. Clutton-Brock et al. 1982, Holand et al. 2012). In cecopithecine primates, offspring are born into a rank immediately below their mothers, and rank is primarily transferred through behavioural, rather than genetic mechanisms (Engh et al. 2000, Chauvin and Berman 2004). In olive baboons, young females that lose their mothers also lose their former rank (Johnson 1987). Similar patterns of rank transfer have been found in non-primates, such as the spotted hyena (*Crocuta crocuta*) (Engh et al. 2000). In savannah baboons, the relative rank of *matrilines* appears to influence group cohesion and grooming relationships (Silk et al. 1999), but the effect of individual ranks on sociality remains to be investigated. In ungulates, the absence of mothers has been linked to more peripheral positions in groups (Clutton-Brock et al. 1982, Green et al. 1989, Holand et al. 2012), increased transfers between groups, and higher movement rates (Clutton-Brock et al. 1982). In reindeer and bison adolescents receive higher rates of aggression and are excluded from defensible feeding sites when their mothers are absent (Green et al. 1989, Holand et al. 2012). The above observations demonstrate the effect mothers have on offspring dominance, and they

further suggest that mothers may influence offspring sociality through affecting their offsprings' ability to integrate into groups.

Mothers are the starting point for social contact and learning for most mammals, and consequently they may also have great control over the social environment available to their offspring (Fairbanks 2000). As young develop, they tend to have affiliative relationships that resemble those of their mothers (Chauvin and Berman 2004). Nutritional and behavioural dependence dictate that young offspring maintain close association with their mothers (Chauvin and Berman 2004). Because of this, offspring will tend to be exposed to their mother's social ties, and even in the absence of attraction between offspring and kin, offspring networks can come to resemble those of their mothers (Berman 2004). For some mammals, this tendency can be further enhanced when mothers are more apt to tolerate close associates near their offspring (Berman 2004, Chauvin and Berman 2004). Mothers may therefore set the initial social possibilities for their offspring, and this could promote bond formations between offspring and their mother's close associates. In some juvenile primates, mothers enhance their offspring's capacity for social exploration. Because mothers defend their offspring from conspecifics, juveniles learn to use their mothers as a safe point of retreat such as when social exploration elicits aggression (Suomi 2005). In the absence of their mothers, the increased risk of social exploration is expected to reduce explorative behaviours among offspring (van Noordwijk 2012).

Mothers may also affect their offspring's associations with kin through acting as connecting links in the offspring social network (Silk et al. 2006). A striking feature of many mammalian social groups, particularly those of females, is that they are often structured around kin. Among females, maternal lineage often predicts group membership, so that most, if not all, group members share a common female ancestor (Clutton-Brock and Lukas 2011). These matrilineal structures

appear in a diversity of social mammals such as various Old World primates (see Fairbanks 2000), hyenas (Engh et al. 2000), cervids (Clutton-Brock et al. 1982), elephants (Archie 2011), and cetaceans (Foster et al. 2012). In some cases, females maintain ties between their offspring and other relatives (aunts, cousins, nieces etc.) (see Silk et al. 2006). Many mammals associate preferentially with their mothers after weaning, and this is observed in many ungulate orders [e.g. perissodactyls, (Penzhorn 1984); artiodactyls (Clutton-Brock et al. 1982, Lheureux et al. 1995)] and proboscids, (Wittemyer et al. 2009). Therefore, one possible model of how matrilines form is based on a simple rule of association: namely, a one or two directional preference of association exists between mothers and daughters (Figure 2a). In a three-generation matriline, a matriarch's granddaughters would be connected to her based solely on their shared association with the matriarch's daughter. The removal of a mother would thus splinter the matriline so all the descendants of the removed mother would become disassociated but other non-descendants would be unaffected (Figure3a). This mode of "lineage creation" has been captured in recent models of group structure based on parameter estimates from Barbary macaques (Lefebvre et al. 2003) and this splintering pattern was observed in rhesus monkeys after the death of matriarchs (Chepko-Sade and Sade 1979). Another possible model of matriline formation could include attractions between mothers and daughters as well as attractions between sisters. In this case, the death of a mother would cause her daughters to dissociate with kin not descending from their mother. Few studies have investigated this topic, but some work on primates and African elephants provide evidence for the maternal role in structuring matrilines. In baboons, a mother's death increases association rates

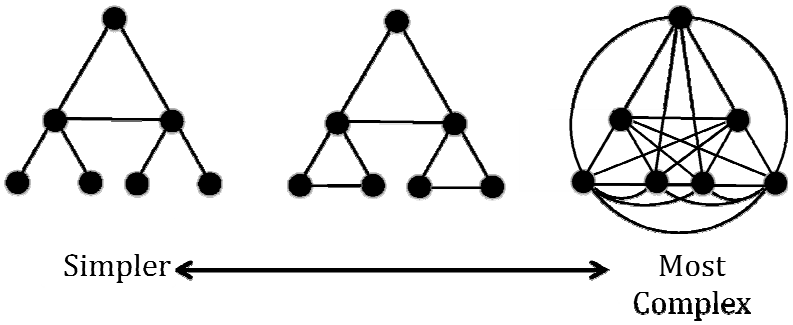

Figure 2. Three possible models of how matrilines are structured. Circles represent females, and lines between circles represent mutual or unidirectional social preference. Models are organized from most complex (left) to simplest (right) of the three. Matriarchs form the apex of the triangle (top), their daughters the middle, and granddaughters the base. In model (a) each member of the matriline has a social attachment to all others, in (b) social attachments are limited to sisters and mothers, and in (c) social attachments only occur between mothers and daughters

between her daughters but reduces associations between her sisters and daughters (Silk et al. 2006). In savannah African elephants that live in matrilineal groups with frequent fission and fusion, the effect of a matriarch's death depends on the family unit size (Moss and Lee 2011). For instance, Moss and Lee (2011) found no effect of a matriarch's death when the matriline originally consisted of the matriarch, a single descendant adult daughter, and the daughter's offspring. In contrast, larger matrilines became divided into mother-offspring groups when the matriarch left behind more than one adult daughter. Further, Moss and Lee (2011) also noted that orphaned adult females can become wanderers if they have no living sisters. The latter suggests that mothers do affect the structure of kin groups, and in both elephants and baboons there also appears to be social attraction among sisters.

