POPULATION DYNAMICS OF EASTERN COYOTES IN SOUTHEASTERN ONTARIO

A Dissertation Submitted to the Committee on Graduate Studies in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy in the Faculty of Arts and Science

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ABSTRACT

Population Dynamics of Eastern Coyotes in Southeastern Ontario

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The ability of animal populations to compensate for harvest mortality provides the basis for sustainable harvesting. Coyote populations are resilient to exploitation, but the underlying mechanisms of compensation and how they inter-relate are not fully understood. Moreover, deficiencies in the quality and quantity of information about eastern coyotes preclude effective management. I combined field work, laboratory work, and genetic profiling to investigate the population dynamics of eastern coyotes in southeastern Ontario. Specifically, I conducted research on coyotes during 2010–2013 in Prince Edward County where coyote hunting and trapping seasons were open all year. First, I investigated their social status dynamics and space-use patterns. Transients exhibited extensive space-use relative to residents, potentially encountering vacant territories and/or breeding positions, and some transients became residents, potentially filling vacant territories and/or breeding positions. Accordingly, the study population demonstrated the potential to compensate for harvest mortality via source-sink dynamics and/or buffering reproductive capacity. Second, I investigated their survival and cause-specific mortality. Residents exhibited greater survival than transients, probably partly because of the benefits of holding a territory, and transients seemingly exhibited greater vulnerability to harvest than residents, probably partly because their movements exposed them to greater cumulative mortality risks over time. Accordingly, harvest mortality disproportionately impacted the non-reproductive segment of the study population and thus may have failed to substantially limit reproduction, and thus recruitment. Third, I investigated their reproduction and breeding histories. Females in the study population exhibited age-specific reproductive rates and litter sizes generally typical of those in exploited coyote populations. Accordingly, increased reproductive rates and increased litter sizes may have offset losses due to harvest mortality. There was at least some breeder turnover in the study population due to harvest mortality, but many breeders survived to reproduce for multiple years and those that died were quickly replaced. My findings have important management implications for eastern coyotes and contribute significantly to better understanding of their resilience to harvest. Indiscriminate killing of coyotes through liberal harvest is unlikely to be effective in reducing their abundance. Management strategies should consider non-lethal alternatives and/or targeted lethal control for dealing with problem coyotes.

Keywords: population dynamics, eastern coyotes, *Canis latrans* var., southeastern Ontario, Prince Edward County, harvest, resilience, social status, space-use, survival, cause-specific mortality, reproduction, breeding

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I participated in all research activities and performed all data analyses described herein. Therefore, throughout my dissertation I have used the pronoun “I” rather than “we” for attributing the performance of research activities and data analyses; however, it should be noted that research activities were carried out by a team of researchers, which comprised me, my supervisor, and several field technicians. The contributions of all those involved in this study were greatly appreciated.

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Chapter 1

General Introduction

Demographic compensation in animal populations

The ability of animal populations to compensate for harvest mortality (e.g., hunting and trapping) facilitates their persistence where they are subject to exploitation by humans and provides the basis for sustainable harvesting. Animal populations can compensate for predation or harvest mortality via responses in demographic rates, including births and deaths, but also spatially via immigration and emigration. Demographic compensation in animal populations is usually related to density dependence, which is assumed to be caused by competition for resources, whereby population density affects resource availability per individual, and thus affects survival and reproduction of individuals. Demographic compensation in animal populations can occur via decreases in natural mortality or increases in reproductive output (Boyce et al. 1999), but also via decreases in emigration or increases in immigration (Adams et al. 2008). Field studies have demonstrated these types of compensatory responses to harvest in a number of species (Boyce et al. 1999; Adams et al. 2008); however, the mechanisms that underlie these processes and how they inter-relate are not fully understood (Pöysä et al. 2004). Also, mechanisms of compensation vary substantially among species and even among populations of the same species (Fretwell 1972). Further research on demographic compensation in harvested species conducted at the scale of the population of interest is required to inform management strategies.

Compensatory mortality in animal populations occurs when predation or harvest mortality is completely or partially compensated for by a density-dependent response in natural mortality

(Boyce et al. 1999). The compensatory mortality hypothesis predicts that an increase in harvest mortality results in a decrease in population density and thereby reduced competition for resources (e.g., food and habitat), which results in a decrease in natural mortality and thereby a relatively stable population size over time (Boyce et al. 1999). Complete compensation for harvest mortality is unlikely to occur in animal populations (Kokko 2001) and is unachievable above certain thresholds of harvest mortality (Lebreton 2005). Partial compensation for harvest mortality is more likely to occur in animal populations (Kokko 2001), whereby the total mortality rate increases with harvest, but not in direct proportion to the harvest mortality rate (Lebreton 2005). Compensatory mortality in response to harvest has been documented for waterfowl species (Burnham & Anderson 1984; Nichols et al. 1984) and grouse species (Ellison 1991; Sedinger et al. 2010). Explicit partial compensation has been documented for experimentally harvested willow ptarmigan (Sandercock et al. 2011) and non-experimentally harvested wildlife species, including wolves (Murray et al. 2010) and cougars (Wolfe et al. 2015).

Compensatory natality in animal populations occurs when predation or harvest mortality is compensated for by a density-dependent response in reproductive output (Boyce et al. 1999). The compensatory natality hypothesis predicts that an increase in harvest mortality results in a decrease in population density and thereby reduced competition for resources (e.g., food and habitat), which results in an increase in reproductive output and thereby a relatively stable population size over time (Boyce et al. 1999). Compensation for harvest mortality can occur in animal populations via increases in age-specific reproductive rates (Gese 2005; Minnie et al. 2016) or increases in litter size (Knowlton 1972; Cavallini & Santini 1996), but is constrained by the biological limits of the species with respect to reproduction. Compensatory natality in response to harvest has been documented for various wildlife species, including bobwhite

(Roseberry & Klimstra 1984), mountain goats (Swenson 1985), feral pigs (Hanson et al. 2009), coyotes (Knowlton 1972; Gese 2005), wolves (Schmidt et al. 2017), red foxes (Cavallini & Santini 1996), and black-backed jackals (Minnie et al. 2016). Note that compensatory natality is often referred to as compensatory reproduction and both terms are used interchangeably.

Seasonality in density dependence is an important mechanism that underlies compensatory mortality and compensatory natality in animal populations (Kokko & Lindström 1998; Boyce et al. 1999; Kokko 2001). Specifically, the timing of harvest relative to the mortality season (i.e., the period of highest natural mortality risk) and the birthing season (i.e., the period of gestation and parturition) can significantly affect the ability of an animal population to compensate for harvest mortality (Kokko & Lindström 1998; Boyce et al. 1999; Kokko 2001). Density dependence in natural mortality or reproductive output must occur after harvest mortality for compensation to be realized (Boyce et al. 1999). The following rules generally apply: (1) if harvest mortality occurs before natural mortality or breeding, then compensation can be complete; (2) if harvest mortality overlaps with natural mortality or breeding, then compensation can only be partial; and (3) if harvest mortality occurs after natural mortality or breeding, then compensation cannot occur (Kokko & Lindström 1998; Kokko 2001).

Spatial differences in survival and reproduction in relation to intrinsic and extrinsic factors may result in source-sink dynamics in an animal population (Pulliam 1988; Dias 1996; Thomas & Kunin 1999). In a source-sink system, the sources have positive demography (births > deaths) and the sinks have negative demography (births < deaths), with net emigration occurring for sources and net immigration occurring for sinks, thereby stabilizing the overall demographic system (Pulliam 1988; Dias 1996; Thomas & Kunin 1999). Source-sink theory has generally been considered in the context of spatial differences in habitat quality (Pulliam & Danielson

1991; Diffendorfer 1998), but also has been considered in the context of spatial differences in harvest pressure (Novaro et al. 2000; Delibes et al. 2001). Indeed, source-sink dynamics in response to harvest have been documented for various wildlife species, including the Iberian lynx (Gaona et al. 1998), culpeo foxes (Novaro et al. 2005), cougars (Robinson et al. 2008; Andreasen et al. 2012), and Eurasian woodcocks (Péron et al. 2012). Density-dependent dispersal from areas of low harvest (sources) to areas of high harvest (sinks) is the underlying mechanism that drives source-sink dynamics in response to harvest and may be related to resource availability and/or breeding opportunity. Consistent with source-sink theory, the compensatory immigration hypothesis predicts that harvest mortality in a given area results in a temporary decrease in local density, which results in an increase in immigration from other areas and thereby prevents a permanent decrease in local density. Compensatory immigration in response to harvest has been documented for various wildlife species, including willow grouse (Smith & Willebrand 1999), damselfish (Turgeon & Kramer 2012), black-backed jackals (Minnie et al. 2018), coyotes (Kierepka et al. 2017), cougars (Robinson et al. 2008; Cooley et al. 2009), red foxes (Lieury et al. 2015), and wolverines (Gervasi et al. 2015).

Compensatory mortality, compensatory natality, and source-sink dynamics have been implicated separately in demographic compensation in animal populations. However, these processes are not mutually exclusive, thus interactions among them should be considered. Consistent with this view, Sandercock et al. (2011) proposed five main factors that determine the response of animal populations to harvest under natural conditions: (1) life history strategy (i.e., survival versus reproduction), (2) population status (i.e., low versus high density, below versus above carrying capacity), (3) seasonal timing of harvest and natural mortality (i.e., overlapping versus non-overlapping), (4) individual variation in survival and vulnerability to harvest (i.e., sex, age), and (5) animal movements (i.e., dispersal). Péron (2013) found that life history strategy and population status were important factors with respect to determining the response of animal populations to harvest. Accordingly, investigations of demographic compensation in animal populations should consider as many of these factors as possible to facilitate comprehensive understanding of resilience to harvest.

Demographic compensation can facilitate sustainable harvesting of game species, which can be desirable from a game management standpoint, but for certain predator species it can also facilitate their resilience to lethal control efforts intended to achieve predator population reduction, which can be undesirable from a livestock depredation management standpoint. Indeed, certain predator species are widely subject to persistent lethal control efforts for the purpose of livestock depredation management, but such efforts often have limited success in preventing or reducing conflicts (Peebles et al. 2013; Treves et al. 2016) or achieve only temporary relief from conflicts (Conner et al. 1998; Knowlton et al. 1999). The efficacy of using lethal control for predator population reduction is challenged by compensatory mechanisms that confer resilience (Mosnier et al. 2008; Newsome et al. 2014; Lieury et al. 2015; Doherty & Ritchie 2017). Accordingly, gaining better understanding of the compensatory mechanisms of predator species is important for informing livestock depredation management strategies.

Study species

The coyote (*Canis latrans*) is one of the most widely distributed predators in North America and has been studied extensively (Voigt & Berg 1987; Knowlton et al. 1999; Bekoff & Gese 2003; Mastro et al. 2011). Coyotes are inarguably the most persecuted and yet arguably the most successful of all predators in North America in modern times. The coyote is an archetypal generalist species with respect to habitat and diet (Voigt & Berg 1987; Bekoff & Gese 2003). Consequently, coyotes are remarkably adaptable with respect to changing environmental conditions and anthropogenic disturbances. Coyotes are beneficial both ecologically and economically (Voigt & Berg 1987); however, their perceived impacts on game species (e.g., white-tailed deer) and conflicts with livestock (e.g., sheep and goats) have led to repeated attempts by humans to control them (Young & Jackson 1951; Knowlton et al. 1999). Coyotes have been continually exploited throughout most of their recorded history (Young & Jackson 1951). Indeed, coyotes have been, and continue to be, trapped for fur, hunted for sport, killed for predator control, and often indiscriminately killed as part of bounties or calling contests (Young & Jackson 1951; Knowlton et al. 1999). Repeated attempts by humans to control coyotes through various means have generally proven unsuccessful (Voigt & Berg 1987). Particularly, bounties have been ineffective in controlling coyotes (Young & Jackson 1951; Parker 1995). Despite continual exploitation, coyotes have not only persisted, they have thrived and greatly expanded their range over the past century, demonstrating remarkable resilience to human-caused mortality (Young & Jackson 1951; Voigt & Berg 1987; Knowlton et al. 1999). Therefore, the coyote is an ideal study species for investigating the mechanisms that underlie the processes of demographic compensation in animal populations. A review of relevant background information on coyotes is necessary because consideration of their resilience requires knowledge of their natural history and population dynamics.

Coyotes are medium-sized canids that vary in size, weight, and pelage colour across their range (Voigt & Berg 1987; Bekoff & Gese 2003). Moreover, coyotes are sexually dimorphic with respect to size and weight, whereby adult males are usually larger and heavier than adult females

(Bekoff & Gese 2003). Compared to other canids, coyotes are larger and heavier than foxes but smaller and lighter than wolves (Voigt & Berg 1987). Coyotes can successfully interbreed and produce fertile hybrids with certain other canids, namely wolves (Kolenosky 1971; Schmitz & Kolenosky 1985a) and domestic dogs (Kennelly & Roberts 1969; Mengel 1971).

Coyotes occur throughout North America and occupy a variety of habitats (Voigt & Berg 1987; Bekoff & Gese 2003). Moreover, across their range, coyotes occupy a variety of landscapes, including both forest and rural (Tremblay et al. 1998), but also urban (Gehrt 2007). Historically, coyotes occurred in the western half of North America, and occupied mostly grasslands, prairies, and deserts (Young & Jackson 1951; Moore & Parker 1992; Hody & Kays 2018). Following European colonization of North America, coyotes greatly expanded their range beginning around 1900 (Young & Jackson 1951; Moore & Parker 1992; Hody & Kays 2018). This range expansion was likely facilitated by land clearing associated with logging and agriculture and the decline of larger predators such as wolves (Young & Jackson 1951; Moore & Parker 1992; Hody & Kays 2018). Contemporarily, coyotes occur across most of North America, with the exception of the Arctic tundra and northern portions of the Boreal forest (Moore & Parker 1992; Hody & Kays 2018). The density of coyotes varies spatially and temporally in response to changes in the availability of food (Voigt & Berg 1987; Bekoff & Gese 2003).

Coyotes eat a variety of food items in relation to changes in their respective availabilities (Bekoff & Gese 2003) and thus exhibit spatial and temporal variation in diet (Andelt et al. 1987; Dumond et al. 2001; Morey et al. 2007). The diet of coyotes includes various wild prey items, wild plant items, and anthropogenic food items (Gier 1968; Voigt & Berg 1987). Coyotes are an important part of the ecosystem, because they commonly prey on small mammals such as lagomorphs and rodents (Gier 1968; Voigt & Berg 1987), yet coyotes can be a concern for wildlife managers, because they can prey on game species such as white-tailed deer (Lavigne 1992). Also, coyotes can be a nuisance for livestock producers, because they can depredate livestock such as sheep and goats (Knowlton et al. 1999).

Coyotes exhibit variation in social organization, ranging from solitary individuals to pairs to variable-sized groups (Messier & Barrette 1982; Andelt 1985; Gese et al. 1996; Patterson & Messier 2001). The basic social unit in coyotes is the mated pair (Bekoff & Wells 1986). Packs typically consist of a mated pair and their offspring from the current litter, but can also include pack associates, which typically are non-dispersing offspring from previous litters (Andelt 1985; Gese et al. 1996). Within packs, coyotes exhibit a dominance hierarchy (Knowlton et al. 1999; Bekoff & Gese 2003). Coyotes exhibit a land-tenure system of exclusive territories, which are spaced contiguously across the landscape in relation to the availability of food and habitat (Knowlton et al. 1999; Bekoff & Gese 2003). Coyotes defend exclusive territories either directly by means of confrontation or indirectly by means of scent-marking and howling (Voigt & Berg 1987; Bekoff & Gese 2003). The burden of rearing sedentary pups makes a territory a prerequisite for successfully whelping pups (Messier & Barrette 1982). Breeding positions are typically limited to one individual of each sex per territory (Andelt 1985; Gese et al. 1996). Thus, coyotes must disperse from their natal territory, inherit a breeding position from a parent of the same sex, or displace a parent of the same sex to become a breeder (Andelt 1985; Gese et al. 1996).

Coyote populations consist of residents and transients, which represent distinct social classes of individuals that exhibit disparate space-use patterns (Andelt 1985; Gese et al. 1988; Kamler & Gipson 2000). Residents are territorial, occupying exclusive territories that are spaced contiguously across the landscape (Gese et al. 1988, 1989; Windberg & Knowlton 1988), and typically live together in groups composed of a breeding pair and their offspring (Andelt 1985; Bekoff & Wells 1986). Transients are non-territorial, occupying non-exclusive living areas that are superimposed upon the exclusive territories of residents (Gese et al. 1988, 1989; Windberg & Knowlton 1988), and typically live solitarily (Andelt 1985; Bekoff & Wells 1986). Coyotes can transition between social classes during their lifetime (Andelt 1985; Gese et al. 1988; Kamler & Gipson 2000) and may do so multiple times.

Home range size of coyotes varies geographically and seasonally as well as among individuals within a population (Voigt & Berg 1987; Bekoff & Gese 2003). Specifically, home range size varies with respect to habitat and prey density (Crête et al. 2001; Patterson & Messier 2001; Gese et al. 2012). Moreover, home range size varies with respect to social status, whereby the home ranges of residents are smaller and less variable than the home ranges of transients (Gese et al. 1988; Windberg & Knowlton 1988; Kamler & Gipson 2000). Population density of coyotes is negatively correlated with home range size of residents (Andelt 1985); this is because territory density of coyotes, which determines the breeding capacity of the population, is inversely related to home range size of residents.

Female coyotes are seasonally monoestrous (Kennelly 1978) and are capable of breeding in their first year (Gier 1968; Chambers 1992). Breeding occurs between January and March (Voigt & Berg 1987) and each breeding pair produces a single litter of pups each spring (Knowlton et al. 1999). Gestation lasts 60–63 days (Kennelly 1978) and most pups are whelped in April (Gier 1968; Chambers 1992). Both parents participate in the care and rearing of pups (Harrison & Gilbert 1985; Schell et al. 2018). The fecundity of a coyote population is a function of the proportion of females that breed and litter size (Kennelly 1978). The proportion of females that breed in a coyote population varies with respect to local conditions (Bekoff & Gese 2003) and has been shown to be variable within and between age classes (Windberg 1995). Litter size of coyotes varies with respect to food abundance (Gier 1968) and has been shown to be inversely related to population density (Knowlton 1972). Litter size averages six (Bekoff & Gese 2003) and ranges from one to twelve (Chambers 1992).

Mortality rates of coyotes vary geographically and seasonally (Voigt & Berg 1987; Bekoff & Gese 2003). Specifically, mortality rates depend on the availability of food and the level of exploitation in the population (Bekoff & Gese 2003). Furthermore, mortality rates can vary with respect to age class and social status (Andelt 1985; Windberg et al. 1985; Gese et al. 1989). Juveniles and yearlings tend to have higher mortality rates than adults (Windberg et al. 1985; Gese et al. 1989) and residents tend to have lower mortality rates than transients (Andelt 1985; Gese et al. 1989). Mortality of coyotes is predominantly attributed to human causes, including hunting, trapping, and roadkill, but is also attributed to natural causes, including disease, starvation, and predation (Voigt & Berg 1987; Bekoff & Gese 2003). Most coyotes are harvested during late autumn through late winter (Voigt & Berg 1987).

Dispersal of coyotes usually begins in autumn and continues throughout the winter (Voigt & Berg 1987) and generally involves juveniles or yearlings (Bekoff & Gese 2003). Most coyotes disperse as juveniles, but some coyotes disperse as yearlings (Gese et al. 1989; Harrison 1992a). Delayed dispersal of juveniles may occur in saturated populations (Voigt & Berg 1987), leading to pack formation (Messier & Barrette 1982). Dispersal is related to social and nutritional pressures, but seems to be voluntary rather than forced, whereby subordinate individuals voluntarily leave their natal territory due to mate competition and/or resource competition to seek breeding opportunities and/or food elsewhere (Gese et al. 1996). Coyotes may make exploratory movements outside their natal territory prior to dispersal (Harrison et al. 1991). Dispersal may be into a vacant or occupied territory, which may be a short or long distance from the natal territory (Harrison 1992a; Gese et al. 1996).

An understanding of coyote population dynamics requires information on reproduction, mortality, and emigration/immigration (Voigt & Berg 1987). Coyote populations exhibit seasonal patterns in births, deaths, and dispersal, which affect pack size and population density (Knowlton et al. 1999). Specifically, pack size and population density increase during spring when litters are born and then gradually decrease mostly during autumn and winter as individuals die or disperse (Knowlton et al. 1999). Coyote population regulation involves changes in births, deaths, and dispersal in response to various factors. Food abundance is the most important factor regulating coyote abundance, mediated through social dominance and territoriality (Knowlton et al. 1999; Bekoff & Gese 2003). Specifically, food abundance regulates coyote abundance by influencing reproduction, survival, dispersal, space-use patterns, and territory density (Knowlton et al. 1999; Bekoff & Gese 2003). Also, the level of exploitation by humans is an important factor with respect to coyote population regulation, because it has been shown to influence coyote demography (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). Unexploited or lightly exploited coyote populations tend to have older age structures, lower juvenile survival rates, higher adult survival rates, lower reproductive rates (especially among young individuals), and smaller litter sizes (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). Moderately to heavily exploited coyote populations tend to have younger age structures, higher juvenile survival rates, lower adult survival rates, higher reproductive rates, and larger litter sizes (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). Exploitation of coyotes can decrease population density, thereby resulting in reduced resource competition and reduced social constraints on breeding, which can elicit various demographic responses (Windberg 1995;

Knowlton et al. 1999). Potential demographic responses of coyotes to exploitation can include recolonization from adjacent areas, increased reproduction by young individuals, larger litter sizes, and increased survival rates (Windberg 1995; Knowlton et al. 1999). Indeed, coyote populations are resilient to exploitation, with demographic responses directing population density to levels consistent with food abundance (Windberg 1995; Knowlton et al. 1999). Yet, despite substantial evidence for demographic compensation in coyote populations, the underlying mechanisms of compensation and how they inter-relate are not fully understood.

The colonization of eastern North America by coyotes during the past century involved the hybridization of expanding western coyotes (*C. latrans*) with eastern wolves (*C. lycaon*) and domestic dogs (*C. familiaris*) in the Great Lakes region, which resulted in the formation of the eastern coyote (*C. latrans* var.) (Hilton 1978; Parker 1995). Morphologic and genetic studies have confirmed that eastern coyotes derive from western coyotes that hybridized with eastern wolves and domestic dogs (Lawrence & Bossert 1969; Schmitz & Kolenosky 1985b; Kays et al. 2010; Wheeldon et al. 2013; Monzón et al. 2014). Despite its mixed ancestry, the eastern coyote is predominantly coyote-like morphologically (Lawrence & Bossert 1969; Schmitz & Kolenosky 1985b; Way 2013), genetically (Chambers 2010; vonHoldt et al. 2011; Monzón et al. 2014), and ecologically (Crête et al. 2001; Kays et al. 2008; Benson et al. 2017). However, eastern coyotes differ from western coyotes in some important respects, which could have implications regarding their resilience to harvest. Putatively because of hybridization, eastern coyotes are larger and heavier than western coyotes (Way 2007a; Kays et al. 2010), thus the former presumably have greater energy requirements (Carbone et al. 1999) and larger home ranges (Harestad & Bunnell 1979) than the latter. Possibly also due to lower food availability in the east relative to the west, indeed, eastern coyotes tend to have larger home ranges than western coyotes, thus the former generally occur at lower densities than the latter (Harrison 1992b; Parker 1995). Based on these differences, eastern coyotes may be less resilient to harvest than western coyotes, but supporting evidence is lacking. Wolves are less resilient to harvest than coyotes, as evidenced by the fact that the former were extirpated from much of their historical range following European colonization whereas the latter expanded their range during the same period despite extensive persecution by humans. Wolves have larger home ranges than coyotes, thus the former occur at lower densities than the latter. Also, wolves are less productive than coyotes, in part because the former attain sexual maturity at an older age than the latter. These differences may partly explain why wolves are less resilient to harvest than coyotes. It is not clear how the partial wolf ancestry of eastern coyotes might influence their resilience to harvest.

A review of the literature (Mastro et al. 2011) revealed deficiencies in the quality and quantity of information about eastern coyotes, including all aspects of their ecology and topics relevant to understanding their population dynamics. A clear understanding of the population dynamics of eastern coyotes is critical, especially in areas where predator control and/or sport hunting occur (Gompper 2002), including agricultural landscapes where livestock depredation is a concern. Further investigation of the population dynamics of eastern coyotes is needed to provide wildlife managers with essential information (Gompper 2002; Mastro et al. 2011).

I combined field work, laboratory work, and genetic profiling to investigate the population dynamics of eastern coyotes in southeastern Ontario. Specifically, I investigated the social status dynamics and space-use patterns, the survival and cause-specific mortality, and the reproduction and breeding histories of eastern coyotes from a harvested population in southeastern Ontario. My findings have important management implications for eastern coyotes and contribute significantly to better understanding of their resilience to harvest.

Research objectives

My overall research objective was to gain better understanding of the compensatory mechanisms by which eastern coyote populations might achieve resilience to harvest. My specific research objectives were to gain better understanding of how (1) social status dynamics and space-use patterns, (2) individual variation in survival and cause-specific mortality, and (3) reproduction and breeding histories might contribute to, influence, or inform on resilience to harvest for eastern coyote populations. Essentially, I sought to determine (1) if eastern coyote populations exhibit source-sink dynamics, compensatory mortality, and compensatory natality in response to harvest and (2) the relative importance of these compensatory mechanisms for eastern coyote populations with respect to achieving resilience to harvest. Moreover, I sought to determine the compensatory potential of eastern coyote populations with respect to harvest. The main goal of my study was to provide further insights into eastern coyote populations and their resilience to harvest and thereby better inform management strategies for eastern coyotes.

Study area

I conducted research on coyotes during 2010–2013 in Prince Edward County (PEC), which is located in southeastern Ontario on a large irregular headland in the northeastern region of Lake Ontario (Figure 1.1). This headland is bordered on the north and east by the Bay of Quinte and a canal intersects the only land connection. Thus, PEC is technically an island, but it is connected to the mainland by several bridges. PEC encompassed a land area of approximately 1,050 km^2 (Statistics Canada 2012). Based on the 2011 Census, human population size was 25,258 and density was 24.0 persons per km^2 (Statistics Canada 2012). The landscape was predominantly

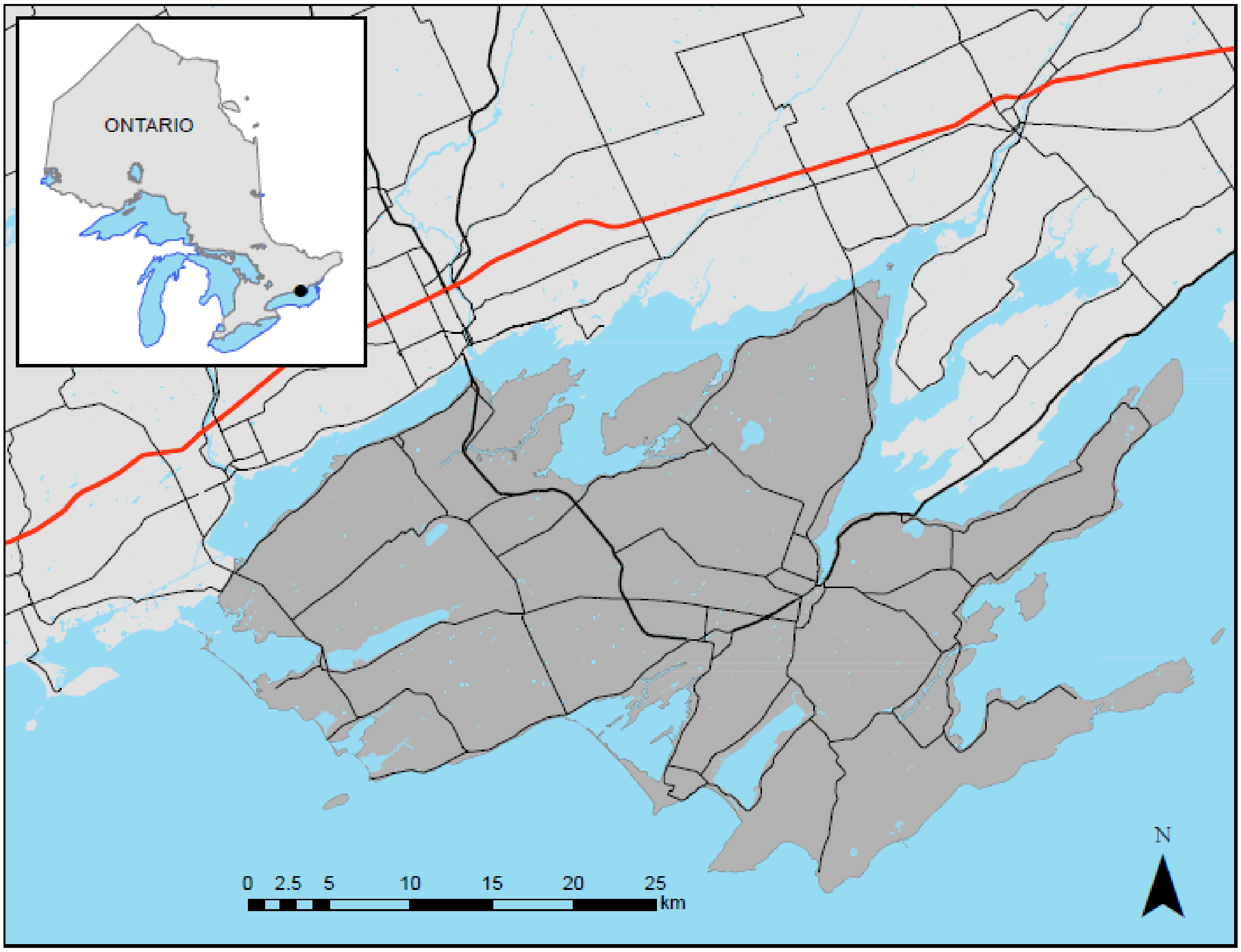

Figure 1.1. Map of the study area. Prince Edward County is shaded in dark gray and the mainland is shaded in light gray. Black lines represent major roads and the red line represents Hwy 401 (multi-lane divided highway). The greater study area included the portion of the mainland south of Hwy 401. The inset map shows the location of the study area (black circle) in Ontario.

agricultural and rural. Agriculture involved pasturing of various livestock, including sheep and cattle, and growing of various crops, including grains, vegetables, and fruits. Multiple orchards and vineyards were in operation. The natural prey base of coyotes in PEC presumably included eastern cottontail (*Sylvilagus floridanus*), white-tailed deer (*Odocoileus virginianus*), and various small rodents (e.g., mice, shrews, and voles). Coyote hunting and trapping seasons were open all year. Coyote hunting with hounds was common during the winter. Based on deer hunter questionnaire data, the relative abundance of coyotes in the study area was relatively stable over the years of the study (Figure 1.2). There was a roughly 3-fold change in the relative abundance of coyotes in the study area over the years 2000–2015, but there was no substantial change in the relative abundance of coyotes in the study area over the years 2010–2013 (Figure 1.2). Notably, the overall trend in relative abundance of coyotes in the study area was generally consistent with that of coyotes across southeastern Ontario (data not shown), and thus presumably reflected large-scale population-level responses to changes in food abundance and landscape conditions, but not necessarily changes in coyote hunting and trapping.

The study area was PEC, but the greater study area included the portion of the mainland south of Hwy 401 (multi-lane divided highway that runs approximately west-to-east) between Port Hope and Kingston. The landscape of the relevant portion of the mainland was similar to that of PEC. Thus, I assumed that the natural prey base was similar for PEC and the relevant portion of the mainland. Likewise, I assumed that coyote harvest was similar for PEC and the relevant portion of the mainland.

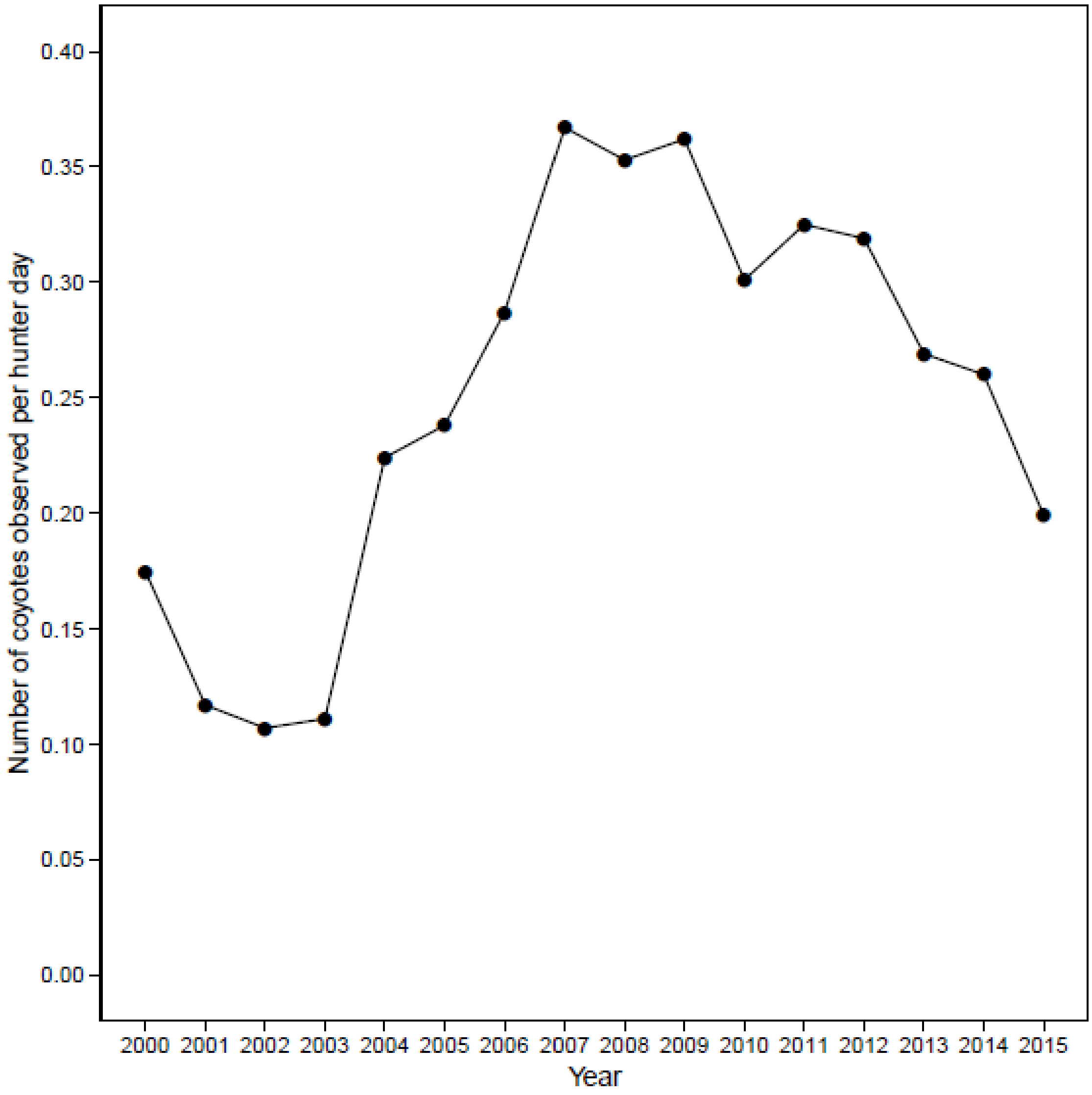

Figure 1.2. Coyote population index for Prince Edward County, Ontario, 2000–2015. This index is based on deer hunter questionnaire data for Wildlife Management Unit 70 provided by the Ontario Ministry of Natural Resources and Forestry.

General methods

I captured coyotes using padded foot-hold traps and either chemically or physically immobilized them to facilitate handling. I weighed, sexed, and aged coyotes. I sampled blood and/or hair from coyotes for genetic profiling. I ear-tagged coyotes and fitted them with either Global Positioning System (GPS) radio-collars or very high frequency (VHF) radio-collars. The capture, handling, and radio-collaring of coyotes was approved by the Trent University Animal Care Committee (protocol no. 10016) and the Ontario Ministry of Natural Resources Wildlife Animal Care Committee (protocol nos. 10-219 through 12-219). I conducted ground VHF telemetry approximately weekly to locate and monitor radio-collared coyotes. I remotely or physically downloaded location data from GPS radio-collars. I retrieved carcasses of radio-collared coyotes. Also, I collected carcasses of non-radio-collared coyotes. I performed necropsies on carcasses in the laboratory. I examined carcasses and (if possible) determined cause of death. I weighed, sexed, and aged carcasses. I extracted a lower canine tooth from each carcass for aging by the cementum annuli technique. I examined the reproductive tracts of females and recorded the presence/absence and (if applicable) number of implants, fetuses, or placental scars. I sampled tissue from carcasses for genetic profiling. I collected fecal swabs from scats found in the field and saliva swabs from bite wounds on depredated livestock. I extracted genomic DNA from the various samples and genetically profiled them. Specifically, I determined genotypes based on 16 autosomal microsatellite loci. Also, I determined maternal and paternal haplotypes based on mitochondrial DNA sequences and four Y-chromosome microsatellite loci, respectively.

Overview of dissertation

This dissertation is organized as follows: Chapter 1 presents a general introduction to review demographic compensation in animal populations and to provide background information on coyotes and their resilience to harvest; Chapter 2 investigates the social status dynamics and space-use patterns of eastern coyotes and considers the role of source-sink dynamics with respect to their resilience to harvest; Chapter 3 investigates the survival and cause-specific mortality of eastern coyotes and considers the role of compensatory mortality with respect to their resilience to harvest; Chapter 4 investigates the reproduction and breeding histories of eastern coyotes and considers the role of compensatory natality with respect to their resilience to harvest; Chapter 5 presents a general discussion to summarize the findings of this dissertation and to provide suggestions for future research and management recommendations.

Chapter 2

Social status dynamics and space-use patterns of eastern coyotes from a harvested population in southeastern Ontario

Abstract

Animal movements are an important factor to consider when investigating the compensatory potential of harvested animal populations. Coyotes are liberally harvested across much of their range, but most coyote populations demonstrate considerable resilience to harvest, suggesting that they exhibit some mechanisms of compensation. The social system of the coyote includes territorial individuals and non-territorial individuals, referred to as residents and transients, respectively. However, individuals can undergo transitions in social status. Coyotes exhibit variable space-use with respect to social status and a social hierarchy with respect to breeding. The social status dynamics and space-use patterns of coyotes are fundamentally important with respect to the resilience of harvested coyote populations, but better understanding is sought. I investigated the social status dynamics and space-use patterns of eastern coyotes from a harvested population in southeastern Ontario. I presumed (1) that coyotes in the study population would include residents and transients, which would be discernable based on their disparate space-use patterns, and (2) that coyotes in the study population would undergo transitions in social status, both because of and despite harvest mortality. I captured and radio-collared 147 coyotes. I determined the social status of individuals based on thorough assessment of their space-use patterns. I observed 63 residents and 27 transients, and also 40 individuals that changed social status. I recorded 44 transitions in social status, including 34 transitions from resident to transient and 10 transitions from transient to resident. I generated 95% fixed kernel home ranges and 99% Brownian bridge movement model home ranges for residents and transients, respectively. Both residents and transients exhibited considerable variation in space-use; mean (± SD) home range size was 13.9 ± 5.9 km^2 (range = 1.9–27.0 km^2) and 162.0 ± 99.6 km^2 (range = 28.7–464.0 km^2) for residents and transients, respectively. Indeed, transients exhibited extensive space-use relative to residents, potentially encountering vacant territories and/or breeding positions, and some transients became residents, potentially filling vacant territories and/or breeding positions. Accordingly, the study population demonstrated the potential to compensate for harvest mortality via source-sink dynamics and/or buffering reproductive capacity. My findings corroborate research that challenges the efficacy of liberal harvest for reducing coyote abundance and livestock depredation.

Introduction

The ability of animal populations to compensate for harvest mortality (e.g., hunting and trapping) depends on various intrinsic and extrinsic factors (see Sandercock et al. 2011). Animal movements are an important factor to consider when investigating the compensatory potential of harvested animal populations. Dispersal in particular can be important with respect to achieving compensation for harvest mortality in animal populations (e.g., Adams et al. 2008). Wildlife species with low dispersal capabilities may have limited capacity to compensate for harvest mortality, but wildlife species with high dispersal capabilities may have substantial capacity to compensate for harvest mortality. Dispersal capability differs among wildlife species (Bowman et al. 2002; Whitmee & Orme 2013), but many predators are highly mobile (e.g., cougars and wolves), and thus may have substantial capacity to compensate for harvest mortality. Therefore, gaining better understanding of the movements of predators is important for informing management strategies.

Spatial differences in survival and reproduction in relation to intrinsic and extrinsic factors may result in source-sink dynamics in an animal population (Pulliam 1988; Dias 1996; Thomas & Kunin 1999). Source-sink theory has generally been considered in the context of spatial differences in habitat quality (Pulliam & Danielson 1991; Diffendorfer 1998), but also has been considered in the context of spatial differences in harvest pressure (Novaro et al. 2000; Delibes et al. 2001). Source-sink dynamics can occur in harvested animal populations through density-dependent dispersal, possibly related to resource availability and/or breeding opportunity, whereby individuals disperse from areas of low harvest (i.e., sources where births exceed deaths) to areas of high harvest (i.e., sinks where deaths exceed births). Source-sink dynamics in response to harvest have been documented for various wildlife species (e.g., Eurasian woodcocks: Péron et al. 2012), including predators such as the Iberian lynx (Gaona et al. 1998), culpeo foxes (Novaro et al. 2005), and cougars (Robinson et al. 2008; Andreasen et al. 2012). Consistent with source-sink theory, compensatory immigration can occur in harvested animal populations when harvest mortality in a given area results in a temporary decrease in local density, which results in an increase in immigration from other areas and thereby prevents a permanent decrease in local density. Compensatory immigration in response to harvest has been documented for various wildlife species (e.g., willow grouse: Smith & Willebrand 1999), including predators such as black-backed jackals (Minnie et al. 2018), cougars (Robinson et al. 2008; Cooley et al. 2009), red foxes (Lieury et al. 2015), and wolverines (Gervasi et al. 2015).

Coyotes (*Canis latrans*) are liberally harvested across much of their range, but most coyote populations demonstrate considerable resilience to harvest, suggesting that they exhibit some mechanisms of compensation (Knowlton et al. 1999). However, some stakeholders remain convinced that liberal harvest is effective for reducing coyote abundance (e.g., Bartel & Brunson 2003). The onus remains on wildlife managers to better explain how coyote abundance can remain relatively stable across years despite consistently liberal harvest regimes.

The social system of the coyote includes territorial individuals and non-territorial individuals, referred to as residents and transients, respectively (Andelt 1985; Gese et al. 1988; Kamler & Gipson 2000). However, individuals can undergo transitions in social status, whereby residents can become transients and transients can become residents (Andelt 1985; Gese et al. 1988; Kamler & Gipson 2000), thereby demonstrating social status dynamics. Coyotes exhibit variable space-use with respect to social status, whereby residents typically exhibit localized space-use with fidelity to a specific area and transients typically exhibit nomadic space-use with no fidelity to any specific area (Gese et al. 1988, 1989; Windberg & Knowlton 1988). Resident home ranges typically do not overlap or overlap minimally, whereas transient home ranges typically overlap considerably and also overlap resident home ranges (Gese et al. 1989; Kamler & Gipson 2000). Residents typically live together in groups composed of a breeding pair and their offspring, whereas transients typically live solitarily (Andelt 1985; Bekoff & Wells 1986). Furthermore, coyotes exhibit a social hierarchy with respect to breeding, whereby typically residents but not transients can hold breeding positions and successfully whelp (Messier & Barrette 1982; Knowlton et al. 1985; Gese 2001). Thus, coyote socio-spatial organization typically involves breeding groups occupying contiguous territories and solitary individuals occupying living areas superimposed upon those territories (Camenzind 1978; Messier &

Barrette 1982). The space-use patterns of residents and transients reflect their respective objectives of defending a territory in which to raise offspring and searching for a vacant territory or breeding position. Accordingly, transients serve as an important reserve of individuals that can fill vacant territories and/or breeding positions (Camenzind 1978; Windberg & Knowlton 1988); however, supporting evidence for this has been meager (Gese et al. 1989; Gese 2005). The social status dynamics and space-use patterns of coyotes are fundamentally important with respect to the resilience of harvested coyote populations, but better understanding is sought.

