

## **Mortality and survival of white-tailed deer *Odocoileus virginianus* fawns on a north Atlantic coastal island**

Authors: Long, Robert A., O'Connell, Allan F., and Harrison, Daniel J.

Source: *Wildlife Biology*, 4(4) : 237-247

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.1998.021>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Mortality and survival of white-tailed deer *Odocoileus virginianus* fawns on a north Atlantic coastal island

Robert A. Long, Allan F. O'Connell, Jr. & Daniel J. Harrison

Long, R.A., O'Connell, A.F., Jr. & Harrison, D.J. 1998: Mortality and survival of white-tailed deer *Odocoileus virginianus* fawns on a north Atlantic coastal island. - Wildl. Biol. 4: 237-247.

Mortality and survival of white-tailed deer *Odocoileus virginianus* fawns (N = 29) were studied from birth to one year of age during 1991-95 on Mount Desert Island (MDI), Maine, where deer hunting is prohibited, coyotes *Canis latrans* have become recently established, and protected U.S. National Park lands are interspersed with private property. The rate of predator-caused mortality was 0.52, with coyote predation (N = 8) accounting for at least 47% of mortalities from all causes (N = 17). Mortality rate from drowning was 0.24 (N = 3), and from vehicles 0.14 (N = 3). For fawns radio-collared as neonates, 10 of 14 mortalities occurred during the first two months of life. Annual rate of fawn survival was 0.26. Survival rate from six months to one year was 0.65 and four mortalities (two predation, two drowning) were observed during this interval. A subgroup of fawns (N = 11) captured near a residential area and along the periphery of a coyote territory had a higher rate of survival to one year of age (S = 0.67) than did fawns from all other areas (N = 18, S = 0.00). Recruitment to one year of age was lower than that observed in other deer populations in the northeastern United States. Low recruitment associated with coyote predation and mortality sources associated with humans appears to be limiting white-tailed deer populations in some segments of this insular landscape.

*Key words:* coyotes, *Canis latrans*, fawn, Maine, mortality, *Odocoileus virginianus*, survival, white-tailed deer

Robert A. Long\* & Daniel J. Harrison, Department of Wildlife Ecology, Nutting Hall, University of Maine, Orono, Maine 04469, USA  
Allan F. O'Connell, Jr., Cooperative Park Studies Unit, Biological Resources Division, U.S. Geological Survey, University of Maine, South Annex A, Orono, Maine 04469, USA - e-mail: [connell@umenfa.maine.edu](mailto:connell@umenfa.maine.edu)

\*Present address: Greater Laurentian Wildlands Project, 4 Laurel Hill Drive, South Burlington, Vermont 05403, USA

Received 9 September 1997, accepted 6 May 1998

Associate Editor: Jean-Michel Gaillard

Mortality in ungulate populations typically follows a 'U'-shaped pattern divided into three age stages: juvenile, prime adulthood, and adult senescence, with the highest mortality in the youngest and oldest age classes (Caughley 1966). Statistical verification of these stages and variability in mortality sources and

survival rates for ungulates are poorly documented, despite their importance for clarifying the dynamics of age-structured populations (Gaillard, Delorme, Boutin, van Laere, Boisauvert & Pradel 1993, Linnell, Aanes & Andersen 1995). Understanding the relative magnitude of mortality factors will strength-

en our predictive capabilities (Kunkel & Mech 1994) and enhance our knowledge of ungulate population dynamics (Linnell et al. 1995).

In response to changing land-use patterns, a decline in sport hunting, and the absence of most mammalian predators, white-tailed deer *Odocoileus virginianus* populations throughout the eastern U.S. have increased in the last four decades to densities previously unrecorded (Porter 1991). This trend is especially evident in parks and other protected areas where hunting is often not permitted, and the interspersed parks and refuges with agriculture, forests, and increasing suburbanization have created a vegetation mosaic that encourages deer population growth. Because deer seem to lack intrinsic mechanisms to maintain their populations below K-carrying capacity (McCullough 1979:186-190, Warren 1991), studies of eastern deer populations have focused on the concept of overabundance (McShea, Underwood & Rappole 1997), management alternatives such as immunocontraception (McShea, Monfort, Hakim, Kirkpatrick, Liu, Turner, Chassy & Munson 1997) and the social and cultural implications of deer management (Curtis & Richmond 1992, Decker & Gavin 1987). Conversely, with the exception of legal hunting (where it occurs), little information is available on white-tailed deer mortality in the northeastern U.S., particularly for fawns. Furthermore, although the chronology of fawn mortality varies widely (Linnell et al. 1995), few studies have documented fawn mortality between six months and one year of age. Only two studies have examined fawn mortality in the northeastern U.S. (Mathews 1989, Decker, Healy & Williams 1992), yet elsewhere fawns often suffer high rates of mortality and are highly vulnerable to predation (Cook, White, Trainer & Glazener 1971, Beasom 1974, Nelson & Mech 1986, Fuller 1990, Kunkel & Mech 1994).

Predation can be a limiting factor in ungulate populations and exceeds all other mortality causes for neonatal ungulates, but little is known about the long-term effects of predation on ungulate population dynamics (Linnell et al. 1995). In the northeastern U.S. the role of predation in deer population dynamics is unclear because of unusually high deer densities, recent range expansion of the coyote (Moore & Parker 1992), the range reduction of other potential predators like black bears *Ursus americanus* (Maehr 1984) or bobcats *Lynx rufus* (Rolley 1987), and an increasing array and intensity of anthropogenic mortality sources. Predator-prey relationships may be

different within isolated or fragmented habitats because of concomitant changes in resource availability and use. For example, on an island in central Norway a population of red fox *Vulpes vulpes* preyed heavily on fawns in a roe deer *Capreolus capreolus* population at low densities. Fawn sex, time of birth, and type of habitat used by deer were important factors in survival (Aanes & Andersen 1996). Thus, documentation of age and time-specific mortality is needed to assess how deer populations respond to different landscapes and predator communities.