At present, most literature on maternally-mediated sociality has focused on hypothetical mechanisms, and little work has sought to test for outcomes (i.e. an actual effect of the loss of mothers on their daughter's sociality). To test whether mothers affect offspring social ties, the change in social ties that occur after maternal loss must be determined. However, social changes following maternal loss (orphaning) cannot be considered as good evidence of a maternal effect. To gain such evidence, the social changes experienced by orphans must be compared to those experienced by non-orphans of similar age. In this study, we use the second approach to test for signatures of maternally-mediated social ties in a wild population of red deer. We do not distinguish between various mechanisms such as those outlined above. Rather, we test the hypothesis that mothers affect offspring social ties, and we use these results as a starting point to discuss possible mechanisms. The specific hypotheses tested include:

H_1: Mothers affect the number of social ties held by their daughters.

H_2: Mothers influence the strength of social ties held by their daughters.

H_3: Mothers affect the loss and gain of social ties.

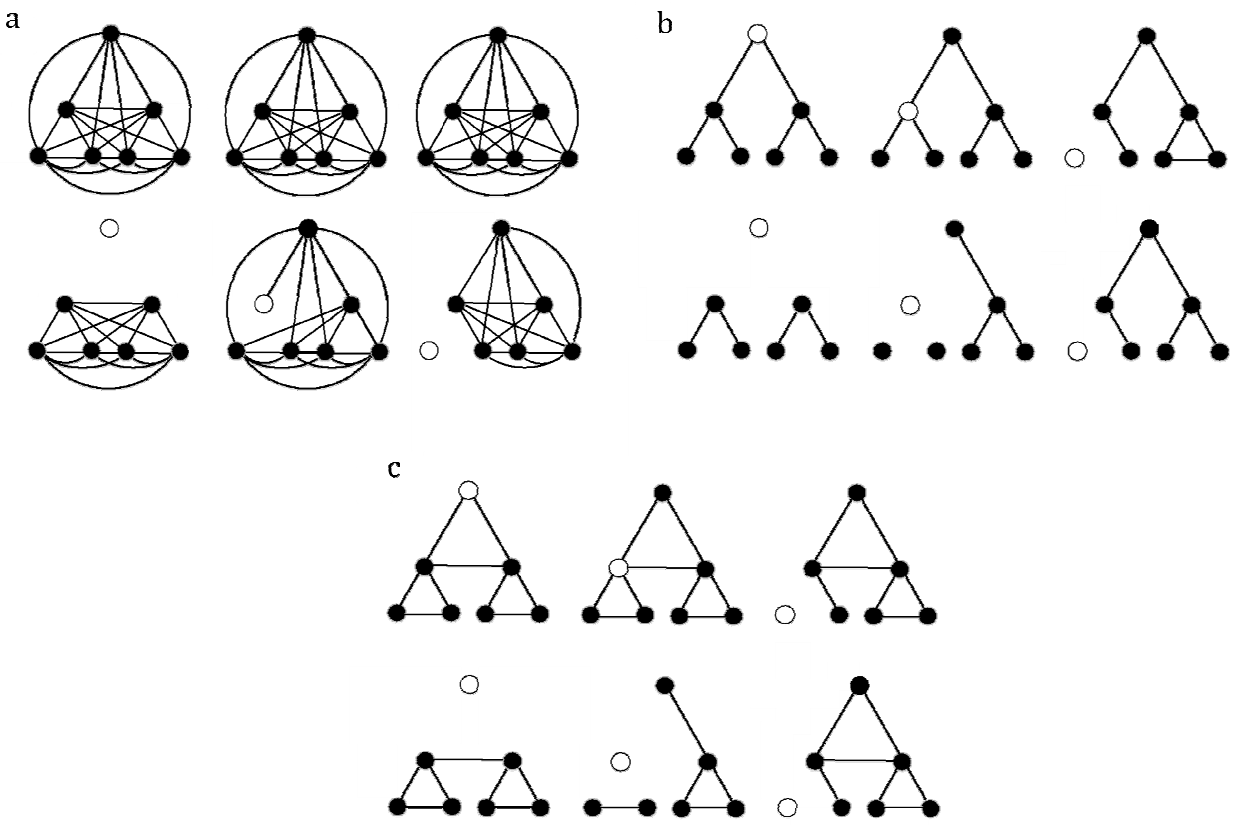

Figure 2. Three models (a, b, c) of matriline structure and predicted splintering patterns following the removal of matrilineal members (see Figure 2 caption for model details and symbology). Open circles show the females selected for removal. Within each model diagram, the top diagrams shows the intact group connections and the bottom diagrams show the connections that are lost following the female's removal. Nodes connected in a chain and those unconnected represent separate groups.

3.3 Methods

3.3.1 Study Area and Animals

The study occurred between 1978 and 2011 in the North Block of the Isle of Rum, Scotland ($57^{o}01'N$, $06^{o}17'W$, NM-402996). A detailed description of the study site is found in Clutton-Brock et al. (1982). During the study years, all individuals residing within the North Block of the island were individually recognizable based on artificial markings and idiosyncrasies. Information was collected on the associative relationships between deer available through monthly censuses (minimum of 5 per month). During censuses, researchers walked set routes in the study area and took note of the identities of deer that were in association with one another (Coulson et al. 1997). Association was inferred using a 50-meter chain rule: each individual is visually linked to its closest neighbour when the distance between their noses is less than 50 meters. The successive links form a chain, and each complete chain represents a group. Further details regarding methods and the study can be found in Clutton-Brock et al. (1982).