Considerable research exists on the space-use of western coyotes, but comparatively limited research exists on that of eastern coyotes, especially in agricultural landscapes where livestock depredation is a concern (see Mastro et al. 2011). Geographic differences in prey density and landscape conditions influence the space-use of coyotes across their range (Harrison 1992b; Ellington & Murray 2015). Moreover, hybridization influences the space-use of coyotes in the east relative to that of those in the west (Ellington & Murray 2015). Indeed, eastern coyotes generally have larger home ranges and thus lower population densities than western coyotes (Harrison 1992b; Ellington & Murray 2015). Consequently, eastern coyotes may be potentially exposed to greater hazards (e.g., hunters, trappers, roads) and may be less resilient to harvest than western coyotes; however, the latter may be generally exposed to greater harvest intensities than the former, which complicates the issue. Further investigation of the space-use of eastern coyotes is needed to provide wildlife managers with essential information (Mastro et al. 2011).

I investigated the social status dynamics and space-use patterns of eastern coyotes from a harvested population in southeastern Ontario. My objective was to gain better understanding of how social status dynamics and space-use patterns might contribute to resilience to harvest for eastern coyote populations. I presumed that coyotes in the study population would include residents and transients, which would be discernable based on their disparate space-use patterns. I predicted that transients would exhibit extensive space-use relative to residents, potentially encountering vacant territories and/or breeding positions, which would be expected because of harvest mortality. I presumed that coyotes in the study population would undergo transitions in social status, both because of and despite harvest mortality; importantly, this would demonstrate the study population's potential to compensate for harvest mortality. I predicted that, despite harvest mortality, some transients would become residents, potentially filling vacant territories and/or breeding positions. I discuss the implications of my findings concerning the resilience of harvested coyote populations and the efficacy of liberal harvest for reducing coyote abundance and livestock depredation.

Methods

Study area

I conducted research on coyotes during 2010–2013 in Prince Edward County (PEC), which is located in southeastern Ontario on a large irregular headland in the northeastern region of Lake Ontario (see Chapter 1). The landscape was predominantly agricultural and rural. Coyote hunting and trapping seasons were open all year. Based on deer hunter questionnaire data, the relative abundance of coyotes in the study area was relatively stable over the years of the study (see Chapter 1).

Capture, handling, and radio-collaring

I captured coyotes using #3 Soft Catch® (Oneida Victor® Inc. Ltd., Euclid, Ohio, USA) coil spring foot-hold traps and physically restrained them with a Ketch-All Pole (The Ketch All Company, San Luis Obispo, California, USA). Generally, upon capture, I chemically immobilized coyotes with an intramuscular injection of either 1:1 mixture of ketamine (Vetalar®, Bioniche Animal Health Canada Inc., Belleville, Ontario, Canada) and medetomidine (Domitor®, Pfizer Canada Inc., Kirkland, Quebec, Canada) or 2:1 mixture of tiletamine-zolazepam (Telazol®, Fort Dodge Animal Health, Fort Dodge, Iowa, USA) and xylazine (Rompun®, Bayer Inc., Toronto, Ontario, Canada) at dosages of 5 mg/kg : 50 µg/kg and 4 mg/kg : 2 mg/kg, respectively, of estimated body mass. If applicable, prior to release, I reversed coyotes with an intramuscular injection of either atipamezole (Antisedan®, Pfizer Canada Inc., Kirkland, Quebec, Canada) or yohimbine (Yobine®, Novopharm Ltd., Toronto, Ontario, Canada) at dosages of 0.2 mg/kg and 0.2 mg/kg, respectively, of estimated body mass. Alternatively, I physically immobilized coyotes by hobbling and muzzling them for the duration of handling. I weighed coyotes and recorded their body mass. I sexed coyotes and noted evidence of breeding for females. I aged coyotes based on tooth eruption and wear (Gier 1968) and classified them as juvenile (< 12 months old), yearling (12–24 months old), or adult (> 24 months old). I sampled blood and/or hair from coyotes for genetic profiling. I marked coyotes with uniquely numbered Ketchum Kurl-Lock ear tags (Ketchum Manufacturing Inc., Brockville, Ontario, Canada). I fitted coyotes with either Global Positioning System (GPS) radio-collars or very high frequency (VHF) radio-collars; GPS radio-collars were programmed to record locations every 90 or 180 minutes for 12 or 13 days and then every 5 or 15 minutes for 1 day (the date and time of locations was recorded in GMT/UTC). I deployed several types of mortality-sensitive GPS radio-collars (equipped with VHF tracking beacon and fitted with drop-off mechanism) on coyotes: (1) Lotek WildCell SG (Lotek Wireless Inc., Newmarket, Ontario, Canada) with Global System for Mobile communications (GSM) cellular modem for Short Message Service (SMS) communication; (2) Lotek GPS 7000SU with ultra high frequency (UHF) radio modem; and (3) Sirtrack GPS Datalogger (Sirtrack Limited, Havelock North, New Zealand). I deployed several types of mortality-sensitive VHF radio-collars on coyotes: (1) ATS (Advanced Telemetry Systems Inc., Isanti, Minnesota, USA); (2) Sirtrack; and (3) Telonics (Telonics Inc., Mesa, Arizona, USA). Radio-collars generally weighed < 5% of body mass, except for some rapidly growing juveniles. If applicable, radio-collars were fitted with compressible foam and sized to accommodate neck growth. The capture, handling, and radio-collaring of coyotes was approved by the Trent University Animal Care Committee (protocol no. 10016) and the Ontario Ministry of Natural Resources Wildlife Animal Care Committee (protocol nos. 10-219 through 12-219).

Telemetry data

I conducted ground VHF telemetry approximately weekly to locate and monitor radio-collared coyotes. I determined the presence/absence of signals using a vehicle-mounted omnidirectional antenna and receiver; I determined the direction of signals using a hand-held 3-element Yagi antenna and receiver. I located individuals to within a specific tract of land and recorded their estimated location as a compass bearing from a reference location (e.g., road intersection, civic address); however, I did not triangulate their location. I monitored individuals based on the pulse rate of signals and recorded their vital status (i.e., alive or dead). Ontario Ministry of Natural Resources staff conducted aerial VHF telemetry when necessary to locate and monitor missing radio-collared coyotes. I plotted VHF telemetry locations in MapSource (version 6; Garmin Ltd., Schaffhausen, Switzerland). I remotely downloaded location data from applicable GPS radio-collars either regularly via SMS communication with a GSM ground station or irregularly via UHF communication with a hand-held command unit. I physically downloaded location data from GPS radio-collars upon retrieval after drop-off or mortality. I managed GPS radio-collar location data in Telemetry Data System (version 3; Kushneriuk et al. 2011), which transformed/converted WGS84 geographic coordinates to NAD83 (Lambert conformal conic) projected coordinates. I rarefied GPS radio-collar locations to either 90-min or 180-min intervals; the mean (± SD) fix success rate was 0.961 ± 0.039 (range = 0.793–1.000) and 0.923 ± 0.052 (range = 0.823–0.977) for Lotek radio-collars (*n* = 72) and Sirtrack radio-collars (*n* = 8), respectively.

Data screening/censoring

I screened GPS radio-collar location data in a multistep approach. First, I omitted locations recorded before or after deployment periods, which started at the first location recorded post-capture and ended at the first location recorded upon drop-off or mortality or at the last location recorded prior to radio-collar failure. Second, I omitted locations with error index (Keating 1994) values > 10, which were implausible. Third, I omitted locations with horizontal dilution of precision values ≥ 10 (Sirtrack radio-collars only), which were unreliable. Fourth, I omitted locations recorded during recapture for applicable individuals. Additionally, I censored GPS radio-collar location data that might bias space-use analyses. Specifically, I calculated daily movement distances in R (version 3.1.2; R Core Team 2014) using the adehabitatLT package, subjectively assessed daily movement distances during the first 30 days post-capture, and censored locations recorded prior to recovery (i.e., apparent normal movement) for individuals that exhibited apparent reduced movement post-capture, putatively due to capture-related effects. Alternatively, I censored locations recorded on the capture date and first post-capture date for individuals that exhibited no apparent reduced movement post-capture. Also, I censored locations recorded at the end of deployment for an individual that exhibited notably reduced movement prior to mortality.

Social status assessment

I visualized location data (GPS radio-collar locations and/or VHF telemetry locations) in ArcMap (version 10.2; Esri, Redlands, California, USA) and thoroughly assessed the space-use patterns of radio-collared coyotes. Further, using only GPS radio-collar locations, I plotted net displacement over time in R using the rgeos package and generated (95% minimum convex polygon) area-observation curves (Odum & Kuenzler 1955) from sequential-daily locations in R using the adehabitatHR package. I assessed relative variation in net displacement over time and determined whether area-observation curves reached an asymptote. I noted any conspicuous changes in net displacement over time and area-observation curves. I confidently determined the social status of most individuals, classifying them as either resident (exhibited localized space-use with fidelity to a specific area) or transient (exhibited nomadic space-use with no fidelity to any specific area). Ambiguous space-use patterns or insufficient data precluded determination of the social status of some individuals; however, I inferred the social status of some individuals based on pedigree information (see Chapter 4), whereby some individuals determined to be in their natal territory were inferred to be residents. Monitoring gaps precluded determination of the social status of some individuals during specific periods. I recorded transitions in social status of individuals that exhibited both distinct space-use patterns, which were classified as resident and transient during discrete periods. I considered localized space-use within an apparent territory becoming nomadic to be indicative of transition from resident to transient and nomadic space-use becoming localized within an apparent territory to be indicative of transition from transient to resident. I did not consider brief extra-territorial movements by residents or intermittent localized movements by transients to be indicative of transitions in social status.

Space-use analyses

I used only GPS radio-collar locations for quantifying space-use, because VHF telemetry locations were insufficiently accurate for this purpose. I empirically assessed location error of GPS radio-collars using non-rarefied locations recorded during stationary periods after drop-off or mortality. I estimated true locations of GPS radio-collars by averaging the coordinates of ≥ 5 good-quality locations. I calculated location error as the Euclidean distance between recorded locations and estimated true locations; the median location error was 3.7 m and 7.4 m for Lotek radio-collars (1860 locations) and Sirtrack radio-collars (113 locations), respectively.

For residents, I generated fixed kernel (Worton 1989, 1995) home ranges in R using the adehabitatHR package. I estimated utilization distributions over 30-m cell-size grids and extracted 95% contours. I employed the rule-based ad hoc method of bandwidth selection described by Kie (2013) because my goal was to delineate a continuous contour representing a home range as described by Burt (1943), i.e., ‘that area traversed by the individual in its normal activities of food gathering, mating, and caring for young'. I assessed bandwidths comprising the reference bandwidth (h_{ref}) and sequentially reduced proportions (0.1 increments from 0.9 to 0.1) of the reference bandwidth ($\supset h_{ad\ hoc}$). Generally, I selected the smallest bandwidth that produced a continuous home range contour that contained no lacuna. Alternatively, I selected the smallest bandwidth that produced a discontinuous home range contour that contained no lacuna or a continuous home range contour that contained a lacuna. I visualized home range contours and locations in ArcMap and identified excursions, defined as movements (i.e., sequential locations) generally > 1 km outside the home range contour that lasted ≥ 1 day, but also included final movements outside the home range contour that lasted < 1 day. I omitted excursions and regenerated home ranges for applicable residents. I generated home ranges for residents with datasets that spanned > 4 weeks. I truncated the datasets of two residents such that they spanned 365 days. Further, I generated (95% fixed kernel) area-observation curves from sequential-daily locations in R using the adehabitatHR package and determined whether home ranges plateaued, defined as deviating ≤ 10% below the maximum area for ≥ 4 weeks or not exceeding the maximum area for ≥ 4 weeks. I retained home ranges that plateaued or spanned ≥ 180 days. Finally, I clipped home range contours that overlapped ≥ 1 waterbody (i.e., lake > 0.5 km^2 in area) with respect to the Ontario Hydro Network waterbody layer (OMNR 2010) and recalculated areas of applicable home range contours in ArcMap; exceptions applied for two residents that frequented a specific waterbody during presumed ice cover. For residents, I generated seasonal fixed kernel home ranges similarly as described above, but found no significant difference in home range size between seasons (Appendix A), and therefore do not report on them herein.

For transients, I generated Brownian bridge movement model (Horne et al. 2007; Sawyer et al. 2009) home ranges in R using the BBMM package. I estimated utilization distributions over

30-m cell-size grids and extracted 99% contours. I specified a location error of 20 m and a time step of 10 units. Also, I specified a maximum time lag of 400 minutes to ensure that movement paths were not estimated between locations > 400 minutes apart, because ‘including large time gaps in [datasets] can artificially inflate/deflate the Brownian motion variance and potentially bias estimates of probability of use’ (refer to the BBMM package reference manual). The main routine estimated the Brownian motion variance via maximum likelihood. I generated home ranges for transients with datasets that spanned > 4 weeks. I truncated the dataset of one transient because frequently missed fixes associated with radio-collar battery failure resulted in long time lags between locations. I employed the Brownian bridge movement model rather than a kernel-based approach to quantify space-use of transients because my goal was to estimate the expected movement paths and thus overall space-use of transients; this technique is well suited for describing space-use of animals during migration or dispersal (Horne et al. 2007).

Statistical analyses

I computed summary statistics for the home range sizes of residents and transients in R using the base package. Also, I plotted the frequency distributions of the home range sizes of residents and transients in R using the ggplot2 package. Prior to doing so, I averaged the home range sizes of residents that shared the same territory (i.e., parent-offspring or breeding pair) to avoid pseudo-replication. For both residents and transients, I determined if variation in home range size was independent of time span by fitting a linear regression to the data and plotting it in R using the stats package and the ggplot2 package. Note that I excluded juvenile residents and one duplicate resident from statistical analyses.

Results

Radio-collar deployments

I captured and radio-collared 147 coyotes (63 females and 84 males), but also recaptured and fitted new radio-collars to three coyotes, and thus performed 150 radio-collar deployments (86 GPS and 64 VHF). Specifically, I deployed radio-collars on 67 juveniles, 32 yearlings, and 51 adults (Appendix B). Generally, I deployed VHF radio-collars on juveniles and GPS radio-collars on yearlings and adults. However, I deployed GPS radio-collars on some juveniles captured in late summer or early autumn and VHF radio-collars on some yearlings and adults.

Social status dynamics

I observed 63 residents and 27 transients, both of which included individuals of each sex and age class combination. Also, I observed 40 individuals that changed social status, four of which did so twice. I recorded 44 transitions in social status (Appendix C), including 34 transitions from resident to transient and 10 transitions from transient to resident. The transitions from resident to transient included individuals of each age class (Table 2.1), but mostly juveniles, and mainly involved younger individuals dispersing from their natal territory, but also older individuals vacating their territory; four individuals subsequently reverted to residents. The transitions from transient to resident included individuals of each age class (Table 2.1), but mostly adults, and implicitly involved individuals settling in either a vacant territory or an occupied territory, but including two individuals returning to their respective natal territories after attempting dispersal. Accounting for transitions in social status, I observed 103 residents and 67 transients. Social status was undetermined for 17 individuals, and also for several additional individuals during

Table 2.1. Summary of transitions in social status of radio-collared coyotes in Prince Edward County, Ontario, 2010–2013. Frequencies are provided for each age class.

Transition type	Juveniles	Yearlings	Adults	Total
resident-transient	18	8	8	34
transient-resident	1	2	7	10
both combined	19	10	15	44

specific periods. Notably, two individuals of undetermined social status that exhibited ambiguous space-use patterns showed periodic fidelity to a specific area (i.e., putative home range) but made frequent excursions of variable duration.

Resident space-use

I generated 51 resident home ranges based on variable numbers of locations (range = 258–3684). I retained 38 resident home ranges that plateaued or spanned ≥ 180 days; however, I excluded seven of them (six juveniles and one duplicate) from statistical analyses. Mean (± SD) home range size of residents was 13.9 ± 5.9 km^2 (range = 1.9–27.0 km^2) and the most commonly observed binned home range size was 10–15 km^2 (Figure 2.1a). Variation in home range size of residents was independent of time span ($r^2 = 0.084$, $P = 0.11$; Figure 2.2a), which ranged from 56 to 365 days. Details of resident home ranges are provided in Appendix D. Residents exhibited considerable variation in space-use and home range configuration (Figure 2.3). Numerous resident home ranges were partly bounded by ≥ 1 waterbody (Figure 2.3), and some were bounded by roads (not shown), whereas others spanned multiple roads (not shown). Several residents exhibited repeated space-use of one or two areas outside their respective main home range areas, resulting in several discontinuous home ranges (Figure 2.3). There was limited spatial overlap among adjacent resident home ranges (Figure 2.3), suggesting territoriality. Therefore, I estimated that there were approximately 75 territories within PEC based on the size of the study area (1045 km^2) and the mean home range size of residents (13.9 km^2), but this may be an overestimation because certain areas within PEC may not have been part of any resident home ranges.

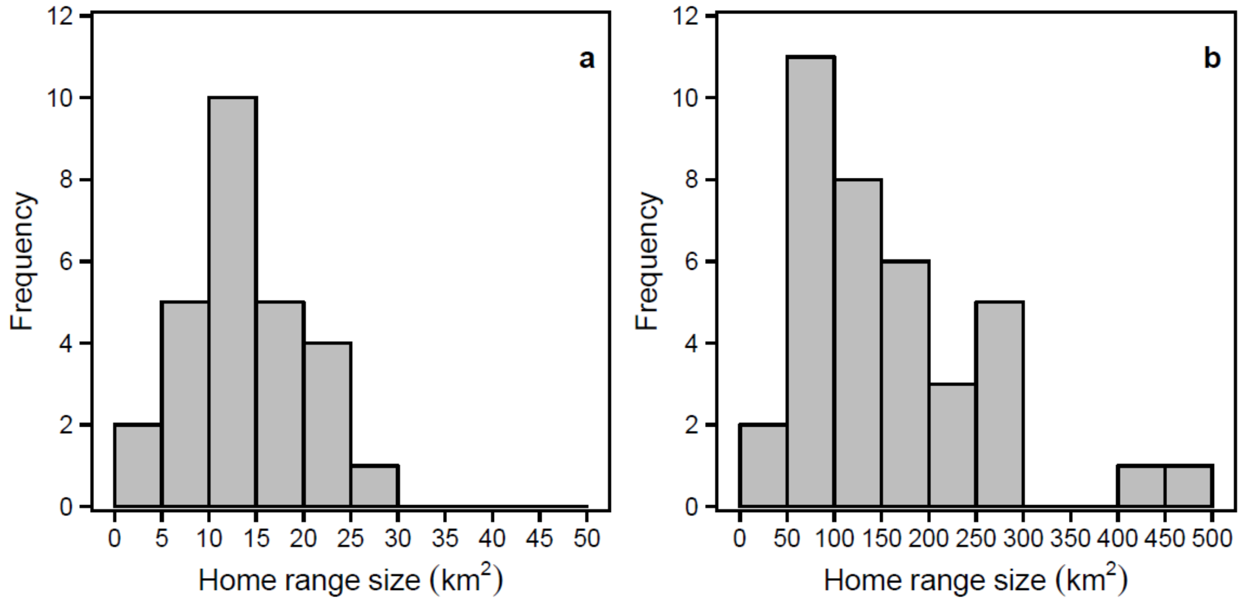

Figure 2.1. Binned frequency distribution of the home range sizes of (a) resident and (b) transient coyotes in Prince Edward County, Ontario, 2010–2013. Note that the home range sizes of residents that shared the same territory were averaged to avoid pseudo-replication.

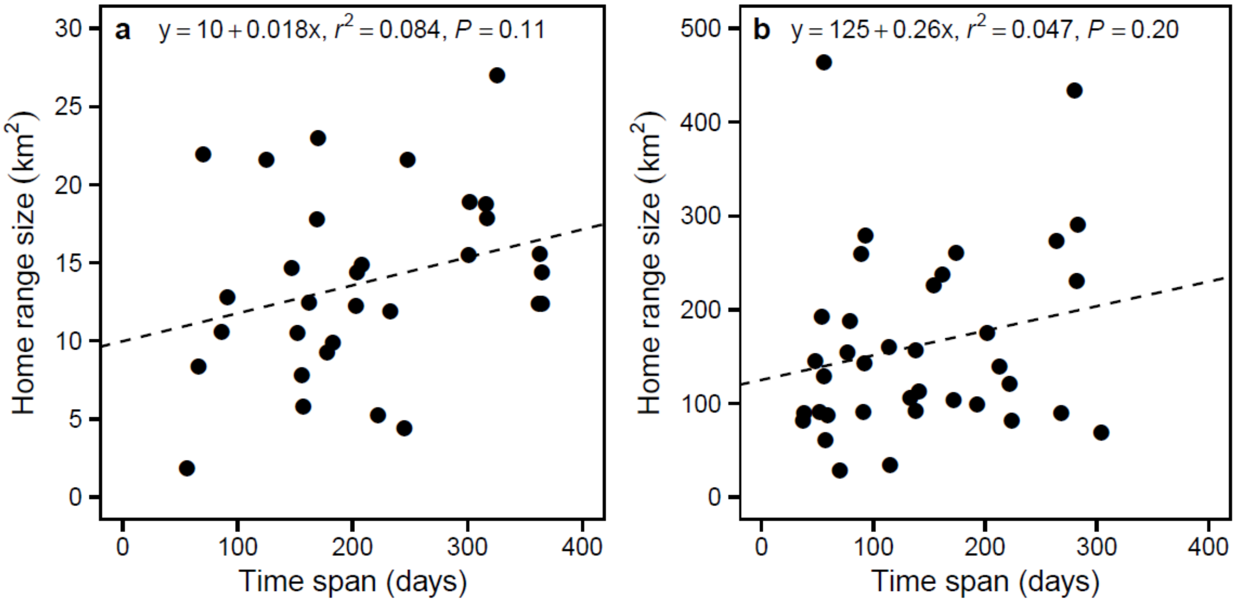

Figure 2.2. Scatterplot of home range size versus time span with linear regression fitted to the data for (a) resident and (b) transient coyotes in Prince Edward County, Ontario, 2010–2013.

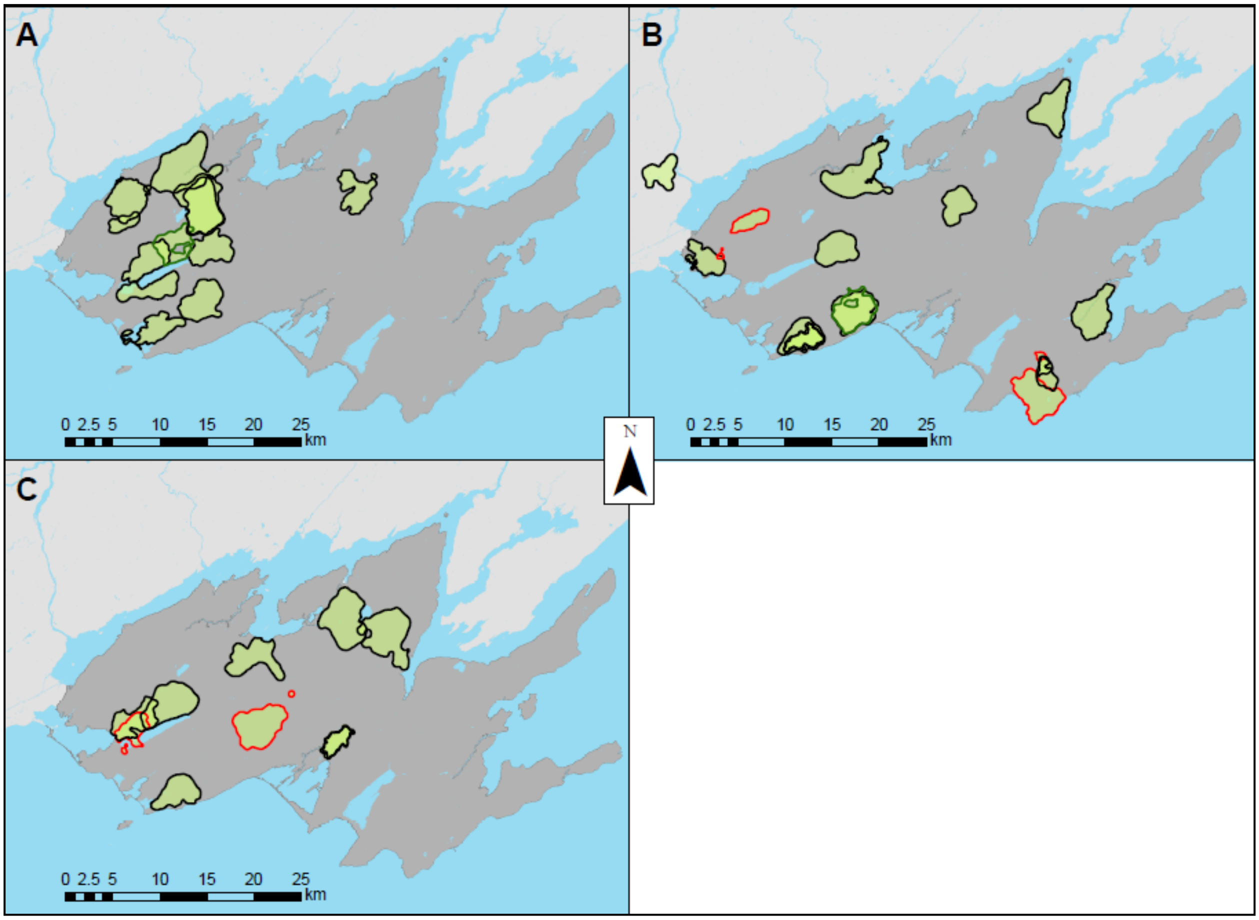

Figure 2.3. Home range contours of resident coyotes in Prince Edward County, Ontario, 2010–2013. Home range contours (95% fixed kernel) are shown in Lambert conformal conic projection. Panels: (A) individuals radio-collared during 2010–2011; (B) individuals radio-collared during 2011–2012; (C) individuals radio-collared during 2012–2013. Contour colours: black = continuous and contains no lacuna; red = discontinuous and contains no lacuna; green = continuous and contains a lacuna.

Transient space-use

I generated 37 transient home ranges based on variable numbers of locations (range = 286–2330). Mean (± SD) home range size of transients was 162.0 ± 99.6 km^2 (range = 28.7–464.0 km^2) and the most commonly observed binned home range size was 50–100 km^2 (Figure 2.1b). Variation in home range size of transients was independent of time span ($r^2 = 0.047$, $P = 0.20$; Figure 2.2b), which ranged from 37 to 304 days. Details of transient home ranges are provided in Appendix D. Transients exhibited considerable variation in space-use, whereby some exhibited relatively localized movements and others exhibited relatively nomadic movements (Figure 2.4). Therefore, some transients exhibited movements over relatively small areas spanning relatively few resident territories and other transients exhibited movements over relatively large areas spanning relatively many resident territories (Figure 2.5). Multiple transients alternately exhibited relatively localized movements and relatively nomadic movements for variable periods. Most transients (70%) restricted their movements to within the study area, but some transients (30%) made movements out of the study area; eight individuals left the study area and returned at least once and three individuals left the study area and did not return.

Discussion

Coyotes in the study population included residents and transients, which exhibited disparate space-use patterns, and they underwent transitions in social status, both because of and despite harvest mortality. As predicted, transients exhibited extensive space-use relative to residents, potentially encountering vacant territories and/or breeding positions, and some transients became residents, potentially filling vacant territories and/or breeding positions. Accordingly, the study

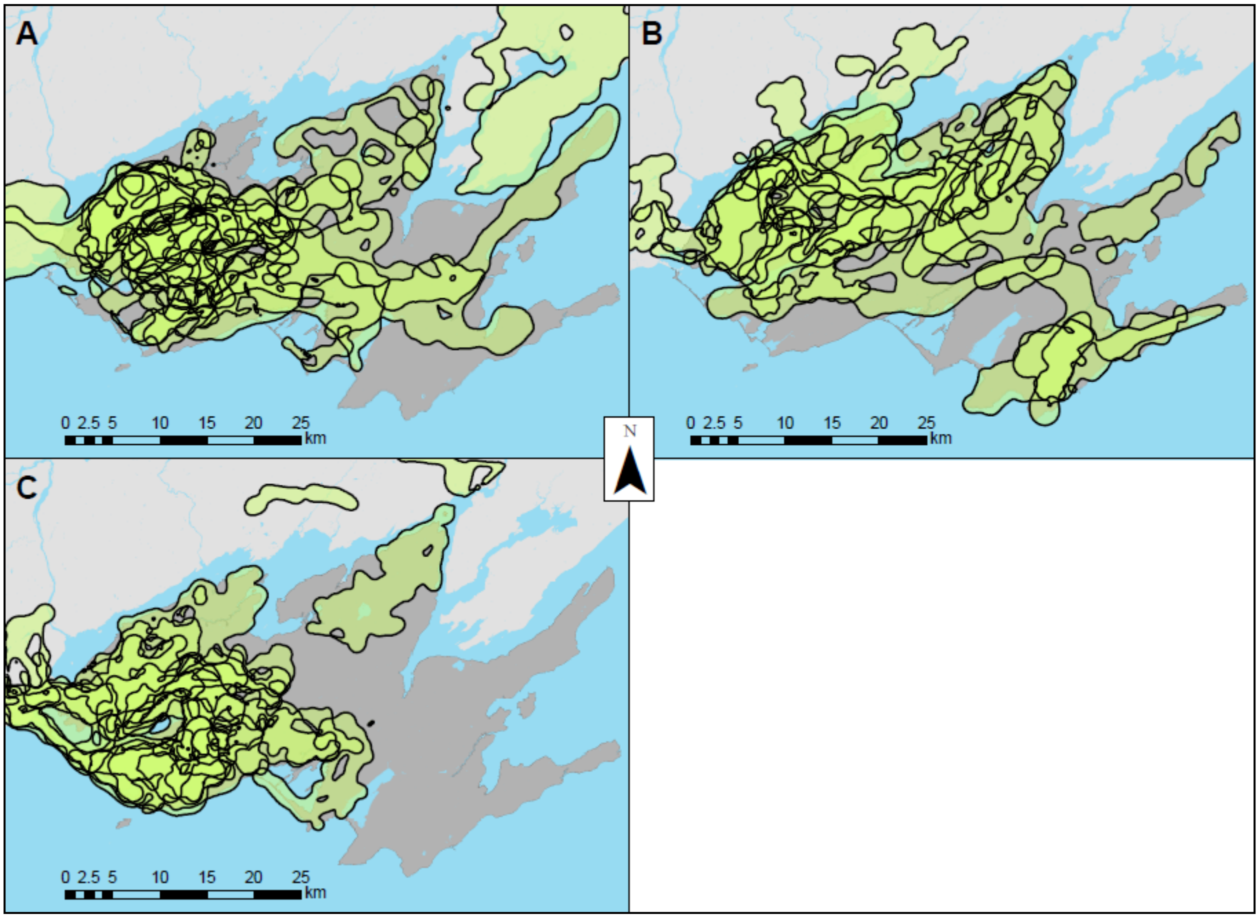

Figure 2.4. Home range contours of transient coyotes in Prince Edward County, Ontario, 2010–2013. Home range contours (99% Brownian bridge movement model) are shown in Lambert conformal conic projection. Panels: (A) individuals radio-collared during 2010–2011; (B) individuals radio-collared during 2011–2012; (C) individuals radio-collared during 2012–2013. Note that many contours are discontinuous and/or contain ≥ 1 lacuna and some contours extend beyond the area displayed.

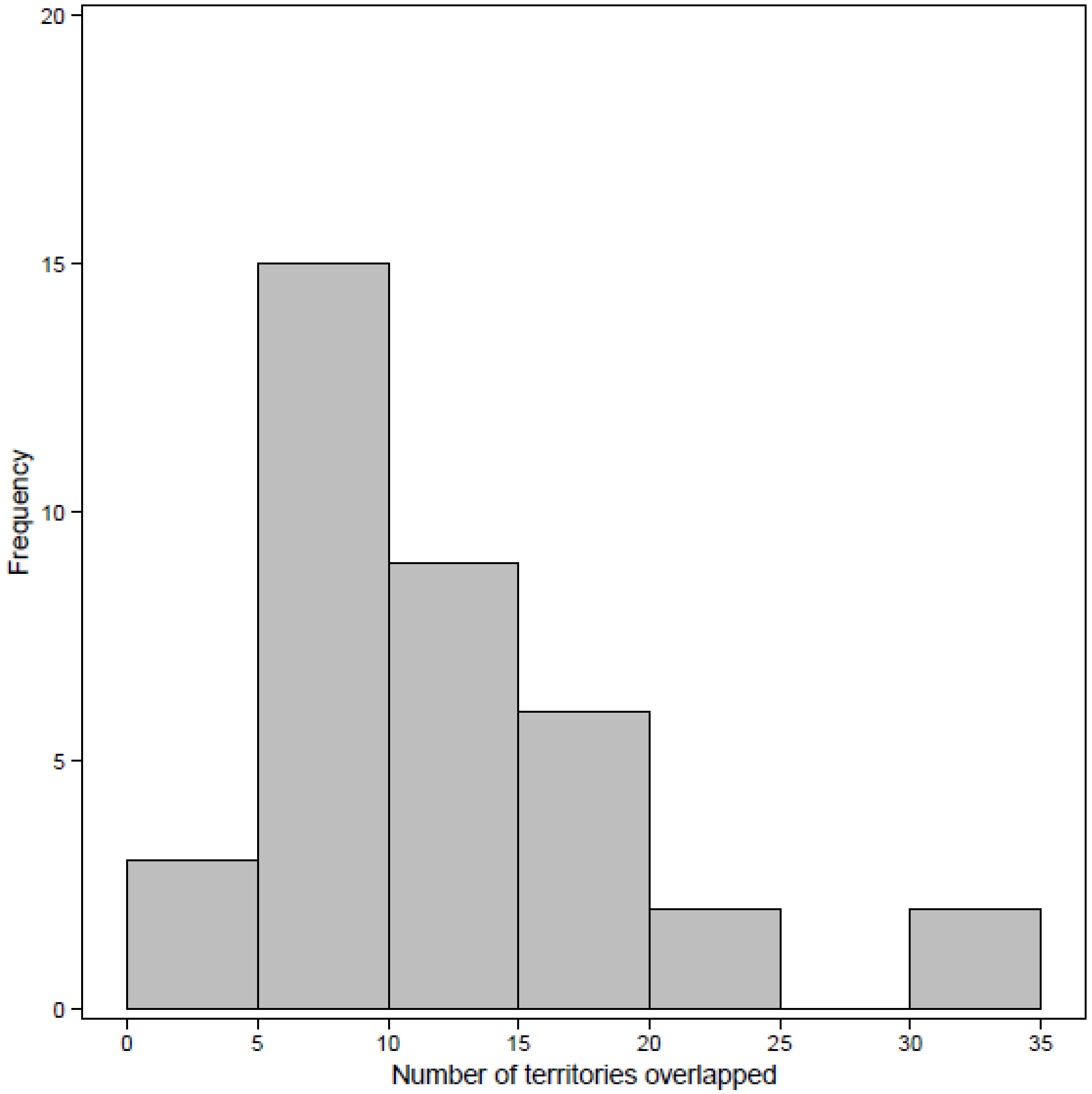

Figure 2.5. Binned frequency distribution of the number of territories overlapped by transients. The number of territories overlapped by each transient was estimated by dividing the home range size of each transient by the mean home range size of residents.

population demonstrated the potential to compensate for harvest mortality via source-sink dynamics and/or buffering reproductive capacity. Hereafter, I discuss my findings and explore them in the context of resilience to harvest for coyote populations. Furthermore, I discuss the relevant implications of my findings.

The transitions in social status of radio-collared coyotes warrant further elaboration. Residents that became transients either dispersed from their natal territory (younger individuals) or vacated their territory (older individuals), the latter of which might have involved territory abandonment caused by various factors (Bowen 1982; Gese 1998; Way & Timm 2008) or territory displacement by another individual (Andelt 1985; Gese 1998; Way 2010). Transients that became residents implicitly settled in either a vacant territory or an occupied territory, the latter of which might have involved filling a vacant breeding position (Hinton et al. 2015a) or assuming an occupied breeding position (Andelt 1985), but the first scenario seems most probable. Note that settling in a vacant territory might have also involved filling a vacant breeding position by acquiring a mate (Gese 2005; Way 2007b). Details of transitions in social status of coyotes provide context for interpreting their social status dynamics, but are challenging to ascertain, requiring long-term monitoring of many individuals.

Consider source-sink dynamics within a hypothetical harvested coyote population, wherein spatial variability in harvest mortality might promote density-dependent responses in emigration and immigration with respect to territories (Conner et al. 2008). Specifically, an individual might disperse from its natal territory (i.e., emigration) located in an area of low harvest mortality, because of limited resource availability and breeding opportunity (Gese et al. 1996), and subsequently that individual might settle in a vacant territory (i.e., immigration) located in an area of high harvest mortality, because of greater resource availability and breeding opportunity (Gese et al. 1996). Harvest intensity was spatially heterogeneous across the study area based on the spatial distribution of harvest mortalities of radio-collared coyotes (see Chapter 3). It seems reasonable to assume that spatial variability in harvest mortality reflected spatial variability in harvest intensity. Personal communication with hunting groups in the study area and knowledge of their hunting activities support the notion that harvest intensity was spatially heterogeneous across the study area. The study population demonstrated the potential for source-sink dynamics in response to spatial variability in harvest intensity considering that many transients overlapped multiple territories (Figure 2.5) and some consequently settled. Plausibly, density-dependent dispersal of coyotes from areas of low harvest intensity (i.e., sources; high coyote density) to areas of high harvest intensity (i.e., sinks; low coyote density) might occur (Knowlton 1972; Davison 1980; Gese 2005), because areas of high harvest intensity presumably have more vacant territories and breeding positions than areas of low harvest intensity, thus transients are presumably more likely to settle in the former than in the latter (Gese 2001, 2005). Accordingly, spatial variability in settlement rates might be indicative of source-sink dynamics operating in the study population in response to spatial variability in harvest intensity. Regrettably, I did not obtain sufficient data (i.e., I recorded only 10 settlements) to investigate spatial variability in settlement rates; limited deployment time spans (< 1 year) might have precluded observation of additional settlements and/or low survival of transients (see Chapter 3) might have precluded occurrence of additional settlements. For future research, improvements in radio-collar efficiency should facilitate longer deployment time spans and thus potentially observation of additional settlements, but long-term study of many individuals may be required to investigate spatial variability in settlement rates in the context of source-sink dynamics.

Dispersing individuals may fill vacant territories in areas of high harvest intensity and thereby stabilize local coyote abundance over time (Knowlton 1972; Gese 2005). However, overall coyote abundance may decrease over time unless non-dispersing individuals experience reduced natural mortality (i.e., compensatory mortality) and/or produce additional offspring (i.e., compensatory natality) in areas of low harvest intensity, because dispersal from sources to sinks has the potential to deplete sources over time (Gundersen et al. 2001), without some density-dependent response to reduced competition for resources. Clearly, the long-term operation of source-sink dynamics in harvested coyote populations requires the maintenance of reproductive capacity. Accordingly, demonstrating that transients exhibit reproductive behavior following settlement is important for understanding the compensatory potential of harvested coyote populations. Notably, during the study, two transients that settled subsequently exhibited evidence of reproductive behavior. Specifically, an adult male transient that settled apparently subsequently paired with an estrus female (based on snow-tracking observations during the breeding period) and an adult female transient (previously breeding resident) that settled apparently subsequently denned (based on spike in missed fixes during the denning period). Thus, some transients probably filled vacant breeding positions during the study, thereby buffering the reproductive capacity of the study population. However, the low number of settlements recorded during the study might imply that some non-breeding residents (i.e., pack associates) filled vacant breeding positions within territories (Gese et al. 1996; Patterson & Messier 2001). Molecular genetics techniques in combination with radio-telemetry may facilitate investigation of breeder replacement in harvested coyote populations. Regardless, observations of transients filling vacant breeding positions (Gese et al. 1989; Gese 2005) and simulations of an individual-based model of coyote populations (Pitt et al. 2003) suggest that transients play an important role in buffering the reproductive capacity of harvested coyote populations.

Furthermore, transients may buffer residents (including breeders) against harvest mortality. Therefore, investigating the relative survival of residents and transients in harvested coyote populations may further inform on their resilience to harvest.

Breeding positions are held exclusively by residents and limited to one individual of each sex per territory (Messier & Barrette 1982; Gese 2001); indeed, I noted evidence of breeding for resident females only, except for one transient female with mange that was probably a resident at the time of breeding/whelping. Thus, the breeding capacity of coyote populations is constrained by territory density (Knowlton et al. 1999). The observed configuration of resident home ranges (Figure 2.3) suggests that the study area was probably saturated with territories, implying that the number of breeding positions was probably maximized based on available resources. Territory density in coyote populations may affect the capacity for source-sink dynamics in response to harvest. Specifically, low territory density would be expected to reduce settlement opportunities for transients, because there would be relatively few vacant territories and/or breeding positions, whereas high territory density would be expected to increase settlement opportunities for transients, because there would be relatively many vacant territories and/or breeding positions. Thus, the capacity for source-sink dynamics in response to harvest may be positively related to territory density (negatively related to resident home range size) in coyote populations.

Logically, settlement probability may be positively related to degree of nomadism, because greater space-use may result in greater probability of encountering a vacant territory and/or breeding position; however, mortality risk may be positively related to degree of nomadism, because greater space-use may result in greater probability of encountering harvest threats (see Chapter 3). Therefore, as an ad hoc test of this hypothesis, I contrasted the space-use estimates of transients that settled and those that did not. Four of five transients that settled had a home range size above the median home range size of transients. Similarly, four of five transients that settled had a space-use rate (i.e., home range size divided by time span) above the median space-use rate of transients. Thus, although limited, my data suggest that settlement probability may be positively related to degree of nomadism, but further investigation is required. Importantly, any relationship between settlement probability and degree of nomadism must be considered in the context of spatial variability in harvest intensity.

I have used the term “home range” to describe space-use areas with specific probability of use for both residents and transients. Maintaining a true home range requires some degree of site fidelity (Powell 2000). Clearly, residents have home ranges, but transients may or may not have home ranges. Transients that are particularly nomadic obviously do not have home ranges, but those that restrict their space-use to any specific area overlapping several territories could be construed as displaying home range behavior. Notably, multiple transients exhibited periods of temporary localized space-use similar to that of residents; these periods presumably corresponded with failed settlement attempts or temporary use of biding areas (Hinton et al. 2012, 2015a; Morin & Kelly 2017) where localized resources might have been exploited.

I confidently determined the social status of most radio-collared coyotes, but some individuals exhibited somewhat ambiguous movements during specific periods, thus I might have made some misclassifications. Specifically, transients exhibiting localized movements in biding areas might have been misclassified as residents and residents exhibiting nomadic movements on prolonged excursions might have been misclassified as transients. Accordingly, some supposed transitions in social status might have been erroneous. Furthermore, some actual transitions in social status might have been missed because of insufficient data. Regardless, I clearly demonstrated social status dynamics in the study population (Table 2.1).

I employed modern techniques for quantifying coyote space-use, but some biases were still evident. Specifically, space-use was overestimated for some residents because their home range contour overlapped ≥ 1 waterbody, but such bias was offset by clipping their home range contour with respect to a waterbody layer. Similarly, space-use was overestimated for some transients because their home range contour overlapped ≥ 1 waterbody, but the degree of such bias was uncertain because their movement paths might have crossed ice-covered waterbodies. Conversely, space-use was underestimated for some transients because their movement paths were not estimated between locations > 400 minutes apart. Regardless, the biases in home range size were low or negligible in comparison to the variability in home range size observed across individuals for both residents and transients (Figure 2.1).

The island-like nature of PEC probably constrains emigration and immigration of coyotes throughout much of the year, because water deflects such movements through the northwest region of PEC where only a narrow canal separates it from the mainland. However, winter ice cover facilitates movement across the Bay of Quinte. Notably, during the study, one transient left PEC and settled on the mainland and another transient left PEC and did not return there during approximately one year of subsequent monitoring. Thus, emigration occurred, but immigration presumably also occurred. However, the multi-lane divided highway (Hwy 401) that runs approximately west-to-east just north of PEC was a barrier to movement (although three radio-collared coyotes were killed north of Hwy 401) and thus probably constrains emigration and immigration of coyotes year-round. Plausibly, the island-like nature of PEC and nearby presence of a high-traffic road effectively limits potential compensatory immigration into PEC, but promotes settlement within PEC. Accordingly, the study population's apparent resilience to harvest probably derives from local intra-population dynamics rather than regional interpopulation dynamics. Compensatory immigration may be more likely for mainland coyote populations than island coyote populations (e.g., PEC and Manitoulin Island), because emigration and immigration of coyotes is presumably relatively unconstrained on the mainland, except where roads present barriers to movement.