We examined mortality and survival of white-tailed deer fawns exposed to a unique set of circumstances that are likely to be representative of deer populations in the future: an island with a patchy mosaic of private and public lands, a newly established predator population, and a long-term absence of legal sport hunting. In this context, information on cause-specific mortality and survival is critical for evaluating management options. For example, restoration of predators is often proposed as a management alternative for controlling deer populations in eastern North America, yet this hypothesis remains to be tested (Porter 1991, 1996). Few areas in the region provide the opportunity to evaluate predation without the impact of hunting. Thus, our objectives were to document the timing and causes of mortality and survival rates for fawns to one year of age, evaluate the relative importance of individual mortality sources, and compare survival against various physical and geographic parameters.

## Study area

This study was conducted on Mount Desert Island (MDI), Hancock County, Maine (44°12' - 44°27'N, 68°10' - 68°27'W). MDI is the largest island (281 km<sup>2</sup>) in the Gulf of Maine, and about 47% of its area comprises the Acadia National Park (Fig. 1). MDI is divided east-west by a 10-km long fjord oriented north to south and the island is characterized by granite mountains and glaciated valleys, with elevations ranging from sea level to 465 m a.s.l. (Garman 1991). The climate of MDI is "cool, moist and maritime" (Patterson, Saunders & Horton 1983). Mean temperatures range from -6.8°C in January to 18.3°C in July and mean precipitation between 1982 and 1989 was 279 cm, with annual snowfall averaging 153 cm (U.S. National Climatic Data Center 1980-1989).

MDI is connected to the mainland via a 1-km road-

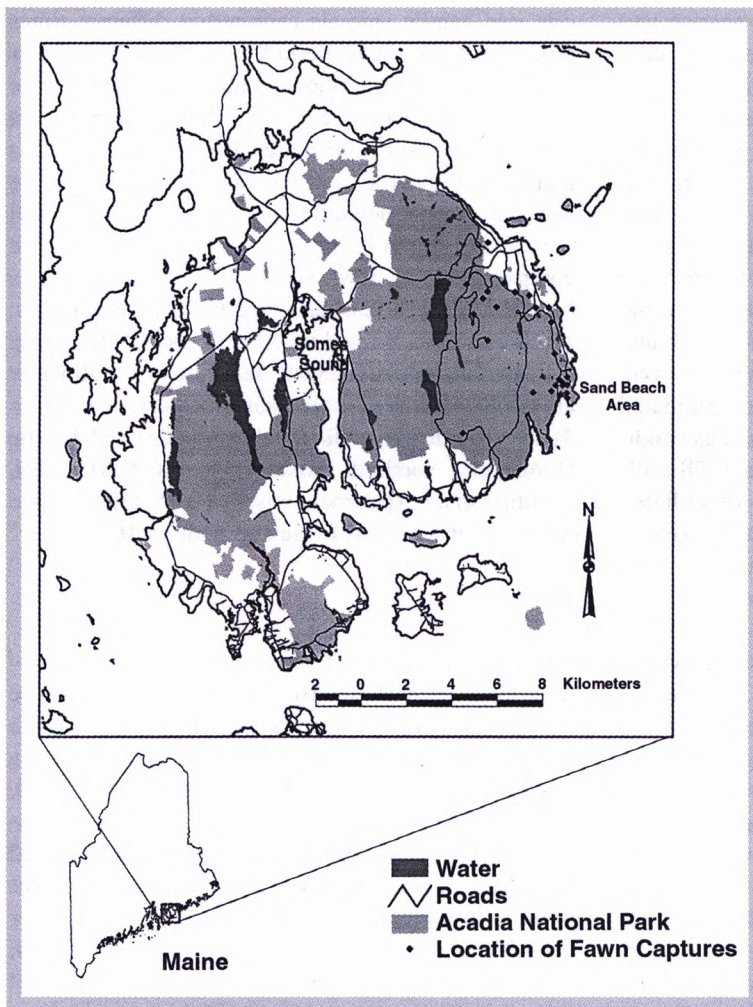


Figure 1. Location of Mount Desert Island (MDI), Maine, including boundaries of the Acadia National Park, water bodies, primary roads, and white-tailed deer fawn captures, 1991-1995.

way. Mainland - island movement for non-flying animals is also possible, across a narrow strait (0.06 - 0.6 km wide) via mud flats at low tide or via sporadic ice formation in winter. The boundary of Acadia National Park is highly fragmented; several towns are located on MDI and permanent residents total about 10,000. Visitation and recreational use on MDI increases greatly during summer and autumn. Zoning regulates land use outside the park, but development continues under local ordinances. Sand Beach (SB) is an area located within the Acadia National Park, which is a focal point for recreation during the summer months and is bordered by Bar Harbor, MDI's largest town (see Fig. 1).

Forests on MDI are primarily spruce-fir and northern hardwood (Westveld, Ashmann, Baldwin, Holds-

worth, Johnson, Lambert, Lutz, Swain & Standish 1956). Deciduous tree species predominate on the east side of MDI where a fire burned 6,880 ha in 1947. Much of this area has regenerated to an overstory of aspen *Populus* spp. and birch *Betula* spp. with an understory of red spruce *Picea rubens* and balsam fir *Abies balsamea* (Garman 1991). Red spruce stands, intermixed with balsam fir, are the dominant forest community in areas that were not influenced by fire. Black spruce *P. mariana*, eastern larch *Larix laricina*, and northern white cedar *Thuja occidentalis* inhabit wetter sites. Northern hardwood stands of American beech *Fagus grandifolia*, red maple *Acer rubrum*, and sugar maple *A. saccharum* occupy valley basins where soils are deeper and more fertile.

Legal hunting of deer on MDI has been prohibited since the early 1900s. Deer numbers on MDI increased after the 1947 fire in response to changes in vegetative succession; during 1960-67 over 700 deer were removed from MDI by direct reduction using sharpshooters. Since 1967 the deer population on MDI has not been actively managed. Indirect evidence, via browse availability and via fecal nitrogen levels, indicates that current densities of deer on MDI are

below forage carrying capacity (Saeki 1991). Due to natural range expansion, coyotes have occurred on the island since the early 1980s (Winter 1990). In addition to deer, common foods for coyotes on MDI include raccoons *Procyon lotor*, small mammals (Cricetidae, Soricidae, Zapodidae), snowshoe hare *Lepus americanus*, and blueberries *Vaccinium angustifolium*, a fruit common in the region (O'Connell, Harrison, Connery & Anderson 1992). The red fox is the only other potential predator of deer that occurs on MDI in appreciable numbers (Winter 1990).