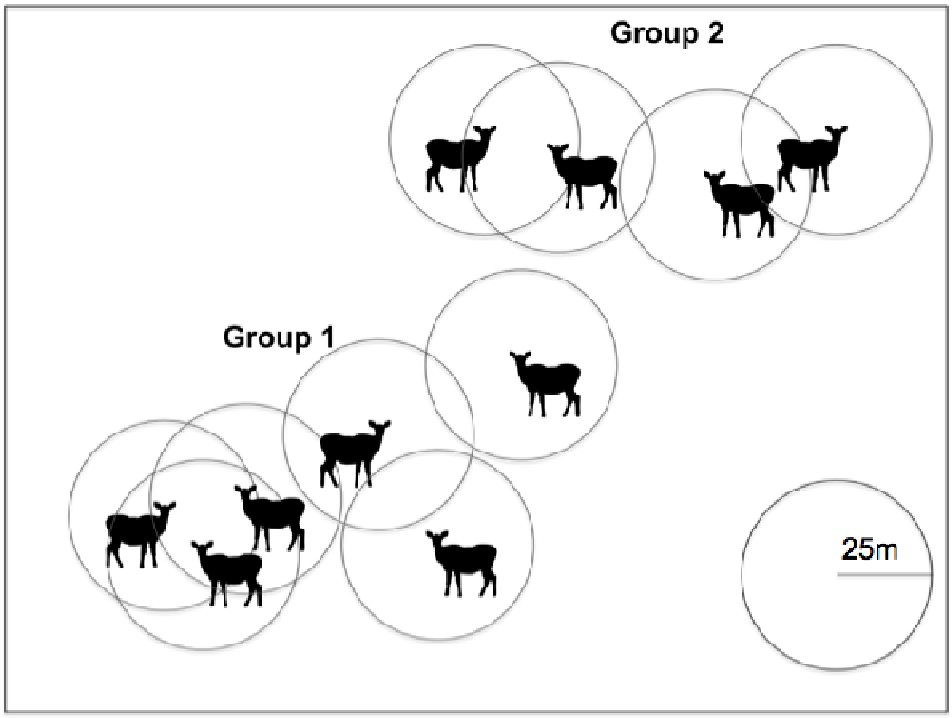

Figure 3. Schematic of the 50 meter chain rule. Each individual is visually linked to its closest neighbor when the distance between their noses is under 50 meters. The successive links form a chain, and each complete chain represents a group.

3.3.2 General Study Design

The census data and associations among deer were the focus of this study: specifically, we assessed the effect mothers have on their daughters' ego networks (individual-specific social ties) during adolescence (5 to 22 months of age). Here, we use ego networks to refer to social characteristics of individuals. This includes the total number of associates and number of close associates held by an individual (see definitions below). To do so, we compared the ego network change experienced by deer whose mothers died (orphans) to that experienced by same cohort non-orphans. This involved the division of an orphan's ego network into a pre- and post-orphaning period and the matching of orphans to non-orphans (see below). Because non-orphans can continue to associate with their

mothers but orphans cannot, the social environments for the two are not directly comparable. Based on the fact that non-orphans have an additional available associate, maternal loss automatically produces a difference between the two groups. However, this does not reflect the mother's influence over her offspring's non-maternal ties. Therefore we omitted mothers from ego networks to remove this effect. In doing so, both orphans and non-orphans had no registered ties with their mothers, yet the social network for the latter group did have the potential to be influenced by their mother's presence.

3.3.3 Data Structure and Matching

We considered females as orphans if they lost their mothers prior to 13 months. For all orphans we divided the census dataset into pre- (T1) and post-orphaning (T2) periods. The pre-orphaning period included all census observations that occurred between a focal orphan's birth date and the date of orphaning. This period was always between 5 and 10 months, as no orphaning events occurred at earlier ages. When orphans survived for greater than 12 months after they lost their mothers, we set the post-orphaning period at 12 months after orphaning. When orphans died prior to 13 months after orphaning, the post-orphaning period was set as the time between orphaning and death.

We used a matched design in our analyses, so that each orphan was compared to one matched non-orphan. Deer were eligible for matching to a specific orphan if they: (1) were born in the same year as the orphan; (2) had a known death date or were still alive; (3) had a mother whose death date was known, or their mother was still alive; (4) did not lose their mother prior to the end of the orphan's T2 period; and (5) were observed a minimum of 5 times in the T1 period and a minimum of 5 in the T2 period. Criteria 2, 3, and 5 applied to orphans as well, so that all orphans not

matching the criteria were excluded from analysis. We randomly selected a single match from the pool of potential matches. We did not permit individuals to be matched with more than one orphan.

3.3.4 Statistical Analysis

We calculated various ego-network measures and tested whether the change (slope) between the T1 and T2 periods differed between orphans and non-orphans. All measures used the half-weighted association index as calculated in SOCPROG (Whitehead 2008). The half-weighted association index provides an estimate of the proportion of time two individuals spend together, and it controls for biases that can exist in the probability of sighting particular individuals. We performed two major groups of analyses. The first group (see analyses [a-c] below) focused on the general change in association patterns, and we did not adjust for demographic changes (e.g. the death and birth of individuals in the population). The second type of analysis (see analysis [d] below) did control for demographic changes; thus we focused on changes in relationships with individuals that were potential social partners in both the T1 and T2 periods. A total of 32 orphans and 32 non-orphans were used in the analyses that follow.

Further definitions of the measures analyzed and their associated analytical methods are as follows:

a) Association index change – Average association was calculated by averaging the half-weighted association index values for the orphans and non-orphans in the separate T1 and T2 periods. We analyzed the change in average association between the T1 and T2 periods with a general linear mixed model. We implemented the model with PROC MIXED in the SAS® system. Average association served as the response variable, and orphaning status (yes/no), time period (T1, T2) and their interaction appeared as fixed effects. A square-root transformation of the response variable improved normality, and therefore the analysis proceeded with this transformed variable. Since the interaction between time period and orphaning status was part of the design of the study, we did not

use any model selection techniques (Bolker et al. 2009). Because we had paired individuals and repeated measures on individuals, we modeled individual identity nested within matched pair as a random effect. We used an unstructured variance-covariance matrix to model the random component. All parameter estimates were back-transformed to the original scale for interpretation.

b) Probability of association change – This is the change in probability of associating with a given individual in the population. In other words, it is the number of different individuals that a deer was observed with over a given time period (T1 or T2) relative to the number of individuals available for association (observed in the population in the specified time period). Hence, it can be thought of as a set of Bernoulli trials, where success is an observed association with a given individual, and the number of trials is the number of individuals observed in the population within a given time period. We modeled this with a generalized linear mixed model (GLMM) with a binomial error structure and logit link function. Proc glimmix in the SAS ® system was used. As before, predictor variables included orphaning status and time period, plus their interaction. We included individual identity nested within matched pair as a random effect, and we adjusted for overdispersion through modeling R-side random effects using an unstructured covariance matrix with the Cholesky-root reparameterization (see Kiernan et al. 2012 for details). Plots of residuals were used to assess normality. In testing the fixed effects, the Kenward-Roger method was used to calculate the denominator degrees of freedom.

c) Probability of strong association – The analysis here is similar to that in (b), except strong associations are used to represent the number of 'successes'. We defined strong associates in two ways. In the first, herein *degree 1* associate, a strong associate is considered to be one with a shared association index value greater than two times the average association for a focal deer. Similar methods have been used previously to identify important social affiliates (Durrell et al. 2004). This

average includes zero values. In the second definition, herein *degree 2* associate, we exclude zero values from the average. This definition has a higher cutoff for being classed as a strong associate.