The efficacy of liberal harvest for reducing coyote abundance and livestock depredation needs to be addressed. Liberal harvest of coyotes is essentially a means of uncoordinated and indiscriminate lethal control. Based on the space-use patterns of coyotes, it is apparent that uncoordinated and indiscriminate lethal control of coyotes is unlikely to be effective in reducing coyote abundance or livestock depredation (Windberg & Knowlton 1988; Knowlton et al. 1999; Conner et al. 2008). The disparate space-use patterns of residents and transients demonstrate the potential for transients to fill vacant territories following removal of residents (Knowlton 1972; Gese 2005) and the potential for transients to comprise a substantial proportion of removals relative to residents (Gese et al. 1989; Windberg & Knowlton 1990). Liberal harvest may temporarily reduce coyote abundance locally, but repopulation via influx of transients is probable (Knowlton 1972; Gese 2005), thus necessitating continual removal of coyotes, which is an inefficient strategy. Transients may depredate livestock, but they are less likely than residents to be responsible for repeated depredations on specific farms (Sacks et al. 1999a; Blejwas et al. 2002, 2006), thus liberal harvest likely involves removal of many non-offending coyotes, which has been shown to be ineffective at reducing livestock depredation (Conner et al. 1998; Sacks et al. 1999a). For example, a juvenile coyote that dispersed from its natal territory exhibited highly nomadic movements over an area of 464 km^2 during a 56-day period, covering much of the study area, until it was killed near a sheep farm as part of predator control approximately 21 km east of its natal territory. Given that individual’s recorded movements, it could not have been responsible for repeated depredations on that sheep farm. This type of scenario was seemingly common in PEC during the study. Management strategies that seek to reduce conflicts between coyotes and livestock should consider non-lethal alternatives and/or targeted lethal control, which may prove effective (Knowlton et al. 1999).

In conclusion, the compensatory potential of harvested animal populations may be explained partly by animal movements. This is particularly true for predators that exhibit variable space-use with respect to social status and a social hierarchy with respect to breeding, such as coyotes, which are commonly subject to lethal control efforts of questionable efficacy. Therefore, wildlife managers should consider the space-use patterns of such predators when assessing the efficacy of management practices.

Chapter 3

Survival and cause-specific mortality of eastern coyotes from a harvested population in southeastern Ontario

Abstract

Individual variation in survival and vulnerability to harvest is an important factor to consider when investigating the compensatory potential of harvested animal populations. Coyotes are liberally harvested across much of their range, but most coyote populations demonstrate considerable resilience to harvest, suggesting that they exhibit some mechanisms of compensation. The social system of the coyote includes residents and transients, which have different roles in coyote populations with respect to reproduction and dispersal. Residents and transients exhibit disparate space-use patterns, which may expose them to different mortality risks. Individual variation in survival and vulnerability to harvest is likely important with respect to the resilience of harvested coyote populations, but better understanding is sought. I investigated the survival and cause-specific mortality of eastern coyotes from a harvested population in southeastern Ontario. I hypothesized that residents and transients in the study population would experience different cumulative mortality risks due to their disparate space-use patterns; specifically, I hypothesized that transients would encounter more harvest-related threats on average than residents due to their more extensive movements. I captured and radio-collared 147 coyotes. The study cohort included individuals of each sex, age class, and social status combination. Sex and age class did not have any significant effects on the annual or seasonal survival of radio-collared coyotes; however, social status had a marginally significant effect on

the survival of radio-collared coyotes for the period November–April, whereby mortality risk was 65% higher for transients than residents for that period, and correspondingly, the survival rate was higher for residents (0.620) than transients (0.414) for that period. Mortality of radio-collared coyotes was predominantly attributed to harvest (67.6%), but also roadkill (13.5%) and other causes (18.9%). Notably, social status did not have a significant effect on the harvest mortality of radio-collared coyotes for the period November–April, although the harvest mortality rate was seemingly higher for transients than residents for that period. Indeed, residents exhibited greater survival than transients, probably partly because of the benefits of holding a territory, and transients seemingly exhibited greater vulnerability to harvest than residents, probably partly because their movements exposed them to greater cumulative mortality risks over time. Accordingly, harvest mortality disproportionately impacted the non-reproductive segment of the study population and thus may have failed to substantially limit reproduction, and thus recruitment. My findings corroborate research that challenges the efficacy of liberal harvest for reducing coyote abundance and livestock depredation.

Introduction

The ability of animal populations to compensate for harvest mortality (e.g., hunting and trapping) depends on various intrinsic and extrinsic factors (see Sandercock et al. 2011). Individual variation in survival and vulnerability to harvest is an important factor to consider when investigating the compensatory potential of harvested animal populations. This is partly because individuals belonging to different sexes or age classes, or even those of different social status, can have different roles in animal populations with respect to important biological processes such as reproduction and dispersal. Important biological processes such as reproduction and dispersal may be differentially impacted in harvested animal populations depending on the nature of individual variation in survival and vulnerability to harvest. Individual variation in survival and vulnerability to harvest has been observed for various wildlife species, including predators (e.g., bears: Koehler & Pierce 2005; bobcats: Blankenship et al. 2006; cougars: Wolfe et al. 2015; wolves: Murray et al. 2010). Therefore, gaining better understanding of individual variation in survival and vulnerability to harvest of predators is important for informing management strategies.

Compensatory mortality can occur in harvested animal populations through density dependence, whereby harvest mortality decreases population density, which results in reduced competition for resources (e.g., food and habitat), and thereby decreases natural mortality (Boyce et al. 1999). The timing of harvest is an important factor to consider when investigating the potential for compensatory mortality to occur in harvested animal populations (Boyce et al. 1999; Kokko 2001). If harvest mortality and natural mortality are temporally non-overlapping then harvest mortality can be partially or completely compensatory to natural mortality, but if harvest mortality and natural mortality are temporally overlapping then harvest mortality can be partially or completely additive to natural mortality (Kokko 2001). Density dependence must occur after harvest for compensation to be realized (Boyce et al. 1999). Complete compensation for harvest mortality is unachievable above certain thresholds, but partial compensation for harvest mortality has been demonstrated for various wildlife species (e.g., willow ptarmigan: Sandercock et al. 2011), including predators such as wolves (Murray et al. 2010; but see Sparkman et al. 2011) and cougars (Wolfe et al. 2015; but see Cooley et al. 2009).

Coyotes (*Canis latrans*) are liberally harvested across much of their range, but most coyote populations demonstrate considerable resilience to harvest, suggesting that they exhibit some mechanisms of compensation (Knowlton et al. 1999). However, some stakeholders remain convinced that liberal harvest is effective for reducing coyote abundance (e.g., Bartel & Brunson 2003). The onus remains on wildlife managers to better explain how coyote abundance can remain relatively stable across years despite consistently liberal harvest regimes.

The social system of the coyote includes territorial individuals and non-territorial individuals, referred to as residents and transients, respectively (Andelt 1985; Gese et al. 1988; Kamler & Gipson 2000). Residents and transients have different roles in coyote populations with respect to reproduction and dispersal. The reproductive segment of coyote populations generally includes residents but not transients (Messier & Barrette 1982; Knowlton et al. 1985; Gese 2001) and the dispersing segment of coyote populations implicitly includes transients but not residents. Residents and transients exhibit disparate space-use patterns (Gese et al. 1988, 1989; Windberg & Knowlton 1988), which may expose them to different mortality risks. Therefore, residents and transients may exhibit different survival and cause-specific mortality rates. Indeed, survival of coyotes has been shown to vary with respect to social status, whereby survival of residents was greater than that of transients (Andelt 1985; Gese et al. 1989; Harrison 1992a; Kamler & Gipson 2000). Also, survival of coyotes has been shown to vary with respect to age class, whereby survival of adults was greater than that of juveniles (Windberg et al. 1985; Gese et al. 1989; Crête et al. 2001; Van Deelen & Gosselink 2006); however, the relative survival of adults and juveniles may depend on the level of exploitation, given that moderately to heavily exploited coyote populations typically exhibit lower adult survival rates and higher juvenile survival rates than unexploited or lightly exploited coyote populations (Knowlton et al. 1999; Jackson 2014).

Notably, survival of coyotes has been shown not to vary with respect to sex (Windberg et al. 1985; Gese et al. 1989; Crête et al. 2001; Van Deelen & Gosselink 2006; but see Holzman et al. 1992). Differences in survival and cause-specific mortality of residents and transients, or that of adults and juveniles, may have implications for mechanisms of compensation related to reproduction and dispersal in harvested coyote populations. Individual variation in survival and vulnerability to harvest is likely important with respect to the resilience of harvested coyote populations, but better understanding is sought.

Harvest intensity varies temporally for coyote populations in many areas, despite year-round hunting and trapping seasons. This is partly because of seasonal differences in hunting effort and trapping effort associated with landscape conditions and pelt quality, respectively. Hunting effort is typically highest during the cold season when vegetative cover is limited (Van Deelen & Gosselink 2006) and snow cover facilitates tracking with hounds. Trapping effort is typically highest during the cold season when coyotes have prime pelts (Voigt & Berg 1987). Survival and cause-specific mortality of coyotes has been shown to vary seasonally with respect to harvest intensity (Chamberlain & Leopold 2001; Crête et al. 2001; Van Deelen & Gosselink 2006; Schrecengost et al. 2009). Temporal variation in survival and cause-specific mortality of coyotes may impact the resilience of harvested coyote populations, particularly if harvest mortality overlaps natural mortality or the breeding period, because such would limit their compensatory potential.

Considerable research exists on the survival and cause-specific mortality of western coyotes, but comparatively limited research exists on that of eastern coyotes, especially in agricultural landscapes where livestock depredation is a concern (see Mastro et al. 2011). Geographic differences in the density of domestic stock and fowl might be associated with differences in harvest pressure for coyotes (Harrison 1992b), suggesting that the survival and cause-specific mortality of eastern coyotes may differ from that of western coyotes. Specifically, lower density of domestic stock and fowl might be associated with lower harvest pressure for eastern coyotes, which might be associated with lower harvest mortality rates and thus higher survival rates for eastern coyotes. Also, geographic differences in prey density and landscape conditions likely influence the survival and cause-specific mortality of coyotes across their range (see Jackson 2014). Lower prey density might be associated with higher natural mortality rates and thus lower survival rates for eastern coyotes. Moreover, eastern coyotes differ from western coyotes in that they have partial wolf ancestry due to hybridization (Kays et al. 2010; Wheeldon et al. 2013; Monzón et al. 2014). Partial wolf ancestry might be associated with higher mortality risk and thus lower survival for eastern coyotes, given that wolves have larger home ranges than coyotes, and thus they are potentially exposed to greater hazards (e.g., hunters, trappers, roads) than them. It is not clear how partial wolf ancestry might influence the survival and cause-specific mortality of eastern coyotes. Despite limited data on the survival and cause-specific mortality of eastern coyotes, human-caused mortality is thought to be extremely important (Gompper 2002). Further investigation of the survival and cause-specific mortality of eastern coyotes is needed to provide wildlife managers with essential information (Mastro et al. 2011).

I investigated the survival and cause-specific mortality of eastern coyotes from a harvested population in southeastern Ontario. My objective was to gain better understanding of how individual variation in survival and cause-specific mortality might influence resilience to harvest for eastern coyote populations. I hypothesized that residents and transients in the study population would experience different cumulative mortality risks due to their disparate space-use patterns; specifically, I hypothesized that transients would encounter more harvest-related threats on average than residents due to their more extensive movements. I predicted (1) that the survival rate would be higher for residents than transients, (2) that the harvest mortality rate would be higher for transients than residents, and (3) based on the assumption that the study population was moderately to heavily exploited, that the survival rate would be similar between sexes and across age classes. Also, I hypothesized that survival of coyotes in the study population would vary seasonally due to temporal differences in harvest intensity. I predicted that harvest mortality would be higher, and that survival would be lower, during the cold season than the warm season. Additionally, I sought to determine if the study population exhibited compensatory mortality in response to harvest. I hypothesized that high harvest mortality of coyotes would be compensated for by low natural mortality of coyotes. I predicted that survival would be consistent across years, because increases or decreases in harvest mortality would lead to compensatory decreases or increases in natural mortality, respectively. I discuss the implications of my findings concerning the resilience of harvested coyote populations and the efficacy of liberal harvest for reducing coyote abundance and livestock depredation.

Methods

Study area

I conducted research on coyotes during 2010–2013 in Prince Edward County (PEC), which is located in southeastern Ontario on a large irregular headland in the northeastern region of Lake Ontario (see Chapter 1). The landscape was predominantly agricultural and rural. Coyote hunting and trapping seasons were open all year. Based on deer hunter questionnaire data, the relative abundance of coyotes in the study area was relatively stable over the years of the study (see Chapter 1).

Capture, handling, and radio-collaring

I captured coyotes using padded foot-hold traps and physically restrained them with a noose pole. Generally, upon capture, I chemically immobilized coyotes with an intramuscular injection of an agonist drug mixture (see Chapter 2). If applicable, prior to release, I reversed coyotes with an intramuscular injection of an antagonist drug (see Chapter 2). Alternatively, I physically immobilized coyotes by hobbling and muzzling them for the duration of handling. I weighed coyotes and recorded their body mass. I sexed coyotes and noted evidence of breeding for females. I aged coyotes based on tooth eruption and wear (Gier 1968) and classified them as juvenile (< 12 months old), yearling (12–24 months old), or adult (> 24 months old). I sampled blood and/or hair from coyotes for genetic profiling. I marked coyotes with uniquely numbered metal ear tags. I fitted coyotes with either Global Positioning System (GPS) radio-collars or very high frequency (VHF) radio-collars; GPS radio-collars were programmed with variable fix schedules (see Chapter 2). I deployed several types of mortality-sensitive GPS radio-collars and VHF radio-collars on coyotes (see Chapter 2); mortality sensors were set to trigger after 12 hours of motionlessness. Radio-collars generally weighed < 5% of body mass, except for some rapidly growing juveniles. If applicable, radio-collars were fitted with compressible foam and sized to accommodate neck growth. The capture, handling, and radio-collaring of coyotes was approved by the Trent University Animal Care Committee (protocol no. 10016) and the Ontario Ministry of Natural Resources Wildlife Animal Care Committee (protocol nos. 10-219 through 12-219).

Telemetry data

I conducted ground VHF telemetry approximately weekly to locate and monitor radio-collared coyotes. I determined the presence/absence of signals using a vehicle-mounted omnidirectional antenna and receiver; I determined the direction of signals using a hand-held 3-element Yagi antenna and receiver. I located individuals to within a specific tract of land and recorded their estimated location as a compass bearing from a reference location (e.g., road intersection, civic address); however, I did not triangulate their location. I monitored individuals based on the pulse rate of signals and recorded their vital status (i.e., alive or dead). Ontario Ministry of Natural Resources staff conducted aerial VHF telemetry when necessary to locate and monitor missing radio-collared coyotes. I plotted VHF telemetry locations in MapSource (version 6; Garmin Ltd., Schaffhausen, Switzerland). I remotely downloaded location data from applicable GPS radio-collars (see Chapter 2). I physically downloaded location data from GPS radio-collars upon retrieval after drop-off or mortality. I managed GPS radio-collar location data in Telemetry Data System (version 3; Kushneriuk et al. 2011). I rarefied GPS radio-collar locations to constant intervals (see Chapter 2). Details of the protocols used for screening/censoring GPS radio-collar location data are provided elsewhere (see Chapter 2).

Social status assessment

I visualized location data (GPS radio-collar locations and/or VHF telemetry locations) in ArcMap (version 10.2; Esri, Redlands, California, USA) and thoroughly assessed the space-use patterns of radio-collared coyotes. Details of further space-use-based techniques employed for social status assessment are provided elsewhere (see Chapter 2). I confidently determined the social status of most individuals, classifying them as either resident (exhibited localized space-use with fidelity to a specific area) or transient (exhibited nomadic space-use with no fidelity to any specific area). Ambiguous space-use patterns or insufficient data precluded determination of the social status of some individuals; however, I inferred the social status of some individuals based on pedigree information (see Chapter 4), whereby some individuals determined to be in their natal territory were inferred to be residents. Monitoring gaps precluded determination of the social status of some individuals during specific periods. I recorded transitions in social status of individuals that exhibited both distinct space-use patterns, which were classified as resident and transient during discrete periods. I considered localized space-use within an apparent territory becoming nomadic to be indicative of transition from resident to transient and nomadic space-use becoming localized within an apparent territory to be indicative of transition from transient to resident. I did not consider brief extra-territorial movements by residents or intermittent localized movements by transients to be indicative of transitions in social status.

Carcass necropsy

I retrieved carcasses of radio-collared coyotes after detecting mortality signals via VHF telemetry or receiving reports of dead coyotes. Generally, I determined the mortality date for individuals based on telemetry data, mortality site evidence, and/or reported information. Alternatively, I estimated the mortality date for individuals by taking the midpoint between the last date that they were recorded alive and the first date that they were recorded dead (Fieberg & DelGiudice 2008). I stored carcasses in freezers until necropsy. I performed necropsies on carcasses in the laboratory; decomposition precluded some aspects of necropsy for several carcasses. I examined carcasses for traumatic injuries and/or evidence of poor health (e.g., emaciation, mange) and (if possible) determined cause of death, with consideration given to mortality site evidence and/or reported information. I weighed carcasses and recorded their body mass. I sexed carcasses and noted evidence of breeding for females. I aged carcasses based on tooth eruption and wear (Gier 1968) and classified them as juvenile (< 12 months old), yearling (12–24 months old), or adult (> 24 months old). Moreover, I extracted a lower canine tooth from each carcass and submitted teeth to Matson's Laboratory (Manhattan, Montana, USA) for aging by the cementum annuli technique (Linhart & Knowlton 1967). I sampled tissue from carcasses for genetic profiling.

Datasets for analyses

I defined a 365-day biological year beginning May 1 and ending April 30 that approximately coincided with the biological cycle of the study population. Also, I defined two seasons of similar duration: (1) the warm season spanned May 1–October 31 (184 days) and coincided with warm months when crops were grown and vegetative cover was relatively abundant; and (2) the cold season spanned November 1–April 30 (181 days) and coincided with cold months when crops were harvested and vegetative cover was relatively scarce. The transitions between seasons coincided with the presumed beginning of the dispersal period (warm season to cold season) and the presumed midpoint of the parturition period (cold season to warm season). The study spanned three biological years (2010–2011, 2011–2012, 2012–2013) and thus six seasons (because both seasons occurred three times). I prepared three datasets for survival and cause-specific mortality analyses: (1) annual dataset, which included only adults and yearlings; (2) warm season dataset, which included only adults and yearlings; and (3) cold season dataset, which included adults, yearlings, and juveniles. I excluded juveniles from the annual and warm season datasets because most juveniles were not captured and radio-collared until mid-summer to early-autumn and therefore sample size of juveniles was zero or negligible during part of the biological year and the warm season. Sample sizes of yearlings and adults were non-zero and non-negligible throughout the biological year and the warm season, partly because juveniles and yearlings advanced into the next age class as biological years passed. Therefore, excluding juveniles from the annual and warm season datasets was appropriate, because their time span for assessment was neither complete nor comparable to that of yearlings and adults. I structured the datasets with either an annually or seasonally recurrent time of origin (as defined above) for survival and cause-specific mortality analyses, which allowed for re-entry of individuals that survived the previous year (Fieberg & DelGiudice 2009).

Study cohort design

I used a dynamic study cohort design for survival and cause-specific mortality analyses of radio-collared coyotes. Specifically, new individuals were recruited into the study cohort as individuals already in the study cohort died or were censored for various reasons. Therefore, the study cohort design involved both left-truncation and right-censoring. Individuals were entered into the risk set on the day following capture and censored from the risk set upon emigration from the greater study area, radio-collar drop-off/fall-off, radio-collar failure, or termination of the study. For the annual dataset, individuals that were monitored across biological years were censored from the risk set on the last day of a given biological year, advanced to the next age class (if applicable), and re-entered into the risk set on the first day of the next biological year. For the seasonal datasets, individuals that were monitored in a given season across biological years were censored from the risk set on the last day of that season in a given biological year, advanced to the next age class (if applicable), and re-entered into the risk set on the first day of that season in the next biological year. Individuals that changed social status were censored from the risk set upon transition in social status, re-classified, and re-entered into the risk set.

Survival analyses

I tested for effects of several categorical variables on annual and seasonal survival of radio-collared coyotes using the Anderson-Gill extension to the Cox Proportional Hazards (CPH) regression model (Therneau & Grambsch 2000), which allowed for discontinuous time intervals. The categorical variables tested were biological year, sex, age class, and social status. I coded dichotomous variables for sex (female or male), age class[1] (adult or yearling), and social status (resident or transient); if social status was undetermined, it was coded as missing data. I coded dummy variables for each biological year (1, 2, 3) and each age class[2] (adult, yearling, juvenile) and considered models retaining two-thirds of these dummy variables such that one value was always withheld as the reference value. I modeled survival in a stepwise manner for the annual and seasonal datasets. First, I tested for an effect of biological year on survival, pooling data across other strata, based on the assumption that any effect of biological year on survival would be similar across other strata (initial model). Second, I tested for effects of sex, age class, and social status on survival, including interaction terms and pooling data across biological years (interactive model). Third, I tested for effects of sex, age class, and social status on survival,

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[1] Applicable for annual and warm season datasets only

[2] Applicable for cold season dataset only

excluding interaction terms and pooling data across biological years (additive model). Fourth, I re-tested for an effect of any significant ($P < 0.05$) or marginally significant ($0.05 \leq P < 0.10$) variable on survival, pooling data across other strata (final model). I assessed significance of variables across models based on robust *z*-tests and hazard ratios (exponentiated β coefficients) with 95% confidence intervals; I computed robust standard errors for regression coefficients by clustering observations by individual (Therneau & Grambsch 2000). I tested the proportional hazards assumption for variables across models using the statistical test based on scaled Schoenfeld residuals (Therneau & Grambsch 2000). Additionally, I estimated annual and seasonal survival functions for radio-collared coyotes using the nonparametric Kaplan-Meier estimator modified for staggered entry of individuals (Pollock et al. 1989); note that the cold season survival functions were estimated conditional on survival to the cold season. I performed survival analyses and related plotting in R (version 3.1.2; R Core Team 2014) using the survival package and the ggplot2 package, respectively.

I performed CPH regression model selection using an information-theoretic approach to corroborate the findings from stepwise CPH regression modeling, because of the criticisms of stepwise procedures (e.g., Quinn & Keough 2002) and to quell concerns about data dredging and multiple testing problems. Details of CPH regression model selection are provided elsewhere (Appendix E). I chose to model survival in a stepwise manner due to sample size considerations. Missing data for social status resulted in sample size differences across the categorical variables. Model selection required equal sample sizes across the categorical variables, therefore records with missing data were omitted, which resulted in reduced sample size for sex and age class; stepwise modeling avoided reduced sample size for sex and age class.

Hazard estimation

I estimated annual and seasonal hazard functions for radio-collared coyotes using the nonparametric method based on B-splines from the perspective of generalized linear mixed models implemented in the R package bshazard (Rebora et al. 2014) to illustrate temporal variation in mortality risk. The smoothing parameter and over-dispersion parameter were estimated from the data. I used the default values for the number of knots and other parameters. Data were pooled across biological years for hazard estimation.

Cause-specific mortality analyses

I grouped causes of mortality into categories (harvest, roadkill, and other causes) for analyses and plotting. I estimated annual and seasonal cause-specific mortality rates for radio-collared coyotes using the nonparametric cumulative incidence function (CIF) estimator (Heisey & Patterson 2006); note that the cold season cause-specific mortality rates were estimated conditional on survival to the cold season. Additionally, I tested for an effect of any significant or marginally significant variable from stepwise CPH regression modeling on cause-specific mortality of radio-collared coyotes using a previously described approach (Heisey & Patterson 2006). First, I replicated the applicable dataset within a single data table once for each category of mortality and created an associated stratification variable indicating the category of mortality (Lunn & McNeil 1995). Second, I coded dummy variables representing interactions between a given significant or marginally significant variable and the stratification variable. Third, I ran a stratified CPH regression model using the applicable dataset and including the dummy variables. I performed cause-specific mortality analyses and related plotting in R using the survival package with modified code from Heisey and Patterson (2006) and the ggplot2 package, respectively. Data were pooled across biological years for cause-specific mortality analyses.

Assumptions of analyses

I made the following assumptions for survival and cause-specific mortality analyses (Tsai et al. 1999): (1) individuals comprised a random sample of the study population; (2) survival times were independent across individuals; (3) radio-collars did not impact the survival of individuals; (4) newly radio-collared individuals had the same survival function as previously radio-collared individuals; (5) death times were known exactly for individuals; and (6) censoring was random (i.e., not related to the fate of individuals). I considered these assumptions and determined that they were adequately met. I excluded four individuals from survival and cause-specific mortality analyses because their deaths may have been capture-related or hastened due to capture-related effects. Radio-collar failure might have resulted from damage associated with an undetected mortality event; however, in several cases, an individual was killed after radio-collar failure. Details of several data issues regarding the survival and cause-specific mortality analyses are provided elsewhere (Appendix F).

Results

Radio-collar deployments

I captured and radio-collared 147 coyotes (63 females and 84 males), but also recaptured and fitted new radio-collars to three coyotes, and thus performed 150 radio-collar deployments (86

GPS and 64 VHF). Specifically, I deployed radio-collars on 67 juveniles, 32 yearlings, and 51 adults (Appendix B). Generally, I deployed VHF radio-collars on juveniles and GPS radio-collars on yearlings and adults. However, I deployed GPS radio-collars on some juveniles captured in late summer or early autumn and VHF radio-collars on some yearlings and adults.

Social status dynamics

I observed 63 residents and 27 transients, both of which included individuals of each sex and age class combination. Also, I observed 40 individuals that changed social status, four of which did so twice. I recorded 44 transitions in social status (Appendix C), including 34 transitions from resident to transient and 10 transitions from transient to resident. Accounting for transitions in social status, I observed 103 residents and 67 transients. Social status was undetermined for 17 individuals, and also for several additional individuals during specific periods.

Survival

The study cohort comprised 147 radio-collared coyotes (Table 3.1), including individuals of each sex, age class, and social status combination. I recorded mortalities of 78 radio-collared coyotes, but I excluded four individuals from survival analyses for reasons previously noted (Table 3.1). The remaining 69 radio-collared coyotes were censored for various reasons, typically because of radio-collar drop-off/fall-off or radio-collar failure (Table 3.1). Observation periods for radio-collared coyotes that were included in survival analyses ranged from 2–959 days (median = 184 days); note that observation periods for recaptured individuals were based on cumulative time.

Table 3.1. Fates of radio-collared coyotes in Prince Edward County, Ontario, May 2010–April 2013. Text in parentheses refers to whether individuals were included or excluded with respect to survival analyses.

Fate	Females	Males	Total
Mortality (included)	29	45	74
Mortality (excluded)	1	3	4
Collar failed*	11	7	18
Collar fell off†	6	6	12
Planned collar drop‡	6	12	18
Unplanned collar drop‡	1	1	2
Emigrated	0	2	2
Unknown (lost contact)	1	1	2
Not applicable§	8	7	15
Total	63	84	147

*Mostly GPS radio-collars (premature failure or battery depletion).

†Mostly VHF radio-collars (fitted with compressible foam and deployed on juveniles).

‡Only GPS radio-collars (programmed to drop-off approximately one year after deployment).

§Censored upon termination of the study.

Note that three individuals were recaptured; therefore, the fates for their second deployments are included in the table, but the fates for their first deployments (one planned collar drop and two collar replacements) are not included in the table.

Stepwise CPH regression modeling indicated that the categorical variables generally did not have any significant effects on the annual or seasonal survival of radio-collared coyotes (Appendix G). Biological year was not significant in the initial models for the annual and seasonal datasets (all $P > 0.05$), thus pooling data across biological years for the subsequent CPH regression models was appropriate. Interaction terms were not significant in the interactive model for the annual dataset (all $P > 0.05$). Sex, age class, and social status were not significant in the additive model for the annual dataset (all $P > 0.05$), but social status showed a significant violation of proportionality ($\chi^2 = 10.1$, $P = 0.001$), which was confirmed by crossing survival curves of residents and transients (not shown). The overall annual survival rate (± SE) for radio-collared coyotes (adults and yearlings) was 0.400 ± 0.055 (95% CI = 0.304–0.524) (Figure 3.1a); mortality risk was relatively low during the first half of the biological year and relatively high during the second half of the biological year (Figure 3.1b). Certain interaction terms were significant in the interactive model for the warm season dataset ($P < 0.001$), but were deemed spurious and disregarded (certain stratum combinations had no events; results are provided in Appendix G). Sex, age class, and social status were not significant in the additive model for the warm season dataset (all $P > 0.05$), but social status showed a marginally significant violation of proportionality ($\chi^2 = 3.0$, $P = 0.083$). The overall warm season survival rate (± SE) for radio-collared coyotes (adults and yearlings) was 0.830 ± 0.047 (95% CI = 0.743–0.928) (Figure 3.2a); mortality risk was relatively low during the warm season (Figure 3.2b). Interaction terms were not significant in the interactive model for the cold season dataset (all $P > 0.05$). Sex and age class were not significant in the additive model for the cold season dataset (all $P > 0.05$); however, social status was marginally significant in the additive model for the cold season dataset ($z = 1.9$, $P = 0.064$), although social status showed a marginally significant violation of proportionality ($\chi^2 = 2.8$, $P = 0.093$). The overall cold season survival rate (± SE) for radio-

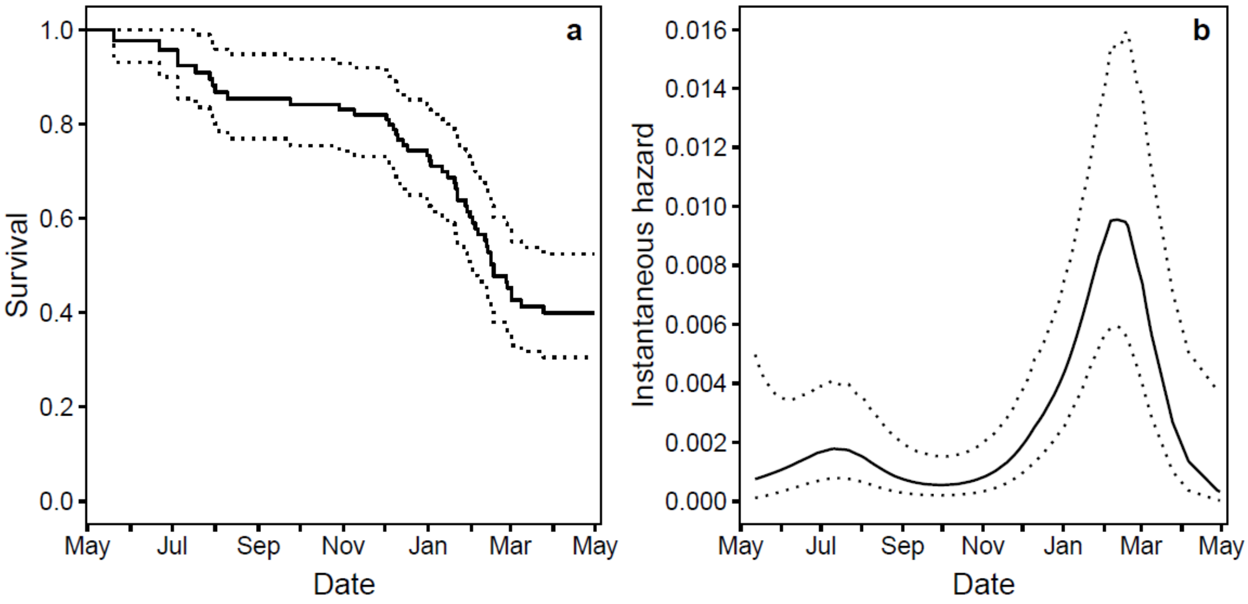

Figure 3.1. Overall annual survival function and related hazard function for radio-collared coyotes in Prince Edward County, Ontario, May 2010–April 2013. Panels: (a) Kaplan-Meier cumulative survival curve; (b) smoothed instantaneous hazard curve. Dotted lines represent 95% confidence intervals. Data were pooled across three biological years. Dataset included adults and yearlings.

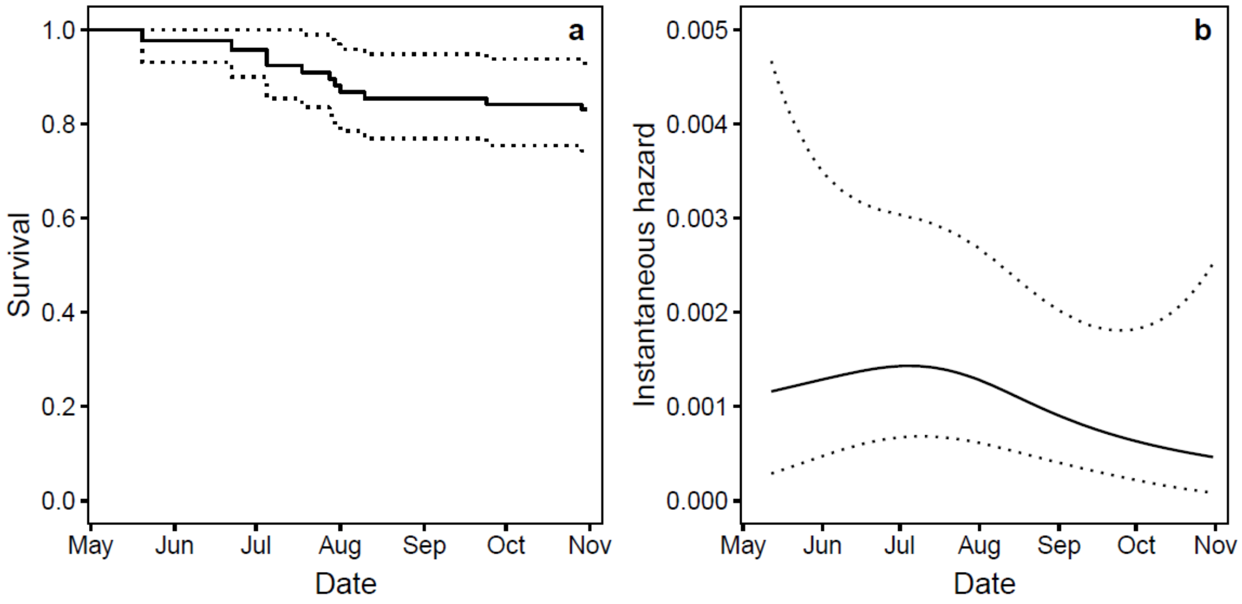

Figure 3.2. Overall warm season survival function and related hazard function for radio-collared coyotes in Prince Edward County, Ontario, May 2010–April 2013. Panels: (a) Kaplan-Meier cumulative survival curve; (b) smoothed instantaneous hazard curve. Dotted lines represent 95% confidence intervals. Data were pooled across three biological years. Dataset included adults and yearlings.

collared coyotes (adults, yearlings, and juveniles) was 0.525 ± 0.047 (95% CI = 0.441–0.625) (Figure 3.3a); mortality risk was relatively high during the cold season (Figure 3.3b). Moreover, social status was also marginally significant in the final model for the cold season dataset (z = 1.9, P = 0.057), whereby the hazard ratio (± robust SE) was 1.65 ± 0.26 (95% CI = 0.99–2.77), indicating that mortality risk was 65% higher for transients than residents; importantly, social status showed no violation of proportionality ($\chi^2 = 2.1$, $P = 0.147$) in the final model for the cold season dataset. Cold season survival rates (± SE) for residents and transients were 0.620 ± 0.064 (95% CI = 0.507–0.759) and 0.414 ± 0.071 (95% CI = 0.296–0.580), respectively (Figure 3.4a); mortality risk was noticeably higher for transients than residents during the latter half of the cold season (Figure 3.4b). Additional stratum-specific survival rates for the annual and seasonal datasets are provided elsewhere (Appendix H).

Notably, the findings from CPH regression model selection corroborated those from stepwise CPH regression modeling, whereby the categorical variables generally did not influence the annual or seasonal survival of radio-collared coyotes (Appendix I). However, the findings from CPH regression model selection also corroborated that social status influenced the cold season survival of radio-collared coyotes (Appendix I).

Cause-specific mortality

Mortality of radio-collared coyotes was attributed to shooting (n = 38), hunting dogs (n = 1), trapping (n = 2), snaring (n = 9), roadkill (n = 10), human causes (n = 2), natural causes (n = 6), and unknown causes (n = 6). Human causes included unknown causes attributed to humans. Natural causes included apparent starvation and presumed exposure caused by the effects of

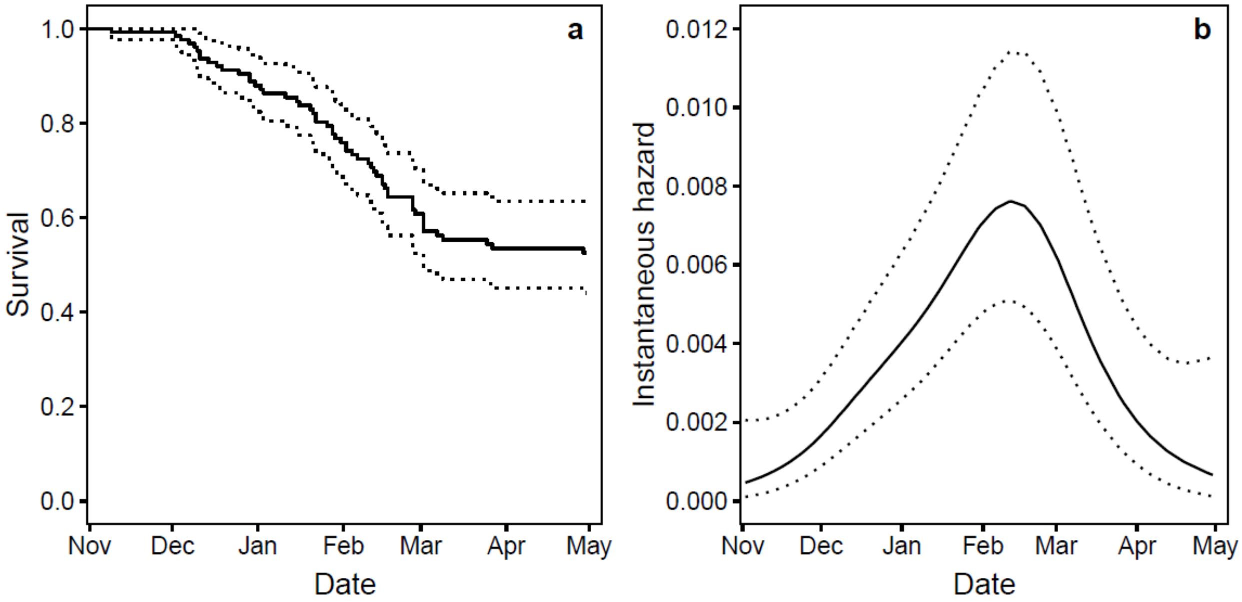

Figure 3.3. Overall cold season survival function and related hazard function for radio-collared coyotes in Prince Edward County, Ontario, May 2010–April 2013. Panels: (a) Kaplan-Meier cumulative survival curve; (b) smoothed instantaneous hazard curve. Dotted lines represent 95% confidence intervals. Data were pooled across three biological years. Dataset included adults, yearlings, and juveniles.

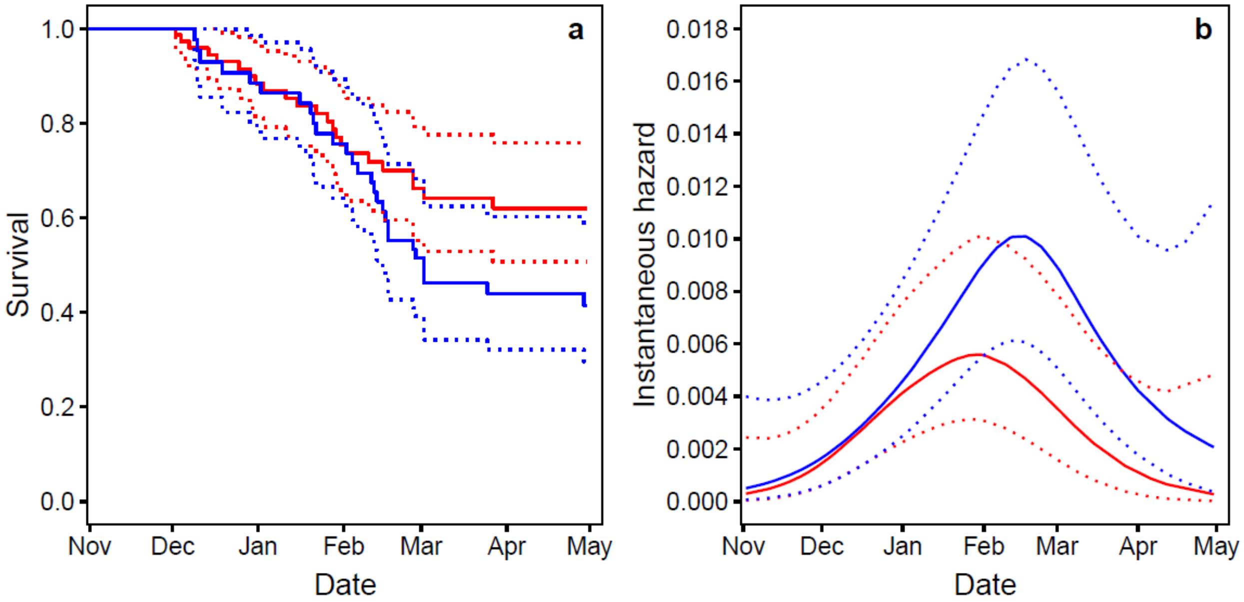

Figure 3.4. Cold season survival functions and related hazard functions for resident and transient coyotes in Prince Edward County, Ontario, May 2010–April 2013. Panels: (a) Kaplan-Meier cumulative survival curves; (b) smoothed instantaneous hazard curves. Colours: red = residents; blue = transients. Dotted lines represent 95% confidence intervals. Data were pooled across three biological years. Dataset included adults, yearlings, and juveniles.

mange. Unknown causes might have included human causes (e.g., poisoning) that were not detected. Mortality of radio-collared coyotes was predominantly attributed to harvest[3] (67.6%), but also roadkill (13.5%) and other causes[4] (18.9%). Cause-specific mortality of radio-collared coyotes varied throughout the year, whereby harvest occurred predominantly during the winter and roadkill and other causes occurred intermittently throughout the year (Figure 3.5). The overall annual cause-specific mortality rates for radio-collared coyotes (adults and yearlings) differed markedly (Appendix J), whereby the overall annual mortality rate due to harvest was higher than that due to roadkill or other causes (Figure 3.6). The overall warm season cause-specific mortality rates for radio-collared coyotes (adults and yearlings) differed slightly (Appendix J), reflecting the low overall warm season mortality rate (Figure 3.7). The overall cold season cause-specific mortality rates for radio-collared coyotes (adults, yearlings, and juveniles) differed markedly (Appendix J), whereby the overall cold season mortality rate due to harvest was higher than that due to roadkill or other causes (Figure 3.8). Cold season cause-specific mortality rates for residents and transients showed similar differences (Appendix J), whereby the cold season mortality rate due to harvest was higher than that due to roadkill or other causes for both residents and transients (Figure 3.9). A stratified CPH regression model indicated that social status did not have a significant effect on the cause-specific mortality of radio-collared coyotes for the cold season dataset (all $P > 0.05$; Appendix K), although the cold season cause-specific mortality rates were seemingly higher for transients than residents (Figure 3.9). Additional stratum-specific cause-specific mortality rates for the annual and seasonal datasets are provided elsewhere (Appendix J).

