AGE-SPECIFIC CAUSES OF MORTALITY AMONG MALE WHITE-TAILED DEER SUPPORT MATE-COMPETITION THEORY

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Abstract: Mate-competition theory predicts that males will invest resources toward intrasexual competition for mates until reproductive benefits are outweighed by costs to future fitness. In populations that have a substantial proportion of mature males, theory predicts that young males will forego reproduction to reduce exposure to mortality that may result from breeding efforts. We examined age-specific mortality of males in a white-tailed deer (*Odocoileus virginianus*) population in which >50% of the males were ≥3.5 years old to determine whether patterns of male mortality conform to mate-competition theory. Annual mortality rates were relatively stable throughout adulthood (0.26–0.38), but causes of mortality changed with age. Young males (1.5 and 2.5 years old) were most susceptible to human-induced mortality (e.g., hunting and vehicle accidents), whereas males ≥3.5 years old tended to die from non-human causes (e.g., fighting, predation) more frequently than did younger deer. Proportional hazard models also indicated that as antler size increased, likelihood of mortality increased. Age- and cause-specific patterns of mortality in adult male deer from a population with >50% mature males reflected patterns predicted by mate-competition theory. When managing deer populations with high proportions of mature males, it is important to account for shifts in susceptibility to human-induced and natural mortality agents.

Mate-competition theory states that populations with a substantial proportion of mature males should possess mating systems dominated by mature males. Young males in these populations should not actively participate in reproduction early in life because of low probability of successfully acquiring a mate. Such a strategy is likely based upon expected costs of mate competition and probability of success (Roff 1992, Stearns 1992). Although young males that commit substantial resources to mate competition may increase current reproductive success, they may jeopardize lifetime reproductive success because of decreased probability of survival in the future (Geist 1971, Hutchings 1994, Hogg and Forbes 1997). Clutton-Brock et al. (1982) noted that reproduction in red deer (*Cervus elaphus*) populations was dominated by mature males, and similar findings have been reported for mule deer

(*Odocoileus hemionus*; Bowyer 1986), moose (*Alces alces*; Van Ballenberghe and Miquelle 1993), fallow deer (*Dama dama*; Komers et al. 1997), and pronghorn antelope (*Antilocapra americana*; Byers 1997).

White-tailed deer populations have been subjected to intensive hunting pressure across most of their range, resulting in demographic conditions—such as younger age distributions—that differ from those in which they evolved (Miller et al. 1995). Young males in these populations may exert greater reproductive effort than those in populations with greater numbers of mature males (Miller and Marchinton 1995). However, the paucity of older-aged populations has resulted in few investigations of the reproductive strategies of male white-tailed deer in populations that have a substantial proportion of mature males.

We examined mortality of male white-tailed deer in a population with a large proportion of mature males (>50% of males ≥3.5 years old; Ditchkoff et al. 2000) to improve our understanding of reproductive strategies of males under these demographic conditions. We hypothesized that if younger males were committing fewer resources to breeding or competition for mates than mature males, they would not be as susceptible to natural mortality agents as

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mature deer. Additionally, we predicted that increased body size and antler development—traits associated with reproductive success (Hirth 1977, Clutton-Brock et al. 1982, Bowyer 1986)—would be associated with increased competition for mates and subsequently result in greater mortality.

STUDY AREA

We conducted this study at the McAlester Army Ammunition Plant (McAAP) in southeastern Oklahoma, United States. The McAAP was an ammunition production and storage facility owned and operated by the U.S. Department of Defense. Public access on the area was restricted. This facility encompassed 18,212 ha, 98.6% of which was composed of native vegetation. Dominant vegetation included post oak (*Quercus stellata*)–blackjack oak (*Q. marilandica*) uplands and riparian drainages of mainly water oak (*Q. nigra*), red oak (*Q. shumardii*), and bur oak (*Q. macrocarpa*). Large areas of native prairie grasses, including broomsedge bluestem (*Andropogon virginicus*), little bluestem (*Schizachyrium scoparium*), and panicums (*Panicum* spp.), were maintained as hay meadows and were bisected by brushy draws. Approximately 200 ha of food plots planted with a mixture of rye, wheat, and clover were dispersed over much of the area. A more detailed description of the study area was described by Ditchkoff et al. (1996, 1997).