For degree 1 associates, the analysis methods are identical to those used in (b). In contrast, for degree 2 associates we altered the specified error structure. Instead of a binomial process, we modeled the number of strong associates using a negative binomial error structure, and we included only matched pair as a random effect. This eliminated overdispersion and improved the assumption of normality. To test the fixed effects we used the Kenward-Roger method for calculating the denominator degrees of freedom.

d) Strong ties lost and gained – This analysis focused on changes in strong ties and controls for demographic changes. Hence, we only used data from individuals that we observed in both the T1 and T2 periods. As before, we defined strong ties as degree 1 and 2. We enumerated the number of individuals that were strong ties in the T1 period but were no longer strong ties in the T2 period; the difference was the number of strong ties lost. Similarly, we determined the number of deer that were *not* strong ties in T1 but became strong ties in T2. We modeled the data using the same methods as in (b) except the response variable was the number of strong ties lost (success) relative to the total number of strong tie changes (lost + gained, i.e. the number of trials). Therefore, this analysis answers the question: if a strong tie change occurs, is there a difference between orphans and non-orphans in the probability that this change involves the loss of a strong tie? Strong tie change values greater than 0.5 indicate that a deer lost more strong ties than it gained, while values below 0.5 indicate that more strong ties were gained than lost.

If orphans and non-orphans experience an equal number of strong tie changes, then the above measure reflects the change in social environment linked to orphaning. Even if there is no difference in the probability that a strong tie change involves the loss of a strong associate, a

difference in the number of strong tie changes would still indicate a social change linked to orphaning. Therefore, we compared the number of strong tie changes between orphans and non-orphans as well. A GLMM with Poisson error structure and log link function was used for this analysis. The identity of the matched pair appeared as a random effect in the model, and the R-side random effects were modeled using an unstructured variance-covariance matrix with Cholesky-root reparameterization. The denominator degrees of freedom were calculated with the Kenward-Roger method.

3.4.1 Results

Orphaning did not significantly influence the change in average association strength (average with null associations included) between the T1 and T2 periods ($F_{1\ df,\ 62\ ddf}$ =1.09, P=0.30) (Table 1). The change in number of associates between the T1 and T2 periods was not affected by orphaning ($F_{1\ df,\ 62.01\ ddf}$ = 1.44, P=0.23) (Table 1). Similarly, the change in number of strong ties (1st degree) shown by orphans did not differ significantly from that of non-orphans ($F_{1\ df,\ 62.03\ ddf}$ = 0.34, P=0.56) (Table 1). Orphaning did not affect the probability that a strong tie change (1st degree) between T1 and T2 would involve a loss of a strong tie ($F_{1\ df,\ 32.52\ ddf}$ = 0.77, P=0.39) (Table 2). The number of strong tie changes was unrelated to orphaning ($F_{1\ df,\ 31.57\ ddf}$ = 0.00, P=0.98) (Table 2).

Conclusions did not change when we repeated some of the above analyses with zero values excluded in the calculation of average associations. The change in average association strength (excluding null associations) did not differ significantly between orphans and non-orphans ($F_{1\ df,\ 621.6ddf}$ =0.03, P=0.86) (Table 1). The change in number of strong ties (2nd degree) between T1 and T2 was also not affected by orphaning ($F_{1\ df,\ 95..19\ ddf}$ = 1.05, P=0.31) (Table 1). Orphaning did not significantly affect the probability that a strong tie (2nd degree) change would involve the loss

of a strong tie ($F_{1\ df,\ 30.5\ ddf} = 1.26$, P=0.27), nor was there an influence on the number of 2nd degree strong tie changes ($F_{1\ df,\ 60\ ddf} = 0.08$, P=0.77) (Table 2).

Table 4. Various social metrics and 95% confidence intervals for deer orphaned in the period T2 and those that were not orphaned in this period. Ties of the 1st degree include those with association index values greater than two times the average association for a focal deer; the average includes zero values. Ties of the 2nd degree are determined as above, except zero values are excluded from determining the average.

		Parameter Estimate (95% CI)	
Response Variable	Time Period	Orphan	Non-Orphan
Average Association 1st degree	T1	0.042 (0.034,0.051)	0.042 (0.034,0.052)
	T2	0.033 (0.026,0.041)	0.039 (0.031,0.048)
Average Association 2nd degree	T1	0.382 (0.354,0.409)	0.390 (0.363,0.417)
	T2	0.406 (0.368,0.444)	0.410 (0.372,0.448)
No. ties/No. possible ties	T1	0.291(0.252,0.333)	0.296 (0.256,0.338)
	T2	0.232 (0.189, 0.281)	0.276 (0.230,0.327)
No. 1 degree ties/No. possible ties	T1	0.175 (0.161,0.190)	0.177 (0.162,0.192)
	T2	0.142 (0.115,0.173)	0.155 (0.127,0.187)
No. 2 degree ties	T1	10.87 (7.94 ,14.89)	10.63 (7.78 ,14.53)
	T2	10.70 (7.81 ,14.66)	13.66 (9.97,18.70)

Table 5. Comparison of strong tie changes between orphans and non-orphans using two definitions of strong ties. Ties of the 1st degree include those with association index values greater than two times the average association for a focal deer; the average includes zero values. Ties of the 2nd degree are determined as above, except zero values are excluded from determining the average.