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[3] Includes shooting, hunting dogs, trapping, and snaring

[4] Includes human causes, natural causes, and unknown causes

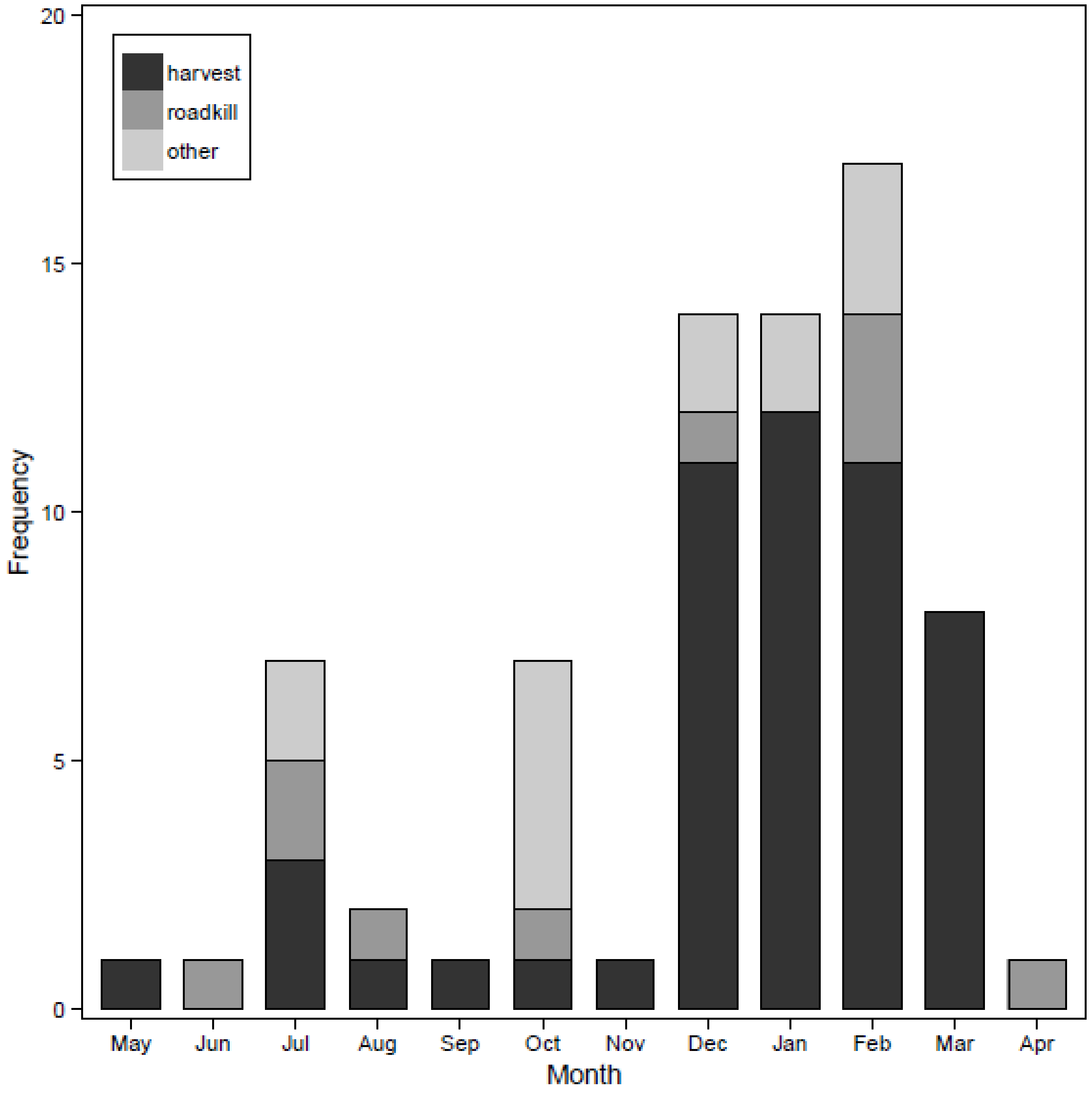

Figure 3.5. Monthly frequency of total mortality and cause-specific mortality of radio-collared coyotes in Prince Edward County, Ontario, May 2010–April 2013. Data were pooled across three biological years.

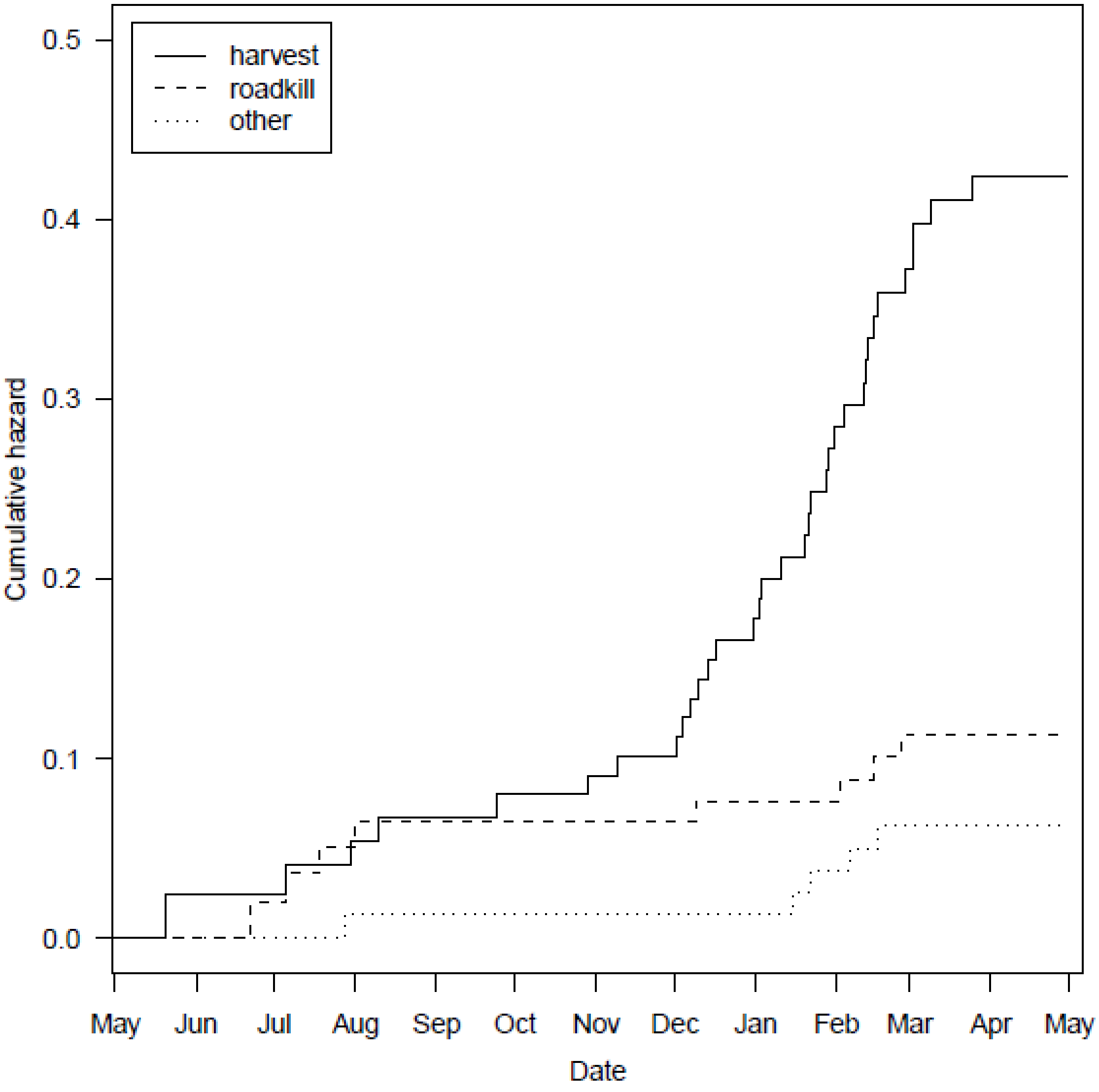

Figure 3.6. Overall annual cumulative incidence functions for radio-collared coyotes in Prince Edward County, Ontario, May 2010–April 2013. Cumulative hazard curves depicting cause-specific mortality rates of radio-collared coyotes are shown. Data were pooled across three biological years. Dataset included adults and yearlings.

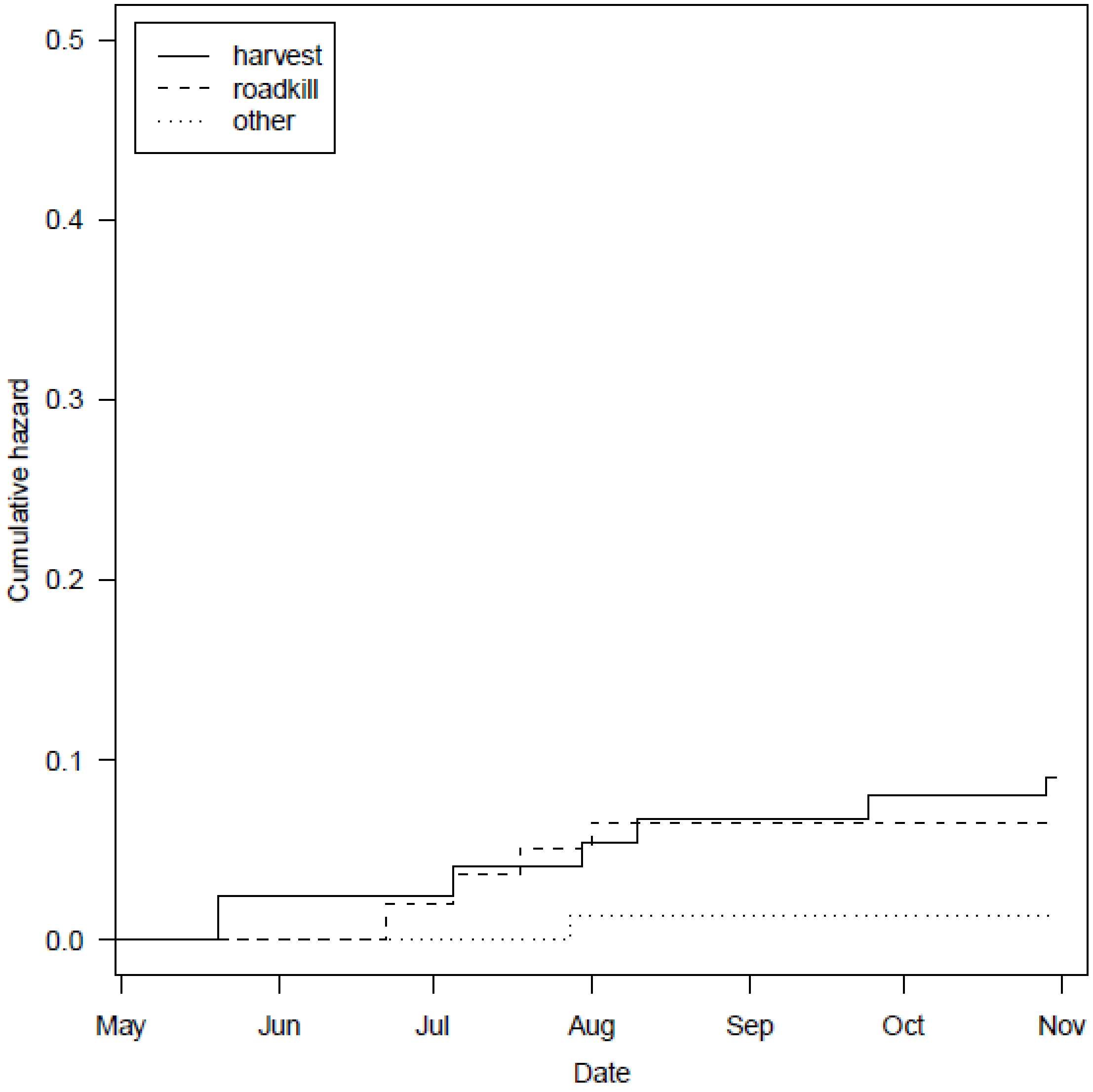

Figure 3.7. Overall warm season cumulative incidence functions for radio-collared coyotes in Prince Edward County, Ontario, May 2010–April 2013. Cumulative hazard curves depicting cause-specific mortality rates of radio-collared coyotes are shown. Data were pooled across three biological years. Dataset included adults and yearlings.

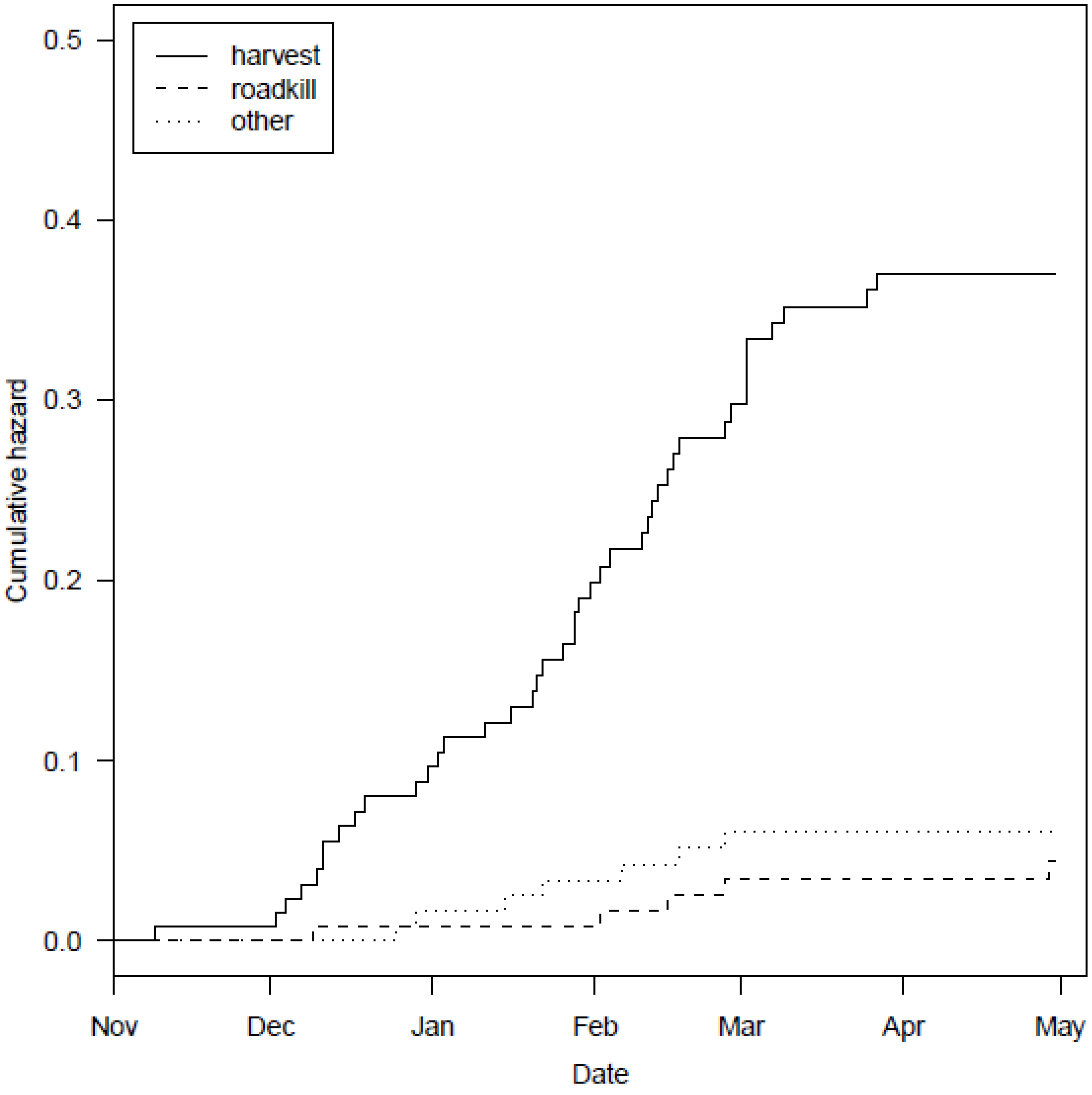

Figure 3.8. Overall cold season cumulative incidence functions for radio-collared coyotes in Prince Edward County, Ontario, May 2010–April 2013. Cumulative hazard curves depicting cause-specific mortality rates of radio-collared coyotes are shown. Data were pooled across three biological years. Dataset included adults, yearlings, and juveniles.

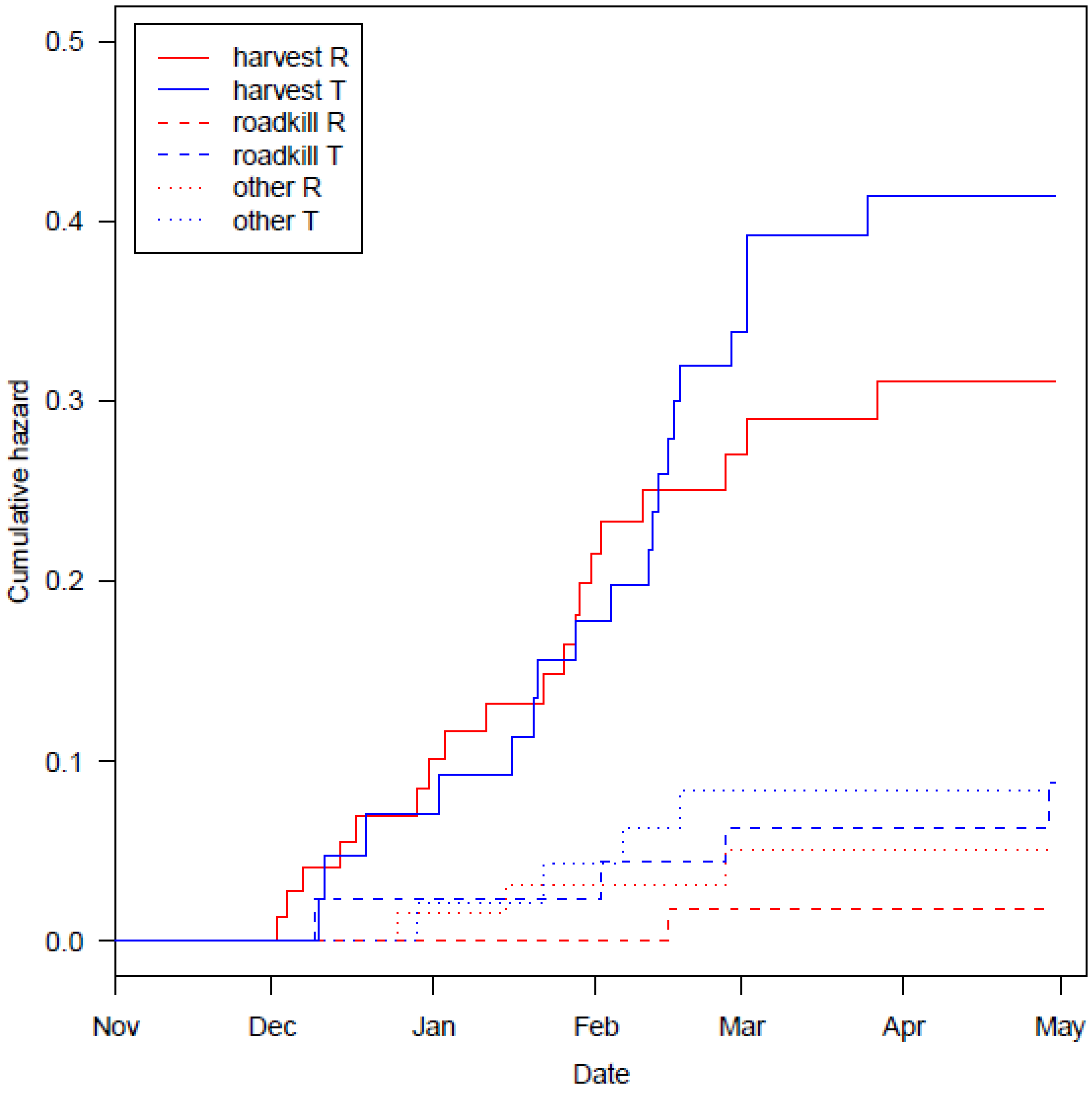

Figure 3.9. Cold season cumulative incidence functions for resident and transient coyotes in Prince Edward County, Ontario, May 2010–April 2013. Cumulative hazard curves depicting cause-specific mortality rates of residents and transients are shown. Abbreviations: R = residents; T = transients. Data were pooled across three biological years. Dataset included adults, yearlings, and juveniles.

Mortality of radio-collared coyotes occurred across the study area (Figure 3.10), but was not uniformly distributed, which presumably reflects a combination of spatial differences in mortality risk and capture effort. Regardless of uneven capture effort across the study area, the spatial distribution of harvest mortalities of radio-collared coyotes suggests that harvest intensity was spatially heterogeneous across the study area (Figure 3.10).

Discussion

Coyotes in the study population exhibited different survival rates with respect to social status but not sex or age class; however, they did not exhibit different harvest mortality rates with respect to social status. Evidently, residents and transients in the study population experienced different cumulative mortality risks, but apparently they encountered similar harvest-related threats on average (but see below). As predicted, the survival rate was higher for residents than transients; social status had a marginally significantly effect on survival. Not as predicted, the harvest mortality rate was not higher for transients than residents; social status did not have a significant effect on harvest mortality. As predicted, the survival rate was similar between sexes and across age classes; neither sex nor age class had a significant effect on survival. Also, survival of coyotes in the study population varied seasonally due to temporal differences in harvest intensity. As predicted, harvest mortality was higher, and survival was lower, during the cold season than the warm season. Additionally, harvest mortality was high but natural mortality was low in the study population. Thus, the study population may have exhibited compensatory mortality (but see below). Hereafter, I discuss my findings and explore them in the context of resilience to harvest for coyote populations. Furthermore, I discuss the relevant implications of my findings.

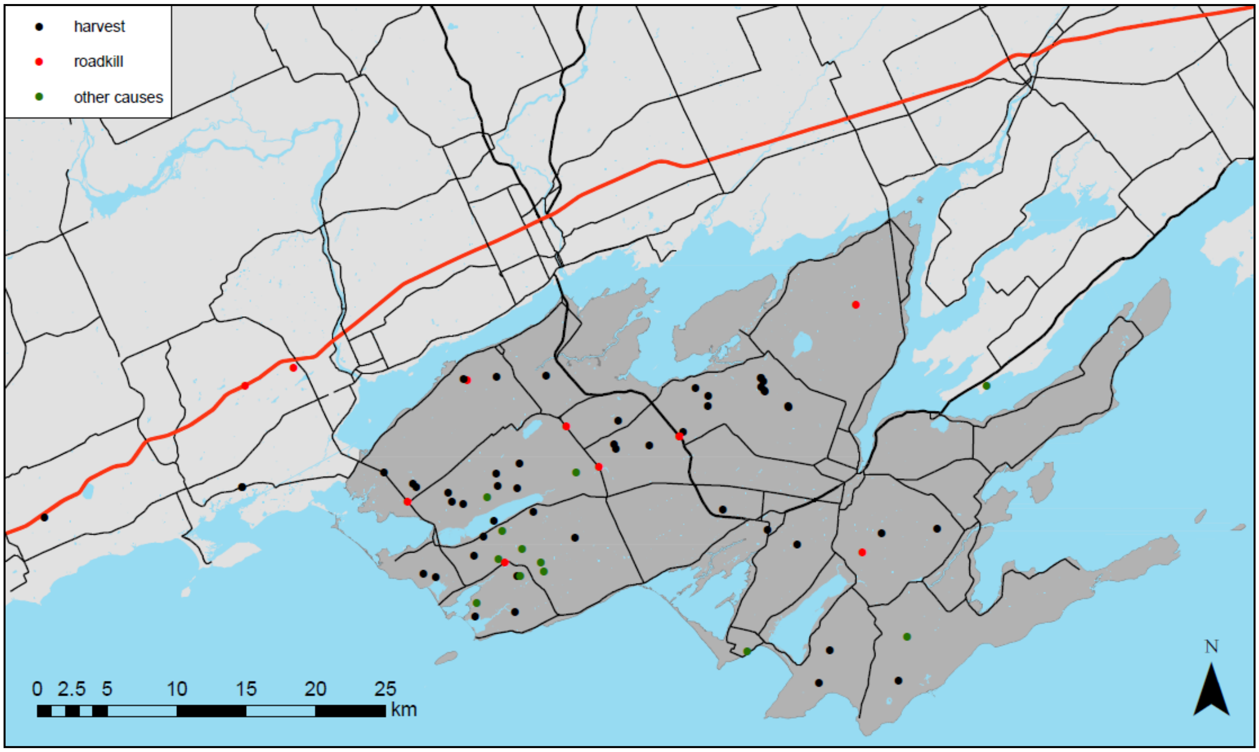

Figure 3.10. Locations of cause-specific mortalities of radio-collared coyotes in Prince Edward County, Ontario, May 2010–April 2013. Four individuals that were excluded from survival analyses are not depicted. Two individuals are not depicted because the location of their death was unknown.

The survival of coyotes in the study population did not differ with respect to biological year. This finding is consistent with the findings of several other studies (Windberg et al. 1985; Gese et al. 1989; Chamberlain & Leopold 2001; Crête et al. 2001). Specifically, the overall survival and cause-specific mortality rates of radio-collared coyotes were not significantly different across biological years for the annual or seasonal datasets, as evidenced by overlapping confidence intervals (Appendix H; Appendix J). Regardless, for the annual and seasonal datasets, the overall survival rate of radio-collared coyotes was noticeably lower for the third biological year than the first or second biological year (Appendix H). Moreover, for the annual and seasonal datasets, the overall harvest mortality rate of radio-collared coyotes was noticeably higher for the third biological year than the first or second biological year, whereas the overall non-harvest (i.e., roadkill and other causes) mortality rates of radio-collared coyotes were generally similar across biological years (Appendix J). Thus, my findings suggest that harvest mortality was at least partially additive to non-harvest mortality for the study population. The relative abundance of coyotes declined in 2013 following the end of the study (see Chapter 1), which was consistent with the decrease in survival in the third biological year, suggesting that the increase in harvest mortality in the third biological year was sufficient to cause a noticeable decline in coyote abundance. The relative abundance of coyotes continued to decline after 2013, suggesting that changes in food abundance and landscape conditions may also have contributed to the decline in coyote abundance.

The study population exhibited low overall annual survival across the years of the study. Despite on average < 50% of individuals (adults and yearlings) surviving annually (Figure 3.1a) and > 40% of them being harvested annually (Figure 3.6), the study population was apparently stable over the years of the study, given that there was no substantial increase or decrease in relative abundance observed across the years of the study (see Chapter 1). Therefore, either recruitment into the population was adequate to offset annual losses or compensatory mechanisms operating in the population were adequate to offset annual losses. My findings support the notion that coyote populations can tolerate substantial harvest mortality (Knowlton et al. 1999), calling into question the efficacy of liberal harvest for reducing coyote abundance.

The magnitude of harvest mortality in a coyote population obviously has a direct effect on the survival of individuals, because it determines how many of them are killed. However, the nature of harvest mortality also has an effect on the survival of individuals, because it determines which of them are killed. Specifically, indiscriminate shooting and trapping of coyotes for overall population reduction undoubtedly results in the non-selective killing of individuals belonging to different sexes, age classes, and social statuses. Alternatively, targeted lethal control of coyotes in response to livestock depredation can result in the selective killing of breeding residents (e.g., Blejwas et al. 2002). The indiscriminate nature of harvest mortality in the study area indicated that all individuals were exposed to harvest mortality risks; indeed, individuals belonging to different sexes, age classes, and social statuses were harvested (Appendix J).

The survival of coyotes in the study population did not differ with respect to sex. This finding is consistent with the findings of several other studies (Windberg et al. 1985; Gese et al. 1989; Crête et al. 2001; Van Deelen & Gosselink 2006). Nevertheless, the survival rate was noticeably lower for males than females for the cold season (Appendix H), partly because the harvest mortality rate was noticeably higher for males than females for the cold season (Appendix J). Harvest mortality of pregnant females during the cold season has the potential to limit recruitment into the population. The loss of post-breeding males during the latter portion of the cold season will have less effect on the compensatory potential of the population than the loss of pregnant females, given that lone females can successfully raise offspring to independence (Sacks & Neale 2001). Presumably, if an adequate proportion of pregnant females survive to whelp, then coyote populations will be able to maintain adequate recruitment into the population to offset losses due to harvest mortality, and thereby maintain a stable population size over time, assuming relatively constant resource availability.

The survival of coyotes in the study population did not differ with respect to age class. This finding is consistent with the findings of several other studies (Holzman et al. 1992; Grinder & Krausman 2001; Gehrt et al. 2011; Stevenson et al. 2016). Nevertheless, surprisingly, the survival rate was noticeably lower for adults than yearlings and juveniles for the cold season (Appendix H), partly because the harvest mortality rate was noticeably higher for adults than yearlings and juveniles for the cold season (Appendix J). Notably, certain studies have found that survival of coyotes differed with respect to age class, whereby survival of adults was greater than that of juveniles (Windberg et al. 1985; Gese et al. 1989; Crête et al. 2001; Van Deelen & Gosselink 2006). Although the survival rate of juveniles was not estimated for the warm season, the survival rate was presumably lower for juveniles than adults for the warm season, because the former were presumably more susceptible to natural mortality than the latter; several juveniles, but no adults, died of natural causes during the warm season. Consequently, the survival rate may have been higher for adults than juveniles for the biological year. Research suggests that the relative survival of adults and juveniles in coyote populations depends on the level of exploitation (Knowlton et al. 1999; Jackson 2014), whereby increased levels of exploitation result in decreased adult survival and consequently increased juvenile survival. Indeed, moderately to heavily exploited coyote populations typically exhibit lower adult survival rates and higher juvenile survival rates than unexploited or lightly exploited coyote populations (Knowlton et al.

1999; Jackson 2014). Juveniles are presumed to be less competitive than adults with respect to acquiring and/or defending resources (Gese et al. 1996). Thus, juveniles presumably benefit from decreased competition for resources resulting from harvest mortality of adults and consequently exhibit increased survival. Adults are generally expected to exhibit better survival probability than juveniles, because the latter are generally presumed to be naïve with respect to hazards, such as hunting and trapping, due to their lack of experience (Windberg et al. 1985; Van Deelen & Gosselink 2006); however, social learning could render this presumption somewhat unjustified, considering that juvenile coyotes can learn avoidance of traps or general “wariness” from their parents or other coyotes (Sacks et al. 1999b). The unpredictable nature of hunting with hounds in the study area may have resulted in adults and juveniles being equally susceptible to harvest mortality; this consideration could partly explain my findings. Tracking with hounds reduces the possibility that coyotes can avoid the hazard, because the hazard seeks them, but adults may be better than juveniles at evading and/or confronting hounds, and thus surviving chases.

The survival of coyotes in the study population differed with respect to social status, whereby the survival of residents was greater than that of transients, albeit only seasonally. This finding is generally consistent with the findings of several other studies (Andelt 1985; Gese et al. 1989; Harrison 1992a; Kamler & Gipson 2000). Specifically, social status had a marginally significant effect on the survival of radio-collared coyotes for the cold season, when the harvest mortality rate was high, but not for the warm season, when the harvest mortality rate was low. Based on the CPH regression model, mortality risk was 65% higher for transients than residents over the cold season (Appendix G). Consequently, the survival rate was lower for transients than residents for the cold season (Figure 3.4a). Based on the stratified CPH regression model, cause-specific mortality risks were not significantly different between social statuses over the cold season; however, harvest mortality risk was seemingly higher for transients than residents over the cold season (Appendix K). Consequently, the harvest mortality rate was seemingly higher for transients than residents for the cold season (Figure 3.9). Thus, during the cold season, residents survived better than transients, partly because they were seemingly less vulnerable to harvest than them. Residents exhibited greater survival than transients, probably partly because of the benefits of holding a territory with available resources (Gese 2001), and transients seemingly exhibited greater vulnerability to harvest than residents, probably partly because their movements exposed them to greater cumulative mortality risks over time in a landscape where harvest intensity varied spatially (Gese et al. 1989; Stevenson et al. 2016). Accordingly, harvest mortality disproportionately impacted the non-reproductive segment of the study population and thus may have failed to substantially limit reproduction, and thus recruitment.

Harvest intensity presumably varies across the landscape for many coyote populations. Indeed, harvest intensity was spatially heterogeneous across the study area based on the spatial distribution of harvest mortalities of radio-collared coyotes (Figure 3.10). It seems reasonable to assume that spatial variability in harvest mortality reflected spatial variability in harvest intensity. Personal communication with hunting groups in the study area and knowledge of their hunting activities support the notion that harvest intensity was spatially heterogeneous across the study area. The movements of residents are generally restricted to within their respective territories, which occur at fixed locations across the landscape, but the movements of transients are generally nomadic, spanning multiple territories across the landscape (see Chapter 2). The instantaneous mortality risk for either residents or transients may be low or high at any given time, depending on where they occur on the landscape with respect to the distribution of harvest intensity, because some individuals will occur in areas of low harvest intensity and other individuals will occur in areas of high harvest intensity. Similarly, the cumulative mortality risk for residents may be low or high over time, depending on where their territories occur on the landscape with respect to the distribution of harvest intensity, because some territories will occur in areas of low harvest intensity and other territories will occur in areas of high harvest intensity. However, the cumulative mortality risk for transients is more likely to be high than low over time, because they will most likely repeatedly occur in areas of high harvest intensity over time due to their nomadic movements. Accordingly, if harvest intensity is spatially heterogeneous, residents and transients are likely to experience different cumulative mortality risks over time and thus exhibit different survival probabilities. Conversely, if harvest intensity is spatially homogeneous, residents and transients are likely to experience similar cumulative mortality risks over time and thus exhibit similar survival probabilities. However, familiarity with the landscape and its hazards is also an important factor, because it influences the survival of coyotes and their vulnerability to trapping (Knowlton et al. 1999). Residents are territorial and thus exhibit site fidelity, such that they should be aware of the hazards within their territory, whereas transients are non-territorial and thus do not exhibit site fidelity, such that they often encounter hazards for the first time during their nomadic wanderings. Accordingly, residents should be better than transients at navigating the landscape while avoiding its hazards, such that residents should exhibit higher survival probability than transients (e.g., Gese et al. 1989; Harrison 1992a). Regardless, the relative survival of residents and transients may partly depend on the degree of spatial heterogeneity in harvest intensity, whereby increasing spatial heterogeneity in harvest intensity may result in increasing cumulative mortality risk and thus decreasing survival probability for transients relative to residents, but further investigation is required.

The magnitude of differences in survival with respect to social status may affect the strength of source-sink dynamics in harvested coyote populations and the means of buffering reproductive capacity (i.e., filling vacant breeding positions) therein. Specifically, if survival of residents is very high and that of transients is very low, then source-sink dynamics operating in response to harvest mortality may be weak, because vacant territories and breeding positions are expected to be relatively uncommon and transients are expected to be relatively unlikely to survive and encounter them, thus implying that pack associates may be primarily responsible for buffering reproductive capacity. Conversely, if survival of residents is only moderately high and that of transients is only moderately low, then source-sink dynamics operating in response to harvest mortality may be strong, because vacant territories and breeding positions are expected to be relatively common and transients are expected to be relatively likely to survive and encounter them, thus implying that transients may be primarily responsible for buffering reproductive capacity. The latter scenario is likely typical for exploited coyote populations, but further investigation is required.

Survival probability may differ among transients with respect to degree of nomadism. Specifically, transients that are locally nomadic might experience greater survival than transients that are widely nomadic. The cumulative mortality risk for locally nomadic transients may be low or high over time, depending on where they occur on the landscape with respect to the distribution of harvest intensity, because some will occur in areas of low harvest intensity and others will occur in areas of high harvest intensity. The cumulative mortality risk for widely nomadic transients is more likely to be high than low over time, because they will most likely repeatedly occur in areas of high harvest intensity over time due to their widespread movements. Accordingly, if harvest intensity is spatially heterogeneous, transients with different space-use patterns are likely to experience different cumulative mortality risks over time and thus exhibit different survival probabilities. Further, familiarity with the landscape might convey increased resource acquisition and/or reduced mortality risk for locally nomadic transients relative to widely nomadic transients. Particularly, transients using biding areas (Hinton et al. 2012, 2015a; Morin & Kelly 2017) may benefit from increased resource acquisition and/or experience reduced mortality risk relative to transients roaming nomadically, but further investigation is required.

As an ad hoc test of the hypothesis that cumulative mortality risk is positively related to degree of nomadism for transients, I contrasted the space-use estimates of transients (see Chapter 2) that were harvested during their monitoring period and those that were not (i.e., survived or died from roadkill or other causes). An approximately equal number of transients that were harvested had a home range size below versus above the median home range size of transients. Similarly, an approximately equal number of transients that were harvested had a space-use rate (i.e., home range size divided by time span) below versus above the median space-use rate of transients. Thus, my data suggest that cumulative mortality risk did not differ among transients with respect to degree of nomadism in my study area, although different trends might be observed in other areas under different circumstances. The relative survival of locally nomadic transients and widely nomadic transients may depend on the degree of spatial heterogeneity in harvest intensity, whereby increasing spatial heterogeneity in harvest intensity may result in increasing cumulative mortality risk and thus decreasing survival probability for widely nomadic transients relative to locally nomadic transients, but further investigation is required.

A resident coyote that had previously made excursions but always returned to its territory was harvested (snared) while off territory and thus on a putative excursion. Regardless of whether this individual was actually a resident or a transient when it died, it is clear that it was harvested while making transient-like movements. This nuance may have biased the survival analyses with respect to social status, because the individual was coded as a resident rather than a transient in the dataset, but actually provides further support for my results concerning the effect of social status on survival of radio-collared coyotes. Coyotes have been shown to exhibit site-dependent vulnerability to certain removal techniques, whereby they were more vulnerable to traps and snares outside of the core areas of their territories (Sacks et al. 1999b) and more vulnerable to traps along the edge of or outside their home ranges (Windberg & Knowlton 1990). Interestingly, excursions might expose residents to harvest-related threats that are absent within their territory or they have learned to avoid only within their territory, but further investigation is required.

The cause-specific mortality of coyotes in the study population differed, whereby harvest mortality was greater than non-harvest mortality; the survival of coyotes in the study population was primarily influenced by harvest mortality. This finding is consistent with the findings of several other studies (Windberg et al. 1985; Gese et al. 1989; Crête et al. 2001; Van Deelen & Gosselink 2006). Specifically, the overall harvest mortality rate of radio-collared coyotes was significantly higher than the overall non-harvest mortality rates of radio-collared coyotes for both the biological year and the cold season, as evidenced by non-overlapping confidence intervals (Appendix J); similarly, the overall harvest mortality rate of radio-collared coyotes was slightly higher than the overall non-harvest mortality rates of radio-collared coyotes for the warm season, but the confidence intervals overlapped (Appendix J). Harvest mortality of coyotes in the study population was predominantly attributed to shooting, which was generally associated with hunting with hounds, but was also attributed to trapping and snaring, which was generally associated with lethal control on a specific sheep farm. Across much of North America, the survival of coyotes is likely primarily influenced by harvest mortality (Bekoff & Gese 2003), either due to hunting for sport, trapping for fur, and/or lethal control for reducing livestock depredation. The density of domestic stock and fowl is likely an important determinant of harvest mortality for coyotes across their range (Harrison 1992b), but landscape conditions likely also influence coyote hunting and trapping.

The survival of coyotes in the study population differed with respect to season, whereby survival was lower for the cold season than the warm season, because harvest mortality was higher for the cold season than the warm season. This finding is consistent with the findings of several other studies (Windberg et al. 1985; Chamberlain & Leopold 2001; Crête et al. 2001; Van Deelen & Gosselink 2006). Notably, Van Deelen and Gosselink (2006) found that the survival of coyotes in a farming region of central Illinois varied seasonally due to differences in harvest mortality risk associated with changes in vegetative cover related to the planting and harvesting of agricultural crops (growing season versus fallow season), despite a year-round open hunting season on coyotes; a similar situation at least partly occurred in my study area. Juveniles were included in the cold season dataset but were excluded from the warm season dataset; therefore, seasonal comparisons based on overall rates might be biased. Regardless, trends in overall rates remained the same when juveniles were excluded from the cold season dataset (results not shown). Instantaneous mortality risk for coyotes in the study population was relatively low throughout much of the year (Figure 3.1b), but was relatively high throughout the winter months (Figure 3.3b), primarily because of hunting with hounds. My findings demonstrate that seasonal variation in the survival of coyotes in the study population was caused by seasonal variation in harvest mortality risk, which was caused by seasonal variation in harvest intensity.

Harvest intensity varied temporally in the study area, mainly because of seasonal hunting trends associated with landscape conditions. Particularly, hunting occurred mostly during the cold season when vegetative cover was limited and snow cover facilitated tracking with hounds. Thus, the timing of harvest mortality coincided with the expected period of natural mortality; during the cold season, prey scarcity may lead to coyotes dying from starvation and sub-zero temperatures may lead to mange-afflicted coyotes dying from exposure. Indeed, although limited, natural mortality occurred during the cold season, but also during the warm season (Figure 3.5). Accordingly, because harvest mortality and natural mortality overlapped temporally in the study population, harvest mortality must have been at least partially additive to natural mortality; compensatory mortality could have been only partial, because there would have been limited capacity for improved survival of unharvested individuals. Notably, prey and anthropogenic food sources were seemingly abundant in the study area, thus density-dependence related to food resources may have been trivial for the study population. Indeed, body condition indices (Wheeldon unpublished data) suggested that coyotes in the study area were generally in good condition, thus food resources in the study area may not have been a limiting factor for the study population. Accordingly, low natural mortality in the study population may have been the result of abundant food resources rather than a partial compensatory response to high harvest mortality. Furthermore, the timing of harvest mortality coincided with the breeding period and at least part of the gestation period. Harvest mortality of breeders, especially pregnant females, may impact the compensatory potential of coyote populations by limiting recruitment into the population. Notably, if harvest mortality of breeders occurs prior to the breeding period, then transients and/or pack associates may fill vacant breeding positions and thereby buffer the reproductive capacity of the population. However, if harvest mortality of breeders occurs during the breeding period, then vacant breeding positions will not be filled and the reproductive capacity of the population will be reduced. Similarly, if harvest mortality of breeders occurs during the gestation period, then recruitment into the population will be reduced. None of the radio-collared coyotes that were harvested during the gestation period were pregnant females. The study population evidently achieved adequate recruitment to maintain a stable population size over time, despite harvest mortality; based on deer hunter questionnaire data, the relative abundance of coyotes in the study area was relatively stable over the years of the study (see Chapter 1).

Eleven radio-collared coyotes with mange died during the study (one of them died after a planned collar drop); specifically, two of them died of natural causes (i.e., presumed exposure) and nine of them died of human-related causes (six were shot, two were snared, and one was killed by hunting dogs). Although mange was rarely the proximate cause of mortality for radio-collared coyotes, the effects of mange may have predisposed radio-collared coyotes to human-related mortality risk in some cases, and thus mange could be considered the ultimate cause of mortality in those cases; for example, one coyote suffering from severe mange sought shelter in a barn and was shot by the landowner. Gehrt et al. (2011) noted that some coyotes suffering from severe mange were shot during their study, but they classified those cases as mortalities caused from mange, because they 'deemed the disease to be the ultimate cause of mortality that caused the animal to be euthanized'. Regardless, several radio-collared coyotes with mange were harvested under seemingly typical circumstances during my study. Accordingly, harvest mortality may have been partially compensatory to natural mortality in the study population, because some radio-collared coyotes with mange likely would have died from natural causes had they not been harvested.

The efficacy of liberal harvest for reducing coyote abundance and livestock depredation needs to be addressed. Liberal harvest of coyotes is essentially a means of uncoordinated and indiscriminate lethal control. Based on the observed survival and cause-specific mortality of coyotes in the study population, it is apparent that uncoordinated and indiscriminate lethal control of coyotes is unlikely to be effective in reducing coyote abundance or livestock depredation. During the cold season, when most harvest occurred, residents survived better than transients, partly because they were seemingly less vulnerable to harvest than them. Accordingly, liberal harvest may prove ineffective in reducing coyote abundance, other than temporarily, because harvest mortality may disproportionately impact the non-reproductive segment of the population and thus fail to substantially limit reproduction, and thus recruitment. Transients may depredate livestock, but they are less likely than residents to be responsible for repeated depredations on specific farms (Sacks et al. 1999a; Blejwas et al. 2002, 2006), thus liberal harvest likely involves removal of many non-offending coyotes, which has been shown to be ineffective at reducing livestock depredation (Conner et al. 1998; Sacks et al. 1999a). Furthermore, depending on the spatial distribution of livestock with respect to that of harvest intensity, liberal harvest may involve the killing of many coyotes with territories distant from livestock, which would be unlikely to depredate livestock. Therefore, liberal harvest may prove inefficient in reducing livestock depredation. Management strategies that seek to reduce conflicts between coyotes and livestock should consider non-lethal alternatives and/or targeted lethal control, which may prove effective (Knowlton et al. 1999).

In conclusion, the compensatory potential of harvested animal populations may be explained partly by individual variation in survival and vulnerability to harvest. This is particularly true for predators that exhibit a social hierarchy with respect to reproduction and dispersal, such as coyotes, which are commonly subject to lethal control efforts of questionable efficacy. Therefore, wildlife managers should consider the survival and cause-specific mortality of such predators when assessing the efficacy of management practices.