This facility has been open to public hunting via lottery since 1962, and it has been managed under the objectives of quality deer management since 1989 (Ditchkoff et al. 1997). As a result, the male segment of the herd contained ≥50% mature (≥3.5 years old) deer (Ditchkoff et al. 2000). Such an age structure is uncommon across most of the range of white-tailed deer (Miller and Marchinton 1995). The deer herd at the facility was below carrying capacity (density was approximately 12–13 deer/km^2), and the buck:doe ratio was 1:2.2 (Ditchkoff et al. 1997). The primary mechanism used to control hunter success and maintain a suitable proportion of mature deer in the population was restriction of hunters to traditional archery equipment (e.g., recurve or longbows). Hunter success at this facility has averaged about 10% since inception of the traditional archery rule (Ditchkoff et al. 1996), and harvest data suggested that approximately 15% of the males were harvested annually (Ditchkoff et al. 1998). A more detailed description of management on the study area was provided by Ditchkoff et al. (1997).

METHODS

Capture and Survival

We captured adult (≥1.5 years old) male deer during December 1994–January 1995 (*n* = 50), January 1996 (*n* = 13), and January 1997 (*n* = 17) using dropnets (Ramsey 1968) on food plots prebaited with whole corn and persimmons. The study ended on 31 December 1997. Deer were not sedated during capture and handling. Age of captured deer was estimated by tooth wear and eruption (Severinghaus 1949), and each deer was fitted with a collar-mounted transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). Each radiocollar was equipped with a mortality sensor that was triggered whenever the radiocollar was stationary for a period >4 hours. Prior to release, we measured chest girth, body length, and antler characteristics. We calculated a Boone and Crockett score (Nesbitt and Wright 1981) for each set of antlers to estimate antler size by summing the measurements (inches) of beam length, all tines, greatest inside spread, and 4 circumferences of the main beam. Each inch of length, spread, and circumference counted as a point using this scoring system. We enumerated ectoparasitic ticks on the sternum within a 5- × 25-cm template. We also collected whole blood via jugular venipuncture into a 10-ml, evacuated, serum-separating tube (SST, Becton Dickinson Vacutainer Systems, Rutherford, New Jersey, USA). Serum was separated from blood by centrifugation and stored at –80°C. Serum was analyzed for blood urea nitrogen (BUN), total protein, creatinine phosphokinase (CPK), and albumin (Vet-Pro Labs, Tulsa, Oklahoma, USA). Blood urea nitrogen and other measures of protein in serum of deer (e.g., total protein and albumin) can be used as indices to nutritional condition (LeResche et al. 1974), and CPK can be used as an index to stress and muscle trauma (DelGiudice et al. 1990).

Cause-specific mortality was determined by locating dead deer and performing in-field necropsies (Roffe et al. 1994). We used evidence of predation or scavenging, hunting wounds, and condition assessments based on femur marrow fat (Klein 1964) to determine cause of death. We classified mortalities caused by hunting, poaching, and vehicular collisions as human-induced and all others as natural (e.g., not caused by humans: predation, intrasexual combat, rut-related stress). If the specific cause of death could not be determined, it was classified as unknown. However, in all situations where mortality was classified as unknown we were able to rule out

Table 1. Sample sizes[a] (*n*) of adult male white-tailed deer monitored using radiotelemetry during 1995–1997 at the McAlester Army Ammunition Plant in southeastern Oklahoma.

	Age (years)						
Time period	1.5	2.5	3.5	4.5	5.5	6.5	≥7.5
1 Jan 1995 to 31 Mar 1995	16	16	6	5	3	1	2
1 Apr 1995[b] to 31 Mar 1996	8	17	16	7	6	4	3
1 Apr 1996 to 31 Mar 1997	3	13	14	9	7	7	5
1 Apr 1997 to 31 Dec 1997	0	3	12	9	5	4	8

[a] Animals were trapped during January each year in an attempt to maintain 50 radiocollared animals at all times and replace individuals lost to mortality. However, total animals present during listed time periods may exceed 50 because of staggered entry (Pollock et al. 1989).

[b] Study animals were considered to leave 1 age category and enter the next on 1 April.

human-induced mortality and thus categorized these as natural mortality. Because there was only 1 entrance to the study area and all deer harvested had to be brought to a check station, we were aware of all study deer that were legally harvested.

Data Analysis

We calculated Kaplan-Meier estimates modified for a staggered-entry design (Pollock et al. 1989) to determine annual survival and compared survival curves between age classes using PROC LIFETEST (SAS Institute 1988, Allison 1995). Ages of study animals were based upon age in November and recorded as 1.5, 2.5, 3.5, etc., and animals were assumed to enter the next age class on 1 April. We separated animals into 3 groups based on age: 1.5–2.5 years old, 3.5–4.5 years old, and ≥5.5 years old. Antler development in white-tailed deer >5.5 years old approached maximum while deer <3.5 years old lacked substantial antler development relative to older animals (Ditchkoff et al. 2000).