		Parameter Estimate (95% CI)	
Analysis Type	Response Variable	Orphan	Non-Orphan
1st degree strong ties	No. Tie Changes	51.49 (43.3,61.2)	51.6 (43.1, 61.8)
	No. ties lost/total changes	0.62 (0.52,0.72)	0.57 (0.49,0.64)
2nd degree strong ties	No. Tie Changes	15.8 (12.4,20.0)	15.5 (12.2,19.7)
	No. ties lost/total changes	0.36 (0.25,0.49)	0.29 (0.20,0.42)

3.5.1 Discussion

Research on cercopithecine primates has shown that mothers can influence their offspring's social status within groups, and this is because maternal dominance is behaviourally transferred to offspring (see Kapsalis 2004). Similar conclusions can be drawn from studies on ungulates as well (see Clutton-Brock et al. 1982, Green et al. 1989, Holand et al. 2012). Further, in ungulates changes in positions *within* groups and frequency of group transfers have been linked to maternal loss (Clutton-Brock et al. 1982, Green et al. 1989), and in elephants as well as some primates, the loss of mothers appears to result in severance of social ties with some kin (Chepko-Sade and Sade 1979, Moss and Lee 2011). This work shows that mothers can indeed affect offspring sociality, though distinctions between various models of matriline formation have not been explored. In ungulates, the maternal role in mediating associations with other individuals has only recently been considered (Ruckstuhl et al. 2013, submitted). Ruckstuhl et al. (2013, submitted) studied the social changes

following maternal loss in red deer, but this analysis was strictly focused on kin-based associations. In the current study, we do not distinguish between kin and non-kin, though for females the majority of close associations typically occur between close relatives (Clutton-Brock et al. 1982). We broadly assessed whether mothers influenced the social ties of their juvenile daughters but failed to find any evidence of this. Mothers did not appear to affect the number of associates their daughters had, nor did they influence the probability that their daughters held strong ties. The number of changes (gain or loss) in strong ties experienced by offspring was also unrelated to maternal presence. When strong tie changes occurred, orphaning did not influence the chance that it involved a lost tie. Therefore, we found no support for the hypothesis that mothers influence the social environment of their offspring.

In earlier studies on the same population of red deer, Clutton-Brock et al. (1982) noted that orphans received increased rates of aggression, and for one two-year-old orphan, more group transfers and peripheral group positions were observed. Assuming similar effects occurred for the orphans used in the present study, why were we unable to detect social changes? It is possible that orphaned females increased the rate of group transfers but still maintained stable association patterns. As long as orphans associated with the same number of groups, and so long as group transfers do not take much time, the average time an orphan spends with its associates will only be modestly reduced. The data available does not permit us to test these assumptions.

The lack of maternal effects on sociality can also be explained if deer form relationships equivalent to those they had with their mothers. Indeed, this type of behaviour has been observed in several cercopithecine primates (see (Fairbanks 2000). In a supplementally fed population of Japanese macaques orphans were adopted by grandmothers and close adult kin (Nozaki 2009). Similarly, Fairbanks (2000) found no effect of maternal removal on grooming and aggressive

behaviour in 2 year old vervet monkeys, nor was there an effect on the probability that the animals would be alone versus in a group. Work on other primates reveals that the substitutive relationships formed after maternal loss can be virtually indistinguishable from true maternal associations (see Fairbanks 2000). Moreover, in nearly all cercopithecine monkeys studied, daughters remain in their natal group in the absence of their mother (Fairbanks 2000). In baboons, sisters increase the strength of association between one another after their mother's death, and this could buffer the costs of maternal loss (Silk 2006). The same observation comes from red deer sisters that lose their mothers (Ruckstuhl et al. 2013, submitted), which suggests that females may attempt to compensate for lost bonds in this species as well.

In the present study we found a lack of social effects following orphaning. This would also suggest that maternal loss did not compromise social ties with kin. This is based on the observation that female red deer typically form close associations with kin, and associations of similar strength are rare between non-kin (Clutton-Brock et al. 1982). Under a model where mothers bind layers of matrilines together, an increased chance of strong tie loss would be expected following orphaning. Yet in this study, such changes were not observed. Therefore, unlike African elephants, mothers do not seem to be brokers in their matrilines: it would appear that preferential associations exist between kin that are both descendant and non-descendant of the dead mothers. Unfortunately, we could not test this specifically. We did not match orphans to non-orphans based on the structure of their matrlines. In elephants, the death of a mother only produced social changes when she left behind more than one adult daughter (Moss and Lee 2011). In rhesus monkeys the death of matriarchs was associated with dissolution of matrilines, but not consistently so (Chepko-Sade and Sade 1979), and in baboons daughters increased their association with sisters but not aunts (Silk et al. 2006). Therefore, in order to distinguish between various models of how matrilines are

structured, analyses must be restricted to those matrilines composed of a matriarch and at least two adult daughters, and attempts should be made to control for matriline size as well. These studies must also focus on cases where one of the matriarch's daughters dies rather than the matriarch herself. This is because the various models of matriline structure can only be distinguished following the death of a matriarch's daughter (Figure 3). Future studies should seek to identify the social bonds that structure matrilines in various species, because different structures will respond differently to demographic changes. For instance, if matrilines are formed due to social attractions among all members of the matriline, then they will be much more robust to deaths of matriline members. Indeed, groups would not be expected to splinter. As the structure of matrilines becomes simpler (see Figure 2), the death of matriline members would be expected to produce greater structural changes in groups (Figure 3).

In this study, we used an observational approach to test the general hypothesis that mothers affect their offspring's social environment. We had a limited ability to control for environment and social effects in our analyses. Researchers that seek to understand animal social networks and the benefits of social bonds should test specific hypotheses based on various models of social bonding. Experimental manipulations of group structure will prove to be an effective method for enhancing our understanding of animal sociality. In the future, wildlife management decisions and wildlife translocations may benefit from an increased understanding of how social bonds and grouping patterns, specifically matrilines, are structured. Determining what social consequences follow from demographic changes will be especially important.

3.6.1 Acknowledgements

We would like to thank Scottish Natural Heritage for permission to work on the Isle of Rum, the UK NERC for funding the project and the many dedicated field personnel for collecting the detailed data necessary to perform this study, especially Sean and Ali Morris, Martyn Baker, and Fiona Guinness. I thank Tak Fung from the statistical consulting department at the University of Calgary, for his help with the GLMM analysis. This research was supported by the National Sciences and Engineering Research Council of Canada CGS and MSFSS scholarships awarded to D. Andres, and an NSERC DG to KER.