Chapter 4

Reproduction and breeding histories of eastern coyotes from a harvested population in southeastern Ontario

Abstract

Life history strategy is an important factor to consider when investigating the compensatory potential of harvested animal populations. Coyotes are liberally harvested across much of their range, but most coyote populations demonstrate considerable resilience to harvest, suggesting that they exhibit some mechanisms of compensation. Evidence suggests that coyote populations can respond to decreasing population density due to exploitation by increasing the proportion of females breeding in the population and increasing litter sizes. Reproduction is fundamentally important with respect to the resilience of harvested coyote populations, but better understanding is sought. Furthermore, breeding histories of coyotes in wild populations remain largely unexplored. I investigated the reproduction and breeding histories of eastern coyotes from a harvested population in southeastern Ontario. I hypothesized that females in the study population would exhibit age-specific reproductive rates and litter sizes typical of those in exploited coyote populations. Also, I hypothesized that there would be considerable breeder turnover in the study population due to harvest mortality. I determined the reproductive status of 81 females. The proportion of females that were reproductive differed significantly with respect to age class, whereby 10.3% of juveniles, 14.3% of yearlings, and 90.5% of adults were reproductive. I estimated litter size for 18 reproductive females based on counts of fetuses or placental scars. Mean (± SE) litter size of females was 6.2 ± 0.6 (range = 1─10). I genetically profiled 398 coyotes. I determined the maximum likelihood relationship for each pair of individuals and subsequently determined breeding histories for 58 individual parents. The number of litters observed for individual parents ranged from 1–7 (median = 2; mode = 1). Specifically, 1–2 litters were observed for 39 individual parents (67%) and 3–7 litters were observed for 19 individual parents (33%). The number of mates observed for individual parents with multiple litters ranged from 1–3 (median = 1; mode = 1). Specifically, only one mate was observed for 25 individual parents with multiple litters (83%) and 2–3 mates were observed for five individual parents with multiple litters (17%). Indeed, females in the study population exhibited age-specific reproductive rates and litter sizes generally typical of those in exploited coyote populations. Accordingly, increased reproductive rates and increased litter sizes may have offset losses due to harvest mortality. There was at least some breeder turnover in the study population due to harvest mortality, but many breeders survived to reproduce for multiple years and those that died were quickly replaced. My findings corroborate research that challenges the efficacy of liberal harvest for reducing coyote abundance and livestock depredation.

Introduction

The ability of animal populations to compensate for harvest mortality (e.g., hunting and trapping) depends on various intrinsic and extrinsic factors (see Sandercock et al. 2011). Life history strategy is an important factor to consider when investigating the compensatory potential of harvested animal populations. Wildlife species that exhibit high survival and low fecundity often do not produce a reproductive surplus and thus may have limited capacity to compensate for harvest mortality, whereas wildlife species that exhibit high fecundity and low survival often do produce a reproductive surplus and thus may have substantial capacity to compensate for harvest mortality (Sandercock et al. 2011; Péron 2013). Life history strategy differs among wildlife species (Stearns 1983; Oli 2004; Bielby et al. 2007; Dobson & Oli 2007), including predators (e.g., bears and wolves), thus so may their capacity to compensate for harvest mortality. Therefore, gaining better understanding of the life history strategy of predators is important for informing management strategies.

Compensatory natality can occur in harvested animal populations through density dependence, whereby harvest mortality decreases population density, which results in reduced competition for resources (e.g., food and habitat), and thereby increases reproductive output (Boyce et al. 1999). The timing of harvest is an important factor to consider when investigating the potential for compensatory natality to occur in harvested animal populations (Boyce et al. 1999; Kokko 2001). If harvest mortality occurs prior to the breeding period then compensation can be complete, but if harvest mortality occurs during the breeding period then compensation can be only partial (Kokko 2001). Density dependence must occur after harvest for compensation to be realized (Boyce et al. 1999). Compensatory natality, also known as compensatory reproduction, has been demonstrated for various wildlife species (e.g., mountain goats: Swenson 1985), including predators such as red foxes (Cavallini & Santini 1996) and black-backed jackals (Minnie et al. 2016). Compensatory reproduction in harvested animal populations may manifest itself as increases in age-specific reproductive rates (e.g., Minnie et al. 2016) and/or increases in litter size (e.g., Cavallini & Santini 1996).

Coyotes (*Canis latrans*) are liberally harvested across much of their range, but most coyote populations demonstrate considerable resilience to harvest, suggesting that they exhibit some mechanisms of compensation (Knowlton et al. 1999). However, some stakeholders remain convinced that liberal harvest is effective for reducing coyote abundance (e.g., Bartel & Brunson 2003). The onus remains on wildlife managers to better explain how coyote abundance can remain relatively stable across years despite consistently liberal harvest regimes.

Coyotes are monoestrous (Kennelly 1978) with each breeding pair producing a single litter of pups each spring (Knowlton et al. 1999). Coyotes exhibit a social hierarchy with respect to breeding, whereby typically territorial individuals (i.e., residents) but not non-territorial individuals (i.e., transients) can hold breeding positions and successfully whelp (Messier & Barrette 1982; Knowlton et al. 1985; Gese 2001). Reproductive rates and litter sizes of coyotes vary geographically and over time (Jean & Bergeron 1984; Chambers 1992; Gese et al. 1996). Food abundance is the primary limiting factor with respect to reproduction in coyote populations (Gier 1968). Food abundance determines the proportion of females breeding in the population and litter size (Gier 1968). Litter size of coyotes has been shown to be inversely related to population density (Knowlton 1972), suggesting that compensatory reproduction may occur in coyote populations. Exploitation of coyote populations may lead to a decrease in their density, which may result in reduced competition for food and reduced social constraints on breeding, and thus may lead to an increase in their reproductive output (Knowlton et al. 1999). The level of exploitation has been shown to influence reproductive parameters in coyote populations (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). Specifically, unexploited or lightly exploited coyote populations typically exhibit relatively low reproductive rates (especially among young individuals) and small litter sizes, whereas moderately to heavily exploited coyote populations typically exhibit relatively high reproductive rates and large litter sizes (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). Thus, evidence suggests that coyote populations can respond to decreasing population density due to exploitation by increasing the proportion of females (especially young ones) breeding in the population and increasing litter sizes (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). Reproduction is fundamentally important with respect to the resilience of harvested coyote populations, but better understanding is sought.

Considerable research exists on the reproductive parameters of western coyotes, but comparatively limited research exists on those of eastern coyotes, especially in agricultural landscapes where livestock depredation is a concern (see Mastro et al. 2011). Geographic differences in the density of domestic stock and fowl might be associated with differences in harvest pressure for coyotes (Harrison 1992b), suggesting that the reproductive parameters of eastern coyotes may differ from those of western coyotes. Specifically, lower density of domestic stock and fowl might be associated with lower harvest pressure for eastern coyotes, which might be associated with lower reproductive rates and litter sizes for eastern coyotes. Also, geographic differences in prey density and landscape conditions likely influence the reproductive parameters of coyotes across their range (Chambers 1992). Lower prey density might be associated with lower reproductive rates and litter sizes for eastern coyotes, despite apparently contrary findings (Chambers 1992), given that they are now longer established across the northeast. Moreover, eastern coyotes differ from western coyotes in that they have partial wolf ancestry due to hybridization (Kays et al. 2010; Wheeldon et al. 2013; Monzón et al. 2014). Partial wolf ancestry might be associated with lower productivity for eastern coyotes, given that wolves are less productive than coyotes. It is not clear how partial wolf ancestry might influence the reproductive parameters of eastern coyotes. A clear understanding of the reproductive parameters of eastern coyote populations is critical (Gompper 2002). Further investigation of the reproductive parameters of eastern coyotes is needed to provide wildlife managers with essential information (Mastro et al. 2011).

Reproduction of coyotes has typically been investigated based on the examination of reproductive tracts collected from female carcasses (e.g., Gier 1968; Sacks 2005). The presence of fetuses or placental scars in reproductive tracts confirms breeding for females and the number of them provides an estimate of litter size (Gier 1968; Sacks 2005); however, reproductive tracts provide information only on recent reproduction of coyotes and do not facilitate investigation of the breeding histories of coyotes. Although some studies have investigated pairwise genetic relatedness among coyotes in wild populations (Kohn et al. 1999; Williams et al. 2003), breeding histories of coyotes in wild populations remain largely unexplored. Hennessy et al. (2012) genetically investigated pedigree relationships among urban coyotes and reported on long-term pair bonding and genetic evidence for monogamy. Moreover, Hennessy et al. (2012) determined breeding histories of urban coyotes and documented a case of breeder turnover. Indeed, genetic investigation of pedigree relationships among individuals can inform on breeder turnover for social carnivores, such as wolves (Ausband et al. 2017). Mortality of breeders can occur frequently in harvested animal populations, but quick replacement of breeders can maintain reproductive capacity and thus prevent population decline. Thus, exploring the breeding histories of coyotes in wild populations, especially those that are liberally harvested, might yield novel insights regarding breeder turnover and thereby inform on resilience to harvest for coyote populations.

I investigated the reproduction and breeding histories of eastern coyotes from a harvested population in southeastern Ontario. My objective was to gain better understanding of how reproduction and breeding histories might inform on resilience to harvest for eastern coyote populations. I hypothesized that females in the study population would exhibit age-specific reproductive rates and litter sizes typical of those in exploited coyote populations; importantly, this would be indicative of demographic compensation for harvest mortality. First, I predicted that > 70% of adults and > 10% of juveniles would be reproductive; these thresholds are the proposed average age-specific reproductive rates of females in an unexploited coyote population (Connolly & Longhurst 1975). Second, I predicted that mean litter size would be > 4.5; this threshold is the proposed average litter size of females in an unexploited coyote population (Connolly & Longhurst 1975). Also, I hypothesized that there would be considerable breeder turnover in the study population due to harvest mortality. First, I predicted that the number of litters observed for individual parents would be relatively low (i.e., 1–2) in most cases, because many of them would not have survived to reproduce for multiple years. Second, I predicted that the number of mates observed for individual parents with multiple litters would be two or more in most cases, because many of them would have suffered mate loss. I discuss the implications of my findings concerning the resilience of harvested coyote populations and the efficacy of liberal harvest for reducing coyote abundance and livestock depredation.

Methods

Study area

I conducted research on coyotes during 2010–2013 in Prince Edward County (PEC), which is located in southeastern Ontario on a large irregular headland in the northeastern region of Lake Ontario (see Chapter 1). The landscape was predominantly agricultural and rural. Coyote hunting and trapping seasons were open all year. Based on deer hunter questionnaire data, the relative abundance of coyotes in the study area was relatively stable over the years of the study (see Chapter 1).

Capture, handling, and radio-collaring

I captured coyotes using padded foot-hold traps and physically restrained them with a noose pole. Generally, upon capture, I chemically immobilized coyotes with an intramuscular injection of an agonist drug mixture (see Chapter 2). If applicable, prior to release, I reversed coyotes with an intramuscular injection of an antagonist drug (see Chapter 2). Alternatively, I physically immobilized coyotes by hobbling and muzzling them for the duration of handling. I weighed coyotes and recorded their body mass. I sexed coyotes and noted evidence of breeding for females. I aged coyotes based on tooth eruption and wear (Gier 1968) and classified them as juvenile (< 12 months old), yearling (12–24 months old), or adult (> 24 months old). I sampled blood and/or hair from coyotes for genetic profiling. I marked coyotes with uniquely numbered metal ear tags. I fitted coyotes with radio-collars (see Chapter 2). The capture, handling, and radio-collaring of coyotes was approved by the Trent University Animal Care Committee (protocol no. 10016) and the Ontario Ministry of Natural Resources Wildlife Animal Care Committee (protocol nos. 10-219 through 12-219).

Carcass necropsy

I retrieved carcasses of radio-collared coyotes that were killed or died in the greater study area. Also, I collected carcasses of non-radio-collared coyotes that were killed or died in the study area. Carcasses were reported/provided to me by various people, including hunters, trappers, farmers, road-crew workers, and landowners; several carcasses were found by chance. I stored carcasses in freezers until necropsy. I performed necropsies on carcasses in the laboratory; decomposition/scavenging precluded some aspects of necropsy for several carcasses. I examined carcasses and (if possible) determined cause of death. I weighed carcasses and recorded their body mass. I sexed carcasses and noted evidence of breeding for females. I aged carcasses based on tooth eruption and wear (Gier 1968) and classified them as juvenile (< 12 months old), yearling (12–24 months old), or adult (> 24 months old). Moreover, I extracted a lower canine tooth from each carcass and submitted teeth to Matson's Laboratory (Manhattan, Montana, USA) for aging by the cementum annuli technique (Linhart & Knowlton 1967). I examined the reproductive tracts of females and recorded the presence/absence and (if applicable) number of implants (i.e., localized uterine swellings), fetuses, or placental scars. I sampled tissue from carcasses for genetic profiling.

Female reproduction assessment

I determined the reproductive status of females based on the presence/absence of implants, fetuses, or placental scars. The presence of implants or fetuses indicated that females were pregnant and the presence of placental scars indicated that females were postpartum. I classified females as either reproductive or non-reproductive. I assessed reproduction only for females aged ≥ 10 months, because those aged < 10 months were too young to have either bred or shown signs of pregnancy. The assessment age for females was as follows: (1) the mortality age less one year for females that died during May–February, because they would have bred (if applicable) during the previous biological year; and (2) the mortality age for females that died during March–April, because they would have bred (if applicable) during the current biological year. This approach was appropriate because reproductive females that died during March–April had only implants or fetuses and those that died during May–February had only placental scars; therefore, overlap of implants/fetuses and placental scars was not an issue. I determined the proportion of females in each age class that were reproductive. I tested for differences in the proportions of females that were reproductive among age classes using the Chi-squared test for equality of proportions in R (version 3.1.2; R Core Team 2014). I plotted the frequency distribution of the breeding ages of females in R using the ggplot2 package. I estimated litter size for reproductive females based on counts of fetuses or placental scars, but not implants. I counted only dark scars of similar colour to avoid including those from resorbed fetuses and/or previous litters. Note that estimated litter sizes were maximums, because actual litter sizes might have been reduced by late-term abortions. I plotted the frequency distribution of the litter sizes of females in R using the ggplot2 package.

Population age structure

I investigated the age structure of the study population using tooth-age data from carcasses of radio-collared coyotes that were killed or died in the greater study area and non-radio-collared coyotes that were killed or died in the study area. I determined the proportion of carcasses that belonged to each age class. I plotted the frequency distribution and the proportion distribution of the ages of carcasses in R using the ggplot2 package. I limited the dataset to carcasses of coyotes that were killed or died between November and April to avoid biasing the dataset; juveniles would be less likely than yearlings or adults to be harvested between May and October, because their movements would be largely restricted to their natal territory prior to the dispersal period.

Sample collection

I collected various samples from coyotes for genetic profiling. I collected blood samples from captured coyotes and applied them to Whatman FTA® Classic Cards (GE Healthcare, Little Chalfont, Buckinghamshire, UK) for dry storage until processing. I collected tissue samples from carcasses and placed them in Whirl-Pak® bags (Spectrum Nasco, Newmarket, Ontario, Canada) for frozen storage until processing. I collected hair samples from captured coyotes and carcasses and placed them in paper coin envelopes for dry storage until processing. I collected fecal swabs from scats found in the field, including those found on roads or near traps. I collected saliva swabs from bite wounds on depredated livestock, which included mostly sheep, but also cattle and poultry. I collected multiple swabs from some scats and depredated livestock. I collected fecal/saliva swabs using cotton-tipped applicators and transferred them to tubes containing lysis buffer for frozen storage until processing. Additionally, I collected an estrus blood sample found on snow, a hair sample found at a bedding site, a hair sample found at a depredation site, a tissue sample found in a trap, blood samples from two carcasses, and tissue samples from fetuses found in the reproductive tracts of three females.

DNA extraction and quantification

I extracted genomic DNA from 599 samples using either the DNeasy® Blood & Tissue Kit (Qiagen, Hilden, Germany) or the MagneSil® Blood Genomic, Max Yield System (Promega, Madison, Wisconsin, USA) on the JANUS® Automated Workstation (PerkinElmer, Waltham, Massachusetts, USA). Specifically, I extracted genomic DNA from 93 blood samples, 282 tissue samples, 6 hair samples, 121 fecal swabs, and 97 saliva swabs. I included negative controls throughout the extraction process to monitor for contamination. Generally, I determined the DNA concentration of samples using the PicoGreen® dsDNA quantitation assay (Life Technologies, Carlsbad, California, USA) and standardized the DNA concentration of samples to 2.5 ng/μl. Alternatively, I estimated the DNA concentration of samples by attempting polymerase chain reaction (PCR) amplification of autosomal microsatellite locus cxx204 (Ostrander et al. 1993) and visualizing PCR products, including controls of known DNA concentration, on an agarose gel stained with ethidium bromide.

Sex confirmation/determination

I genetically confirmed/determined the sex of samples. Generally, I attempted PCR amplification of *Zfx/Sry* fragments using previously described primer pairs (Aasen & Medrano 1990; Fain & LeMay 1995). Alternatively, I attempted PCR amplification of *Zfx/Zfy* introns using previously described primers (Shaw et al. 2003). I electrophoresed and visualized PCR products on an agarose gel stained with ethidium bromide. I sexed samples based on banding pattern; females had one band and males had two bands. Primer sequences and details of PCR amplification are provided in Appendix L and Appendix M, respectively.

Autosomal microsatellite genotyping

I attempted PCR amplification of 16 autosomal microsatellite loci in four multiplex reactions (Ostrander et al. 1993: cxx2, cxx109, cxx123, cxx147, cxx172, cxx204, cxx225, cxx250, cxx253; Fredholm & Winterø 1995: CPH11; Ostrander et al. 1995: cxx377, cxx383, cxx410, cxx442; Francisco et al. 1996: c2010; Wagner et al. 1996: c2202). PCR products were genotyped on a 3730 DNA Analyzer (Applied Biosystems, Foster City, California, USA). I scored alleles in GeneMarker (version 1.9; Softgenetics LLC, State College, Pennsylvania, USA). I re-amplified loci with uncertain alleles to confirm locus-specific genotypes. Locus cxx2 had some 1 base pair (bp) allele differences, but they were considered useful for investigating relatedness; therefore, locus cxx2 was not excluded. Details of PCR amplification are provided in Appendix M.

Mitochondrial DNA (mtDNA) sequencing

I attempted PCR amplification of the mtDNA control region using previously described primers. Generally, I attempted PCR amplification of a 420–425 bp fragment of the mtDNA control region using primers described in Leonard et al. (2002). Alternatively, I attempted PCR amplification of a 343–347 bp fragment of the mtDNA control region using primers described in Wilson et al. (2000). PCR products were purified using Exonuclease 1 and Antarctic Phosphatase (New England BioLabs Inc., Ipswich, Massachusetts, USA) and bi-directionally sequenced with the BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) on a 3730 DNA Analyzer. I edited and aligned sequences in MEGA (version 5; Tamura et al. 2011). I determined haplotypes based on 223–228 bp sequences; note that fragments amplified with different primers contained the same variable region used to determine haplotypes. Primer sequences and details of PCR amplification are provided in Appendix L and Appendix M, respectively.

Y-chromosome microsatellite genotyping

I attempted PCR amplification of four Y-chromosome microsatellite loci in two duplex reactions (Sundqvist et al. 2001: MS34A, MS34B, MS41A, MS41B). PCR products were genotyped on a 3730 DNA Analyzer. I scored alleles in GeneMarker. I re-amplified loci with uncertain alleles to confirm locus-specific genotypes. I determined composite haplotypes based on the alleles present at the four loci, which are located in the non-recombining region of the canine Y chromosome (Sundqvist et al. 2001). Details of PCR amplification are provided in Appendix M.

Genetic analyses

I obtained 457 autosomal microsatellite genotypes based on variable numbers of loci. I estimated the genotyping error rate by comparing genotypes of paired samples from individuals (n = 8) and genotypes of replicate samples from scats (n = 6). I observed no discrepancies between genotypes of paired samples or replicate samples and therefore assumed that the genotyping error rate was negligible, but probably not null. I retained 450 genotypes based on 13–16 loci (92% based on 16 loci); I omitted three genotypes based on ≤ 9 loci and four known duplicate genotypes. Two loci (c2202 and CPH11) had some off-ladder alleles, which were coded as missing data for genetic analyses. I identified matching genotypes using GeneCap (version 1.4; Wilberg & Dreher 2004). I identified 29 genotype matches that comprised 2–6 samples. I identified 404 unique genotypes based on 14–16 loci (94% based on 16 loci). I retained 398 unique genotypes based on 14–16 loci (95% based on 16 loci); I omitted four genotypes of domestic dogs (based on mtDNA haplotype), one genotype of a coyote sampled from beyond the greater study area, and one suspect genotype from a fecal swab. I performed subsequent genetic analyses on 398 unique genotypes, which included 169 females, 209 males, and 20 individuals of undetermined sex; four individuals of undetermined sex that had Y-haplotypes were inferred to be males.

I calculated the probability of identity ($P_{\text{(ID)}}$) and the probability of identity for siblings ($P_{\text{(ID)sib}}$) across loci using GenAlEx (version 6.5; Peakall & Smouse 2006, 2012). Across loci, $P_{\text{(ID)}}$ and $P_{\text{(ID)sib}}$ were 4.7×10^{-19} and 2.8×10^{-7}, respectively. I calculated the number of alleles (Na), the effective number of alleles (Ne), the observed heterozygosity (Ho), and the expected heterozygosity (He) for each locus using GenAlEx. Across loci, mean (± SE) Na was 10.5 ± 1.9 (range = 5–33), mean (± SE) Ne was 5.4 ± 0.8 (range = 1.5–13.3), mean (± SE) Ho was 0.751 ± 0.038 (range = 0.339–0.927), and mean (± SE) He was 0.757 ± 0.036 (range = 0.331–0.925) (Appendix N). I tested for locus-specific deviations from Hardy-Weinberg equilibrium (HWE) and locus-pair deviations from linkage equilibrium (LE) using Genepop (version 4.2; Rousset 2008); significance levels were adjusted for multiple tests using the sequential Bonferroni technique (Rice 1989). Seven of 16 loci exhibited significant deviations from HWE and 89 of 120 locus pairs exhibited significant deviations from LE. The deviations from HWE and LE were presumably due to the presence of many related individuals in the dataset; this was supported based on preliminary analyses of the genotypes of adult individuals (i.e., the reproductive segment of the population), for which only one of 16 loci exhibited significant deviations from HWE and only two of 120 locus pairs exhibited significant deviations from LE.

I calculated maximum likelihood estimates of relatedness (*r*) between individuals using ML-Relate (Kalinowski et al. 2006). ML-Relate is useful for discriminating among four common pedigree relationships: unrelated (U), half-siblings (HS), full-siblings (FS), and parent-offspring (PO). Accordingly, I calculated the log-likelihood of four relationships (U, HS, FS, and PO) for each pair of individuals and determined the maximum likelihood relationship for them using ML-Relate. Allele frequencies were estimated from the genotypes of all individuals, rather than the genotypes of adult individuals (i.e., the reproductive segment of the population), because there were 11 additional alleles observed across five loci for the genotypes of all individuals relative to the genotypes of adult individuals. I tested for the presence of null alleles at each locus using the Hardy-Weinberg test for excess homozygotes with 10,000 randomizations; significance levels were adjusted for multiple tests using the sequential Bonferroni technique. Two loci (cxx2 and cxx123) exhibited a significant excess of homozygotes. I specified which loci had null alleles; when null alleles are present, ML-Relate uses maximum likelihood estimates of the frequency of null alleles in all calculations. I generated summary statistics for overall and relationship-specific pairwise relatedness based on the initial ML-Relate results.

Following a multistep approach, I thoroughly investigated the maximum likelihood relationships for 79003 dyads to ensure that they were correct, plausible, and logically consistent. First, I compiled lists of 82 known relationships (64 FS [fetus-fetus] and 18 PO [mother-fetus]) and 61 presumed relationships (51 FS [juveniles caught on the same date and property and/or in the same year and natal territory] and 10 PO [breeding female and pup]) and determined whether the maximum likelihood relationship was correct for applicable dyads. Second, I determined the plausibility of FS dyads and PO dyads based on haplotypes, whereby FS dyads were considered plausible if individuals had the same mtDNA haplotype (female-female dyads, male-male dyads, and mixed-sex dyads) and Y-haplotype (male-male dyads only) and PO dyads were considered plausible if individuals had the same mtDNA haplotype (female-female dyads) or Y-haplotype (male-male dyads). I did not determine the plausibility of mixed-sex PO dyads at this step, because the parent and the offspring had not yet been determined for PO dyads. Third, I revised relationships for applicable dyads based on findings from the previous two steps. Fourth, I determined the parent and the offspring for PO dyads based on the ages of individuals, whereby the older individual was the parent and the younger individual was the offspring. I determined the parent and the offspring for PO dyads with missing or ambiguous age data based on detailed consideration of the relationships among individuals. Also, at this step, I determined the plausibility of female-male PO dyads based on haplotypes, whereby they were considered plausible if the mother and the son had the same mtDNA haplotype; however, I could not determine the plausibility of male-female PO dyads based on haplotypes due to inheritance patterns. Fifth, I revised relationships for applicable dyads based on findings from the previous step. Sixth, I assessed the logical consistency of relationships by comparing them across three dyads that collectively comprised three individuals (i.e., A-B, B-C, and A-C). I employed the following rule for assessing the logical consistency of relationships: if A-B are FS and B-C are FS then A-C must be FS. I queried two FS dyads (A-B and B-C) and the relevant third dyad (A-C) and checked the relationship of the latter to assess the logical consistency of relationships. I determined which dyad had the logically inconsistent relationship for applicable cases. Seventh, I revised relationships for applicable dyads based on findings from the previous step. Much of this multistep approach was implemented using custom scripts in R (available upon request). Subsequently, I repeated steps two, four, and six. I generated summary statistics for overall and relationship-specific pairwise relatedness based on the revised ML-Relate results.

Breeding histories

I investigated PO dyads from the revised ML-Relate results and determined breeding histories for individual parents and breeding pairs (i.e., individual parents that shared offspring). I determined the number of offspring and the number of litters observed for individual parents and breeding pairs. The number of litters was uncertain for some individual parents and breeding pairs, because the year of birth was unknown for ≥ 1 offspring due to missing or ambiguous age data. Note that the numbers of offspring and litters observed were minimums, because only offspring and litters that were sampled could be detected. Also, I investigated the temporal distribution of litters for individual parents and breeding pairs with multiple litters. Additionally, I determined the number of mates observed for individual parents by counting the number of known breeding pairs and/or unknown breeding pairs to which they belonged; the latter was inferred by checking the haplotypes of their offspring, whereby multiple marker-specific haplotypes among offspring indicated multiple mates for them, although they might have had multiple mates with the same marker-specific haplotype. Note that the numbers of mates observed were minimums, because only offspring and litters that were sampled could be detected and thus used to determine the number of mates observed for individual parents.

Results

Female reproduction

I determined the reproductive status of 81 females, including 39 juveniles, 21 yearlings, and 21 adults. I observed 26 reproductive females, including two (1 adult and 1 juvenile) with implants, three (2 adults and 1 yearling) with fetuses, and 21 (16 adults, 2 yearlings, and 3 juveniles) with placental scars; I observed 55 non-reproductive females. The proportion of females that were reproductive differed significantly with respect to age class ($\chi^2 = 44.4$, $df = 2$, $P < 0.001$), whereby 10.3% of juveniles, 14.3% of yearlings, and 90.5% of adults were reproductive. Specifically, the proportion of females that were reproductive was significantly higher for adults than yearlings ($\chi^2 = 21.5$, $df = 1$, $P < 0.001$) or juveniles ($\chi^2 = 33.8$, $df = 1$, $P < 0.001$), but was similar for yearlings and juveniles ($\chi^2 = 0.002$, $df = 1$, $P = 0.966$). The proportion of females that were reproductive was generally high (≥ 88.9%) across breeding ages for adults (Figure 4.1). Breeding age of females ranged from less than one to nine years and the most commonly observed breeding age was two years (Figure 4.2). I estimated litter size for 18 reproductive females (14 adults, 3 yearlings, and 1 juvenile) based on counts of fetuses (*n* = 3) or placental scars (*n* = 15); I did not estimate litter size for six reproductive females (4 adults and 2 juveniles) with ambiguous placental scars. Mean (± SE) litter size of females was 6.2 ± 0.6 (range = 1—10) and the most commonly observed litter sizes were five and nine (Figure 4.3). Small sample size precluded assessment of age-specific differences in litter size; also, small sample size precluded assessment of whether the sex ratio of fetuses was at parity across litters. For comparison, the age-specific reproductive rates and mean litter sizes of female coyotes reported in relevant publications and this study are provided in Table 4.1.

Population age structure

I investigated the age structure of the study population using tooth-age data from 225 carcasses; most were harvested (*n* = 207), but some were road-killed (*n* = 9) or died of other causes (*n* = 9). The study population comprised 39% juveniles (*n* = 88), 25% yearlings (*n* = 57), and 36% adults

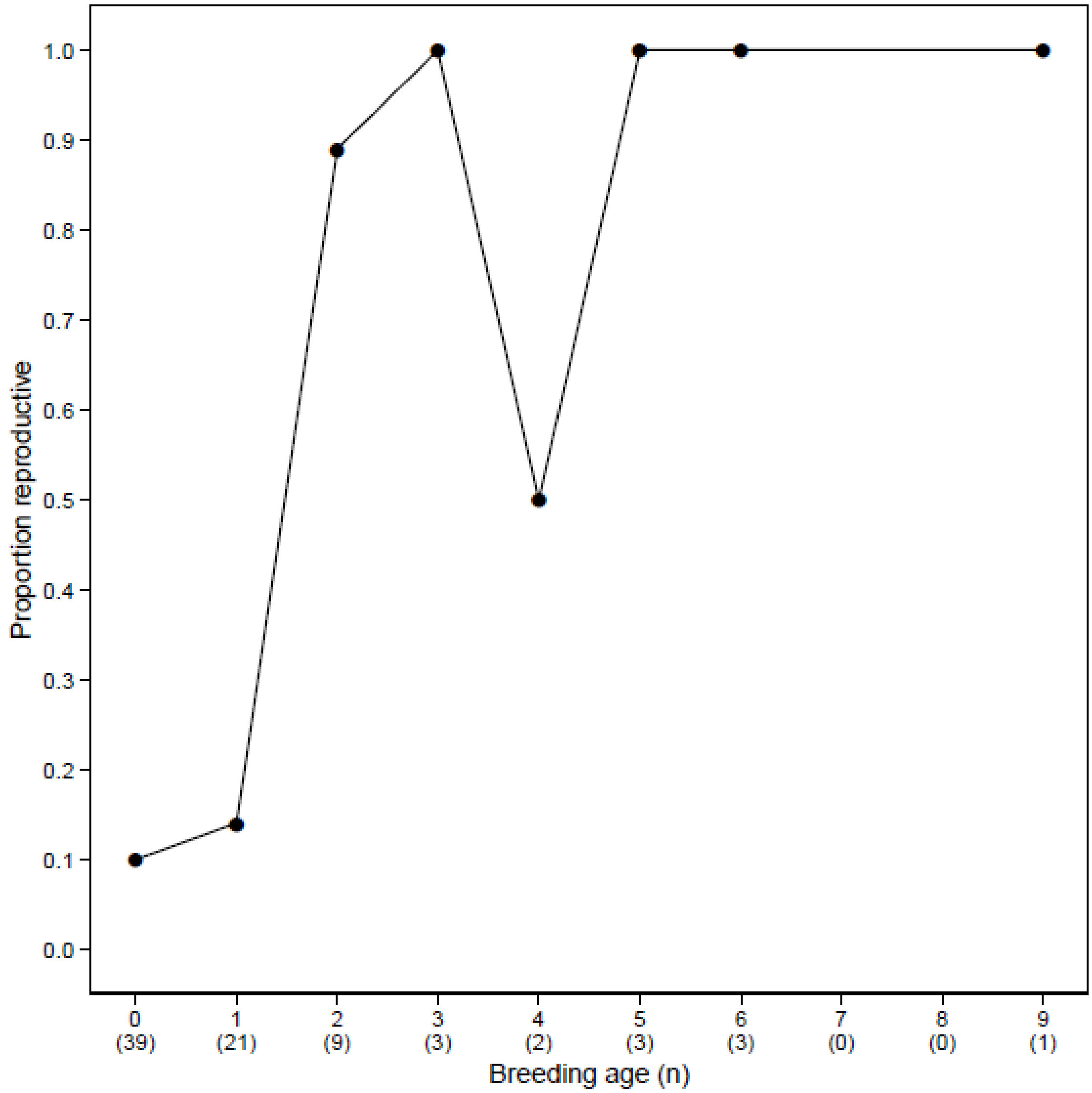

Figure 4.1. Proportion of female coyotes that were reproductive across breeding ages.

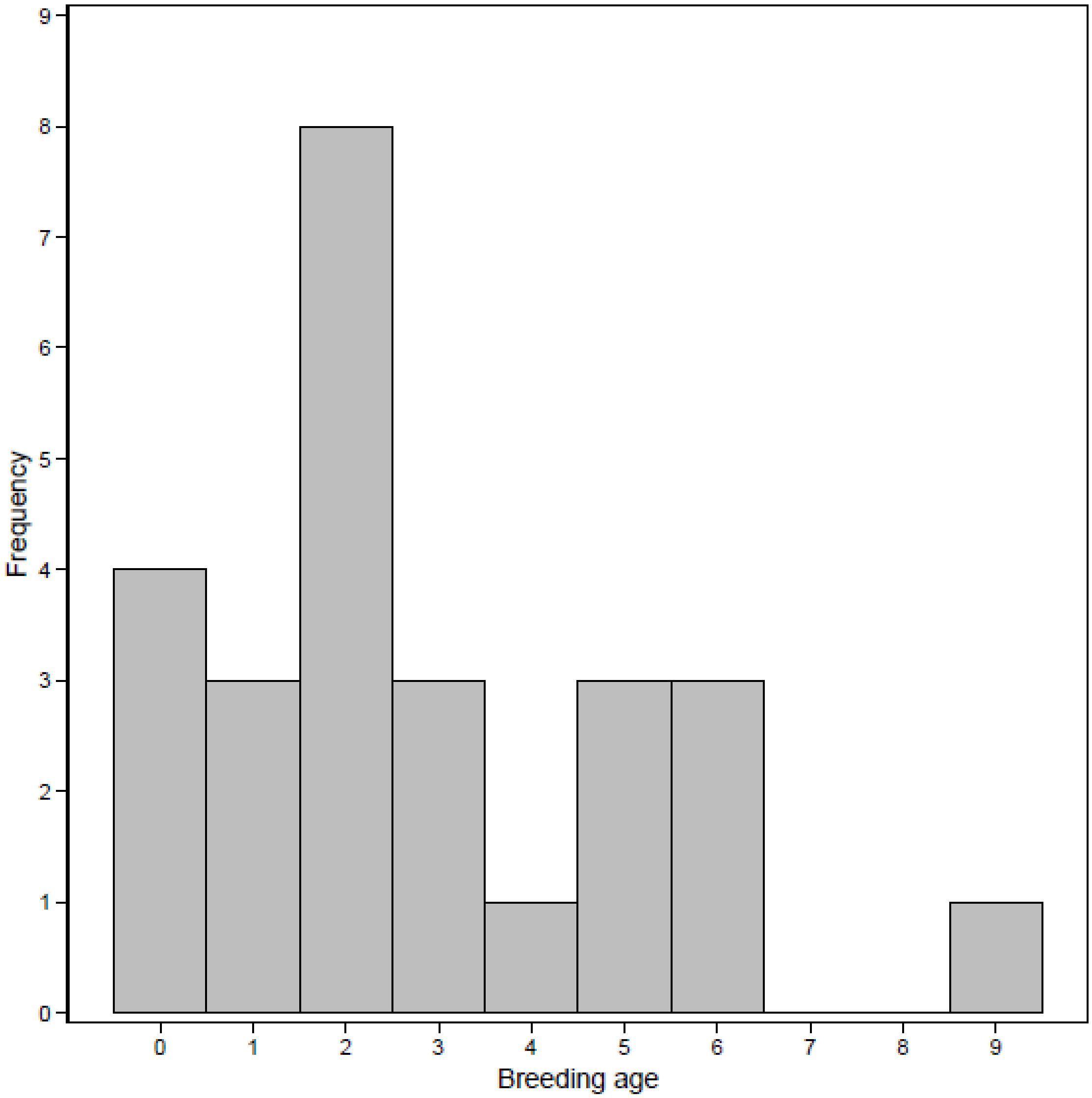

Figure 4.2. Frequency distribution of the breeding ages of female coyotes in Prince Edward County, Ontario, 2010–2013.

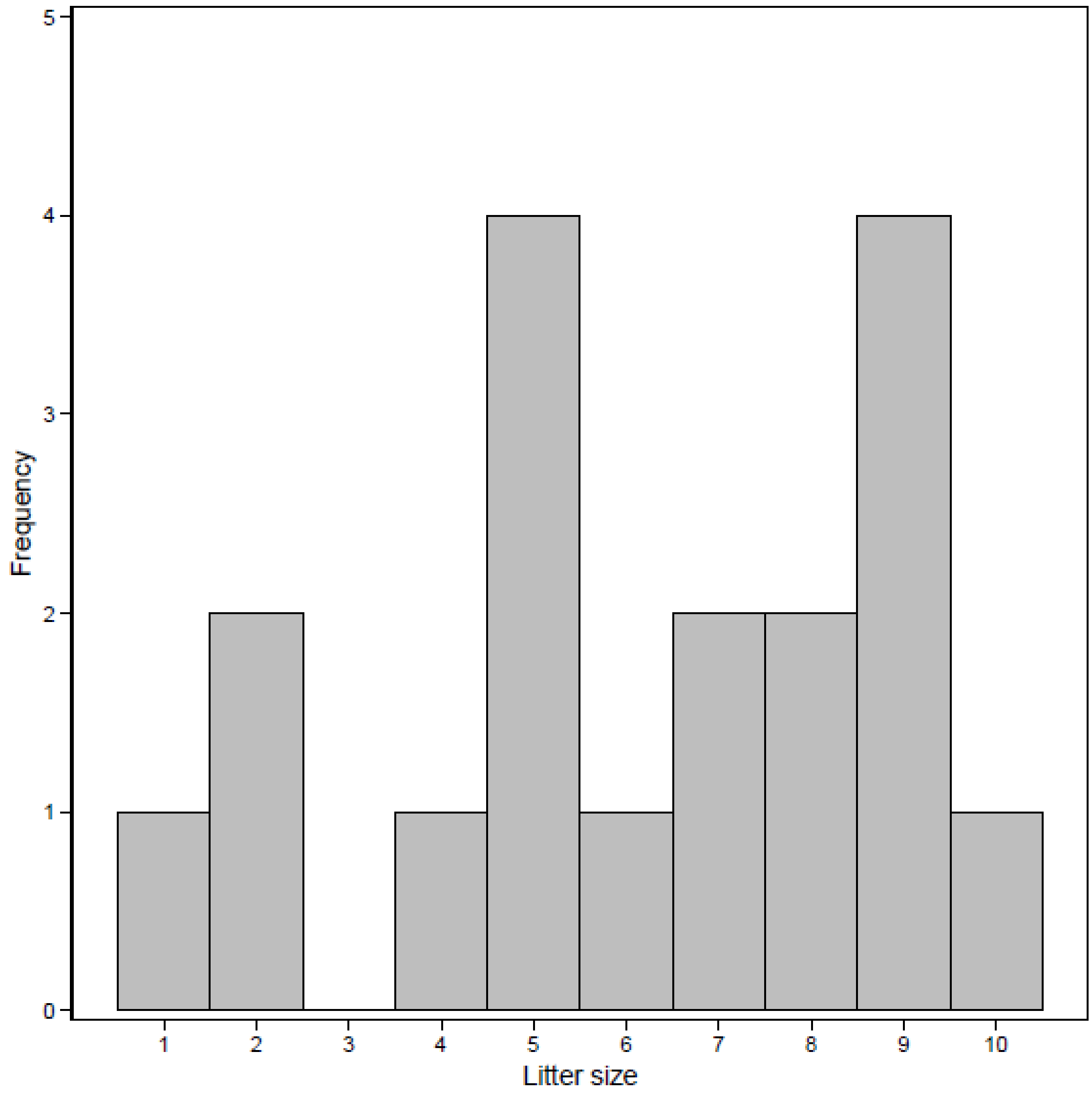

Figure 4.3. Frequency distribution of the litter sizes of female coyotes in Prince Edward County, Ontario, 2010–2013.

Table 4.1. Age-specific reproductive rates and mean litter sizes of female coyotes reported in relevant publications and this study.

Publication	Exploitation level*	Reproductive rate			Mean litter size§
		Juveniles	Yearlings	Adults	
Gese et al. 1989	Light	0%	n/a	100%	3.3
Windberg 1995	Light	2%	42%	65%	5.7
Dumond & Villard 2000	Light	0%	0%	40.9%	6.6
Gese 2005 (pre-removal)	Light	0%	n/a	n/a	3.3
Kilgo et al. 2017 (pre-removal)	Light†	0%	25%	39%	5.4
Nellis & Keith 1976	Moderate	14%	n/a	94%	5.8
Nelson & Lloyd 2005	Mod. to heavy	44%	56%	88%	4.9
this study	Mod. to heavy‡	10.3%	14.3%	90.5%	6.2
Knudsen 1976	Heavy	53%	71%	100%	6.2
Gese 2005 (post-removal)	Heavy	20%	n/a	n/a	6.3
Kilgo et al. 2017 (post-removal)	Heavy†	< 10%	29%	60%	7.0

*Taken from Jackson (2014) unless otherwise noted

†Inferred from publication

‡Determined based on several considerations (see Chapter 5)

§Refer to publication for method of determination (e.g., placental scars, fetuses, uterine swellings, litter sizes, and combinations thereof) and age classes included for determination

Note that the reproductive rate for adults includes yearlings if the reproductive rate is not available for yearlings.

(*n* = 80). Age of individuals in the study population ranged from less than one to 13 years (median = 1 year; mode = < 1 year). The study population was skewed towards individuals aged less than three years (Figure 4.4), which comprised 82% of individuals (Figure 4.5).

ML-Relate analysis

Mean (± SD) relatedness between individuals was 0.05 ± 0.09 (range = 0.00–0.79). Based on the initial ML-Relate results, the maximum likelihood relationships for the 79003 dyads included the following: 69400 U, 8508 HS, 761 FS, and 334 PO. Findings from the multistep approach are described in detail elsewhere (Appendix O). I made the following 328 revisions: 4 U to FS, 84 HS to FS, 2 HS to PO, 15 FS to U, 148 FS to HS, 16 FS to PO, 13 PO to HS, and 46 PO to FS. Based on the revised ML-Relate results, the maximum likelihood relationships for the 79003 dyads included the following: 69411 U, 8583 HS, 716 FS, and 293 PO. Findings from repeating steps two, four, and six of the multistep approach are described in detail elsewhere (Appendix O). Summary statistics for relationship-specific pairwise relatedness based on the initial ML-Relate results (Table 4.2) were similar to those for relationship-specific pairwise relatedness based on the revised ML-Relate results (Table 4.3). Prior to determining breeding histories for individual parents, I excluded a PO dyad that was implausible because the putative parent was a juvenile that died prior to the breeding period. I investigated 275 PO dyads to determine breeding histories for individual parents and breeding pairs.