## Methods

Fawns (<1 month of age) were captured by hand, following intensive radio-monitoring of pregnant does

(as part of a companion study on deer >1 year of age) during pre and post-parturition. We attempted to capture fawns as soon as possible after they were 48 hours old because fawns >2 days of age are less likely to be abandoned (White, Knowlton & Glazener 1972). Searches also were conducted where unmarked does were known to occur, and fawns were captured during their first winter (7-11 months of age) in clover traps (McCullough 1975). Fawns were equipped with radio-transmitters (Telonics, Mesa, AZ) attached to collars designed to expand and detach using latex tubing (wall thickness = 2.38 mm, inside diameter = 6.35 mm). Ages were estimated according to hoof growth, hoof and umbilicus condition, and behaviour (Haugen & Speake 1958). We checked pulse rates from transmitters of collared neonates 1-3 times daily between June and November and 2-5 times per week thereafter. All radios were equipped with a mortality switch designed to change the pulse rate after four hours of inactivity. If pulse rates exceeded 80 beats/minute we visually observed fawns to verify an animal's condition. All deaths were evaluated to distinguish the sources of mortality. We used wound and kill site characteristics, carcass location, collar condition, and presence of physical evidence (scats, tracks, hair) to distinguish predators (Cook et al. 1971, White 1973, Garner, Morrison & Lewis 1976).

We calculated survival rates (survival of an individual for one day) and functions (survival rate by week of life) using the Kaplan-Meier procedure (Kaplan & Meier 1958), modified by Pollock, Winterstein, Bunck & Curtis (1989) to allow the 'staggered entry' of new animals throughout the study. This method does not require the assumption of constant probability of survival over all time peri-

ods, can handle animals captured at different times throughout the study period, and allows for collar loss (i.e. censoring, Pollock et al. 1989). Fawns were reported by cohort year (e.g., fawns captured in January 1993 were considered 1992 fawns). We estimated year-specific survival rates to six months of age to avoid the potential bias associated with small numbers of fawns in the estimator after this age. We compared annual fawn survival rates and functions between years, sexes, surviving and perishing fawns, and fawns from SB and all other areas of MDI, using the log-rank test and Z-tests, respectively (Pollock et al. 1989). Multiple comparisons between years ( $N = 3$ ) were evaluated with  $\alpha$  adjusted (0.0168) by the Dunn-Sidak method (Sokal & Rohlf 1981: 242), resulting in an experiment wise  $\alpha = 0.05$ . Significance for all other tests was evaluated with  $\alpha = 0.05$ .

## Results

Despite a concerted effort, we were not able to capture fawns on MDI's west side, presumably because of lower densities of deer (Saeki 1991). We captured and monitored 29 fawns (15 males, 13 females, 1 unknown); 1 in 1991, 9 in 1992, 8 in 1993, 8 in 1994, and 3 in 1995 (Table 1). Seventeen fawns were captured by following radio-collared does. We captured 26 fawns by hand as neonates, and three in clover traps at >6 months of age. Median age at capture for neonates was estimated at 4.0 days (range = 1-30,  $N = 25$ ). Backdating to estimate birth date indicated that parturition occurred from 27 May to 20 June (median = 7 June). Mean weight of neonates at capture was 4.7 kg (SD = 1.3 kg, range = 2.6-7.3,  $N = 21$ ).

Thirteen fawns died before 180 days of age. At

Table 1. Year and sex-specific estimates of Kaplan-Meier survival rates for white-tailed deer fawns on Mount Desert Island, Maine, 1991-1995.

Sex	1992		1993		1994		1991-1995 Pooled	
	Survival to 6 months of age	N	Survival to 6 months of age	N	Survival to 6 months of age	N	Survival to 1 year of age	N
Female	0.00 (0.00-1.00) <sup>a</sup>	3	0.50 (0.00-1.00)	3	0.50 (0.01-0.99)	4	0.27 (0.00-0.71)	13
Male	0.25 (0.00-0.67)	6	0.75 (0.33-1.00)	4	0.17 (0-0.38)	4	0.22 (0.00-0.49)	15
Both sexes	0.18 (0.00-0.50)	9	0.71 (0.38-1.00)	8 <sup>b</sup>	0.30 (0.05-0.55)	8	0.26 (0.01-0.52)	29 <sup>c</sup>

<sup>a</sup> 95% confidence interval.

<sup>b</sup> One fawn was of undetermined sex.

<sup>c</sup> One additional female fawn captured during 1991 and three fawns captured during 1995 (two female, one male) are not shown because of the bias in estimating survival rates using few animals. These four fawns are, however, included in the pooled sample (1991-1995).

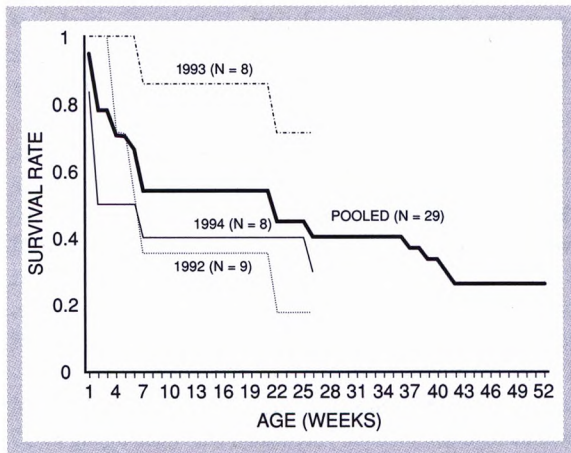


Figure 2. Year-specific survival functions (survival rate by week of life) to six months of age and pooled survival functions to one year of age for white-tailed deer fawns on Mount Desert Island (MDI), Maine, 1991-1995.

least nine fawns captured as neonates survived to a minimum of 180 days of age, and at least three of these fawns survived to one year. Four fawns slipped collars at ages of 23, 24, 39, and 271 days, four fawns shed their collars when the expandable rubber tubing broke (range 316-331 days of age), and one fawn was censored at 53 days of age when the study ended on 31 July 1995. Fawns that lost collars were included in our sample until the date when the collar was shed.