Chapter 4: Conclusion

Social bonds are increasingly being viewed as important contributors to fitness, but for most mammals the fitness benefits and factors involved in maintaining social bonds are still poorly understood (Silk 2007a). In many mammals, offspring maintain preferential associations with their mothers well after weaning (Clutton-Brock 1991; Fairbanks 2000). This suggests that mothers continue to care for their offspring beyond milk dependence, and this has been established in a few cases involving primates, elephants, dolphins, and one rodent species (Fairbanks 2000; McComb et al. 2001; Moses and Miller 1994). This thesis is the first to provide evidence that ungulate mothers benefit their offspring after weaning, and it is the first study to evaluate whether ungulate mothers affect the social environment of their juvenile daughters.

The evidence that ungulate mothers benefit the fitness of their offspring comes from both survival analyses and data on correlates of reproductive success. First, I observed that the risk of mortality was elevated for sons and daughters who lost their mothers before weaning. Second, males that lost their mother prior to weaning also experienced reduced antler growth. As antler growth is positively correlated with body growth and adult reproductive success (Clutton-Brock et al. 1982), orphaning is also likely to affect male breeding success. In contrast to males, reproduction in females was not influenced by maternal care prior to weaning or in the first 2.5 years of life. These results demonstrate that mothers affect the fitness of their juvenile (under 13 month old) offspring, but the components of fitness (survival, reproduction) that are influenced by the mother may differ between the sexes. Studies that evaluate only reproductive and body growth parameters may fail to detect benefits of social bonds even when they exist. My results highlight the importance of using measures of both reproductive performance and survival in testing the fitness value of social bonds.

In addition to demonstrating maternal care prior to 13 months, I also provide evidence that mothers care for their sons and daughters after weaning. I observed that deer orphaned after weaning were at an increased risk of death. In males this effect disappeared after 24 months of age, but in females it persisted throughout life. This is attributed to the fact that females are socially philopatric while males disperse within approximately 2 years of weaning. The pattern of female philopatry and male dispersal is common among social mammals. Therefore, such lifelong benefits of mothers to daughters may be widespread, and future studies on a variety of mammals are needed to test the generality of this pattern.

Although red deer mothers appear to affect offspring fitness, I did not find evidence that they affected the social environment of their juvenile (under 13 month old) daughters. It may be that mothers have little or no effect on the social environment during the ages I investigated. Alternatively, mothers may affect the social environment of their daughters, but these effects remained undetected. One possibility is that the measures used might not capture this effect. Higher resolution social data, such as those on grooming interactions and aggressive interactions, might reveal a maternal effect. Such social data have revealed maternal social effects in primates, dolphins, and elephants (McComb et al. 2001; Silk 2007a, b; Stanton et al. 2011). A maternal social effect might also be undetected because other social partners, possibly kin, serve as adequate surrogates for the mother. In such cases, an effect would only be detectable if all possible surrogates were also removed as potential social partners. It is clear that these questions are so far underexplored, and much remains to be discovered.

An understanding of how individuals respond to the loss of social bonds will be important for future wildlife management and conservation efforts. The human impact on animal societies has been given less attention than the direct human influence on demographics (Sutherland 1998). Yet,

through its potential effects on individual fitness and grouping dynamics, individual level social disruption can scale up to population level effects. Many current methods of wildlife management likely promote social disruptions, and this appears especially true of ungulate management programs. My research on red deer has demonstrated that orphaning both before and after weaning is likely to reduce offspring survival. Therefore, frequent orphaning will have demographic side effects that extend beyond the loss of mothers. Most Cervid populations in North America and Europe are managed through hunting, and this accounts for a large proportion of annual mortality (Milner et al. 2006) and probably orphaning as well. The selective removal of females is used as a tool for managing population sizes (Milner et al. 2006), and although hunting seasons are typically timed to occur after weaning, hunts invariably result in the orphaning of weaned offspring. In some European countries, managers encourage professional deerstalker to kill red deer hinds without calves or to remove both hinds and their calves. These practices aim to reduce the chances of orphaning, but genetic analyses show that deerstalkers are unable to consistently match mothers with their young (Milner et al. 2002). Therefore, such attempts to eliminate orphaning are unlikely to be successful. Alternative hunting methods can be used to limit population growth in ungulates while at the same time minimizing orphaning. Female removal could be limited to young of the year and females below reproductive age. This strategy is used successfully to manage moose (*Alces alces*) populations in Scandinavia (Lavsund et al. 2003). Further research will be needed to determine how populations can be managed effectively while simultaneously reducing the risk of orphaning.

This thesis has highlighted the many possible benefits of social bonds. My primary research has demonstrated that ungulate mothers can benefit their offspring after weaning, and this helps to explain certain aspects of ungulate social behaviour. These findings should be used to inform future

deer management, and the results should also serve as incentive for additional research on other ungulate species. Future work will need to determine the fitness benefits of social bonds in general, not just those between mothers and offspring. This is currently a developing field of research, and it holds promise for explaining many commonly observed patterns of social behaviour.

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Appendix A: Comparison of capture weight of orphans and non-orphans

Confounding factors are an obvious concern in analyzing the effect of orphaning on survival. For example, orphaning may tend to occur because maternal condition is poor, and since maternal condition likely affects birth weight and survival (Clutton-Brock et al. 1982), orphans would be at an increased risk of death irrespective of changes in maternal care. One option to control for this is to include capture weight as a covariate in the modeling of survival; in our study, this would result in a loss of data, since not all individuals were captured and weighed. The other alternative is to test for a difference in birth weight between orphans and non-orphans: if no systematic bias is found, one could ignore the effects of birth weight and accept a level of unexplained variation in survival time. The analysis presented below indicates that failure to include capture weight in our survival models would potentially bias results. Therefore, as outlined in the methods section of the paper, we included capture weight in our survival models. The results here are presented as a justification for the survival methods outlined in the main body of the paper.