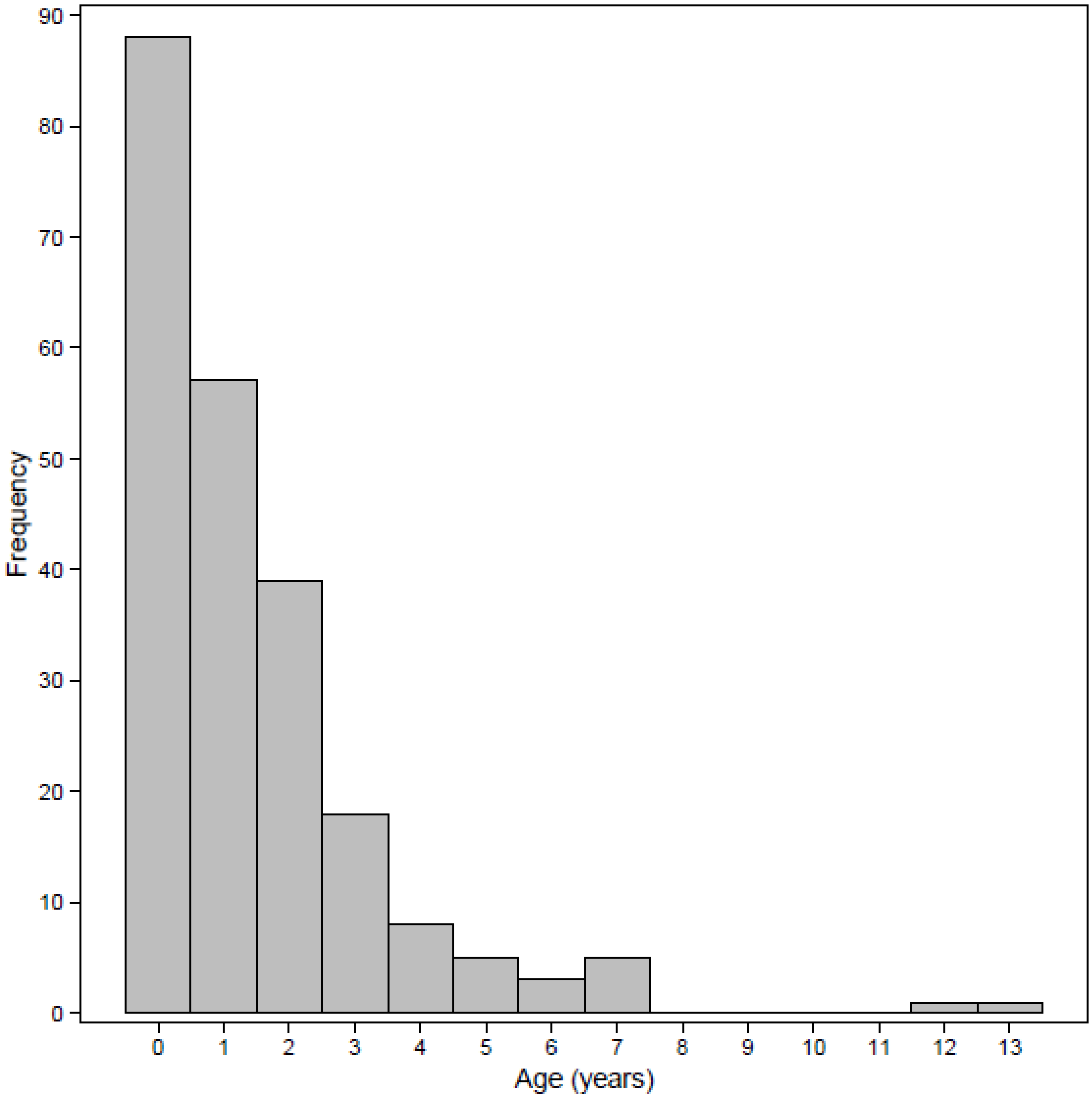

Figure 4.4. Frequency distribution of the ages of coyotes in Prince Edward County, Ontario, 2010–2013. Dataset was limited to 225 coyotes that were killed or died between November and April.

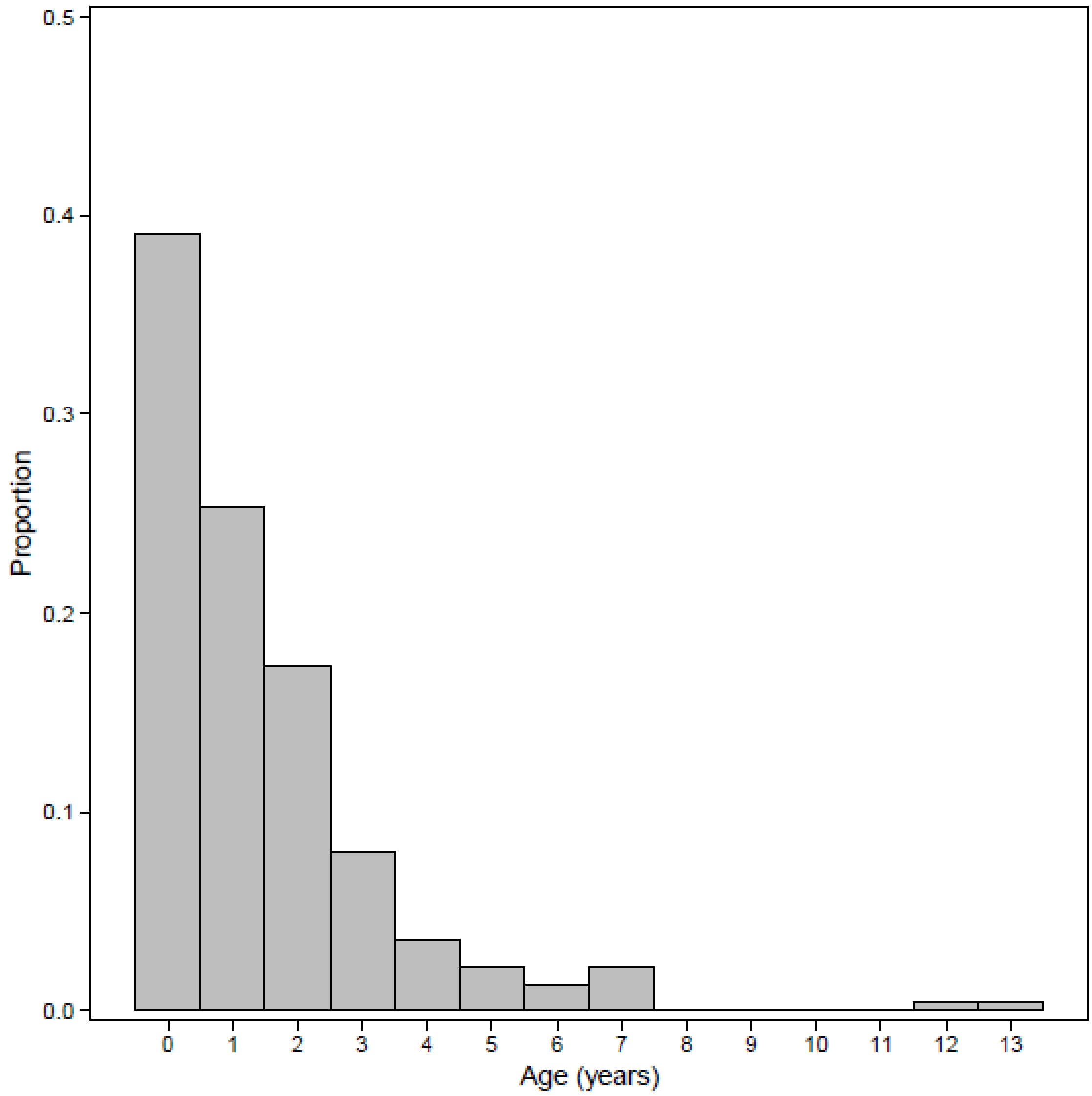

Figure 4.5. Proportion distribution of the ages of coyotes in Prince Edward County, Ontario, 2010–2013. Dataset was limited to 225 coyotes that were killed or died between November and April.

Table 4.2. Summary statistics for relationship-specific pairwise relatedness based on the initial ML-Relate results. Note that pairwise relatedness could be less than 0.50 for PO dyads due to null alleles or scoring issues.

Relationship	Frequency	Mean	Standard deviation	Minimum	Maximum
U	69400	0.03	0.04	0.00	0.34
HS	8508	0.20	0.06	0.06	0.45
FS	761	0.48	0.11	0.22	0.79
PO	334	0.52	0.04	0.45	0.68

Table 4.3. Summary statistics for relationship-specific pairwise relatedness based on the revised ML-Relate results. Note that pairwise relatedness could be less than 0.50 for PO dyads due to null alleles or scoring issues.

Relationship	Frequency	Mean	Standard deviation	Minimum	Maximum
U	69411	0.03	0.04	0.00	0.45
HS	8583	0.20	0.07	0.06	0.60
FS	716	0.48	0.12	0.08	0.79
PO	293	0.52	0.05	0.43	0.77

Breeding histories

I determined breeding histories for 58 individual parents (Appendix P) and 15 breeding pairs (Appendix Q); the former included 25 females, 31 males, and two individuals of undetermined sex, and the latter comprised 12 mothers and 14 fathers. The number of offspring observed for individual parents ranged from 1–18 (median = 3; mode = 1) and that for breeding pairs ranged from 1–12 (median = 6; mode = 1). The number of litters observed for individual parents ranged from 1–7 (median = 2; mode = 1) and that for breeding pairs ranged from 1–4 (median = 2; mode = 1); the number of litters was uncertain for 13 individual parents and five breeding pairs. Specifically, 1–2 litters were observed for 39 individual parents (67%) and 3–7 litters were observed for 19 individual parents (33%), and 1–2 litters were observed for ten breeding pairs (67%) and 3–4 litters were observed for five breeding pairs (33%).

I investigated the temporal distribution of litters for 30 individual parents and eight breeding pairs with multiple litters. Twenty individual parents and seven breeding pairs with multiple litters had them over consecutive years without any gap years between them. Specifically, seven individual parents and three breeding pairs had two litters over consecutive years, seven individual parents and two breeding pairs had three litters over consecutive years, five individual parents and two breeding pairs had four litters over consecutive years, and one individual parent had seven litters over consecutive years. One individual parent with multiple litters likely had them over consecutive years without any gap year between them. Specifically, this individual parent had three litters likely over consecutive years; however, this individual parent had one offspring for which the birth year was uncertain due to ambiguous age data, and therefore may have had three litters over partially consecutive years (one litter, then no litter, then two litters). Four individual parents with multiple litters had them over partially consecutive years with one to three gap years between them. Specifically, three individual parents had three litters over partially consecutive years (one litter, then no litter(s), then two litters) and one individual parent had five litters over partially consecutive years (one litter, then no litter, then four litters). One breeding pair with multiple litters had them over partially consecutive years with one gap year between them. Specifically, this breeding pair had three litters over partially consecutive years (one litter, then no litter, then two litters); however, this breeding pair had one offspring for which the birth year was unknown due to missing age data, and therefore may have had four litters over consecutive years. Five individual parents with multiple litters had them over non-consecutive years with one to three gap years between them. Specifically, four individual parents had two litters over non-consecutive years and one individual parent had three litters over non-consecutive years.

The number of mates observed for individual parents ranged from 1–3 (median = 1; mode = 1). Moreover, the number of mates observed for individual parents with multiple litters (n = 30) ranged from 1–3 (median = 1; mode = 1). Specifically, only one mate was observed for 25 individual parents with multiple litters (83%) and 2–3 mates were observed for five individual parents with multiple litters (17%).

Discussion

Females in the study population exhibited age-specific reproductive rates and litter sizes generally typical of those in exploited coyote populations. First, as predicted, > 70% (90.5%) of adults and > 10% (10.3%) of juveniles were reproductive, although the difference was negligible in the case of juveniles (but see below). Second, as predicted, mean litter size was > 4.5 (6.2).

Accordingly, increased reproductive rates and increased litter sizes may have offset losses due to harvest mortality. Also, there was at least some breeder turnover in the study population due to harvest mortality. First, as predicted, the number of litters observed for individual parents was relatively low (i.e., 1–2) in most cases (67%), but was relatively high (i.e., 3–7) in some cases (33%). Second, not as predicted, the number of mates observed for individual parents with multiple litters was only one in most cases (83%), but was 2–3 in some cases (17%). Many breeders survived to reproduce for multiple years and those that died were quickly replaced. Hereafter, I discuss my findings and explore them in the context of resilience to harvest for coyote populations. Furthermore, I discuss methodological considerations and relevant implications of my findings.

The reproductive rates of females in the study population differed with respect to age class, whereby a high proportion of adults (90.5%) were reproductive and low proportions of yearlings (14.3%) and juveniles (10.3%) were reproductive. Notably, Connolly and Longhurst (1975) included yearlings with respect to the proposed average reproductive rate of adult females in an unexploited coyote population; however, I separated yearlings and adults for assessment of reproductive rates. Consequently, not as predicted, < 70% of adults (52.4%) were reproductive when yearlings were included for assessment. Regardless, the reproductive rate of adult females in the study population was consistent with expectation for an exploited coyote population based on available data from more recent studies (discussed below). There has been a lack of consistency across studies with respect to whether or not yearlings were included with adults for assessments of reproductive rates (see Chambers 1992). Indeed, some studies have included yearlings with adults (e.g., Gier 1968; Nellis & Keith 1976; Gese et al. 1989) whereas other studies have separated yearlings and adults (e.g., Knudsen 1976; Windberg 1995; Nelson &

Lloyd 2005; Kilgo et al. 2017). Moreover, certain studies have separated individuals based on their age in years (e.g., Sacks 2005) or unique age classes (e.g., Dumond & Villard 2000). Nevertheless, studies have consistently separated adults (which may or may not have included yearlings) and juveniles for assessments of reproductive rates (e.g., Gier 1968; Knudsen 1976; Nellis & Keith 1976; Gese et al. 1989; Windberg 1995; Nelson & Lloyd 2005; Kilgo et al. 2017). Therefore, I made predictions regarding the reproductive rates of adults and juveniles, but made no prediction regarding the reproductive rate of yearlings. As a further matter, researchers need to exercise caution when interpreting the reproductive rates of young individuals reported in some studies (e.g., Gese 2005) due to confusion regarding whether they concern juveniles or yearlings. Pregnancy rates for juveniles are analogous to parturition rates for yearlings, because juveniles that become pregnant subsequently whelp when they become yearlings. The reproductive rate of yearlings reported in some studies is actually the reproductive rate of juveniles (e.g., Gese 2005); note that juveniles have been referred to as short-yearlings (e.g., Gier 1968).

Reproductive rates of coyotes vary geographically and over time (Jean & Bergeron 1984; Chambers 1992; Gese et al. 1996), particularly with respect to the level of exploitation (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). A high proportion of adult females (90.5%) and a non-zero proportion of juvenile females (10.3%) in the study population were reproductive, which may have been indicative of compensatory reproduction in response to decreased population density due to harvest mortality, whereby the proportion of females that were reproductive may have been increased due to reduced social constraints on breeding (Windberg 1995; Knowlton et al. 1999). However, no formal test of compensatory reproduction (e.g., comparing pre-exploitation and post-exploitation age-specific reproductive rates) was possible for the study population. Regardless of this obvious limitation, my finding that a high proportion of adult females (90.5%) and a non-zero proportion of juvenile females (10.3%) in the study population were reproductive was consistent with expectations for an exploited coyote population (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). Specifically, the reproductive rate of adult females in the study population was fairly similar to the reproductive rates of adult females reported for some moderately to heavily exploited coyote populations (Knudsen 1976; Nellis & Keith 1976; Nelson & Lloyd 2005) and generally higher than the reproductive rates of adult females reported for some lightly exploited coyote populations (Windberg 1995; Dumond & Villard 2000; but see Gese et al. 1989). Further, the reproductive rate of adult females in the study population was higher than the post-exploitation reproductive rate of adult females reported in a study that compared the pre-exploitation and post-exploitation reproductive rate of adult females (Kilgo et al. 2017). Also, the reproductive rate of juvenile females in the study population was lower than the reproductive rates of juvenile females reported for some moderately to heavily exploited coyote populations (Knudsen 1976; Nellis & Keith 1976; Nelson & Lloyd 2005), but was higher than the reproductive rates of juvenile females reported for some lightly exploited coyote populations (Gese et al. 1989; Windberg 1995; Dumond & Villard 2000). Further, the reproductive rate of juvenile females in the study population was fairly consistent with the post-exploitation reproductive rates of juvenile females reported in two studies that compared the pre-exploitation and post-exploitation reproductive rate of juvenile females (Gese 2005; Kilgo et al. 2017); notably, the pre-exploitation reproductive rate of juvenile females was zero in both studies. Accordingly, the study population may have compensated for harvest mortality via increased reproductive rates, but primarily with respect to adults rather than juveniles.

A low proportion of yearling females (14.3%) in the study population were reproductive, which may have been partly due to high dispersal and low settlement by yearlings (see below). Comparatively, the reproductive rate of yearling females in the study population was lower than the reproductive rates of yearling females reported for some moderately to heavily exploited coyote populations (Knudsen 1976; Nelson & Lloyd 2005), but was higher than the reproductive rate of yearling females reported for a lightly exploited coyote population (Dumond & Villard 2000; but see Windberg 1995). Although yearling females contributed to reproduction in the study population, similar to juvenile females, their contribution to reproduction was minor compared to that of adult females. Indeed, the reproductive rate of yearling females in the study population was lower than expected for an exploited coyote population; however, most studies of exploited populations have involved western coyotes rather than eastern coyotes (Jackson 2014). It is plausible that eastern coyotes, which have partial wolf ancestry, might exhibit delayed sexual maturity on average relative to western coyotes, considering that wolves attain sexual maturity at an older age than coyotes, but further investigation is required.

Litter sizes of coyotes vary geographically and over time (Jean & Bergeron 1984; Chambers 1992; Gese et al. 1996), particularly with respect to the level of exploitation (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). The mean litter size of females in the study population was high (6.2), which may have been indicative of compensatory reproduction in response to decreased population density due to harvest mortality, whereby litter sizes may have been increased due to reduced competition for food (Windberg 1995; Knowlton et al. 1999). However, no formal test of compensatory reproduction (e.g., comparing pre-exploitation and post-exploitation mean litter size) was possible for the study population. Moreover, food abundance in the study area was not considered, but was obviously important, because litter size of coyotes is determined by food abundance (Gier 1968). Notably, an increase in rabbit abundance confounded the effects of population reduction and an observed increase in litter size for a coyote population in Colorado (Gese 2005). Accordingly, the mean litter size of females in the study population may have been high as a result of the seemingly abundant prey and anthropogenic food sources in the study area rather than compensatory reproduction in response to decreased population density due to harvest mortality. Food abundance may not have been a limiting factor with respect to reproduction for coyotes in the study population, thus the capacity for compensatory reproduction in response to decreased population density due to harvest mortality may have been limited. Regardless of this potential confounding factor, my finding that the mean litter size of females in the study population was high (6.2) was consistent with expectation for an exploited coyote population (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). Specifically, the mean litter size of females in the study population was similar to or higher than the mean litter sizes of females reported for some moderately to heavily exploited coyote populations (Knudsen 1976; Nellis & Keith 1976; Nelson & Lloyd 2005) and generally higher than the mean litter sizes of females reported for some lightly exploited coyote populations (Gese et al. 1989; Windberg 1995; but see Dumond & Villard 2000). Furthermore, the mean litter size of females in the study population was fairly consistent with the post-exploitation mean litter sizes of females reported in two studies that compared pre-exploitation and post-exploitation mean litter size of females (Gese 2005; Kilgo et al. 2017). Accordingly, the study population may have compensated for harvest mortality via increased litter sizes.

Litter size was not estimated for six reproductive females with ambiguous placental scars. Specifically, it was uncertain which placental scars may have been from a current litter versus a previous litter and/or which placental scars may have been from a whelped pup versus a resorbed fetus. Possibly by coincidence, the potential litter size (taking into account uncertainty) was relatively low for most of the reproductive females with ambiguous placental scars. Thus, mean litter size may have been biased due to not estimating litter size for reproductive females with ambiguous placental scars. Furthermore, three reproductive females with placental scars had tissue residue associated with all but one of their placental scars; the estimated litter size for each of them was one less than the number of placental scars, because it was assumed that the placental scar without tissue residue represented a resorbed fetus, although this may not have been the case. Thus, mean litter size may have been biased due to underestimating litter size for three reproductive females. Regardless of potential biases with respect to mean litter size, the value presented herein (i.e., 6.2) seems reasonable for an exploited coyote population.

Telemetry data from radio-collared coyotes in the study population indicated that the dispersal rate was approximately 50% for juveniles and 100% for yearlings (data not shown). Therefore, the juveniles and yearlings that were reproductive were probably settled transients; however, I recorded only a few settlements by juvenile or yearling transients (see Chapter 2). Based on necropsy evidence (reproductive tracts of females), low proportions of juveniles and yearlings were reproductive; this may have been partly due to delayed dispersal in the case of juveniles but not in the case of yearlings. Breeding positions may have been saturated in the study population, despite harvest mortality of some breeders, because transients may have quickly filled vacant breeding positions (e.g., Gese et al. 1989; Gese 2005). Transients included individuals of all age classes, but older individuals may have been more competitive with respect to filling vacant breeding positions than younger individuals; this might explain why a high proportion of adults and a low proportion of yearlings were reproductive.

Considerable harvest mortality of coyotes occurred during the breeding period and the gestation period (see Chapter 3), which may have limited the compensatory potential of the study population. The loss of breeders prior to the breeding period may have a limited impact on recruitment, because transients may quickly fill vacant breeding positions (e.g., Gese et al. 1989; Gese 2005), but the loss of breeders during the breeding period may have a substantial impact on recruitment, because breeding females may fail to become pregnant if the loss of breeding males occurs prior to copulation. Moreover, the loss of pregnant females during the gestation period will obviously have a direct impact on recruitment, because litters will be lost. Indeed, four pregnant females were harvested in the study area; also, one pregnant female was road-killed in the study area. Recruitment into the study population was obviously reduced by the harvest mortality of some pregnant females. Regardless, the study population evidently achieved adequate recruitment to maintain a stable population size over time, despite harvest mortality; based on deer hunter questionnaire data, the relative abundance of coyotes in the study area was relatively stable over the years of the study (see Chapter 1).

The level of exploitation has been shown to influence the age structure of coyote populations (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). Unexploited or lightly exploited coyote populations are characterized by older age structures, whereas moderately to heavily exploited coyote populations are characterized by younger age structures (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). The age structure of the study population appeared to be somewhat intermediate to that of the lightly exploited coyote population and that of the highly exploited coyote population depicted in Knowlton et al. (1999). Thus, the study population was likely moderately exploited, evidently comprising predominantly younger individuals (64% were juveniles or yearlings and 82% were aged less than 3 years).

The number of litters observed for individual parents was relatively low (i.e., 1–2) in most cases (67%), but was relatively high (i.e., 3–7) in some cases (33%), and that for breeding pairs was relatively low (i.e., 1–2) in most cases (67%), but was relatively high (i.e., 3–4) in some cases (33%). Sampling of offspring was undoubtedly incomplete for most individual parents and breeding pairs, thus the number of litters observed for them was undoubtedly underestimated. Indeed, the number of litters observed for three females was known to be less than the actual number of litters that they had. One female with one litter was known to have whelped pups near the end of the study, thus it is not surprising that offspring from her additional litter were not sampled. Two females with multiple litters were both known to have had an additional litter prior to their death (based on placental scars), but offspring from their additional litter were not sampled. Accordingly, it was uncertain whether the number of litters observed for individual parents and breeding pairs was low in most cases because many of them did not survive to reproduce for multiple years and because many of them were disrupted due to harvest mortality, respectively, or because sampling of offspring was incomplete. Notably, most individual parents and breeding pairs with one litter were also those with only one offspring. Logically, the number of litters observed was constrained to one for individual parents and breeding pairs with only one offspring. Regardless, most individual parents and breeding pairs with multiple offspring had multiple litters, thus most individual parents and breeding pairs produced litters for multiple years. My findings demonstrate that individual parents and breeding pairs can produce litters for multiple years despite considerable harvest mortality occurring in a coyote population.

Most of the individual parents and breeding pairs with multiple litters had them over consecutive years rather than partially consecutive years or non-consecutive years (individual parents only). The number of litters was uncertain for some individual parents and breeding pairs with multiple litters. Moreover, offspring from possible additional litters of individual parents and breeding pairs may not have been sampled. Accordingly, some individual parents and breeding pairs with multiple litters may have had them and others over consecutive years rather than partially consecutive years (as previously noted for a breeding pair) or non-consecutive years (individual parents only), and some individual parents and breeding pairs with multiple litters may have had them and others over partially consecutive years rather than consecutive years (as previously noted for an individual parent) or non-consecutive years (individual parents only). Pedigree relationships between sampled individuals were used to confirm that individual parents and breeding pairs had a litter in a given year, but could not be used to confirm that they did not have a litter in a given year, because sampling of offspring was undoubtedly incomplete for most of them. My findings confirm that individual parents and breeding pairs had multiple litters over consecutive years, but do not confirm that they had multiple litters over partially consecutive years or non-consecutive years (individual parents only).

The number of mates observed for individual parents with multiple litters was only one in most cases (83%), but was two or three in some cases (17%). Sampling of offspring was undoubtedly incomplete for most individual parents, thus the number of mates observed for them was potentially underestimated, because additional litters produced with different mates may not have been observed. Accordingly, it was uncertain whether the number of mates observed for individual parents with multiple litters was only one in most cases because many of them did not suffer mate loss or because sampling of offspring was incomplete. Notably, the majority of individual parents with one mate were also those with only one litter. Logically, the number of mates observed was constrained to one for individual parents with only one litter (except in the case of polyandry). Regardless, some individual parents with multiple litters had multiple mates, thus some individual parents likely suffered mate loss. However, many individual parents with multiple litters had one mate, thus many individual parents evidently exhibited social monogamy. My findings provide further genetic evidence that coyotes are typically socially monogamous (Bekoff & Gese 2003; Hennessy et al. 2012), but more importantly they demonstrate that pair-bonds can persist for multiple years despite considerable harvest mortality occurring in a coyote population.

Seven breeding pairs with multiple litters had them over consecutive years without any gap years between them, and thus were stable for multiple years, confirming that coyotes in the study population were socially monogamous. However, there were six individual parents with multiple mates, although one of them was an apparent case of polyandry (discussed below). Thus, I documented multiple cases of breeder turnover, which could have involved mate loss (coyotes: Gese et al. 1996; Hennessy et al. 2012; red wolves: Sparkman et al. 2012; Hinton et al. 2015b), mate abandonment (kit foxes: Ralls et al. 2007), or mate displacement (coyotes: Andelt 1985; Gese et al. 1996; red wolves: Sparkman et al. 2012; kit foxes: Ralls et al. 2007). Indeed, I documented two cases of mate loss. In the first case, a known breeding pair had three litters, but then the known male breeder was harvested; subsequently, the known female breeder paired with a new known male breeder, and then the new known breeding pair had two litters, although one of them was not whelped (i.e., fetuses found in the reproductive tract). In the second case, a known breeding pair had three litters, but then the known male breeder was harvested; subsequently, the known female breeder paired with a new unknown male breeder, and then the new unknown breeding pair had one litter. In both cases, there were no gap years between litters produced by the different breeding pairs. Accordingly, although some breeders suffered mate loss in a given biological year, they were able to acquire another mate quickly and have a litter the next biological year. This finding is consistent with the findings of two other studies (Gese et al. 1996; Hennessy et al. 2012). Also, I documented a case of either mate abandonment or mate displacement. Specifically, a known female breeder and a known male breeder had a litter in a given year and subsequently each of them had a litter with a different known breeder in a later year; therefore, mate loss was not a possibility. The impact of mate abandonment on reproduction is similar to that of mate loss, because a breeding pair is disrupted and thus reproduction may not occur unless a new breeding pair is formed. The impact of mate displacement on reproduction is negligible, because a breeding pair is not disrupted (i.e., a new breeding pair is formed implicitly) and thus reproduction will likely still occur. Given the level of exploitation in the study area, it seems likely that breeder turnover in the study population primarily involved mate loss rather than mate abandonment or mate displacement.

Breeder turnover in the study population was not observed as frequently as expected. Sampling of offspring was incomplete for most individual parents, thus the number of mates observed for them was potentially underestimated, because additional litters produced with different mates may not have been observed. Accordingly, breeder turnover in the study population may have occurred more frequently than observed based on limited sampling. Regardless, some breeding pairs were stable for multiple years, which may have been the result of spatially variable harvest intensity across the study area. Indeed, breeding pairs in some areas were likely subject to low harvest mortality risk and breeding pairs in some areas were likely subject to high harvest mortality risk. Offspring from breeding pairs with territories located in areas of low harvest intensity may have been likely to disperse, because of limited breeding opportunities (Gese et al. 1996), and subsequently they may have been likely to fill vacant breeding positions in territories located in areas of high harvest intensity, because of breeder turnover (Gese 2005).

Known breeding pairs (*n* = 15) exhibited low pairwise relatedness values. Mean (± SD) relatedness between individuals of known breeding pairs was 0.08 ± 0.11 (range = 0.00–0.31); the maximum likelihood relationship for known breeding pairs was either unrelated (*n* = 10) or half-siblings (*n* = 5). Known breeding pairs in the study population were not highly related, indicating that non-breeding individuals must have dispersed to find unrelated mates and that breeding individuals must have selected unrelated mates. Accordingly, dispersers (i.e., unrelated transients) rather than pack associates (i.e., related residents) were likely responsible for filling vacant breeding positions in the study population. Presumably coyotes can recognize close kin based on visual and olfactory cues. Thus, coyotes can avoid inbreeding by selecting unrelated mates, which are presumably readily available and often encountered in coyote populations, because they typically include substantial numbers of transients. Williams et al. (2003) reported findings that were consistent with limited inbreeding in a coyote population as a consequence of transients filling vacant territories and breeding positions; this scenario seems plausible for the study population. Hennessy et al. (2012) found that breeding pairs in their study population were not highly related, supporting the notion that coyotes generally avoid inbreeding. There is also evidence of inbreeding avoidance in other social carnivores, including grey wolves (vonHoldt et al. 2008) and red wolves (Sparkman et al. 2012). Researchers have proposed various potential mechanisms for inbreeding avoidance in social carnivores, including absolute avoidance of breeding with related pack members in the case of grey wolves (vonHoldt et al. 2008), reproductive suppression prior to dispersal in the case of red wolves (Sparkman et al. 2012), and dispersal in the cases of both grey wolves (vonHoldt et al. 2008) and red wolves (Sparkman et al.

2012). Indeed, dispersal is likely important with respect to inbreeding avoidance in coyotes (Harrison 1992a; Gese et al. 1996); this was likely the case in the study population.

Multiple paternities were observed for the offspring of a female with only one litter. Specifically, four offspring were observed for the mother and three of them (offspring 1–3) had the same father, but one of them (offspring 4) had a different father. The primary father was genetically excluded as a parent of offspring 4 based on allele mismatches at three loci and the secondary father was genetically excluded as a parent of offspring 1–3 based on allele mismatches at three or more loci; despite an allele mismatch at one locus that showed evidence of a null allele, the secondary father was not genetically excluded as a parent of offspring 4. Notably, the fathers were full-siblings, but the primary father was older than the secondary father. The natal territory of the fathers was adjacent to the territory of the mother; therefore, it seems plausible that she bred with both of them. Accordingly, an apparent case of polyandry was observed in the study population; however, this finding should be treated with caution, given the lack of confirmatory field observation and the potential that genotyping errors may have resulted in pedigree relationships being falsely excluded. Additionally, the only individual parent with three mates was a male that may have bred with two females in a specific year on two separate occasions. The male had one known female mate that was identified based on shared offspring, but also had two unknown female mates that were identified based on two mtDNA haplotypes being observed among his offspring from litters that were not produced by the known female mate. First, in one specific year, the male apparently had offspring with both unknown female mates, based on two mtDNA haplotypes being observed among three offspring that were born in that specific year. Second, in one specific year, the male apparently had offspring with the known female mate and an unknown female mate, based on the known female mate being genetically excluded as a parent for one of two offspring that were born in that specific year. Accordingly, an apparent case of polygyny was observed in the study population; however, this finding should be treated with caution, given the lack of confirmatory field observation and the potential that inaccurate age estimates may have resulted in offspring that were actually born in different years appearing to have been born in the same year. Regardless, although social monogamy is typically observed for coyotes (Bekoff & Gese 2003; Hennessy et al. 2012), polyandry and polygyny may be observed in rare cases (Gese et al. 1996; Way et al. 2001), which my findings apparently confirm.

I compared 24 females that were classified as reproductive based on necropsy evidence (i.e., reproductive tract) against 26 females that were determined to be parents based on pedigree relationships to check for consistency. Overall, 38 females were considered. Twelve females were classified as reproductive based on necropsy evidence and also determined to be parents based on pedigree relationships. Twelve females were classified as reproductive based on necropsy evidence but were not determined to be parents based on pedigree relationships, presumably because their offspring were not sampled. Eleven females were determined to be parents based on pedigree relationships but were not necropsied. Notably, three females were determined to be parents based on pedigree relationships but were classified as non-reproductive based on necropsy evidence; one of those females was a juvenile that died prior to the breeding period (excluded for determining breeding histories) and two of those females were yearlings that had no placental scars (included for determining breeding histories). It is unlikely that placental scars would have faded in less than one year for the two females (Kennelly 1978), thus they likely had not bred and were not parents. Regardless, excluding the two females did not impact the range/median/mode for the number of litters/mates observed for individual parents and did not impact the conclusions drawn from the breeding histories of individual parents.

I previously determined the social status of radio-collared coyotes in the study population (see Chapter 2) and subsequently investigated the social status of 23 radio-collared coyotes that were determined to be parents based on pedigree relationships. Across those parents, I observed 21 residents, six transients, and one individual of undetermined social status; note that three individuals were classified as resident and transient during discrete periods and two individuals were classified as resident twice during discrete periods. The social status of parents at the time of reproduction (i.e., breeding, gestation, and/or whelping) with respect to their sampled offspring was unknown for most parents, because their monitoring period did not overlap the reproduction period and/or their sampled offspring were born before or after their monitoring period. However, I determined that seven parents were residents at the time of reproduction with respect to their sampled offspring from a specific litter. Furthermore, two females were residents at the time of reproduction with respect to their known offspring from a specific litter that was not sampled (i.e., pups found at den/whelp site) and one female was probably a resident at the time of reproduction with respect to its known offspring from a specific litter that was not sampled (i.e., pups evidenced by placental scars). Interestingly, for parents that were transients, their sampled offspring were born before their monitoring period, suggesting that they were likely previously residents that had abandoned their territory or had been displaced from their territory; this was likely the case for one female and one male, both of which were adults. Territory abandonment could occur as a consequence of mate loss (e.g., Bowen 1982; Gese 1998) if an individual is forced to leave its territory to find a new mate or as a consequence of mate displacement if an individual is relegated to non-breeder status and voluntarily leaves its territory to find a new mate. Territory displacement could occur as a consequence of mate loss if an individual cannot effectively defend its territory against intruders or as a consequence of mate displacement (e.g., Andelt 1985; Way 2010) if an individual is forced to leave its territory by the new mate. Notably, for parents that were transients, although their sampled offspring were not born after their monitoring period, two of them apparently bred post-settlement based on field observation or radio-collar data (see Chapter 2). My findings confirm that typically residents but not transients can hold breeding positions and successfully whelp (Messier & Barrette 1982; Knowlton et al. 1985; Gese 2001), but transients can fill vacant breeding positions (Gese et al. 1989; Gese 2005).

The efficacy of liberal harvest for reducing coyote abundance and livestock depredation needs to be addressed. Liberal harvest of coyotes is essentially a means of uncoordinated and indiscriminate lethal control. Based on the reproduction of coyotes, it is apparent that uncoordinated and indiscriminate lethal control of coyotes is unlikely to be effective in reducing coyote abundance or livestock depredation. Coyote populations can respond to decreasing density by increasing their reproductive output (Knowlton et al. 1999). Accordingly, liberal harvest may prove ineffective in reducing coyote abundance, other than temporarily, because increased reproductive rates and increased litter sizes may offset losses due to harvest mortality (Gese 2005; Kilgo et al. 2017). Breeders are more likely than non-breeders to be responsible for repeated depredations on specific farms (Sacks et al. 1999a; Blejwas et al. 2002, 2006), primarily because breeders must provision food for their pups. Although breeder turnover can be exacerbated by harvest mortality, breeders can survive to reproduce for multiple years and those that die can be quickly replaced, most likely by transients (Gese et al. 1989; Gese 2005). Therefore, liberal harvest may prove inefficient in reducing livestock depredation. Management strategies that seek to reduce conflicts between coyotes and livestock should consider non-lethal alternatives and/or targeted lethal control, which may prove effective (Knowlton et al. 1999).

In conclusion, the compensatory potential of harvested animal populations may be explained partly by life history strategy. This is particularly true for predators that exhibit high fecundity and low survival, such as coyotes, which are commonly subject to lethal control efforts of questionable efficacy. Therefore, wildlife managers should consider the reproduction of such predators when assessing the efficacy of management practices.

Chapter 5

General Discussion

Summary of findings

This dissertation provides a detailed assessment of the population dynamics of eastern coyotes in southeastern Ontario. I combined field work, laboratory work, and genetic profiling to investigate the social status dynamics and space-use patterns, the survival and cause-specific mortality, and the reproduction and breeding histories of eastern coyotes from a harvested population in southeastern Ontario during 2010–2013. I found that coyotes in the study population included residents and transients, which exhibited disparate space-use patterns, and that they underwent transitions in social status, both because of and despite harvest mortality (see Chapter 2). Transients exhibited extensive space-use relative to residents, potentially encountering vacant territories and/or breeding positions, and some transients became residents, potentially filling vacant territories and/or breeding positions (see Chapter 2). Accordingly, the study population demonstrated the potential to compensate for harvest mortality via source-sink dynamics and/or buffering reproductive capacity. I found that residents and transients in the study population experienced different cumulative mortality risks, but they encountered similar harvest-related threats on average (see Chapter 3). Residents exhibited greater survival than transients, probably partly because of the benefits of holding a territory, and transients seemingly exhibited greater vulnerability to harvest than residents, probably partly because their movements exposed them to greater cumulative mortality risks over time (see Chapter 3). Accordingly, harvest mortality disproportionately impacted the non-reproductive segment of the study population and thus may have failed to substantially limit reproduction, and thus recruitment. I found that females in the study population exhibited age-specific reproductive rates and litter sizes generally typical of those in exploited coyote populations, which may have been indicative of compensatory reproduction (see Chapter 4). Accordingly, increased reproductive rates and increased litter sizes may have offset losses due to harvest mortality. I found that there was at least some breeder turnover in the study population due to harvest mortality, but many breeders survived to reproduce for multiple years and those that died were quickly replaced (see Chapter 4). Hereafter, I provide a synthesis of my findings and suggestions for future research. Also, I provide management recommendations and concluding remarks.

Synthesis of findings

Research has revealed that demographic parameters typically differ between unexploited coyote populations and exploited coyote populations (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). Thus, premised upon the assumption that exploited coyote populations compensate for harvest mortality, knowledge of demographic parameters can facilitate inference as to whether specific coyote populations might be compensating for harvest mortality. The study population exhibited demographic parameters characteristic of exploited coyote populations (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). I considered the study population to have been moderately to heavily exploited, based on several considerations. First, the study population exhibited a younger age structure that appeared to be somewhat intermediate to that of the lightly exploited coyote population and that of the highly exploited coyote population depicted in Knowlton et al. (1999). Second, adults and juveniles exhibited similar survival rates, which was consistent with lower adult survival rates and higher juvenile survival rates. Third, with respect to females, most adults (90.5%) were reproductive and some yearlings (14.3%) and some juveniles (10.3%) were reproductive, which was generally consistent with higher reproductive rates. Fourth, the mean litter size of females in the study population was high, which was consistent with larger litter sizes. The study population was demographically consistent with an exploited coyote population. Thus, compensation for harvest mortality likely occurred to some extent in the study population.

The relative abundance of coyotes in the study area was relatively stable over the years of the study, despite liberal harvest, suggesting that demographic compensation may have occurred in the study population. Potential processes of demographic compensation may have included compensatory mortality (i.e., reduced natural mortality), compensatory natality (i.e., increased reproductive output), and source-sink dynamics (i.e., density-dependent dispersal). I was unable to document conclusive evidence that the study population compensated for harvest mortality via any of these processes, primarily because I did not quantify coyote density and food abundance across the study area. Quantification of coyote density across the study area was precluded due to the following issues: (1) limitations with respect to trapping effort and capture success resulted in territory sizes for less than a majority of the territories across the study area; and (2) inconsistent snow-tracking conditions during winter resulted in insufficient data for estimation of pack sizes of known territories. Quantification of food abundance across the study area was precluded due to the following issues: (1) limitations with respect to personnel available for additional field work such as small mammal trapping to estimate prey density across the study area; and (2) anthropogenic food sources were readily available across the study area and difficult to quantify. Density-dependence underlies these processes; therefore, data on coyote density is required to document conclusive evidence of these processes. Coyote density is primarily determined by food abundance (Gier 1968); therefore, data on food abundance is required to control for its potential confounding effects on demographic parameters (Gese 2005). Regardless of the limitations of my study, I documented plausible evidence that the study population may have compensated for harvest mortality to some extent via each of these processes.

The harvest mortality rate was high but the natural mortality rate was low in the study population, suggesting that compensatory mortality may have occurred. However, harvest mortality and natural mortality overlapped temporally in the study population, thus harvest mortality must have been at least partially additive to natural mortality. Thus, I documented plausible evidence that partial compensatory mortality may have occurred in the study population in response to harvest. The mean litter size of females was high in the study population, suggesting that compensatory natality may have occurred. However, some pregnant females in the study population were harvested, thus recruitment must have been reduced to some extent by harvest mortality. Thus, I documented plausible evidence that partial compensatory natality may have occurred in the study population in response to harvest. Notably, prey and anthropogenic food sources were seemingly abundant in the study area, thus density-dependence related to food resources may have been trivial for the study population. As such, the low natural mortality rate and the high mean litter size in the study population may have been the result of abundant food resources rather than partial compensatory responses to harvest. Regardless, it is plausible that the study population may have compensated for harvest mortality to some extent via both decreased natural mortality and increased litter size.

The reproductive rate of adult females was high in the study population, such that they were reproducing at near maximum capacity. However, the reproductive rates of yearling females and juvenile females were low in the study population, suggesting that social constraints on breeding must have been maintained to some extent. Accordingly, notwithstanding the aforementioned caveats, my findings suggest that the study population may have compensated for harvest mortality to some extent via increased reproductive rates, but primarily with respect to adults rather than yearlings or juveniles.

The disparate space-use patterns of residents and transients in the study population indicated the potential for source-sink dynamics in response to harvest. Transients overlapped multiple territories of residents and thus were likely to encounter vacant territories and/or breeding positions. Indeed, some transients settled and thus may have filled vacant territories. Moreover, two transients settled and subsequently exhibited evidence of reproductive behavior and thus may have filled vacant breeding positions. Accordingly, I documented plausible evidence that source-sink dynamics may have occurred in the study population in response to harvest, whereby transients may have repopulated areas depleted by harvest and buffered the reproductive capacity of the study population. However, conclusively demonstrating source-sink dynamics in response to harvest would have required clearly demonstrating density-dependent dispersal and settlement in the study population with respect to harvest mortality. This would have required a larger sample size to more adequately document dispersal and settlement rates, as well as data on coyote density and food abundance across the study area. Regardless, my findings suggest that the study population may have compensated for harvest mortality to some extent via source-sink dynamics.

Genetic analysis revealed that known breeding pairs were generally unrelated and that breeders were able to acquire another mate quickly after suffering mate loss, implying that transients likely filled vacant breeding positions and thus buffered the reproductive capacity of the study population. Accordingly, notwithstanding the aforementioned caveats, my findings suggest that the study population likely compensated for harvest mortality to some extent via source-sink dynamics.

Coyotes were liberally harvested in the study area and a common perception among hunters and trappers was that regularly killing coyotes contributed to population reduction and might eventually eliminate coyotes from the study area. However, my assessment of population size and annual reproductive output relative to the overall annual mortality rate, which is based on empirical data, indicates that this perception was not justified. I estimated that there were approximately 75 territories within the study area and the mean litter size of females in the study population was 6.2. Assuming that each territory comprised two breeders and at least 80% of territories produced a litter in a given biological year, it follows that $75 \times 2 = 150$ breeders produced $75 \times 6.2 \times 0.8 = 372$ pups on average in a given biological year, such that the study population comprised at least $150 + 372 = 522$ coyotes on average at the start of a given biological year. Thus, based on annual reproductive output, the study population could have tolerated an overall annual mortality rate of $372 / 522 = 0.71$ and still have maintained a stable population size. The overall annual mortality rate of adults and yearlings combined was only 0.60; note that overall annual mortality of juveniles was not estimated, but mortality of coyotes did not differ with respect to age class during the cold season, and most mortality occurred during the cold season. Evidently, harvest mortality, in addition to other causes of mortality, was insufficient to cause a decline in population size (but see Chapter 3). The population size estimate above is almost certainly an underestimate, because it does not account for non-breeding pack associates and transients, which were known to occur in the study population. This assessment ignores the issues of social status and immigration/emigration, but it serves the purpose of demonstrating that liberal harvest in the study area was insufficient to achieve population reduction, other than temporarily within a given biological year, because annual reproductive output likely offset losses due to harvest mortality, in addition to losses due to other causes of mortality. Liberal harvest certainly resulted in the removal a large number of individuals from the study population annually, but reproduction replaced those individuals annually to maintain a relatively stable population size. Even if, under different circumstances, liberal harvest of coyotes in the study area could reduce their population size, then compensatory mechanisms likely would stabilize their population size at some equilibrium (likely determined by food availability) and prevent continued decline. Based on the population trend, liberal harvest of coyotes in the study area has not achieved desired levels of population reduction and therefore cannot be considered effective in that regard.

Despite the limitations of my findings, it is clear that the study population was at least moderately resilient to harvest. It is likely that multiple mechanisms of compensation occurred in the study population to achieve this resilience. However, the extent to which specific mechanisms of compensation likely contributed to this resilience is unclear. This study highlights the considerable burden of evidence required to demonstrate potential processes of demographic compensation in coyote populations, but also reinforces that these processes must exist in order to explain the observed resilience of coyote populations.