Pooled results from 1991-1995 indicated that male and female fawns did not differ in survival rates ( $Z = 0.17$ ,  $P = 0.86$ ; see Table 1) or functions ( $\chi^2 = 0.04$ ,  $df = 1$ ,  $P = 0.84$ ) and therefore, sexes were pooled for all subsequent analyses. Survival rate was 0.41 from 0-6 months of age and 0.65 from 6-12 months of age. The pooled rate of annual survival for fawns during 1991-1995 was 0.26. Fawn survival rate to six months of age was higher in 1993 than in 1992 ( $Z =$

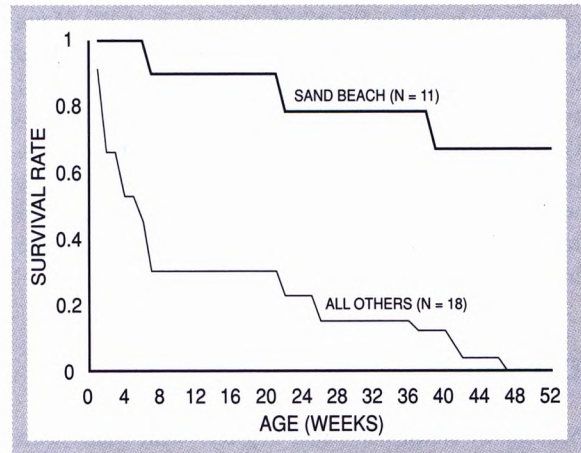


Figure 3. Survival functions (survival rate by week of life) to one year of age for white-tailed deer fawns from Sand Beach (SB) area versus all other areas on Mount Desert Island (MDI), Maine, 1991-1995.

2.28,  $P = 0.02$ ; see Table 1) and the survival function for 1993 also differed from 1992 ( $\chi^2 = 4.03$ ,  $df = 1$ ,  $P = 0.04$ ; Fig. 2).

Eleven of 29 fawns were residents of SB (see Fig. 1). These fawns had a survival rate of 0.67 to one year of age, higher ( $Z = 3.08$ ,  $P = 0.002$ ) than for all other fawns combined (0.00-0.12, 95% CI). Survival functions also differed ( $\chi^2 = 10.41$ ,  $df = 1$ ,  $P = 0.001$ ) between SB fawns and all other fawns (Fig. 3). Six of nine fawns from SB that did not slip or shed collars were still alive at 10 months of age, including three that survived to one year. In contrast, all other fawns that did not slip or shed collars ( $N = 14$ ) died prior to one year of age.

Mortality factors included coyotes ( $N = 8$ ), vehicles (3), drowning (3), domestic dogs (1), unknown predators (1), and unknown causes (1) (Table 2). Annual mortality rate from predation was 0.52, with

Table 2. Cause-specific mortality rate<sup>a</sup> during the first year of life for white-tailed deer fawns on Mount Desert Island, Maine, 1991-1995.

Cause	N	Mortality rate	95% confidence interval	% of perished fawns
All predation	10	0.52	0.10-0.90	59
Coyote	8	0.42	0.00-0.83	47
Domestic dog	1	0.12	0.00-0.47	6
Unknown predator	1	0.06	0.00-0.31	6
Vehicle	3	0.14	0.00-0.30	18
Drowning <sup>b</sup>	3	0.24	0.00-0.66	18
Unknown cause <sup>c</sup>	1	0.10	0.00-0.42	6

<sup>a</sup> Mortality rate estimated using the Kaplan-Meier procedure as modified by Pollock et al. (1989).

<sup>b</sup> Drowned fawns were found floating in the ocean or washed up on shore. Lungs were at least partially filled with water, and none of the fawns showed signs of injury or predation.

<sup>c</sup> The radio-collar from this fawn was located at least five days after the estimated date of death. The latex tubing used to secure the collar had been broken, and the collar had been chewed on by a canid; however, no carcass was found and the cause-of-death could not be determined.

coyotes accounting for  $\geq 80\%$  (at least 8 of 10) of the documented instances of predation. Of 10 fawns killed by predators, eight were killed during the first two months of life. Vehicles accounted for a mortality rate of 0.14 and drownings 0.24. Although the ultimate cause-of-death (why fawns entered the water) was uncertain for fawns that drowned, we found no injuries or trauma other than water in the lungs.

## Discussion

Similar to studies in other regions with high fawn mortality rates for white-tailed deer, coyote predation on MDI was responsible for most (at least 8 of 10) fawn mortalities during the first 60 days of life. Coyotes prey heavily on fawns across North America (Berg & Chesness 1978, Blanton & Hill 1989, Salwasser, Holl & Ashcraft 1978, Litvaitis & Shaw 1980) and white-tailed deer are a common source of food for coyotes in the northeastern United States (e.g. Hilton 1978, Person 1988, Litvaitis & Harrison 1989). The high level of coyote predation on MDI fawns may be explained by a combination of prey availability, coyote energy demands, and canid social ecology. Consumption of fawns by coyotes may be higher in forested habitats when rearing pups where alternate prey species (e.g. rodents, leporids) occur at relatively low densities (Hamilton 1974, Hilton 1978, Harrison & Harrison 1984). The use of large prey was further suggested by companion studies (O'Connell et al. 1992) which indicated that coyotes on MDI used raccoons as a frequent food item. Use of larger prey has been associated with coyote delayed dispersal and pack formation, but sociality was not the causal factor in determining prey size (Gese, Rongstad & Mytton 1988). Delayed dispersal and coyote pack formation have been linked with habitat saturation and lack of exploitation (Andelt 1985, Harrison 1992) and a similar situation has been observed on MDI (S. Glass, D. Harrison & A. O'Connell, unpubl. data). The island environment limits space and hinders dispersal, and coyotes are protected on lands within the Acadia National Park, thus reducing exploitation. These circumstances may have resulted in a higher use of relatively large prey like deer fawns and raccoons, and lower fawn survival rates compared to other areas where coyote-deer relationships have been studied.