In this analysis, we used a matched design to compare weights of orphans and non-orphans. Observations were matched by year of birth, sex, age weighed and 'event age' (see below). The matched set each observation belonged to was fitted as a random effect. All animals were weighed within 13 days of birth. Non-orphan deer were matched to individual orphans if their age at weighing was within plus or minus 12 hours of the orphan's age at weighing. Mortality risk declines with age and birth-weight (Clutton-Brock et al. 1982), and as a consequence animals that survive long enough to lose their mothers will tend to survive longer and be heavier than the starting crop of deer. Therefore, we randomly matched non-orphans to orphans if non-orphan survival time (months) was equal or greater than the age (months) orphans lost their mother; we refer to this as 'event age' matching. Orphans with mothers dying from shooting were excluded from this analysis.

Birth-weight was analyzed using general linear mixed models with orphan status (orphaned or not) as a fixed effect and event age match ID as the random effect. In this analysis, an orphan is defined as any individual losing its mother prior to an age of 36 months. Males and females were analyzed separately in these comparisons. The denominator degrees of freedom was adjusted according to the Kenward-Roger technique assuming the correlation among responses follows compound symmetry; AIC was used to select among compound symmetry, heterogeneous compound symmetry and unstructured covariances). Under compound symmetry, the covariance between treatments is assumed to be the same, as is the variance within treatments.

With the above models the data displayed slight deviations from normality and this was confirmed by Kolmogorov-Smirnov tests ($P<0.15$); deviations were associated with heavy tails and/or outliers, and this could not be remedied with transformations. The departures from normality have the effect of reducing statistical power. In spite of this, we found that orphan males were significantly heavier at birth compared to their non-orphan counterparts (0.37 kg heavier +/- 0.14 SE, $F_{1\ df,\ 333\ ddf} = 2.62$, $P=0.009$). Female orphans were also significantly heavier than non-orphans (0.48 kg heavier +/-0.15 SE, $F_{1\ df,\ 317\ ddf} = 3.18$, $P=0.002$). Therefore, failure to include capture weight as a covariate in our survival models would lead to an under-estimate of the orphaning effect.