Based on my findings, eastern coyotes in southeastern Ontario are resilient to harvest, but the extent to which this resilience is characteristic across their range remains uncertain. Notably, eastern coyotes in agricultural and rural landscapes likely experience similar conditions to many western coyotes due to high prey density and availability of anthropogenic food sources, which might result in comparable resilience between them due to similar population densities. However, eastern coyotes in forest landscapes likely experience poorer conditions than many western coyotes due to low prey density and lack of anthropogenic food sources, which might result in diminished resilience for forest-dwelling eastern coyotes relative to western coyotes due to lower population densities. Thus, the comparability of resilience between eastern coyotes and western coyotes might depend on the landscape in which the former occurs. Further, research has shown that eastern coyotes in habitats with high deer density are genetically more wolf-like than those in habitats with low deer density (Monzón et al. 2014). Eastern coyotes that are genetically more wolf-like may be less resilient to harvest than eastern coyotes that are genetically less wolf-like, but it remains unclear how the partial wolf ancestry of eastern coyotes might influence their resilience to harvest across their range. Differences in prey and habitat across the range of eastern coyotes may influence natural selection for more coyote-like or more wolf-like forms, potentially resulting in differential resilience of eastern coyotes across their range. Additional studies of eastern coyotes across their range are needed to provide insight on this issue of interest that has potential evolutionary consequences.

Conceptual model

The response of a coyote population to harvest may involve multiple processes of demographic compensation that collectively help to maintain the coyote population at its carrying capacity. These processes include compensatory mortality (CM), compensatory natality (CN), and source-sink dynamics (SSD). Logically, the level of response achieved via these processes should be commensurate with the level of harvest, within biological limits, in order to achieve population stability despite harvest. Multiple factors are likely involved in determining the likelihood and strength of these processes in a coyote population, but harvest mortality and food abundance are likely the most important. A conceptual model of the potential responses of a coyote population to harvest (Figure 5.1) facilitates consideration of how certain factors are predicted to affect the likelihood and strength of these processes in a coyote population. If harvest mortality is low and food abundance is low, then CM and CN are likely to occur and be weak, but if harvest mortality is high and food abundance is low, then CM and CN are likely to occur and be strong. Regardless of whether harvest mortality is low or high, if food abundance is high, then CM and CN are unlikely to occur, because density-dependence, which underlies these processes, will not be in effect, thus any reduction in coyote density will not improve the survival or reproduction of the remaining individuals. Regardless of whether food abundance is low or high, if harvest mortality is low, then SSD is likely to occur and be weak, but if harvest mortality is high, then SSD is likely to occur and be strong. If food abundance is approximately uniform across the landscape then it is unlikely to influence SSD, because density-dependent dispersal and settlement is expected to operate with respect to harvest mortality, which largely determines the distribution of vacant territories and breeding positions. However, the degree of spatial variability in harvest mortality is likely to influence how SSD occur in a coyote population. If harvest mortality is spatially heterogeneous within a coyote population, then SSD is likely to occur via local dispersal and settlement, whereby individuals disperse from areas of low harvest mortality and settle in areas of high harvest mortality. If harvest mortality is spatially homogeneous within a coyote population, then SSD is likely to occur via immigration of individuals from surrounding areas, assuming harvest mortality is lower there. Also, the timing of harvest is important to consider, because it can affect the compensatory potential of a coyote population. If harvest mortality occurs prior to natural mortality and reproduction, then CM and CN can be complete, but if harvest mortality occurs during the same period of time as natural mortality and reproduction,

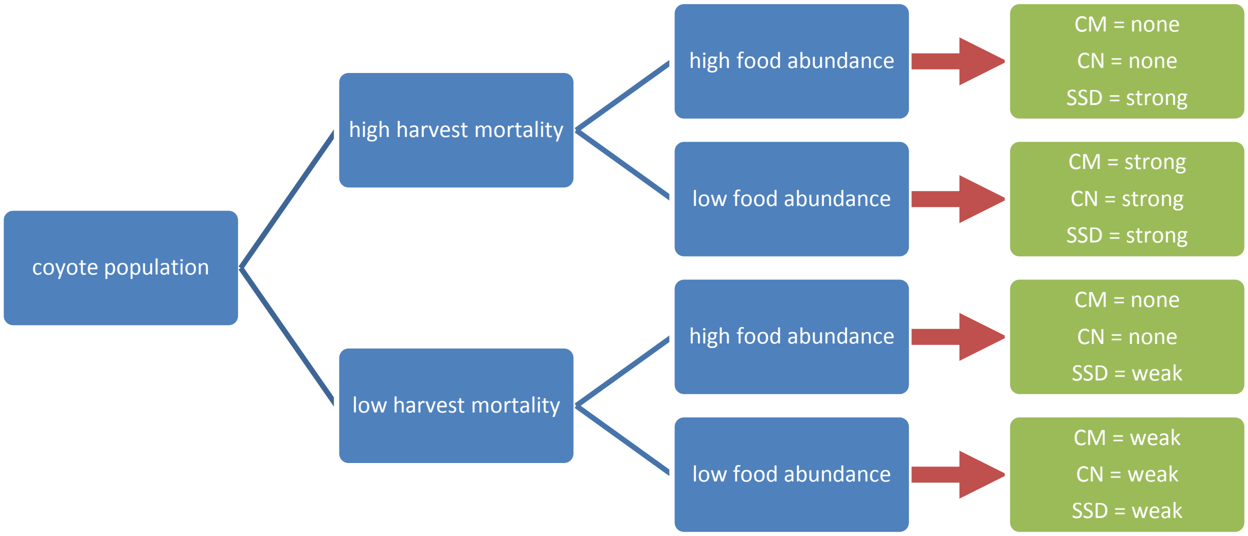

Figure 5.1. Conceptual model of the potential responses of a coyote population to harvest. Abbreviations: CM = compensatory mortality; CN = compensatory natality; SSD = source-sink dynamics.

then CM and CN can only be partial, and if harvest mortality occurs after natural mortality and reproduction, then CM and CN cannot occur. The extent to which the above predictions hold true may be revealed through meta-analysis of demographic data from multiple coyote populations.

Future research

Certain studies of coyote populations have documented evidence of compensatory responses to exploitation by humans (e.g., Gese 2005; Kilgo et al. 2017). However, these studies have involved experimental treatments, whereby coyote populations were subjected to exploitation and their demographic parameters were compared between pre-removal and post-removal periods to document evidence of compensatory responses. While such studies have been valuable and have contributed greatly to better understanding of coyote resilience, I believe that it is important for future studies of coyote populations to investigate variation in their demographic parameters in response to changes in actual harvest pressure rather than experimental treatments. The response of coyote populations to harvest is likely to be both spatially and temporally dynamic, changing over space and time as harvest intensity and food abundance fluctuate. Studying many different coyote populations under natural conditions and using similar methods might facilitate a meta-analysis of their response to exploitation by humans, which should improve understanding of the mechanisms by which coyote populations achieve resilience to harvest. Foremost, future studies of coyote populations and their resilience to harvest should attempt to quantify coyote density and food abundance, which is a prerequisite for documenting conclusive evidence of potential processes of demographic compensation in coyote populations. Although surely challenging, quantifying spatial and temporal variation in coyote density with respect to harvest intensity, while controlling for food abundance, should be a priority for future research.

Many studies of coyote populations have been of relatively short duration (e.g., 2–3 years) and involved relatively few radio-collared individuals. Short-term studies of coyote populations, with small sample sizes, have been useful for understanding the population dynamics of coyotes, but their limitations have precluded obtaining insight regarding some interesting aspects of such. Long-term studies of coyote populations, under natural conditions and with large sample sizes, might facilitate further investigation of the following: 1) spatial variability in settlement rates in the context of source-sink dynamics in response to spatial variability in harvest intensity; 2) the potential relationship between settlement probability and degree of nomadism for transients, considered in the context of spatial variability in harvest intensity; 3) the relative survival of residents and transients in relation to the degree of spatial heterogeneity in harvest intensity; 4) the potential relationship between survival probability and degree of nomadism for transients, considered in the context of spatial variability in harvest intensity. Although costly, long-term studies of coyote populations, under natural conditions and with large sample sizes, should be a priority for future research.

Management recommendations

Promoting liberal harvest of coyotes is essentially a means of implementing uncoordinated and indiscriminate lethal control. This type of management strategy can involve implementation of year-round hunting and trapping seasons, but perhaps most controversially can also specifically involve sport hunting with hounds and calling contests. Promoting liberal harvest of coyotes is offered as a means to reduce coyote abundance, particularly under the guise of preventing and/or curtailing livestock depredation, but also to limit predation on game species and alleviate public safety concerns. However, the efficacy of liberal harvest for reducing coyote abundance and livestock depredation is questionable. Based on the findings of this study and other available evidence, it is apparent that uncoordinated and indiscriminate lethal control of coyotes is unlikely to be effective in reducing coyote abundance or livestock depredation. For instance, transients can fill vacant territories following the removal of residents (Knowlton 1972; Gese 2005), thereby rendering any local reduction in coyote abundance temporary, and transients can fill vacant breeding positions following the removal of residents (Gese et al. 1989; Gese 2005), thereby preventing reductions in the reproductive capacity of the coyote population. Moreover, coyote populations can offset losses due to harvest mortality via increased reproductive rates and increased litter sizes (Knowlton et al. 1999; Gese 2005; Jackson 2014; Kilgo et al. 2017). Harvest mortality can disproportionately impact transients relative to residents (this study; Gese et al. 1989; Harrison 1992a), but transients are less likely than residents to repeatedly depredate livestock on specific farms (Sacks et al. 1999a; Blejwas et al. 2002, 2006), thus liberal harvest likely involves removal of many non-offending coyotes, which has been shown to be ineffective at reducing livestock depredation (Conner et al. 1998; Sacks et al. 1999a). Further, breeders are more likely than non-breeders to repeatedly depredate livestock on specific farms (Sacks et al. 1999a; Blejwas et al. 2002, 2006), but breeders can survive to reproduce for multiple years despite liberal harvest and those that die can be quickly replaced (this study; Gese et al. 1989; Gese 2005), thus liberal harvest is likely to be inefficient at reducing livestock depredation. Management strategies that promote liberal harvest of coyotes with the objective of reducing coyote abundance and livestock depredation are misguided and unlikely to be effective long-term, because coyote populations can effect demographic compensation for harvest mortality and many of the individual coyotes that repeatedly depredate livestock may not be removed through liberal harvest. Accordingly, management strategies that seek to reduce conflicts between coyotes and livestock should consider non-lethal alternatives and/or targeted lethal control, which may prove effective (Knowlton et al. 1999). Specifically, greater consideration should be given to the importance of livestock husbandry practices, adequate fencing, deterrent devices, and aversive conditioning. Targeted lethal control of coyotes can be effective in preventing and/or curtailing livestock depredation in certain situations, but it should be implemented only when and where it is necessitated by livestock depredation. Continually killing coyotes on farms when it is not necessary may lead to sinks, thereby inviting continual ingress from surrounding sources. Importantly, if territorial coyotes that do not depredate livestock live near a farm, then killing them should be discouraged, because doing so might result in other coyotes that do depredate livestock replacing them (Sacks et al. 1999a).

Conclusions

My findings provide further insights into eastern coyote populations and their resilience to harvest. Hopefully my findings will serve to better inform management strategies for eastern coyotes. The persistence of eastern coyotes across their range, despite attempts by humans to control them, suggests that both human-coyote conflicts and livestock-coyote conflicts are likely to remain persistent management issues in northeastern North America. Indeed, eastern coyotes are there to stay, thus humans must strive to better co-exist with them. This means implementing management strategies that: 1) seek to prevent conflicts whenever and wherever possible, 2) advocate the preferential use of non-lethal techniques to deal with problem coyotes, and 3) implement lethal control in a coordinated and selective manner only when and where necessary. Management strategies should not promote liberal harvest of coyotes as a means to reduce coyote abundance or livestock depredation.

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Appendices

Appendix A. Details of seasonal space-use analysis of residents.

For residents, I generated seasonal fixed kernel home ranges similarly as described elsewhere (see Chapter 2). I defined two seasons of similar duration: (1) the warm season spanned May 1–October 31 (184 days) and coincided with warm months when crops were grown and vegetative cover was relatively abundant; and (2) the cold season spanned November 1–April 30 (181 days) and coincided with cold months when crops were harvested and vegetative cover was relatively scarce. I identified excursions and omitted them from the overall dataset for applicable residents prior to generating seasonal home ranges. I generated seasonal home ranges for residents with datasets that spanned > 4 weeks. I retained seasonal home ranges that plateaued or spanned ≥ 90 days. I performed a paired samples *t*-test to test for seasonal differences in home range size of residents; I examined a normal quantile-quantile plot of the paired differences and confirmed that they were normally distributed. The home range size of residents did not differ significantly between seasons (t = -1.2, df = 12, P = 0.25).

Appendix B. Details of radio-collared coyotes in Prince Edward County, Ontario, 2010–2013. Abbreviations: F = female; M = male; A = adult; Y = yearling; J = juvenile. Asterisks indicate individuals that were recaptured. Not applicable (n/a) means that the individual was still alive at the time of censoring (i.e., emigration from the greater study area, radio-collar drop-off/fall-off, radio-collar failure, or termination of the study) and was not known to have died during the study.

Animal ID	Collar type	Sex	Age class	Capture date	Mortality date
PEC001	GPS	M	A	2010-05-27	n/a
PEC002	GPS	M	Y	2010-06-03	2011-02-12
PEC003	VHF	F	Y	2010-06-09	2012-07-28
PEC004	GPS	M	Y	2010-06-16	2010-11-30
PEC005	GPS	M	Y	2010-06-18	n/a
PEC006	GPS	F	A	2010-06-23	2011-03-20
PEC007	GPS	M	A	2010-06-25	2011-02-06
PEC008	GPS	M	A	2010-06-28	2010-07-18
PEC009	GPS	M	A	2010-07-01	2011-02-11
PEC010	VHF	F	A	2010-07-01	2010-12-04
PEC011	GPS	F	Y	2010-07-02	2011-02-02
PEC012	GPS	M	Y	2010-07-11	2012-02-18
PEC013	VHF	M	A	2010-07-11	2011-02-12
PEC014	GPS	M	Y	2010-07-14	n/a
PEC015	GPS	F	A	2010-07-15	n/a
PEC016	VHF	M	J	2010-07-18	2010-07-31
PEC017	VHF	M	Y	2010-07-19	2012-08-10
PEC018	GPS	M	A	2010-07-22	2011-01-02
PEC019	GPS	F	A	2010-07-23	2011-05-25
PEC020	GPS	M	A	2010-07-24	2011-01-03
PEC021	VHF	M	J	2010-08-02	2011-03-19
PEC022	GPS	M	Y	2010-08-10	2010-08-10
PEC023	GPS	M	J	2010-08-19	2011-03-27
PEC024	GPS	F	Y	2010-08-30	2010-10-29
PEC025	VHF	F	J	2010-09-12	2012-02-11
PEC026	VHF	M	J	2010-09-14	n/a
PEC027	GPS	M	Y	2010-09-16	n/a
PEC027*	GPS	M	A	2011-10-20	n/a
PEC028	GPS	M	Y	2010-09-21	n/a

Appendix B (continued).

Animal ID	Collar type	Sex	Age class	Capture date	Mortality date
PEC029	GPS	M	A	2010-09-26	2010-12-31
PEC030	GPS	M	J	2010-10-01	2011-02-26
PEC031	GPS	M	J	2010-10-04	n/a
PEC032	GPS	F	A	2010-10-07	2011-08-01
PEC032*	GPS	F	A	2011-05-20	2011-08-01
PEC033	GPS	F	J	2010-10-08	n/a
PEC034	GPS	F	Y	2010-10-13	n/a
PEC035	GPS	F	A	2010-10-13	2011-01-11
PEC036	GPS	F	A	2010-10-19	2010-11-04
PEC037	GPS	M	A	2010-10-22	2011-12-17
PEC038	GPS	F	J	2010-10-31	n/a
PEC039	GPS	M	J	2010-11-16	2012-02-04
PEC040	GPS	M	A	2011-05-17	2011-07-30
PEC041	GPS	M	A	2011-05-17	2011-12-14
PEC042	GPS	F	Y	2011-05-19	2012-02-26
PEC043	GPS	M	A	2011-05-31	2011-12-02
PEC044	GPS	F	Y	2011-06-09	2012-02-06
PEC045	VHF	F	J	2011-06-30	2011-12-11
PEC046	VHF	M	J	2011-07-08	n/a
PEC047	GPS	F	A	2011-07-13	n/a
PEC048	VHF	M	J	2011-07-15	2012-09-24
PEC049	GPS	M	A	2011-07-16	2012-07-05
PEC050	VHF	F	J	2011-07-17	n/a
PEC051	VHF	M	J	2011-07-24	2012-03-07
PEC052	GPS	M	Y	2011-07-24	n/a
PEC053	GPS	F	A	2011-07-24	2011-12-10
PEC054	GPS	F	Y	2011-07-31	n/a
PEC055	VHF	M	J	2011-08-02	n/a
PEC056	VHF	F	J	2011-08-06	n/a
PEC057	VHF	F	J	2011-08-09	2012-11-12
PEC058	VHF	M	J	2011-08-09	2011-12-29
PEC059	GPS	M	Y	2011-08-10	2012-02-27
PEC060	VHF	F	J	2011-08-10	n/a
PEC061	VHF	M	J	2011-08-10	n/a
PEC062	VHF	M	J	2011-08-10	2012-07-05
PEC063	VHF	F	J	2011-08-11	2012-04-29
PEC064	VHF	F	J	2011-08-13	2013-02-17

Appendix B (continued).

Animal ID	Collar type	Sex	Age class	Capture date	Mortality date
PEC065	VHF	M	J	2011-08-15	n/a
PEC066	GPS	M	A	2011-08-15	2012-02-15
PEC067	VHF	M	J	2011-08-21	2011-10-12
PEC068	GPS	F	A	2011-08-21	n/a
PEC069	VHF	M	J	2011-08-26	2012-02-16
PEC070	GPS	F	A	2011-08-27	n/a
PEC071	GPS	M	A	2011-08-27	2011-08-27
PEC072	VHF	M	J	2011-09-01	2011-12-11
PEC073	VHF	M	J	2011-09-09	2011-10-21
PEC074	GPS	F	A	2011-09-10	n/a
PEC075	VHF	F	J	2011-09-11	n/a
PEC076	VHF	F	J	2011-09-11	2013-01-31
PEC077	VHF	M	J	2011-09-13	2011-09-29
PEC078	VHF	F	J	2011-09-13	2012-06-22
PEC079	GPS	M	J	2011-09-14	n/a
PEC080	GPS	M	J	2011-09-15	n/a
PEC081	VHF	F	J	2011-09-15	n/a
PEC081*	GPS	F	Y	2012-09-12	n/a
PEC082	GPS	M	J	2011-09-16	n/a
PEC083	GPS	M	Y	2011-09-21	n/a
PEC084	VHF	F	J	2011-09-22	n/a
PEC085	VHF	F	J	2011-09-23	2013-02-17
PEC086	GPS	M	A	2011-09-25	2012-01-20
PEC087	GPS	F	A	2011-09-26	2012-02-15
PEC088	GPS	M	A	2011-09-27	n/a
PEC089	GPS	F	A	2011-09-30	2013-01-26
PEC090	GPS	M	A	2011-09-30	2012-02-06
PEC091	GPS	M	J	2011-10-03	2012-02-26
PEC092	GPS	M	A	2011-10-06	n/a
PEC093	GPS	M	J	2011-10-14	2011-12-19
PEC094	GPS	M	J	2011-10-16	2012-01-16
PEC095	GPS	M	A	2011-10-16	n/a
PEC096	VHF	M	A	2011-10-21	2012-01-28
PEC097	VHF	M	J	2011-10-30	2012-07-29
PEC098	VHF	M	Y	2011-11-02	2012-02-04
PEC099	VHF	F	J	2011-11-08	n/a
PEC100	VHF	M	Y	2011-11-11	2012-01-15

Appendix B (continued).

Animal ID	Collar type	Sex	Age class	Capture date	Mortality date
PEC101	GPS	M	A	2012-05-12	2012-12-07
PEC102	GPS	F	Y	2012-05-16	2012-05-20
PEC103	GPS	M	A	2012-05-17	2013-01-22
PEC104	GPS	F	A	2012-06-17	2013-03-02
PEC105	GPS	F	A	2012-06-21	2013-01-22
PEC106	GPS	M	A	2012-06-23	n/a
PEC107	GPS	M	Y	2012-07-01	n/a
PEC108	GPS	F	A	2012-07-02	n/a
PEC109	VHF	F	J	2012-07-05	2012-07-15
PEC110	GPS	M	A	2012-07-09	2013-03-09
PEC111	VHF	F	J	2012-07-28	2013-02-10
PEC112	GPS	F	A	2012-08-01	2012-12-09
PEC113	GPS	F	Y	2012-08-04	n/a
PEC114	GPS	F	Y	2012-08-06	2013-03-02
PEC115	VHF	F	J	2012-08-08	n/a
PEC116	GPS	F	Y	2012-08-10	2013-05-03
PEC117	VHF	F	Y	2012-08-12	n/a
PEC118	VHF	F	J	2012-08-13	2013-02-02
PEC119	VHF	F	J	2012-08-20	2012-10-01
PEC120	GPS	M	A	2012-08-24	2013-03-25
PEC121	VHF	M	J	2012-08-25	2012-10-08
PEC122	GPS	F	A	2012-09-02	2013-01-21
PEC123	VHF	M	J	2012-09-07	n/a
PEC124	VHF	M	J	2012-09-07	n/a
PEC125	VHF	F	J	2012-09-07	2012-10-26
PEC126	VHF	M	J	2012-09-07	2012-10-20
PEC127	VHF	F	J	2012-09-08	2013-03-02
PEC128	VHF	F	J	2012-09-08	2012-12-25
PEC129	GPS	M	Y	2012-09-13	2013-03-02
PEC130	VHF	M	J	2012-09-13	2013-01-28
PEC131	GPS	M	A	2012-09-15	n/a
PEC132	VHF	M	J	2012-09-16	n/a
PEC133	VHF	F	J	2012-09-19	n/a
PEC134	VHF	M	J	2012-09-19	n/a
PEC135	GPS	F	Y	2012-09-28	n/a
PEC136	VHF	F	J	2012-09-28	n/a
PEC137	GPS	M	A	2012-09-29	n/a

Appendix B (continued).

Animal ID	Collar type	Sex	Age class	Capture date	Mortality date
PEC138	VHF	M	J	2012-10-02	2013-03-02
PEC139	VHF	F	J	2012-10-09	2013-01-26
PEC140	GPS	M	Y	2012-10-11	2013-01-29
PEC141	GPS	F	A	2012-10-14	n/a
PEC142	VHF	F	J	2012-10-15	n/a
PEC143	VHF	M	J	2012-10-16	n/a
PEC144	VHF	F	Y	2012-10-20	2013-02-13
PEC145	VHF	M	J	2012-10-21	2012-12-29
PEC146	VHF	M	J	2012-10-26	2013-02-06
PEC147	GPS	M	A	2012-10-28	2012-11-09

Appendix C. Details of transitions in social status of radio-collared coyotes in Prince Edward County, Ontario, 2010–2013. Abbreviations: F = female; M = male; A = adult; Y = yearling; J = juvenile.

Animal ID	Transition #	Transition type	Transition date	Sex	Age class
PEC003	1	resident-transient	2011-02-26	F	Y
PEC003	2	transient-resident	2011-08-01	F	A
PEC009	1	resident-transient	2010-12-10	M	A
PEC017	1	transient-resident	2012-01-21	M	A
PEC020	1	transient-resident	2010-10-27	M	A
PEC026	1	resident-transient	2011-12-17	M	Y
PEC029	1	transient-resident	2010-11-19	M	A
PEC034	1	resident-transient	2011-02-19	F	Y
PEC038	1	resident-transient	2010-12-14	F	J
PEC039	1	resident-transient	2010-12-24	M	J
PEC045	1	resident-transient	2011-11-13	F	J
PEC047	1	resident-transient	2011-10-06	F	A
PEC047	2	transient-resident	2012-03-08	F	A
PEC049	1	transient-resident	2012-04-30	M	A
PEC050	1	resident-transient	2012-02-09	F	J
PEC051	1	resident-transient	2011-12-17	M	J
PEC059	1	resident-transient	2012-01-20	M	Y
PEC062	1	resident-transient	2011-09-11	M	J
PEC062	2	transient-resident	2012-06-01	M	Y
PEC063	1	resident-transient	2011-09-07	F	J
PEC064	1	resident-transient	2012-02-23	F	J
PEC065	1	resident-transient	2012-02-27	M	J
PEC069	1	resident-transient	2011-09-06	M	J
PEC078	1	resident-transient	2012-03-15	F	J
PEC081	1	resident-transient	2012-11-10	F	Y
PEC085	1	resident-transient	2011-12-03	F	J
PEC089	1	resident-transient	2012-02-02	F	A
PEC090	1	resident-transient	2011-11-28	M	A
PEC093	1	resident-transient	2011-10-24	M	J
PEC094	1	resident-transient	2012-01-04	M	J
PEC098	1	resident-transient	2011-12-08	M	Y
PEC105	1	resident-transient	2012-11-26	F	A
PEC112	1	resident-transient	2012-11-02	F	A

Appendix C (continued).

Animal ID	Transition #	Transition type	Transition date	Sex	Age class
PEC115	1	resident-transient	2012-12-20	F	J
PEC115	2	transient-resident	2013-04-12	F	J
PEC117	1	transient-resident	2012-10-18	F	Y
PEC120	1	resident-transient	2012-10-04	M	A
PEC127	1	resident-transient	2013-02-17	F	J
PEC129	1	resident-transient	2012-12-16	M	Y
PEC136	1	resident-transient	2012-11-30	F	J
PEC137	1	transient-resident	2012-11-26	M	A
PEC141	1	resident-transient	2012-12-25	F	A
PEC142	1	resident-transient	2012-11-23	F	J
PEC144	1	resident-transient	2012-11-26	F	Y

Appendix D. Details of resident home ranges and transient home ranges. Superscript letters indicate residents that shared the same territory. Asterisks indicate residents that were excluded from statistical analyses.

Animal ID	Social status	Fix interval (minutes)	Time span (days)	Locations	Home range size (km^2)	Figure panel
PEC001[a]	resident	180	170	1314	23.0	2.3A
PEC002[a]	resident	180	169	1226	17.8	2.3A
PEC004	transient	180	89	689	260.0	2.4A
PEC005	transient	180	174	1353	261.5	2.4A
PEC007	transient	180	193	1538	99.6	2.4A
PEC009	resident	180	152	1207	10.5	2.3A
PEC009	transient	180	59	471	87.8	2.4A
PEC011	transient	180	213	1646	139.5	2.4A
PEC012	transient	180	304	2330	69.7	2.4A
PEC014	resident	180	365	2806	12.4	2.3A
PEC015	resident	180	326	2171	27.0	2.3A
PEC018	transient	180	162	1224	237.6	2.4A
PEC019	resident	180	147	1055	14.7	2.3A
PEC020	transient	180	93	673	279.8	2.4A
PEC023*	resident	180	218	1557	11.1	2.3A
PEC024	transient	180	56	421	129.8	2.4A
PEC027	resident	180	245	1908	4.4	2.3A
PEC027*	resident	180	86	660	6.1	2.3B
PEC028	transient	180	79	607	188.7	2.4A
PEC029	transient	180	52	418	91.0	2.4A
PEC030*	resident	180	147	1151	11.0	2.3A
PEC032[b]	resident	180	203	1542	12.3	2.3A
PEC035	resident	180	86	680	10.6	2.3A
PEC037	resident	180	365	2643	14.4	2.3A
PEC039	transient	180	280	1965	434.2	2.4A
PEC041	resident	180	204	1457	14.4	2.3B
PEC042	transient	180	282	2216	230.9	2.4B
PEC043	resident	180	183	1400	9.9	2.3B
PEC044	transient	180	92	676	143.0	2.4B
PEC047	transient	180	154	1184	226.5	2.4B
PEC047	resident	180	125	827	21.6	2.3B

Appendix D (continued).

Animal ID	Social status	Fix interval (minutes)	Time span (days)	Locations	Home range size (km2)	Figure panel
PEC049	transient	180	283	2226	290.5	2.4B
PEC049	resident	180	66	518	8.4	2.3B
PEC053	transient	180	138	1072	157.3	2.4B
PEC054	transient	180	268	2031	89.6	2.4B
PEC059[b]	resident	180	162	1276	12.5	2.3B
PEC059	transient	180	37	296	82.5	2.4B
PEC066	resident	180	178	1389	9.3	2.3B
PEC074[c]	resident	180	362	2607	12.4	2.3B
PEC079[c]*	resident	180	363	2832	6.4	2.3B
PEC080[d]*	resident	180	362	2869	13.3	2.3B
PEC081	transient	180	222	1734	121.8	2.4C
PEC082[c]*	resident	180	363	2831	5.8	2.3B
PEC083	resident	180	363	2834	15.6	2.3B
PEC086	transient	180	115	910	34.1	2.4B
PEC087	transient	180	141	1120	113.3	2.4B
PEC088[d]	resident	180	301	2372	15.5	2.3B
PEC090	resident	180	56	449	1.9	2.3B
PEC090	transient	180	70	556	28.7	2.4B
PEC091*	resident	180	145	1142	5.2	2.3B
PEC092	resident	180	317	2345	17.9	2.3B
PEC093	transient	180	56	429	464.0	2.4B
PEC095	transient	180	114	891	160.3	2.4B
PEC101	resident	180	208	1577	14.9	2.3C
PEC103	resident	180	248	1930	21.6	2.3C
PEC104	transient	180	133	1038	106.4	2.4C
PEC105[e]	resident	180	157	1157	5.8	2.3C
PEC105	transient	180	57	368	61.4	2.4C
PEC106[e]	resident	180	222	1550	5.3	2.3C
PEC107	resident	180	302	2320	18.9	2.3C
PEC108	transient	180	224	1724	82.0	2.4C
PEC112	resident	180	91	693	12.8	2.3C
PEC112	transient	180	38	286	90.6	2.4C
PEC113	resident	180	316	2446	18.8	2.3C
PEC114	transient	180	202	1569	175.1	2.4C
PEC116	transient	180	264	2038	274.0	2.4C

Appendix D (continued).

Animal ID	Social status	Fix interval (minutes)	Time span (days)	Locations	Home range size (km2)	Figure panel
PEC120	transient	180	172	1258	104.5	2.4C
PEC122	transient	90	138	1841	92.9	2.4C
PEC129	transient	90	77	1213	154.9	2.4C
PEC131[c]	resident	90	233	3684	11.9	2.3C
PEC135	transient	90	91	1439	91.5	2.4C
PEC137	transient	90	54	861	192.5	2.4C
PEC137	resident	90	156	2489	7.8	2.3C
PEC141	resident	90	70	1048	22.0	2.3C
PEC141	transient	90	48	612	145.5	2.4C

Appendix E. Details of CPH regression model selection.

I performed CPH regression model selection using the Akaike Information Criterion with a correction for small sample sizes (AICc; Burnham & Anderson 2002) to determine whether several categorical variables influenced annual and seasonal survival of radio-collared coyotes. The categorical variables tested were biological year, sex, age class, and social status. I coded dichotomous variables for sex (female or male), age class[5] (adult or yearling), and social status (resident or transient); if social status was undetermined, it was coded as missing data. I coded trichotomous variables for biological year (1, 2, 3) and age class[6] (adult, yearling, juvenile) rather than coding dummy variables for each biological year and each age class. I omitted records with missing data for model selection to avoid unequal sample sizes across models. I performed CPH regression model selection in two stages for the annual and seasonal datasets. First, I compared a model with biological year against a null model to determine if that variable influenced survival. Second, I compared models with all possible combinations of sex, age class, and social status (models included 1–3 of those variables) against each other and a null model to determine if those variables influenced survival. I did not consider models with interaction terms, because of sample size limitations and to avoid over-fitting models. I created model selection tables, which included AICc values, Akaike differences (ΔAICc), and Akaike weights, and ranked the models. I considered any model(s) with $\Delta\text{AICc} \leq 2$ that ranked higher than the null model to have substantial empirical support (Burnham & Anderson 2002). I assessed significance of any variable(s) included in any supported model(s) based on robust *z*-tests and hazard ratios (exponentiated β coefficients) with 95% confidence intervals; I computed robust standard errors for regression coefficients by clustering observations by individual (Therneau & Grambsch

---

[5] Applicable for annual and warm season datasets only

[6] Applicable for cold season dataset only

2000). I tested the proportional hazards assumption for any variable(s) included in any supported model(s) using the statistical test based on scaled Schoenfeld residuals (Therneau & Grambsch 2000). I performed CPH regression model selection in R (version 3.5.1; R Core Team 2018) using the survival and AICcmodavg packages.

Burnham KP & Anderson DR (2002) Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Springer, New York.

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Appendix F. Details of several data issues regarding the survival and cause-specific mortality analyses.

Several data issues regarding the survival and cause-specific mortality analyses warrant mention. Social status was uniformly coded as missing data for a juvenile coyote that transitioned from resident to transient, because the timing of dispersal was uncertain and the individual was killed back in its natal territory, such that it was uncertain if the individual was still a transient upon mortality or had reverted to a resident just prior to mortality. Social status was uniformly coded as missing data for a juvenile coyote that had a period of undetermined social status followed by a period of transiency, but separated by a monitoring gap, because the individual might have had a period of residency that was not discerned. For an adult coyote that transitioned from resident to transient and concurrently exhibited an approximately week-long period of ambiguous space-use, social status was coded as missing data for the period of ambiguous space-use rather than interpolating the midpoint of the transition in social status, because the former option was more appropriate than the latter option, considering that misclassification of social status would have affected the risk set and consequently would have biased the results. For a resident coyote that died while off territory and thus on a putative excursion, social status was not coded as transient for the mortality date, because the individual had previously made excursions but always returned to its territory; this particular data issue is discussed further elsewhere (see Chapter 3).