Vegetation on MDI also may play a role in fawn

mortality related to predation. Fawns  $< 3$  weeks of age are usually considered less vulnerable in dense vegetation because hiding seems to be an effective anti-predator behaviour (Carroll & Brown 1977, Nelson & Woolf 1987). Most fawns in Minnesota, however, were  $< 30$  days old when killed by predators despite "relatively dense vegetation" (Kunkel & Mech 1994). We observed a similar situation on MDI where most (all but two) predation events occurred before fawns were eight weeks old, the age at which fawns can generally outrun canids (Nelson & Woolf 1987). Although vegetation in northeastern Minnesota and on MDI is similar, consisting of mixed boreal and deciduous forests, forests on MDI are aging ( $> 50$  years old) with a sparse understory that may aid visibility for predators. Kunkel & Mech (1994) suggested that fawn vulnerability probably varies dependent on local conditions. We concur and propose that physical factors like vegetative cover, although often subtle with respect to predation (Porath 1980, Nelson & Woolf 1987), be carefully considered when evaluating the impact of predators on a prey population (Aanes & Anderson 1996).

Drowning was the proximate cause of three fawn mortalities on MDI in November ( $N = 1$ ) and February and March ( $N = 2$ ). Although we are uncertain as to why fawns entered the water, a plausible explanation is that deer on MDI may forage for seaweeds in the rocky intertidal zone during winter and thus, could lose their footing and fall into the ocean. Saeki (1991: 64, 108) concluded that seaweeds may be an important winter food for white-tailed deer in coastal habitats because of high levels of crude protein combined with a lack of alternate browse. Sitka black-tailed deer *O. hemionus sitchensis* have been reported to feed on seaweeds in the intertidal zone in Alaska (Hanley & McKendrick 1985). Alternatively, white-tailed deer pursued by wolves *Canis lupus* are known to seek out open water (Pimlott 1967, Mech 1970) and drownings could be associated with predator avoidance. Cold ocean temperatures off the Maine coast throughout much of the year and steep, rocky shores covered with knotted wrackweed *Ascophyllum nodosum*, rockweed *Fucus vesiculosus*, and kelp *Alaria esculanta*, might impair the ability of deer to exit the water after fleeing from a predator. We have no evidence that predators chased radio-collared fawns into the ocean but we received one report of a domestic dog cornering a radio-collared doe on coastal rocks, and documented coyotes feeding on a deer carcass shortly after it was washed up on shore.

In the southeast, deer deaths caused by drowning and cold water shock have been attributed to chasing by dogs (Barick 1969).

Although domestic dogs can be occasional predators of newborn fawns (Bryan 1980, Nelson & Woolf 1987, Decker et al. 1992), the overall impact of dogs on deer is not well-quantified (Fuller 1990). Deer may be more susceptible to dogs where snow and cold winter temperatures impact deer physical condition (Fuller 1990) or in suburban areas like northern Idaho; when residential communities were built in deer winter range, 39 instances of dogs chasing deer resulted in 12 direct deer mortalities (Denney 1974). We attributed only one fawn mortality to dog predation; however, MDI is interspersed with small towns and private land which provides numerous opportunities for deer/dog interactions.

Mortality resulting from vehicle-deer collisions can be substantial (e.g. Schaffer & Penland 1985, O'Gara & Harris 1988). In some park areas, where automobile traffic is heavy and deer are concentrated in small areas, collisions can be responsible for maintenance of a stable deer population (Cypher, Yahner & Cypher 1985) in the absence of native predators and hunting. A large increase in visitors and vehicular traffic begins during the fawn rearing season on MDI and most radio-collared fawns that survived >1 month regularly cross paved roads. Visitor use patterns for MDI indicate an increasing number of visitors, especially during spring and autumn (U.S. Department of Interior 1992), thereby increasing the potential for human-deer conflicts. Studies of collisions between deer and vehicles have reported relatively high collision rates in the spring and autumn (Bellis & Graves 1971, Allen & McCullough 1976, Case 1978), and this trend was also evident during autumn on MDI (J. Vinck, unpubl. report). An annual downward trend in the number of deer-automobile accidents on MDI between 1987 and 1992 was evident (J. Vinck, unpubl. report), and corroborates Saeki's (1991) conclusion that deer are declining on MDI.

Previous studies have reported that most fawn mortality occurs within 30 days postpartum. Most studies of neonatal ungulate survival have estimated survival rates to 180 days; thereafter, fawns and adults are assumed to experience similar risks of mortality (Kunkel & Mech 1994). Linnell et al. (1995), however, noted the need for age or time-specific mortality analysis to determine predation patterns. We found three peaks in fawn mortality

throughout the first year of life on MDI; two of these occurred after fawns reached six months of age. Drowning, vehicles, and dog predation contributed to mortality during November (age 22-26 weeks) and late March (age 37-42 weeks) when deer typically increase their movements. Fawn movements and home ranges closely parallel the dam, but fawns may be driven away from their dam by breeding bucks during autumn (Marchinton & Hirth 1984) or by the dam prior to parturition the following spring (Hirth 1977). Deer movements also increase during spring and autumn when distinct seasonality prompts deer to move between summer and winter home ranges (Severinghaus & Cheatum 1956, Verme & Ozoga 1971). Although evidence is limited, movements by bucks seem to increase during late fall, which has been explained by a subordinate social response resulting from sexual competition (Marchinton & Hirth 1984). When deer movements increase on MDI, fawns spend proportionately more time crossing roads, near the immediate coastline, and are probably more likely to encounter vehicles or a potential predator.