Appendix B: Survival Analysis Code

Survival analyses that include time-dependent covariates (e.g. orphaning status) require special coding in statistical programs. I used the SAS statistical system for my analyses of survival time, and here I present the code used. Definitions of variables used and the function of specific programming statements are outlined in the code below. The code covers data formatting, preliminary model diagnostics, and analysis of survival data using Cox regression with time-dependent and time-independent covariates. Separate analyses are conducted for males and females.

```
/* VARIABLE DEFINITIONS:
Sex --> 1=female; 2=male; 3=unknown
BirthDay --> 1-31, with 0=unknown
BirthMonth --> 1-12, with 0=unknown
BirthYear --> 0=unknown
DeathDay, DeathMonth, DeathYear --> as above
Live_or_Dead --> D=dead; L=alive; NA=not available; U=unknown; M=missing
DeathType --> A=accident; B=birthing (females only); C=?; D=?; E=?; W=?
              N=natural winter mortality; S=shot
DataQuality --> 1-9, 1 being most reliable, 9 being least reliable - 0=missing
As above, but applying to mother:
       Mum_DeathMonth, Mum_DeathDay, Mum_DeathYear, Mum_Live_or_Dead, Mum_DataQuality □
Mum_DataQuality: if missing (i.e., NA) replaced with 100 (NA not recognized by SAS when numbers
also present)
*/

/* IMPORT DATAFILE: "deer_life_for_dataset_construction_August_2012_NumericCodes.csv"
Numeric Codes necessary since SAS is not handling nominal IDs properly.
Numeric Codes and their corresponding nominal codes are found in "Numeric_IDCodes_August2012.xls"
*/


data survival_2;
       set survival_1;
       /* CLEANING DATA AND FLAGGING ERRORS */
       if MumCode='' then delete;
       if DataQuality>2 then delete;
       if DataQuality=0 then delete;
       if Live_or_Dead='M' or Live_or_Dead='U' or Live_or_Dead='NA' then delete;
       if Mum_Live_or_Dead='M' or Mum_Live_or_Dead='U' or Mum_Live_or_Dead='NA' then delete;
       if Live_or_Dead='L' and DeathYear>0 then flag='yes!';
       if BirthYear=0 then delete;
       /* CALCULATING EVENT TIME */
       if Live_or_Dead='D' then do;
              if DeathYear=0 or DeathMonth=0 then delete;
              if BirthMonth=0 then delete;
              if BirthYear=DeathYear then Event_Time=DeathMonth-BirthMonth+1;
              if DeathYear-BirthYear=1 then Event_Time=(12-BirthMonth+1)+DeathMonth;
              if DeathYear-BirthYear>1 then Event_Time=(12-BirthMonth+1)+DeathMonth+((DeathYear-
BirthYear-1)*12);
```

```
        end;
        if Live_or_Dead='L' then do;
                if BirthYear=2011 then Event_Time=(12-BirthMonth)+1;
                if 2011-BirthYear=1 then Event_Time=(12-BirthMonth+1)+12;
                if 2011-BirthYear>1 then Event_Time=(12-BirthMonth+1)+12+((2011-BirthYear-1)*12);
        end;
        /* CALCULATING ORPHANING TIME */
        if Live_or_Dead='D' and Mum_Live_or_Dead='L' then orph_status='not orph';
        if Live_or_Dead='L' and Mum_Live_or_Dead='D' then orph_status='orph';
        if Live_or_Dead='L' and Mum_Live_or_Dead='L' then orph_status='not orph';
        if Live_or_Dead='D' and Mum_Live_or_Dead='D' then do;
                if DeathYear=Mum_DeathYear then do;
                        if DeathMonth<Mum_DeathMonth then orph_status='not orph';
                        if DeathMonth>Mum_DeathMonth then orph_status='orph';
                        if DeathMonth=Mum_DeathMonth and DeathDay<MumDeathDay then
                        orph_status='not orph';
                        if DeathMonth=Mum_DeathMonth and DeathDay>MumDeathDay then
                        orph_status='orph';
                end;
        end;
        if Live_or_Dead='D' and Mum_Live_or_Dead='D' then do;
                if DeathYear>Mum_DeathYear then do;
                        if Mum_DeathYear=0 then delete;
                        if Mum_DeathMonth=0 then delete;
                        orph_status='orph';
                end;
                if DeathYear<Mum_DeathYear then do;
                        if DeathYear=0 then delete;
                        orph_status='not orph';
                end;
                if DeathYear=Mum_DeathYear then do;
                        if Mum_DeathMonth=0 then delete;
                        if DeathMonth=Mum_DeathMonth then do;
                                if Deathday=0 then delete;
                                if MumDeathDay=0 then delete;
                                if MumDeathDay=DeathDay then delete;
                        end;
                end;
        end;
        if orph_status='orph' then do;
                if Mum_DeathYear-BirthYear=0 then age_orphaned=(Mum_DeathMonth-BirthMonth)+1;
                if Mum_DeathYear-BirthYear=1 then age_orphaned=(12-BirthMonth+1)+Mum_DeathMonth;
                if Mum_DeathYear-BirthYear>1 then age_orphaned=(12-
                BirthMonth+1)+Mum_DeathMonth+((Mum_DeathYear-BirthYear-1)*12);
        end;
        run;


/* Checked data for inconsistent (negative) event_time and orphaning_time */
        /* Clean out data where variable values are missing. Done as follows: */

data survival_3;
                set survival_2;
                if capture_weight=0 or capture_weight=. then delete;
                if Home_Range=0 then delete;
proc sort data=survival_3;
                by age_orphaned event_time;
proc print data=survival_3;
run;


/* Create additional variables (Mother's age at Birthing) and divide into male and female
datasets */
data survival_4;
        set survival_3;
        if Mum_BirthYear=. or Mum_BirthYear=0 then delete;
        if BirthYear-Mum_BirthYear<11 then
                if BirthYear-Mum_BirthYear<7 then BirthingClass='Y' /* Y=Young */;
                else BirthingClass='M' /* M=Middle */;
                else BirthingClass='O' /* O=Old */;
        if Live_or_Dead='D' then censored_1=2;
```

```
        else censored_1=1;
run;


/* Getting residual capture weight for deer using GLM */
proc glm data=survival_MnF plots=all;
        class Sex;
        model Capture_weight=capture_age sex capture_age*sex;
        /* Capture_weight*Sex interaction is not significant, and excluding this interaction
        both factors are significant. Therefore, I use this model as the source for residuals */
proc glm data=survival_MnF plots=all;
        class Sex;
        model Capture_weight=capture_age sex;
        output out=survival_MnF_Residuals residual=residual;
run;

data survival_M;
        set survival_MnF_Residuals;
        if Sex=1 or Sex=3 then delete;
run;
data survival_F;
        set survival_MnF_Residuals;
        if Sex=2 or Sex=3 then delete;
run;

data survival_MnF_Residuals;
        set survival_4;
        if Sex=3 then delete;
run;

proc print data=survival_M;
proc print data=survival_F;
run;

/* Unadjusted (TypeI) survival Plots for BirthingClass and BirthMonth for Females and Males
seperately */
proc lifetest data=survival_F plots=survival(cl atrisk=0 to 250 by 10);
        time event_time*censored_1(1);
        strata BirthMonth;
run;

proc lifetest data=survival_F plots=survival(cl atrisk=0 to 250 by 10);
        time event_time*censored_1(1);
        strata BirthingClass;
run;

proc lifetest data=survival_F plots=survival(cl atrisk=0 to 250 by 10);
        time event_time*censored_1(1);
        strata Home_range;
run;

proc lifetest data=survival_M plots=survival(cl atrisk=0 to 250 by 10);
        time event_time*censored_1(1);
        strata BirthMonth;
run;

proc lifetest data=survival_M plots=survival(cl atrisk=0 to 250 by 10);
        time event_time*censored_1(1);
        strata BirthingClass;
run;

proc lifetest data=survival_M plots=survival(cl atrisk=0 to 250 by 10);
        time event_time*censored_1(1);
        strata Home_Range;
run;

data survival_M_trash;
        set survival_M;
        event_time=event_time-1;
run;
```

```
/* FINALLY: Analysis of survival using time-dependent and time-independent predictors */
/* Event_Time = the age (months) that a deer died or was lost to follow-up (censored).
Censored_1=1 if the animal was lost to follow-up, and 0 if the deer died.
Ties=Efron → is the method that the model uses to handle tied event times (deaths happening at
the same time). The Efron procedure is necessary for valid estimates when we have many tied event
times. */
proc phreg data=survival_M covs(aggregate);
       class BirthingClass BirthMonth BirthYear MumCode Home_Range
       /* Class variables are categorical */;
       model Event_Time*Censored_1(1)=orph1YR orph2YR orph3YR orph4plus /*BirthingClass*/
       BirthMonth BirthYear BirthMonth*BirthYear residual / RL TIES=EFRON;
/* Now we tell SAS how to define the orph1YR to orph4plus factors. We define them  using
programming statements and tell SAS to treat them as time-dependent factors                (value
allowed to change through time)*/
               if (age_orphaned=. or Event_Time<age_orphaned) then do;
                       orph1YR=0;
                       orph2YR=0;
                       orph3YR=0;
                       orph4plus=0;
/* The above code defines when individuals should be considered non-orphans.
Specifically, whenever the event_time (in the case of the running model, this is the time when
ANY individual dies) is less/comes before the age deer (in the dataset) were orphaned. Proc PHREG
marches through these times sequentially, and in doing so evaluates the probability that the
animal dying was an orphan. All deer alive at that point in time are part of the risk set (those
at risk of dying). */
               end;
               else do;
               if (age_orphaned LE 12) then do;
                       orph1YR=1;
                       orph2YR=0;
                       orph3YR=0;
                       orph4plus=0;
               end;
               if (age_orphaned>12 and age_orphaned LE 24) then do;
                       orph1YR=0;
                       orph2YR=1;
                       orph3YR=0;
                       orph4plus=0;
               end;
               if (age_orphaned>24 and age_orphaned LE 36) then do;
                       orph1YR=0;
                       orph2YR=0;
                       orph3YR=1;
                       orph4plus=0;
               end;
               if (age_orphaned>36) then do;
                       orph1YR=0;
                       orph2YR=0;
                       orph3YR=0;
                       orph4plus=1;
               end;
       if (age_orphaned=. or Event_Time<age_orphaned or (Event_Time-age_orphaned>6)) then do;
               orph_by_time=0;
       end;
       else do;
               orph_by_time=1;
       end;
       end;
       id MumCode;
       strata Home_Range;
run;
```