Appendix G. Results of stepwise CPH regression modeling that tested for effects of several categorical variables on annual and seasonal survival of radio-collared coyotes. Results are presented for the annual and seasonal datasets. Note that the likelihood ratio and score tests assume independence of observations within a cluster, but the Wald and robust score tests do not assume independence of observations within a cluster.

```
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

dummy coded variables: year.1, year.2, year.3, age.class.A, age.class.Y, age.class.J

sex: F (reference) vs M

age.class: A (reference) vs Y

social.status: R (reference) vs T
```

```
##### annual dataset initial model


Call: coxph(formula = my.surv ~ year.1 + year.2 + cluster(id), data = input, ties = "efron")

n = 153, number of events = 47 (1 observation deleted due to missingness)


          coef exp(coef) se(coef) robust se      z Pr(>|z|)

year.1 -0.3785    0.6849   0.3846    0.4032 -0.939    0.348

year.2 -0.3257    0.7220   0.3364    0.3188 -1.021    0.307


       exp(coef) exp(-coef) lower .95 upper .95

year.1    0.6849      1.460    0.3107     1.510

year.2    0.7220      1.385    0.3865     1.349


Concordance = 0.529  (se = 0.041)

Rsquare = 0.009   (max possible = 0.913)

Likelihood ratio test= 1.39  on 2 df,   p=0.5003

Wald test            = 1.41  on 2 df,   p=0.4938

Score (logrank) test = 1.41  on 2 df,   p=0.4932,   Robust = 1.36  p=0.5054


Call: coxph(formula = my.surv ~ year.1 + year.3 + cluster(id), data = input, ties = "efron")

n = 153, number of events = 47 (1 observation deleted due to missingness)


           coef exp(coef) se(coef) robust se      z Pr(>|z|)

year.1 -0.05281   0.94856  0.40931   0.41236 -0.128    0.898

year.3  0.32568   1.38498  0.33638   0.31884  1.021    0.307


       exp(coef) exp(-coef) lower .95 upper .95

year.1    0.9486      1.054    0.4227     2.128

year.3    1.3850      0.722    0.7414     2.587


Concordance = 0.529  (se = 0.041)

Rsquare = 0.009   (max possible = 0.913)
```

```
Likelihood ratio test= 1.39  on 2 df,   p=0.5003
Wald test            = 1.41  on 2 df,   p=0.4938
Score (logrank) test = 1.41  on 2 df,   p=0.4932,   Robust = 1.36  p=0.5054

Call: coxph(formula = my.surv ~ year.2 + year.3 + cluster(id), data = input, ties = "efron")
n = 153, number of events = 47 (1 observation deleted due to missingness)

          coef exp(coef) se(coef) robust se     z Pr(>|z|)
year.2 0.05281   1.05423  0.40931   0.41236 0.128    0.898
year.3 0.37849   1.46008  0.38462   0.40322 0.939    0.348

       exp(coef) exp(-coef) lower .95 upper .95
year.2     1.054     0.9486    0.4698     2.366
year.3     1.460     0.6849    0.6625     3.218

Concordance = 0.529  (se = 0.041)
Rsquare = 0.009   (max possible = 0.913)
Likelihood ratio test= 1.39  on 2 df,   p=0.5003
Wald test            = 1.41  on 2 df,   p=0.4938
Score (logrank) test = 1.41  on 2 df,   p=0.4932,   Robust = 1.36  p=0.5054
```

```
##### annual dataset interactive model


Call: coxph(formula = my.surv ~ sex * age.class * social.status + cluster(id), data = input, ties
= "efron")

n = 130, number of events = 42 (24 observations deleted due to missingness)


                                 coef exp(coef) se(coef) robust se      z Pr(>|z|)

sex                            0.4412    1.5546   0.5841    0.5211  0.847    0.397

age.class                     -1.0569    0.3475   1.1191    1.0547 -1.002    0.316

social.status                  0.5114    1.6676   0.6731    0.5967  0.857    0.391

sex:age.class                  0.5904    1.8046   1.2626    1.2146  0.486    0.627

sex:social.status             -0.5601    0.5712   0.8281    0.7683 -0.729    0.466

age.class:social.status        0.8206    2.2718   1.2634    1.1675  0.703    0.482

sex:age.class:social.status   -0.7835    0.4568   1.5554    1.4394 -0.544    0.586


                              exp(coef) exp(-coef) lower .95 upper .95

sex                              1.5546     0.6433   0.55983     4.317

age.class                        0.3475     2.8775   0.04398     2.746

social.status                    1.6676     0.5996   0.51779     5.371

sex:age.class                    1.8046     0.5541   0.16693    19.509

sex:social.status                0.5712     1.7508   0.12671     2.575

age.class:social.status          2.2718     0.4402   0.23047    22.394

sex:age.class:social.status      0.4568     2.1891   0.02720     7.673


Concordance = 0.6  (se = 0.046)

Rsquare = 0.033   (max possible = 0.92)

Likelihood ratio test= 4.39  on 7 df,   p=0.7341

Wald test            = 4.27  on 7 df,   p=0.7481

Score (logrank) test = 3.74  on 7 df,   p=0.8097,   Robust = 5.48  p=0.6014
```

```
##### annual dataset additive model


Call: coxph(formula = my.surv ~ sex + age.class + social.status + cluster(id), data = input, ties
= "efron")

n = 130, number of events = 42 (24 observations deleted due to missingness)


                  coef exp(coef) se(coef) robust se      z Pr(>|z|)

sex             0.1300    1.1388   0.3204    0.2926  0.444    0.657

age.class      -0.4038    0.6677   0.3296    0.2866 -1.409    0.159

social.status   0.2762    1.3181   0.3159    0.2964  0.932    0.352


               exp(coef) exp(-coef) lower .95 upper .95

sex               1.1388     0.8781    0.6417     2.021

age.class         0.6677     1.4976    0.3808     1.171

social.status     1.3181     0.7587    0.7373     2.356


Concordance = 0.565  (se = 0.046)

Rsquare = 0.018   (max possible = 0.92)

Likelihood ratio test= 2.37  on 3 df,   p=0.4988

Wald test            = 3.37  on 3 df,   p=0.3385

Score (logrank) test = 2.36  on 3 df,   p=0.502,   Robust = 3.12  p=0.3732
```

```
##### warm season dataset initial model

Call: coxph(formula = my.surv ~ year.1 + year.2 + cluster(id), data = input, ties = "efron")

n = 127, number of events = 11

          coef exp(coef) se(coef) robust se      z Pr(>|z|)

year.1 -0.5075    0.6020   0.8190    0.8144 -0.623    0.533

year.2 -0.8585    0.4238   0.8033    0.7801 -1.100    0.271

       exp(coef) exp(-coef) lower .95 upper .95

year.1    0.6020      1.661   0.12199     2.971

year.2    0.4238      2.360   0.09187     1.955

Concordance = 0.582  (se = 0.083)

Rsquare = 0.011   (max possible = 0.509)

Likelihood ratio test= 1.4  on 2 df,   p=0.4961

Wald test            = 1.39  on 2 df,   p=0.5001

Score (logrank) test = 1.36  on 2 df,   p=0.5078,   Robust = 1.44  p=0.4868

Call: coxph(formula = my.surv ~ year.1 + year.3 + cluster(id), data = input, ties = "efron")

n = 127, number of events = 11

         coef exp(coef) se(coef) robust se     z Pr(>|z|)

year.1 0.3509    1.4204   1.0085    1.0131 0.346    0.729

year.3 0.8585    2.3595   0.8033    0.7801 1.100    0.271

       exp(coef) exp(-coef) lower .95 upper .95

year.1      1.42     0.7040    0.1950     10.34

year.3      2.36     0.4238    0.5114     10.89

Concordance = 0.582  (se = 0.083)

Rsquare = 0.011   (max possible = 0.509)
```

```
Likelihood ratio test= 1.4  on 2 df,   p=0.4961
Wald test            = 1.39  on 2 df,   p=0.5001
Score (logrank) test = 1.36  on 2 df,   p=0.5078,   Robust = 1.44  p=0.4868


Call: coxph(formula = my.surv ~ year.2 + year.3 + cluster(id), data = input, ties = "efron")
n = 127, number of events = 11


          coef exp(coef) se(coef) robust se      z Pr(>|z|)
year.2 -0.3509    0.7040   1.0085    1.0131 -0.346    0.729
year.3  0.5075    1.6612   0.8190    0.8144  0.623    0.533


       exp(coef) exp(-coef) lower .95 upper .95
year.2     0.704      1.420   0.09667     5.127
year.3     1.661      0.602   0.33663     8.197


Concordance = 0.582  (se = 0.083)
Rsquare = 0.011   (max possible = 0.509)
Likelihood ratio test= 1.4  on 2 df,   p=0.4961
Wald test            = 1.39  on 2 df,   p=0.5001
Score (logrank) test = 1.36  on 2 df,   p=0.5078,   Robust = 1.44  p=0.4868
```

```
##### warm season dataset interactive model


Call: coxph(formula = my.surv ~ sex * age.class * social.status + cluster(id), data = input, ties
= "efron")

n = 108, number of events = 8 (19 observations deleted due to missingness)


                                     coef  exp(coef)   se(coef)  robust se       z Pr(>|z|)

sex                            -1.325e-01  8.759e-01  9.137e-01  8.643e-01  -0.153    0.878

age.class                      -1.979e+01  2.554e-09  1.963e+04  8.902e-01 -22.226   <2e-16 ***

social.status                  -1.980e+01  2.525e-09  1.949e+04  8.613e-01 -22.986   <2e-16 ***

sex:age.class                   1.989e+01  4.349e+08  1.963e+04  1.245e+00  15.975   <2e-16 ***

sex:social.status               1.170e-01  1.124e+00  2.583e+04  1.137e+00   0.103    0.918

age.class:social.status         3.923e+01  1.091e+17  2.766e+04  1.510e+00  25.984   <2e-16 ***

sex:age.class:social.status    -3.932e+01  8.424e-18  3.807e+04  1.800e+00 -21.845   <2e-16 ***


                               exp(coef) exp(-coef) lower .95 upper .95

sex                            8.759e-01  1.142e+00 1.610e-01 4.766e+00

age.class                      2.554e-09  3.915e+08 4.462e-10 1.462e-08

social.status                  2.525e-09  3.960e+08 4.668e-10 1.366e-08

sex:age.class                  4.349e+08  2.300e-09 3.789e+07 4.991e+09

sex:social.status              1.124e+00  8.896e-01 1.210e-01 1.044e+01

age.class:social.status        1.091e+17  9.169e-18 5.656e+15 2.103e+18

sex:age.class:social.status    8.424e-18  1.187e+17 2.475e-19 2.867e-16


Concordance = 0.686  (se = 0.103)

Rsquare = 0.059   (max possible = 0.451)

Likelihood ratio test= 6.56  on 7 df,   p=0.4763

Wald test            = 1974  on 7 df,   p=0

Score (logrank) test = 4.13  on 7 df,   p=0.7645,   Robust = 6.22  p=0.5139
```

```
##### warm season dataset additive model


Call: coxph(formula = my.surv ~ sex + age.class + social.status + cluster(id), data = input, ties
= "efron")

n = 108, number of events = 8 (19 observations deleted due to missingness)


                    coef exp(coef)  se(coef) robust se      z Pr(>|z|)
sex            -0.005255  0.994759  0.734815  0.640790 -0.008    0.993
age.class      -0.014915  0.985195  0.734461  0.707993 -0.021    0.983
social.status  -1.383023  0.250819  1.081828  0.977024 -1.416    0.157


               exp(coef) exp(-coef) lower .95 upper .95
sex               0.9948      1.005   0.28332     3.493
age.class         0.9852      1.015   0.24597     3.946
social.status     0.2508      3.987   0.03696     1.702


Concordance = 0.606  (se = 0.103)
Rsquare = 0.021   (max possible = 0.451)
Likelihood ratio test= 2.3  on 3 df,   p=0.5133
Wald test            = 2.94  on 3 df,   p=0.4005
Score (logrank) test = 1.95  on 3 df,   p=0.583,   Robust = 3.6  p=0.3074
```

```
##### cold season dataset initial model

Call: coxph(formula = my.surv ~ year.1 + year.2 + cluster(id), data = input, ties = "efron")

n = 173, number of events = 55 (1 observation deleted due to missingness)


          coef exp(coef) se(coef) robust se      z Pr(>|z|)

year.1 -0.3217    0.7249   0.3791    0.3705 -0.868    0.385

year.2 -0.2713    0.7624   0.2985    0.2950 -0.920    0.358


       exp(coef) exp(-coef) lower .95 upper .95

year.1    0.7249      1.379    0.3507     1.498

year.2    0.7624      1.312    0.4276     1.359


Concordance = 0.529  (se = 0.038)

Rsquare = 0.006   (max possible = 0.942)

Likelihood ratio test= 1.1  on 2 df,   p=0.5772

Wald test            = 1.17  on 2 df,   p=0.5574

Score (logrank) test = 1.13  on 2 df,   p=0.5697,   Robust = 1.13  p=0.5676


Call: coxph(formula = my.surv ~ year.1 + year.3 + cluster(id), data = input, ties = "efron")

n = 173, number of events = 55 (1 observation deleted due to missingness)


           coef exp(coef) se(coef) robust se      z Pr(>|z|)

year.1 -0.05034   0.95090  0.38155   0.37884 -0.133    0.894

year.3  0.27131   1.31169  0.29853   0.29504  0.920    0.358


       exp(coef) exp(-coef) lower .95 upper .95

year.1    0.9509     1.0516    0.4526     1.998

year.3    1.3117     0.7624    0.7357     2.339


Concordance = 0.529  (se = 0.038)

Rsquare = 0.006   (max possible = 0.942)
```

```
Likelihood ratio test= 1.1  on 2 df,   p=0.5772

Wald test            = 1.17  on 2 df,   p=0.5574

Score (logrank) test = 1.13  on 2 df,   p=0.5697,   Robust = 1.13  p=0.5676


Call: coxph(formula = my.surv ~ year.2 + year.3 + cluster(id), data = input, ties = "efron")

n = 173, number of events = 55 (1 observation deleted due to missingness)


          coef exp(coef) se(coef) robust se     z Pr(>|z|)

year.2 0.05034   1.05163  0.38155   0.37884 0.133    0.894

year.3 0.32166   1.37942  0.37912   0.37046 0.868    0.385


       exp(coef) exp(-coef) lower .95 upper .95

year.2     1.052     0.9509    0.5005     2.210

year.3     1.379     0.7249    0.6674     2.851


Concordance = 0.529  (se = 0.038)

Rsquare = 0.006   (max possible = 0.942)

Likelihood ratio test= 1.1  on 2 df,   p=0.5772

Wald test            = 1.17  on 2 df,   p=0.5574

Score (logrank) test = 1.13  on 2 df,   p=0.5697,   Robust = 1.13  p=0.5676
```

```
##### cold season dataset interactive model


Call: coxph(formula = my.surv ~ sex * (age.class.A + age.class.Y) * social.status + cluster(id),

            data = input, ties = "efron")

n = 151, number of events = 51 (23 observations deleted due to missingness)


                                   coef exp(coef) se(coef) robust se      z Pr(>|z|)

sex                             -0.1701    0.8436   0.6470    0.6191 -0.275    0.783

age.class.A                     -0.2733    0.7608   0.8671    0.9317 -0.293    0.769

age.class.Y                     -0.6818    0.5057   1.1185    1.2133 -0.562    0.574

social.status                   -0.1359    0.8729   0.7685    0.7926 -0.171    0.864

sex:age.class.A                  1.0051    2.7321   1.0218    1.0707  0.939    0.348

sex:age.class.Y                  0.5777    1.7820   1.3857    1.4624  0.395    0.693

sex:social.status                0.9915    2.6952   1.0036    1.0403  0.953    0.341

age.class.A:social.status        1.3182    3.7367   1.1393    1.1956  1.103    0.270

age.class.Y:social.status        1.2608    3.5284   1.3253    1.4101  0.894    0.371

sex:age.class.A:social.status   -2.0150    0.1333   1.4056    1.4632 -1.377    0.168

sex:age.class.Y:social.status   -1.5359    0.2153   1.7370    1.8061 -0.850    0.395


                                exp(coef) exp(-coef) lower .95 upper .95

sex                                0.8436     1.1855  0.250706     2.838

age.class.A                        0.7608     1.3143  0.122534     4.724

age.class.Y                        0.5057     1.9773  0.046900     5.453

social.status                      0.8729     1.1456  0.184635     4.127

sex:age.class.A                    2.7321     0.3660  0.335069    22.276

sex:age.class.Y                    1.7820     0.5612  0.101415    31.311

sex:social.status                  2.6952     0.3710  0.350833    20.706

age.class.A:social.status          3.7367     0.2676  0.358766    38.920

age.class.Y:social.status          3.5284     0.2834  0.222472    55.960

sex:age.class.A:social.status      0.1333     7.5006  0.007575     2.346

sex:age.class.Y:social.status      0.2153     4.6455  0.006246     7.418
```

```
Concordance = 0.627  (se = 0.042)

Rsquare = 0.059   (max possible = 0.949)

Likelihood ratio test= 9.17  on 11 df,   p=0.6061

Wald test            = 9.83  on 11 df,   p=0.546

Score (logrank) test = 9.42  on 11 df,   p=0.5835,   Robust = 9.05  p=0.6174


Call: coxph(formula = my.surv ~ sex * (age.class.A + age.class.J) * social.status + cluster(id),

            data = input, ties = "efron")

n = 151, number of events = 51 (23 observations deleted due to missingness)


                                    coef exp(coef) se(coef) robust se      z Pr(>|z|)

sex                              0.40758   1.50318  1.22539   1.23590  0.330    0.742

age.class.A                      0.40843   1.50445  1.22547   1.23479  0.331    0.741

age.class.J                      0.68175   1.97734  1.11846   1.21329  0.562    0.574

social.status                    1.12492   3.07999  1.08028   1.03247  1.090    0.276

sex:age.class.A                  0.42735   1.53318  1.45859   1.48177  0.288    0.773

sex:age.class.J                 -0.57771   0.56118  1.38567   1.46240 -0.395    0.693

sex:social.status               -0.54443   0.58017  1.41576   1.36360 -0.399    0.690

age.class.A:social.status        0.05738   1.05905  1.36762   1.34157  0.043    0.966

age.class.J:social.status       -1.26084   0.28342  1.32531   1.41012 -0.894    0.371

sex:age.class.A:social.status   -0.47908   0.61936  1.72530   1.67128 -0.287    0.774

sex:age.class.J:social.status    1.53591   4.64554  1.73701   1.80607  0.850    0.395


                                exp(coef) exp(-coef) lower .95 upper .95

sex                                1.5032     0.6653   0.13336    16.944

age.class.A                        1.5044     0.6647   0.13376    16.921

age.class.J                        1.9773     0.5057   0.18337    21.322

social.status                      3.0800     0.3247   0.40711    23.302

sex:age.class.A                    1.5332     0.6522   0.08401    27.982

sex:age.class.J                    0.5612     1.7820   0.03194     9.861

sex:social.status                  0.5802     1.7236   0.04007     8.400

age.class.A:social.status          1.0591     0.9442   0.07638    14.685
```

```
age.class.J:social.status          0.2834     3.5284   0.01787     4.495

sex:age.class.A:social.status      0.6194     1.6146   0.02341    16.388

sex:age.class.J:social.status      4.6455     0.2153   0.13481   160.091


Concordance = 0.627  (se = 0.042)

Rsquare = 0.059   (max possible = 0.949)

Likelihood ratio test= 9.17  on 11 df,   p=0.6061

Wald test            = 9.83  on 11 df,   p=0.546

Score (logrank) test = 9.42  on 11 df,   p=0.5835,   Robust = 9.05  p=0.6174


Call: coxph(formula = my.surv ~ sex * (age.class.Y + age.class.J) * social.status + cluster(id),

            data = input, ties = "efron")

n = 151, number of events = 51 (23 observations deleted due to missingness)


                                    coef exp(coef) se(coef) robust se      z Pr(>|z|)

sex                              0.83493   2.30465  0.79075   0.87084  0.959    0.338

age.class.Y                     -0.40843   0.66470  1.22547   1.23479 -0.331    0.741

age.class.J                      0.27333   1.31433  0.86714   0.93167  0.293    0.769

social.status                    1.18230   3.26187  0.83842   0.89492  1.321    0.186

sex:age.class.Y                 -0.42735   0.65224  1.45859   1.48177 -0.288    0.773

sex:age.class.J                 -1.00505   0.36602  1.02183   1.07067 -0.939    0.348

sex:social.status               -1.02351   0.35933  0.98467   1.02351 -1.000    0.317

age.class.Y:social.status       -0.05738   0.94424  1.36762   1.34157 -0.043    0.966

age.class.J:social.status       -1.31821   0.26761  1.13930   1.19558 -1.103    0.270

sex:age.class.Y:social.status    0.47908   1.61458  1.72530   1.67128  0.287    0.774

sex:age.class.J:social.status    2.01498   7.50061  1.40559   1.46323  1.377    0.168


                                exp(coef) exp(-coef) lower .95 upper .95

sex                                2.3046     0.4339   0.41816    12.702

age.class.Y                        0.6647     1.5044   0.05910     7.476

age.class.J                        1.3143     0.7608   0.21167     8.161

social.status                      3.2619     0.3066   0.56456    18.846
```

```
sex:age.class.Y                    0.6522     1.5332   0.03574    11.904

sex:age.class.J                    0.3660     2.7321   0.04489     2.984

sex:social.status                  0.3593     2.7829   0.04834     2.671

age.class.Y:social.status          0.9442     1.0591   0.06810    13.093

age.class.J:social.status          0.2676     3.7367   0.02569     2.787

sex:age.class.Y:social.status      1.6146     0.6194   0.06102    42.723

sex:age.class.J:social.status      7.5006     0.1333   0.42618   132.008


Concordance = 0.627  (se = 0.042)

Rsquare = 0.059   (max possible = 0.949)

Likelihood ratio test= 9.17  on 11 df,   p=0.6061

Wald test            = 9.83  on 11 df,   p=0.546

Score (logrank) test = 9.42  on 11 df,   p=0.5835,   Robust = 9.05  p=0.6174
```

```
##### cold season dataset additive model

Call: coxph(formula = my.surv ~ sex + age.class.A + age.class.Y + social.status + cluster(id),
            data = input, ties = "efron")
n = 151, number of events = 51 (23 observations deleted due to missingness)

                   coef exp(coef) se(coef) robust se      z Pr(>|z|)
sex             0.17901   1.19603  0.29123   0.29697  0.603   0.5467
age.class.A     0.45290   1.57287  0.32846   0.33094  1.369   0.1711
age.class.Y    -0.01936   0.98082  0.38387   0.36450 -0.053   0.9576
social.status   0.52460   1.68978  0.28948   0.28317  1.853   0.0639 .

               exp(coef) exp(-coef) lower .95 upper .95
sex               1.1960     0.8361    0.6683     2.141
age.class.A       1.5729     0.6358    0.8222     3.009
age.class.Y       0.9808     1.0196    0.4801     2.004
social.status     1.6898     0.5918    0.9700     2.944

Concordance = 0.609  (se = 0.042)
Rsquare = 0.042   (max possible = 0.949)
Likelihood ratio test= 6.43  on 4 df,   p=0.1694
Wald test            = 7.87  on 4 df,   p=0.09646
Score (logrank) test = 6.69  on 4 df,   p=0.1532,   Robust = 6.82  p=0.1458

Call: coxph(formula = my.surv ~ sex + age.class.A + age.class.J + social.status + cluster(id),
            data = input, ties = "efron")
n = 151, number of events = 51 (23 observations deleted due to missingness)

                  coef exp(coef) se(coef) robust se     z Pr(>|z|)
sex            0.17901   1.19603  0.29123   0.29697 0.603   0.5467
age.class.A    0.47226   1.60362  0.36545   0.31509 1.499   0.1339
age.class.J    0.01936   1.01955  0.38387   0.36450 0.053   0.9576
```

```
social.status  0.52460   1.68978  0.28948   0.28317 1.853   0.0639 .

               exp(coef) exp(-coef) lower .95 upper .95
sex                1.196     0.8361    0.6683     2.141
age.class.A        1.604     0.6236    0.8648     2.974
age.class.J        1.020     0.9808    0.4991     2.083
social.status      1.690     0.5918    0.9700     2.944

Concordance = 0.609  (se = 0.042)
Rsquare = 0.042   (max possible = 0.949)
Likelihood ratio test= 6.43  on 4 df,   p=0.1694
Wald test            = 7.87  on 4 df,   p=0.09646
Score (logrank) test = 6.69  on 4 df,   p=0.1532,   Robust = 6.82  p=0.1458

Call: coxph(formula = my.surv ~ sex + age.class.Y + age.class.J + social.status + cluster(id),
            data = input, ties = "efron")
n = 151, number of events = 51 (23 observations deleted due to missingness)

                  coef exp(coef) se(coef) robust se      z Pr(>|z|)
sex             0.1790    1.1960   0.2912    0.2970  0.603   0.5467
age.class.Y    -0.4723    0.6236   0.3655    0.3151 -1.499   0.1339
age.class.J    -0.4529    0.6358   0.3285    0.3309 -1.369   0.1711
social.status   0.5246    1.6898   0.2895    0.2832  1.853   0.0639 .

               exp(coef) exp(-coef) lower .95 upper .95
sex               1.1960     0.8361    0.6683     2.141
age.class.Y       0.6236     1.6036    0.3363     1.156
age.class.J       0.6358     1.5729    0.3324     1.216
social.status     1.6898     0.5918    0.9700     2.944

Concordance = 0.609  (se = 0.042)
Rsquare = 0.042   (max possible = 0.949)
```

```
Likelihood ratio test= 6.43  on 4 df,   p=0.1694

Wald test            = 7.87  on 4 df,   p=0.09646

Score (logrank) test = 6.69  on 4 df,   p=0.1532,   Robust = 6.82  p=0.1458
```

```
##### cold season dataset final model


Call: coxph(formula = my.surv ~ social.status + cluster(id), data = input, ties = "efron")

n = 151, number of events = 51 (23 observations deleted due to missingness)


                 coef exp(coef) se(coef) robust se     z Pr(>|z|)

social.status  0.5015    1.6513   0.2820    0.2636 1.903    0.057 .


               exp(coef) exp(-coef) lower .95 upper .95

social.status      1.651     0.6056    0.9851     2.768


Concordance = 0.551  (se = 0.036)

Rsquare = 0.021   (max possible = 0.949)

Likelihood ratio test= 3.18  on 1 df,   p=0.07447

Wald test            = 3.62  on 1 df,   p=0.05705

Score (logrank) test = 3.23  on 1 df,   p=0.07236,   Robust = 3.54  p=0.05979
```

Appendix H. Stratum-specific survival rates for radio-collared coyotes in Prince Edward County, Ontario, May 2010–April 2013. Rates are presented for the annual and seasonal datasets; the events value represents the number of mortalities. Abbreviations: SE = standard error; CI = confidence interval; F = female; M = male; A = adult; Y = yearling; J = juvenile; R = resident; T = transient. Note that years 1, 2, and 3 correspond with biological years 2010–2011, 2011–2012, and 2012–2013, respectively.

Dataset	Stratum	Records	Events	Survival rate	SE	Lower 95% CI	Upper 95% CI
annual	overall	153	47	0.400	0.055	0.304	0.524
annual	year = 1	37	10	0.514	0.112	0.336	0.786
annual	year = 2	53	15	0.457	0.095	0.304	0.685
annual	year = 3	63	22	0.293	0.084	0.167	0.514
annual	sex = F	69	19	0.431	0.086	0.292	0.636
annual	sex = M	84	28	0.376	0.072	0.257	0.548
annual	age.class = A	88	30	0.381	0.070	0.265	0.547
annual	age.class = Y	65	17	0.431	0.090	0.286	0.648
annual	social.status = R	72	20	0.520	0.078	0.388	0.697
annual	social.status = T	58	22	0.352	0.082	0.223	0.556
warm season	overall	127	11	0.830	0.047	0.743	0.928
warm season	year = 1	29	2	0.894	0.073	0.763	1.000
warm season	year = 2	42	2	0.899	0.068	0.776	1.000
warm season	year = 3	56	7	0.777	0.074	0.644	0.937
warm season	sex = F	57	5	0.820	0.074	0.687	0.979
warm season	sex = M	70	6	0.838	0.061	0.727	0.966
warm season	age.class = A	77	6	0.851	0.056	0.748	0.969
warm season	age.class = Y	50	5	0.800	0.082	0.655	0.978
warm season	social.status = R	65	7	0.819	0.062	0.707	0.950
warm season	social.status = T	43	1	0.967	0.033	0.905	1.000
cold season	overall	173	55	0.525	0.047	0.441	0.625
cold season	year = 1	40	10	0.578	0.103	0.408	0.818
cold season	year = 2	75	22	0.566	0.070	0.443	0.721
cold season	year = 3	58	23	0.444	0.078	0.314	0.627
cold season	sex = F	83	21	0.579	0.071	0.456	0.735
cold season	sex = M	90	34	0.485	0.062	0.377	0.623

Appendix H (continued).

Dataset	Stratum	Records	Events	Survival rate	SE	Lower 95% CI	Upper 95% CI
cold season	age.class = A	59	24	0.448	0.077	0.319	0.628
cold season	age.class = Y	45	12	0.538	0.098	0.377	0.769
cold season	age.class = J	69	19	0.590	0.072	0.464	0.751
cold season	social.status = R	86	23	0.620	0.064	0.507	0.759
cold season	social.status = T	65	28	0.414	0.071	0.296	0.580

Appendix I. Findings from CPH regression model selection.

CPH regression model selection indicated that the categorical variables generally did not influence the annual or seasonal survival of radio-collared coyotes (Table I). The null model ranked higher than the model with biological year for the annual and seasonal datasets in the first stage of model selection (Table I), indicating that biological year did not influence the annual or seasonal survival of radio-collared coyotes. The null model was the top-ranked model for the annual dataset in the second stage of model selection (Table I), indicating that sex, age class, and social status did not influence the annual survival of radio-collared coyotes. The model with social status was the top-ranked model for the warm season dataset in the second stage of model selection (Table I), but social status was not significant in that model ($z = -1.3$, $P = 0.190$); further, the null model was similarly supported as the top-ranked model (Table I), indicating that sex, age class, and social status did not influence the warm season survival of radio-collared coyotes. The model with social status was the top-ranked model for the cold season dataset in the second stage of model selection (Table I), and social status was marginally significant in that model ($z = 1.9$, $P = 0.057$) and showed no violation of proportionality ($\chi^2 = 2.1$, $P = 0.147$); further, the null model was not similarly supported as the top-ranked model (Table I), indicating that social status, but not sex and age class, influenced the cold season survival of radio-collared coyotes.

Table I. Results of CPH regression model selection performed using an information-theoretic approach to determine whether several categorical variables influenced annual and seasonal survival of radio-collared coyotes. Results are presented for the annual and seasonal datasets. Abbreviations: K = number of parameters; AICc = Akaike Information Criterion with a correction for small sample sizes.

Dataset	Stage	Model	K	AICc	ΔAICc	Akaike weight
annual	1	null	0	329.16	0.00	0.84
annual	1	year	2	332.44	3.28	0.16
annual	2	null	0	329.16	0.00	0.27
annual	2	age.class	1	329.69	0.53	0.21
annual	2	social.status	1	330.73	1.58	0.12
annual	2	sex	1	330.92	1.77	0.11
annual	2	age.class + social.status	2	331.05	1.89	0.11
annual	2	sex + age.class	2	331.65	2.49	0.08
annual	2	sex + social.status	2	332.43	3.27	0.05
annual	2	sex + age.class + social.status	3	332.98	3.82	0.04
warm season	1	null	0	64.73	0.00	0.78
warm season	1	year	2	67.31	2.59	0.22
warm season	2	social.status	1	64.47	0.00	0.29
warm season	2	null	0	64.73	0.26	0.25
warm season	2	age.class + social.status	2	66.54	2.08	0.10
warm season	2	sex + social.status	2	66.55	2.08	0.10
warm season	2	age.class	1	66.72	2.25	0.09
warm season	2	sex	1	66.72	2.25	0.09
warm season	2	sex + age.class + social.status	3	68.66	4.19	0.04
warm season	2	sex + age.class	2	68.76	4.29	0.03
cold season	1	null	0	448.19	0.00	0.82
cold season	1	year	2	451.27	3.09	0.18
cold season	2	social.status	1	447.03	0.00	0.28
cold season	2	null	0	448.19	1.15	0.16
cold season	2	age.class + social.status	3	448.30	1.27	0.15
cold season	2	sex + social.status	2	448.34	1.31	0.15
cold season	2	age.class	2	449.28	2.25	0.09
cold season	2	sex	1	449.92	2.88	0.07
cold season	2	sex + age.class + social.status	4	450.03	3.00	0.06
cold season	2	sex + age.class	3	451.23	4.19	0.03

Appendix J. Stratum-specific cause-specific mortality rates for radio-collared coyotes in Prince Edward County, Ontario, May 2010–April 2013. Rates are presented for the annual and seasonal datasets; the CIF value represents the cause-specific mortality rate. Abbreviations: n = number of mortalities; CIF = cumulative incidence function; SE = standard error; CI = confidence interval; F = female; M = male; A = adult; Y = yearling; J = juvenile; R = resident; T = transient; NA = not applicable. Note that years 1, 2, and 3 correspond with biological years 2010–2011, 2011–2012, and 2012–2013, respectively.

Dataset	Stratum	Category of mortality	n	CIF	SE	Lower 95% CI	Upper 95% CI
annual	overall	harvest	34	0.425	0.058	0.311	0.539
annual	overall	roadkill	8	0.114	0.043	0.030	0.197
annual	overall	other	5	0.062	0.032	0.000	0.124
annual	year = 1	harvest	8	0.368	0.106	0.160	0.577
annual	year = 1	roadkill	2	0.118	0.053	0.015	0.221
annual	year = 1	other	0	NA	NA	NA	NA
annual	year = 2	harvest	10	0.352	0.092	0.172	0.532
annual	year = 2	roadkill	3	0.123	0.074	0.000	0.267
annual	year = 2	other	2	0.069	0.047	0.000	0.161
annual	year = 3	harvest	16	0.518	0.093	0.335	0.700
annual	year = 3	roadkill	3	0.094	0.059	0.000	0.210
annual	year = 3	other	3	0.095	0.066	0.000	0.224
annual	sex = F	harvest	11	0.324	0.081	0.165	0.483
annual	sex = F	roadkill	5	0.157	0.065	0.029	0.285
annual	sex = F	other	3	0.088	0.055	0.000	0.196
annual	sex = M	harvest	23	0.501	0.075	0.353	0.649
annual	sex = M	roadkill	3	0.080	0.034	0.014	0.147
annual	sex = M	other	2	0.043	0.030	0.000	0.101
annual	age.class = A	harvest	22	0.438	0.075	0.291	0.585
annual	age.class = A	roadkill	5	0.118	0.048	0.024	0.212
annual	age.class = A	other	3	0.063	0.040	0.000	0.140
annual	age.class = Y	harvest	12	0.401	0.090	0.225	0.577
annual	age.class = Y	roadkill	3	0.106	0.059	0.000	0.222
annual	age.class = Y	other	2	0.062	0.051	0.000	0.161
annual	social.status = R	harvest	15	0.349	0.072	0.208	0.490

Appendix J (continued).

Dataset	Stratum	Category of mortality	n	CIF	SE	Lower 95% CI	Upper 95% CI
annual	social.status = R	roadkill	3	0.082	0.038	0.009	0.156
annual	social.status = R	other	2	0.049	0.034	0.000	0.115
annual	social.status = T	harvest	16	0.474	0.088	0.301	0.646
annual	social.status = T	roadkill	3	0.087	0.048	0.000	0.181
annual	social.status = T	other	3	0.088	0.055	0.000	0.196
warm season	overall	harvest	6	0.091	0.033	0.026	0.155
warm season	overall	roadkill	4	0.065	0.035	0.000	0.135
warm season	overall	other	1	0.014	0.013	0.000	0.040
warm season	year = 1	harvest	1	0.039	0.038	0.000	0.114
warm season	year = 1	roadkill	1	0.067	NA	NA	NA
warm season	year = 1	other	0	NA	NA	NA	NA
warm season	year = 2	harvest	1	0.048	NA	NA	NA
warm season	year = 2	roadkill	1	0.053	0.051	0.000	0.154
warm season	year = 2	other	0	NA	NA	NA	NA
warm season	year = 3	harvest	4	0.127	0.057	0.016	0.238
warm season	year = 3	roadkill	2	0.065	0.053	0.000	0.170
warm season	year = 3	other	1	0.031	0.030	0.000	0.091
warm season	sex = F	harvest	2	0.073	0.024	0.026	0.120
warm season	sex = F	roadkill	2	0.075	0.051	0.000	0.175
warm season	sex = F	other	1	0.031	0.031	0.000	0.092
warm season	sex = M	harvest	4	0.104	0.041	0.024	0.183
warm season	sex = M	roadkill	2	0.058	0.027	0.006	0.110
warm season	sex = M	other	0	NA	NA	NA	NA
warm season	age.class = A	harvest	2	0.048	0.033	0.000	0.112
warm season	age.class = A	roadkill	3	0.078	0.035	0.010	0.147
warm season	age.class = A	other	1	0.023	0.022	0.000	0.066
warm season	age.class = Y	harvest	4	0.155	0.054	0.048	0.261
warm season	age.class = Y	roadkill	1	0.045	0.044	0.000	0.131
warm season	age.class = Y	other	0	NA	NA	NA	NA
warm season	social.status = R	harvest	4	0.101	0.041	0.021	0.181
warm season	social.status = R	roadkill	2	0.055	0.027	0.002	0.108
warm season	social.status = R	other	1	0.025	0.025	0.000	0.073
warm season	social.status = T	harvest	1	0.033	NA	NA	NA
warm season	social.status = T	roadkill	0	NA	NA	NA	NA
warm season	social.status = T	other	0	NA	NA	NA	NA
cold season	overall	harvest	43	0.371	0.048	0.276	0.465

Appendix J (continued).

Dataset	Stratum	Category of mortality	n	CIF	SE	Lower 95% CI	Upper 95% CI
cold season	overall	roadkill	5	0.044	0.026	0.000	0.095
cold season	overall	other	7	0.060	0.029	0.003	0.117
cold season	year = 1	harvest	8	0.333	0.095	0.147	0.519
cold season	year = 1	roadkill	1	0.044	0.043	0.000	0.130
cold season	year = 1	other	1	0.044	0.043	0.000	0.130
cold season	year = 2	harvest	17	0.333	0.070	0.196	0.469
cold season	year = 2	roadkill	3	0.062	0.043	0.000	0.148
cold season	year = 2	other	2	0.040	0.027	0.000	0.093
cold season	year = 3	harvest	18	0.440	0.080	0.283	0.596
cold season	year = 3	roadkill	1	0.023	0.022	0.000	0.067
cold season	year = 3	other	4	0.094	0.055	0.000	0.202
cold season	sex = F	harvest	14	0.280	0.067	0.148	0.412
cold season	sex = F	roadkill	4	0.082	0.043	0.000	0.167
cold season	sex = F	other	3	0.059	0.039	0.000	0.135
cold season	sex = M	harvest	29	0.439	0.063	0.316	0.562
cold season	sex = M	roadkill	1	0.016	0.016	0.000	0.046
cold season	sex = M	other	4	0.061	0.036	0.000	0.131
cold season	age.class = A	harvest	20	0.459	0.081	0.300	0.617
cold season	age.class = A	roadkill	2	0.046	0.040	0.000	0.124
cold season	age.class = A	other	2	0.047	0.039	0.000	0.124
cold season	age.class = Y	harvest	8	0.308	0.095	0.122	0.494
cold season	age.class = Y	roadkill	2	0.077	0.052	0.000	0.179
cold season	age.class = Y	other	2	0.077	0.052	0.000	0.179
cold season	age.class = J	harvest	15	0.323	0.070	0.185	0.460
cold season	age.class = J	roadkill	1	0.023	0.022	0.000	0.067
cold season	age.class = J	other	3	0.065	0.046	0.000	0.155
cold season	social.status = R	harvest	19	0.311	0.062	0.189	0.434
cold season	social.status = R	roadkill	1	0.018	0.018	0.000	0.053
cold season	social.status = R	other	3	0.051	0.034	0.000	0.118
cold season	social.status = T	harvest	20	0.414	0.072	0.272	0.556
cold season	social.status = T	roadkill	4	0.089	0.037	0.016	0.161
cold season	social.status = T	other	4	0.084	0.044	0.000	0.171

Appendix K. Results of stratified CPH regression model that tested for an effect of social status on the cold season cause-specific mortality of radio-collared coyotes. Note that the likelihood ratio and score tests assume independence of observations within a cluster, but the Wald and robust score tests do not assume independence of observations within a cluster.

```
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
dummy coded variables: social.status.harvest, social.status.roadkill, social.status.other
R (reference) vs T

Call: coxph(formula = my.surv ~ social.status.harvest + social.status.roadkill +
      social.status.other + strata(cause.strata) + cluster(id), data = input, ties = "efron")
n = 453, number of events = 51 (69 observations deleted due to missingness)

                         coef exp(coef) se(coef) robust se     z Pr(>|z|)
social.status.harvest  0.3557    1.4271   0.3211    0.3073 1.157    0.247
social.status.roadkill 1.7262    5.6191   1.1202    1.1330 1.524    0.128
social.status.other    0.5670    1.7629   0.7642    0.7479 0.758    0.448

                       exp(coef) exp(-coef) lower .95 upper .95
social.status.harvest      1.427     0.7007    0.7814     2.607
social.status.roadkill     5.619     0.1780    0.6099    51.770
social.status.other        1.763     0.5672    0.4070     7.636

Concordance= 0.551  (se = 0.055 )
Rsquare= 0.011   (max possible= 0.628 )
Likelihood ratio test= 4.86  on 3 df,   p=0.1827
Wald test            = 4.52  on 3 df,   p=0.2107
Score (logrank) test = 4.82  on 3 df,   p=0.1854,   Robust = 4.71  p=0.194
```

Appendix L. Primer sequences.

P1-5EZ:	5’-ATAATCACATGGAGAGCCACAAGCT-3’	(Aasen & Medrano 1990)
P2-3EZ:	5’-GCACTTCTTTGGTATCTGAGAAAGT-3’	(Aasen & Medrano 1990)
Y53-3C:	5’-CCCATGAACGCATTCATTGTGTGG-3’	(Fain & LeMay 1995)
Y53-3D:	5’-ATTTTAGCCTTCCGACGAGGTCGATA-3’	(Fain & LeMay 1995)
LGL-331:	5’-CAAATCATGCAAGGATAGAC-3’	(Shaw et al. 2003)
LGL-335:	5’-AGACCTGATTCCAGACAGTACCA-3’	(Shaw et al. 2003)
Thr-L:	5’-GAATTCCCCGGTCTTGTAAACC-3’	(Leonard et al. 2002)
DL-Hcan:	5’-CCTGAGGTAAGAACCAGATG-3’	(Leonard et al. 2002)
Primer 1:	5’-GAAGCTCTTGCTCCACCATC-3’	(Wilson et al. 2000)
Primer 2:	5’-GGGCCCGGAGCGAGAAGAGGGAC-3’	(Wilson et al. 2000)

Appendix M. Details of polymerase chain reaction (PCR) amplification.

The *Zfx/Sry* fragments were amplified in a total reaction volume of 15 µl using 5 ng (or 2–4 µl) of genomic DNA, 1X PCR buffer, 0.2 mM dNTPs, 2.5 mM $MgCl_2$, 0.2 µM of each primer, and 0.05 U/µl *Taq* polymerase; 0.10–0.15 µg/µl bovine serum albumin (BSA) was included in some reactions. Products were amplified by PCR under the following conditions: 95°C for 1 min; 94°C for 45 sec, 58°C for 45 sec, and 73°C for 1 min for 35 cycles; 72°C for 2 min.

The *Zfx/Zfy* introns were amplified in a total reaction volume of 15–20 µl using 5 ng (or 2–4 µl) of genomic DNA, 1X PCR buffer, 0.2 mM dNTPs, 1.5 mM $MgCl_2$, 0.2 µM of each primer, and 0.04–0.05 U/µl *Taq* polymerase; 0.1 µg/µl BSA was included in some reactions. Products were amplified by PCR under the following conditions: 94°C for 5 min, 55°C for 30 sec, and 72°C for 30 sec for 1 cycle; 94°C for 30 sec, 55°C for 30 sec, and 72°C for 30 sec for 31–35 cycles; 94°C for 30 sec, 55°C for 30 sec, and 72°C for 10 min for 1 cycle.

The autosomal microsatellite loci were amplified in a total reaction volume of 15 µl using 5 ng (or 2–4 µl) of genomic DNA, 1X PCR buffer, 0.2 mM dNTPs, 1.5 mM $MgCl_2$, 0.2–0.3 µM forward primer (labeled with fluorescent dye: 6FAM, NED or HEX) and 0.2–0.3 µM reverse primer (unlabeled), and 0.05 U/µl *Taq* polymerase; 0.1 µg/µl BSA was included in some reactions. Products were amplified by PCR under the following conditions: 94°C for 5 min; 94°C for 30 sec, 56–58°C for 1 min, and 72°C for 1 min for 30 cycles; 60°C for 45 min.

The 420–425 bp fragment of the mtDNA control region was amplified in a total reaction volume of 20 µl using 5 ng (or 2–4 µl) of genomic DNA, 1X PCR buffer, 0.2 mM dNTPs, 1.5 mM $MgCl_2$, 0.2 µM of each primer, and 0.05 U/µl *Taq* polymerase; 0.1 µg/µl BSA was included in some reactions. Generally, products were amplified by PCR under the following conditions: 94°C for 5 min, 50°C for 2 min, and 72°C for 1.5 min for 1 cycle; 94°C for 1 min, 50°C for 2 min, and 72°C for 1.5 min for 28–34 cycles; 94°C for 1min, 50°C for 2 min, and 72°C for 7 min for 1 cycle. Alternatively, products were amplified by PCR under the following conditions: 94°C for 5 min, 60°C for 30 sec, and 72°C for 30 sec for 1 cycle; 94°C for 30 sec, 60°C for 30 sec, and 72°C for 30 sec for 30 cycles; 94°C for 30 sec, 60°C for 30 sec, and 72°C for 2 min for 1 cycle.

The 343–347 bp fragment of the mtDNA control region was amplified in a total reaction volume of 20 μl using 5 ng (or 2–4 μl) of genomic DNA, 1X PCR buffer, 0.2 mM dNTPs, 1.5 mM $MgCl_2$, 0.2 μM of each primer, and 0.05 U/μl *Taq* polymerase; 0.1 μg/μl BSA was included in some reactions. Products were amplified by PCR under the following conditions: 94°C for 5 min, 60°C for 30 sec, and 72°C for 30 sec for 1 cycle; 94°C for 30 sec, 60°C for 30 sec, and 72°C for 30 sec for 28–35 cycles; 94°C for 30 sec, 60°C for 30 sec, and 72°C for 2 min for 1 cycle.

The Y-chromosome microsatellite loci were amplified in a total reaction volume of 15 μl using 5 ng (or 2–4 μl) of genomic DNA, 1X PCR buffer, 0.2 mM dNTPs, 1.5 mM $MgCl_2$, 0.1–0.2 μM forward primer (labeled with fluorescent dye: 6FAM or HEX) and 0.2–0.3 μM reverse primer (unlabeled), and 0.05 U/μl *Taq* polymerase; 0.1 μg/μl BSA was included in some reactions. Products were amplified by PCR under the following conditions: 94°C for 5 min; 94°C for 30 sec, 58–60°C for 1 min, and 72°C for 1 min for 30 cycles; 60°C for 45 min.

Appendix N. Allele frequency and heterozygosity values for 16 autosomal microsatellite loci.

Abbreviations: N = number of samples; Na = number of alleles; Ne = effective number of alleles; Ho = observed heterozygosity; He = expected heterozygosity.

Locus	N	Na	Ne	Ho	He
c2010	398	5	3.3	0.716	0.701
c2202	380	33	11.8	0.903	0.915
CPH11	397	22	13.3	0.927	0.925
cxx2	398	14	6.4	0.802	0.843
cxx109	398	8	4.4	0.822	0.772
cxx123	398	6	2.6	0.487	0.613
cxx147	398	7	3.0	0.663	0.668
cxx172	398	5	3.2	0.711	0.690
cxx204	398	5	1.5	0.339	0.331
cxx225	398	8	4.9	0.779	0.795
cxx250	396	9	6.0	0.846	0.834
cxx253	398	9	6.8	0.854	0.854
cxx377	398	14	4.8	0.809	0.794
cxx383	397	6	4.0	0.748	0.752
cxx410	398	11	6.4	0.859	0.843
cxx442	398	6	4.6	0.754	0.784

Appendix O. Findings from the multistep approach used to investigate the maximum likelihood relationships for 79003 dyads to ensure that they were correct, plausible, and logically consistent.

Initial ML-Relate results

Step 1

Regarding the known FS relationships (*n* = 64), the maximum likelihood relationship was correct for 47 dyads and incorrect for 17 dyads (11 HS and 6 PO). Regarding the known PO relationships (*n* = 18), the maximum likelihood relationship was correct for 17 dyads and incorrect for 1 dyad (1 FS). Regarding the presumed FS relationships (*n* = 51), the maximum likelihood relationship was correct for 38 dyads and incorrect for 13 dyads (12 HS and 1 PO). Regarding the presumed PO relationships (*n* = 10), the maximum likelihood relationship was correct for all dyads.

Step 2

Based on haplotypes, 590 FS dyads were plausible and 137 FS dyads were implausible; note that the plausibility of 30 FS dyads was unknown due to missing sex data and the plausibility of 4 FS dyads could not be determined due to missing Y-haplotype data. Based on haplotypes, 144 PO dyads were plausible and 5 PO dyads were implausible; note that the plausibility of 40 PO dyads could not be determined due to missing sex data (*n* = 37) or missing Y-haplotype data (*n* = 3) and the plausibility of 145 mixed-sex PO dyads could not be determined because the parent and the offspring had not yet been determined for PO dyads.

Step 3

I made the following 173 revisions based on findings from the previous two steps: 23 HS to FS, 132 FS to HS, 6 FS to PO, 5 PO to HS, and 7 PO to FS.

Step 4

I determined the parent and the offspring for 283 PO dyads; however, I could not determine the parent and the offspring for 45 PO dyads. Based on haplotypes, 73 female-male PO dyads were plausible and 1 female-male PO dyad was implausible; note that the plausibility of 50 male-female PO dyads could not be determined based on haplotypes due to inheritance patterns. Consequently, based on various considerations, I determined that 264 PO dyads were valid and 43 PO dyads were invalid; further, I determined that 2 HS dyads and 4 FS dyads were invalid.

Step 5

I made the following 49 revisions based on findings from the previous step: 2 HS to PO, 4 FS to PO, 8 PO to HS, and 35 PO to FS.

Step 6

I assessed the logical consistency of relationships for 1802 three-dyad combinations and found that 963 of them were logically consistent and 839 of them were logically inconsistent.

Step 7

I made the following 106 revisions based on findings from the previous step: 4 U to FS, 61 HS to FS, 15 FS to U, 16 FS to HS, 6 FS to PO, and 4 PO to FS.

Revised ML-Relate results

Step 2

Based on haplotypes, 681 FS dyads were plausible and none were implausible; note that the plausibility of 30 FS dyads was unknown due to missing sex data and the plausibility of 5 FS dyads could not be determined due to missing Y-haplotype data. Based on haplotypes, 127 PO dyads were plausible and none were implausible; note that the plausibility of 41 PO dyads could not be determined due to missing sex data (*n* = 38) or missing Y-haplotype data (*n* = 3) and the plausibility of 125 mixed-sex PO dyads could not be determined because the parent and the offspring had not yet been determined for PO dyads.

Step 4

I determined the parent and the offspring for 276 PO dyads; however, I could not determine the parent and the offspring for 17 PO dyads. Based on haplotypes, 68 female-male PO dyads were plausible and none were implausible; note that the plausibility of 51 male-female PO dyads could not be determined based on haplotypes due to inheritance patterns. Consequently, based on various considerations, I determined that 276 PO dyads were valid.

Step 6

I assessed the logical consistency of relationships for 1590 three-dyad combinations and found that 1316 of them were logically consistent and 274 of them were logically inconsistent.

Appendix P. Breeding histories for 58 individual parents. The table indicates the number of offspring, the number of litters, and the number of mates observed for each individual parent. Abbreviations: F = female; M = male.

Parent	Sex	Offspring	Litters	Mates	Comment
PEC001	M	7	3	1	
PEC014	M	9	2	1	
PEC015	F	3	3	1	
PEC018	M	1	1	1	
PEC019	F	2	2	2	
PEC027	M	1	1	1	
PEC028	M	1	1	1	
PEC032	F	5	3	1	
PEC036	F	1	1	1	
PEC037	M	10	3	1	number of litters uncertain
PEC047	F	2	1	1	
PEC052	M	3	1	1	
PEC066	M	5	2	1	number of litters uncertain
PEC074	F	10	4	1	
PEC088	M	6	2	1	number of litters uncertain
PEC092	M	1	1	1	
PEC096	M	3	3	1	
PEC103	M	12	3	2	
PEC106	M	3	2	1	
PEC113	F	4	1	2	
PEC120	M	1	1	1	
PEC131	M	17	7	3	
PEC137	M	2	1	1	
PEC153	F	8	3	1	number of litters uncertain
PEC167	M	7	3	1	number of litters uncertain
PEC194	F	5	3	1	
PEC214	F	1	1	1	
PEC217	M	1	1	1	
PEC219	M	8	3	1	number of litters uncertain
PEC221	M	4	1	1	
PEC243	M	2	2	1	
PEC246	F	7	3	1	
PEC249	F	4	2	1	

Appendix P (continued).

Parent	Sex	Offspring	Litters	Mates	Comment
PEC260	M	1	1	1	
PEC268	F	1	1	1	
PEC270	F	2	1	1	
PEC277	F	1	1	1	
PEC291	F	18	5	2	number of litters uncertain
PEC301	F	9	1	1	
PEC322	M	1	1	1	
PEC331	M	1	1	1	
PEC341	M	1	1	1	
PEC346	F	4	2	1	
PEC352	F	1	1	1	
PEC357	M	1	1	1	
PEC367	F	1	1	1	
PEC369	F	12	4	1	number of litters uncertain
PEC370	M	12	4	1	number of litters uncertain
PEC372	F	9	2	1	
PEC374	M	2	1	1	
PEC377	M	1	1	1	
PEC379	M	8	3	1	
PEC380	?	4	2	1	number of litters uncertain
PEC382	M	1	1	1	
PEC384	F	11	4	2	number of litters uncertain
PEC386	F	6	2	1	number of litters uncertain
PEC390	F	1	1	1	
PEC391	?	10	4	1	number of litters uncertain

Appendix Q. Breeding histories for 15 breeding pairs. The table indicates the number of offspring and the number of litters observed for each breeding pair.

Mother	Father	Offspring	Litters	Comment
PEC019	PEC028	1	1	
PEC019	PEC103	1	1	
PEC074	PEC131	10	4	
PEC113	PEC052	3	1	
PEC113	PEC357	1	1	
PEC153	PEC219	8	3	number of litters uncertain
PEC214	PEC331	1	1	
PEC270	PEC137	2	1	
PEC291	PEC103	11	2	
PEC291	PEC167	7	3	number of litters uncertain
PEC367	PEC027	1	1	
PEC369	PEC370	12	4	number of litters uncertain
PEC372	PEC014	9	2	
PEC384	PEC037	10	3	number of litters uncertain
PEC386	PEC088	6	2	number of litters uncertain