Rate of fawn survival on MDI was low relative to most other studies from the central and northeastern U.S.; however, the survival rate of fawns inhabiting SB was similar to survival rates observed in other studies (Logan 1972, Carroll & Brown 1977, Nelson 1984, Dalton 1985, Huegel, Dahlgreen & Gladfelter 1985, Mathews 1989). This area is bordered by the ocean to the east, residential development to the north, and experiences seasonally high human densities. SB is also on the periphery of a coyote territory, but outside its core area of use (S. Glass, D. Harrison & A. O'Connell, unpubl. data). In Minnesota, most traditional summer and winter ranges of white-tailed deer were located in buffer zones between wolf territories, and deer survived despite deteriorating habitat, severe winters, and high wolf densities (Nelson & Mech 1981, Rogers, Mech, Dawson, Peek & Korb 1980). Higher rates of survival for SB fawns may be related to the location of coyote territories and/or areas of high human density that reduce deer encounters with coyotes. We did not observe any apparent factors to account for differences between years (1992-1993) in fawn survival to six months of age and suggest that future work examine survival and mortality over time periods long enough to evaluate year to year variation.

Although evidence indicates that deer on MDI exist at low densities and well below forage carrying



capacity (Saeki 1991), fawns were subject to relatively high mortality rates to one year of age because of coyote predation and a combination of anthropogenic mortality sources. Thus, predation and mortality sources such as vehicle accidents do not appear to be condition dependent. High mortality of fawns in core areas of coyote territories may result in declining deer populations; however, fawns on MDI existing in buffer zones between coyote territories or near human development may exhibit higher survival rates than the general deer population. Fawn captures were limited to the eastern half of MDI (see Fig. 1). The limited distribution of fawn captures, coupled with the relatively high survival of SB fawns suggest that distribution of deer was influenced by spatial patterns of fawn mortality. The long-term result may be a patchy distribution of deer, similar to what has been documented in areas where wolves inflict significant mortality on deer (Nelson & Mech 1981, Kunkel & Mech 1994). The combination of mortality sources is apparently limiting the deer population on MDI in some areas. Where deer and their natural predators coexist, the role of humans may play a significant role in deer population trends. High survival in some areas may be needed to supplement high mortality caused by predators and human influences.

Land use on MDI is varied and contrasted by development on private lands and U.S. National Park Service management policies that allow vegetative succession to proceed naturally in the context of fuel management and wildfire suppression (U.S. Department of Interior 1988, 1992). Thus, as vegetative succession on MDI proceeds toward a mature spruce-fir forest, suburban development outside park boundaries will provide an increasing vegetation mosaic preferred by deer. Deer also approach the edge of their range in the boreal and northern hardwood forests of Maine, and historically, except where deer congregate in winter yards, these communities have not typically supported high deer densities (Mattfield 1984). For coyotes, forest succession will likely result in deer spending a greater proportion of time in areas similar to SB. Further, we expect that densities of alternative prey like small mammals and snowshoe hares will decrease and that anthropogenic food sources (e.g. garbage) for coyotes will increase with increased human encroachment near park boundaries. Because coyotes have the potential to modify their foraging behaviour, spatial requirements, density, and group sizes in response to local food resources and exploitation rates (Harrison 1992), coyote predation

of fawns on MDI will probably remain at relatively high levels for the immediate future, especially in natural habitats. As the landscape changes, however, fawn predation and use of other natural prey by coyotes may decrease as anthropogenic foods become more readily available. Evaluating management options for ungulate populations in parks and other protected areas should incorporate how local landscape changes, especially outside park boundaries, influence interactions between deer and their environment.

*Acknowledgements* - we sincerely appreciate the assistance of Steve Glass, the staff at Acadia National Park, particularly Bruce Connery, and the funding support of the U.S. National Park Service. Many fine individuals participated in field work and logistical support and we thank all involved. Mike Coffey facilitated the funding process, and along with Brian Underwood, provided technical assistance to our field operations. We gratefully acknowledge the two reviewers for providing valuable comments to improve the manuscript.

## References

- Aanes, R. & Andersen, R. 1996: The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. - *Canadian Journal of Zoology* 74: 1857-1865.
- Allen, R.E. & McCullough, D.R. 1976: Deer-car accidents in southern Michigan. - *Journal of Wildlife Management* 40: 317-325.
- Andelt, W.F. 1985: Behavioral ecology of coyotes in south Texas. - *Wildlife Monographs* 94: 1-45.
- Barick, F.B. 1969: Deer predation in North Carolina and other southeastern states. - In: Halls, L.K. (Ed.); White-tailed deer in the southern forest habitat. Proceedings of a symposium in Nacogdoches, Texas. United States Department of Agriculture, U.S. Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, pp. 25-31.
- Beasom, S.L. 1974: Relationships between predator removal and white-tailed deer net productivity. - *Journal of Wildlife Management* 38: 854-859.
- Bellis, E.D. & Graves, H.B. 1971: Deer mortality on a Pennsylvania interstate highway. - *Journal of Wildlife Management* 35: 232-237.
- Berg, W.E. & Chesness, R.A. 1978: Ecology of coyotes in northern Minnesota. - In: Bekoff, M. (Ed.); *Coyotes: biology, behavior and management*. Academic Press, New York, pp. 227-249.
- Blanton, K.M. & Hill, E.P. 1989: Coyote use of white-tailed deer fawns in relation to deer density. - Proceedings of the Annual Conference of Southeast Association of Fish and Wildlife Agencies 43: 470-478.

- Bryan, D.A. 1980: White-tailed deer fawn mortality, home range, and habitat utilization in east central Missouri. - M.Sc. Thesis, University of Missouri, Columbia, 45 pp.
- Carroll, B.K. & Brown, D.L. 1977: Factors affecting neonatal fawn survival in south-central Texas. - *Journal of Wildlife Management* 41: 63-69.
- Case, R.M. 1978: Interstate highway road-killed animals: a data source for biologists. - *Wildlife Society Bulletin* 6: 8-13.
- Caughley, G. 1966: Mortality patterns in mammals. - *Ecology* 47: 906-918.
- Cook, R.S., White, M., Trainer, D.O. & Glazener, W.C. 1971: Mortality of young white-tailed deer fawns in south Texas. - *Journal of Wildlife Management* 35: 47-56.
- Curtis, P.D. & Richmond, M.E. 1992: Future challenges of suburban white-tailed deer management. - *Transactions of the North American Wildlife & Natural Resources Conference* 57: 104-114.
- Cypher, B.L., Yahner, R.H. & Cypher, E.A. 1985: Ecology and management of white-tailed deer at Valley Forge National Historical Park. - National Park Service Technical Report, Mid-Atlantic Region, Philadelphia, Pennsylvania, MAR-15, 244 pp.
- Dalton, C.J. 1985: Mortality and movements of white-tailed deer fawns in the southeastern Missouri Ozarks. - M.Sc. Thesis, University of Missouri, Columbia, 123 pp.
- Decker, D.J. & Gavin, T.A. 1987: Public attitudes toward a suburban deer herd. - *Wildlife Society Bulletin* 15: 173-180.
- Decker, T.A., Healy, W.M. & Williams, S.A. 1992: Survival of white-tailed deer fawns in western Massachusetts. - *Northeast Wildlife* 49: 36-42.
- Denney, R.N. 1974: The impact of uncontrolled dogs. - *Transactions of the North American Wildlife and Natural Resources Conference* 39: 257-291.
- Fuller, T.K. 1990: Dynamics of a declining white-tailed deer population in north-central Minnesota. - *Wildlife Monographs* 110, pp. 1-37.
- Gaillard, J.M., Delorme, D., Boutin, J., van Laere, G., Boisubert, B. & Pradel, R. 1993: Roe deer survival patterns: a comparative analysis of contrasting populations. - *Journal of Animal Ecology* 62: 778-791.
- Garman, S.L. 1991: Habitat associations of small mammals in seral stages of red spruce in Acadia National Park, Maine. - PhD thesis, University of Massachusetts, Amherst, 291 pp.
- Garner, G.W., Morrison, J.A. & Lewis, J.C. 1976: Mortality of white-tailed deer fawns in the Wichita Mountains, Oklahoma. - *Proceedings of the Annual Conference of Southeast Fish & Wildlife Agencies* 30: 493-506.
- Gese, E.M., Rongstad, O.J. & Mytton, W.R. 1988: Relationship between coyote group size and diet in southeastern Colorado. - *Journal of Wildlife Management* 52: 647-653.
- Hamilton, W.J. 1974: Food habits of the coyote in the Adirondacks. - *New York Fish & Game Journal* 21: 177-181.
- Hanley, T.A. & McKendrick, J.D. 1985: Potential nutritional limitations for black-tailed deer in a spruce-hemlock forest, southeastern Alaska. - *Journal of Wildlife Management* 49: 103-114.
- Harrison, D.J. 1992: Social ecology of coyotes in northeastern North America: relationships to dispersal, food resources, and human exploitation. - In: Boar, A.H. (Ed.); *Ecology and management of the eastern coyote*. Wildlife Research Unit, University of New Brunswick, Fredericton, pp. 53-72.
- Harrison, D.J. & Harrison, J.A. 1984: Foods of adult Maine coyotes and their known-aged pups. - *Journal of Wildlife Management* 48: 922-926.
- Haugen, A.O. & Speake, D.W. 1958: Determining age of young fawn white-tailed deer. - *Journal of Wildlife Management* 22: 319-321.
- Hilton, H. 1978: Systematics and ecology of the eastern coyote. - In: Bekoff, M. (Ed.); *Coyotes: biology, behavior and management*. Academic Press, New York, pp. 209-228.
- Hirth, D.H. 1977: Social behaviour of white-tailed deer in relation to habitat. - *Wildlife Monographs* 53, 55 pp.
- Huegel, C.N., Dahlgreen, R.B. & Gladfelter, H.L. 1985: Use of doe behaviour to capture white-tailed deer fawns. - *Wildlife Society Bulletin* 13: 287-289.
- Kaplan, E.L. & Meier, P. 1958: Nonparametric estimation from incomplete observations. - *Journal of the American Statistical Association* 53: 457-481.
- Kunkel, K.E. & Mech, L.D. 1994: Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. - *Canadian Journal of Zoology* 72: 1557-1565.
- Linnell, J.D.C., Aanes, R. & Andersen, R. 1995: Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. - *Wildlife Biology* 1: 209-223.
- Litvaitis, J.A. & Harrison, D.J. 1989: Bobcat-coyote niche relationships during a period of coyote population increase. - *Canadian Journal of Zoology* 67: 1180-1188.
- Litvaitis, J.A. & Shaw, J.H. 1980: Coyote movements, habitat use, and food habits in southwestern Oklahoma. - *Journal of Wildlife Management* 44: 62-68.
- Logan, T. 1972: Study of white-tailed deer fawn mortality on Cookson Hills Deer Refuge, Eastern Oklahoma. - *Proceedings of the Annual Conference of Southeastern Association of Game & Fish Commissioners* 26: 27-38.
- Maehr, D.S. 1984: Distribution of black bears in eastern North America. - *Eastern workshop on black bear ecology and management*. 7: 74.
- Marchinton, R.L. & Hirth, D.H. 1984: Behavior. - In: Halls, L.K. (Ed.); *White-tailed deer ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, pp. 129-168.
- Mathews, N.E. 1989: Social structure, genetic structure

- and anti-predator behaviour of white-tailed deer in the central Adirondacks. - PhD thesis, State University of New York, Syracuse, 168 pp.
- Mattfield, G.F. 1984: Eastern hardwood and spruce fir forests. - In: Halls, L.K. (Ed.); White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania, pp. 305-330.
- McCullough, D.R. 1975: Modification of the clover deer trap. - *California Fish & Game* 61: 242-244.
- McCullough, D.R. 1979: The George Reserve deer herd: population ecology of a K-selected species. - University of Michigan Press, Ann Arbor, 271 pp.
- McShea, W.J., Monfort, S.L., Hakim, S., Kirkpatrick, J., Liu, I., Turner, J.W., Chassy, L. & Munson, L. 1997: The effect of immunocontraception on the behavior and reproduction of white-tailed deer. - *Journal of Wildlife Management* 61: 560-569.
- McShea, W.J., Underwood, H.B. & Rappole, J.H. (Eds.) 1997: *The Science of Overabundance: Deer Population Ecology and Management*. - The Smithsonian Institution Press, Washington, DC, 402 pp.
- Mech, L.D. 1970: *The wolf: the ecology and behavior of an endangered species*. - Doubleday, New York, 381 pp.
- Moore, G.C. & Parker, G.R. 1992. Colonization by the eastern coyote (*Canis latrans*) - In: Boar, A.H. (Ed.); *Ecology and management of the eastern coyote*. Wildlife Research Unit, University of New Brunswick, Fredericton, pp. 22-37.
- Nelson, M.E. & Mech, L.D. 1981: Deer social organization and wolf predation in northeastern Minnesota. - *Wildlife Monographs* 77, pp. 1-53.
- Nelson, M.E. & Mech, L.D. 1986: Mortality of white-tailed deer in northeastern Minnesota. - *Journal of Wildlife Management* 50: 691-698.
- Nelson, T.A. 1984: *The production and survival of white-tailed deer fawns on Crab Orchard National Wildlife Refuge*. - PhD thesis, Southern Illinois University, Carbondale, 178 pp.
- Nelson, T.A. & Woolf, A. 1987: Mortality of white-tailed deer fawns in southern Illinois. - *Journal of Wildlife Management* 51: 326-329.
- O'Connell, A.F., Jr., Harrison, D.J., Connery, B. & Anderson, K.B. 1992: Food use by an insular population of coyotes. - *Northeast Wildlife* 49: 36-42.
- O'Gara, B.W. & Harris, R.B. 1988: Age and condition of deer killed by predators and automobiles. - *Journal of Wildlife Management* 52: 316-320.
- Patterson, W.A., III, Saunders, K.E. & Horton, L.J. 1983: *Fire regimes of the coastal Maine forests of Acadia National Park*. - National Park Service Technical Report, Boston, Massachusetts, OSS-83-3, 96 pp.
- Person, D.K. 1988: Home range, activity, habitat use, and food habits of eastern coyotes in the Champlain Valley region of Vermont. - M.Sc. thesis, University of Vermont, Burlington, 102 pp.
- Pimlott, D.H. 1967: Wolf predation and ungulate populations. - *American Zoology* 7: 267-278.
- Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. 1989: Survival analysis in telemetry studies: the staggered entry design. - *Journal of Wildlife Management* 53: 7-15.
- Porath, W.R. 1980: Fawn mortality estimates in farmland deer range. - In: Hine, R.L. & Nehls, S. (Eds.); *White-tailed deer population management in the north central states*. - Proceedings of a symposium, 41<sup>st</sup> Midwest Fish & Wildlife Conference, Urbana, Illinois, North central section, The Wildlife Society, pp. 55-63.
- Porter, W.F. 1991: *White-tailed deer in eastern ecosystems: Implications for management and research in national parks*. - United States Department of the Interior, National Park Service Technical Report, Washington, DC, NRSUNY/NRR-91/05, 57 pp.
- Porter, W.F. 1996: Management of overabundant species in protected areas: the white-tailed deer as a case example. - In: Wright, R.G. (Ed.); *National parks and protected areas: their role in environmental protection*. Blackwell Science, Cambridge, Massachusetts, pp. 223-248.
- Rogers, L.L., Mech, L.D., Dawson, D.K., Peek, J.M. & Korb, M. 1980: Deer distribution in relation to wolf pack territory edges. - *Journal of Wildlife Management* 44: 253-258.
- Rolley, R.E. 1987: Bobcat. - In: Novak, M., Baker, J.A., Obbard, M.E. & Malloch, B. (Eds.); *Wild furbearer management and conservation in north America*. - Ontario Trappers Association, North Bay, Ontario, pp. 670-681.
- Saeki, M. 1991: *Influence of browsing by white-tailed deer and snowshoe hare on vegetation at Acadia National Park, Maine*. - M.Sc. Thesis, University of Maine, Orono, 120 pp.
- Salwasser, H., Holl, S.A. & Ashcraft, G.A. 1978: Fawn production and survival in the North Kings River deer herd. - *California Fish & Game* 64: 38-52.
- Schaffer J.A. & Penland, S.T. 1985: Effectiveness of Swareflex reflectors in reducing deer-vehicle accidents. - *Journal of Wildlife Management* 49: 774-776.
- Severinghaus, C.W. & Cheatum, E.L. 1956: *Life and times of the white-tailed deer*. - In: Taylor, W.P. (Ed.); *The deer of North America*. Stackpole Books, Harrisburg, Pennsylvania, pp. 57-186.
- Sokal, R.R. & Rohlf, F.J. 1981: *Biometry*. - W.H. Freeman and Company, New York, 859 pp.
- United States Department of the Interior 1988: *National Park Service management policies: management of the national park system*. - Chapter 4, biological resource management. United States Government Printing Office, Washington, DC.
- United States Department of the Interior 1992: *Acadia National Park General Management Plan*. - National Park Service, Boston, Massachusetts, 99 pp.
- United States National Climatic Data Center 1980-1989:

- New England, annual summaries. - Climatological data. National Oceanic and Atmospheric Administration, Asheville, North Carolina, 92-101(13).
- Verme, J.L. & Ozoga, J.J. 1971: Influence of winter weather on the white-tailed deer in Upper Michigan. - In: Haugen, A.O. (Ed.); Proceedings of Snow and Ice in Relation to Wildlife and Recreation Symposium. Iowa State University, Ames, pp. 16-28.
- Warren, R.J. 1991: Ecological justification for controlling deer populations in eastern national parks. - Transactions of the North American Wildlife & Natural Resources Conference 56: 56-66.
- Westveld, M., Ashmann, R.I., Baldwin, H.I., Holdsworth, R.S., Johnson, R.S., Lambert, J.H., Lutz, H.J., Swain, L. & Standish, M. 1956: Natural forest vegetation zones of New England. - *Journal of Forestry* 54: 332-338.
- White, M. 1973: Description of remains of deer fawns killed by coyotes. - *Journal of Mammalogy* 54: 291-293.
- White, M., Knowlton, F.F. & Glazener, W.C. 1972: Effects of dam-newborn fawn behavior on capture and mortality. - *Journal of Wildlife Management* 36: 897-906.
- Winter, L.A. 1990: Home range and spatial relationships of coyotes and red foxes in Acadia National Park, Maine. M.W.C.- report. - University of Maine, Orono, 74 pp.