Annual probability of survival was compared among age classes using *Z*-tests (Heisey and Fuller 1985), and survival curves were compared with Wilcoxon and log-rank tests. Program MICROMORT (Heisey 1985) was used to calculate cause-specific rates of mortality. We used proportional hazard models (Cox 1972, Allison 1995) to determine how morphologic and physiologic parameters influenced likelihood of mortality during the year following capture for 57 individuals; 23 animals that were censored during the year following capture (e.g., lost radio signal) could not be used in this analysis. Unlike traditional survival analyses, proportional hazard models do not calculate probability of survival or mortality but rather estimate how mortality rates change according to changes among independent variables. Proportional hazard models estimate how variables influence mortality during a defined time period, and thus probability estimates refer only to the year following capture (defined period) and not the remainder of a subject's life. Therefore, deer that died after 1 year were considered as survivors for this analysis.

RESULTS

During the study we trapped 80 adult male white-tailed deer but lost radio contact with 6 deer before data could be collected. The 74 deer that were monitored accounted for 45,465 deer–radio days and 39 documented mortalities. Radiocollared animals ranged in age from 1.5 to 10.5 years old (Table 1). Greatest probability of annual mortality was due to hunting (P_m = 0.124), followed by vehicle collisions (P_m = 0.021), poaching (P_m = 0.021), and predation (P_m = 0.021; Table 2). Eight mortalities were classified as

Table 2. Estimated annual probability of mortality (P_m) from various causes for 74 adult, male white-tailed deer in a population from southeastern Oklahoma.

				95% C.I.	
Cause of death	*n*	P_m	SE	Lower	Upper
Hunting	18	0.124	0.027	0.071	0.178
Vehicle collisions	3	0.021	0.012	0.000	0.044
Poaching	3	0.021	0.012	0.000	0.044
Predation	3	0.021	0.012	0.000	0.044
Other[a]	4	0.028	0.014	0.001	0.055
Unknown	8	0.055	0.019	0.018	0.093

[a] Causes of mortality in this category were a leg infection, thoracic puncture during a fight, brain abscess, and exhaustion from breeding activity.
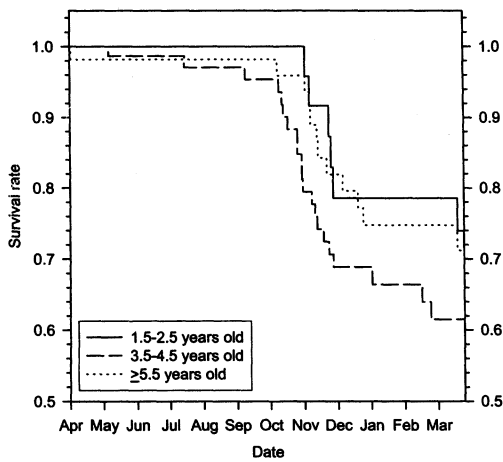
Fig 1. Annual probability of survival of adult male white-tailed deer in a population from southeastern Oklahoma that were 1.5–2.5, 3.5–4.5, and ≥5.5 years old. Survival curves were calculated using the Kaplan-Meier method.

unknown because we could not determine a specific cause of death, and 4 additional mortalities that could not be easily categorized were classified as other. Causes of mortality classified as other were a leg infection, thoracic puncture during intrasexual combat, brain abscess, and exhaustion from excessive breeding activity. Probability of mortality from all natural causes was 0.104 and human-induced causes was 0.166. Most (72%) mortalities occurred during or immediately following the breeding season (1 Oct–15 Dec; Fig. 1). We did not detect differences ($P > 0.20$) in overall survival (curve shape

or endpoint) between age classes, suggesting that seasonal differences in survival among age classes did not occur.

Young males (1.5–2.5 years old) were nearly 5 times as likely ($P = 0.042$) to die from human-induced causes ($P_m = 0.133$) than natural factors ($P_m = 0.027$; Table 3). In contrast, deer ≥5.5 years old had human-induced and natural mortality estimates ($P_m = 0.133$) that were equal. Although human-induced mortality ($P_m = 0.209$) for deer 3.5–4.5 years old tended to be greater than natural mortality ($P_m = 0.129$), the estimates were not statistically different ($P = 0.114$). Young males (1.5–2.5 years old) were less likely to die from natural causes than deer 3.5–4.5 years old ($P = 0.020$) or deer ≥5.5 years old ($P = 0.031$). However, probability of mortality due to human factors did not vary between age classes ($P ≥ 0.145$).

We documented 21 mortalities during the first year following capture, and proportional hazard models indicated that a 1-year increase in age resulted in a 64% decrease ($P = 0.010$) in probability of mortality during the year following capture (Table 4). Antler size and density of sternum ticks both had a positive effect ($P < 0.05$) on likelihood of mortality during the year following capture. Although not significant ($P = 0.065$), there tended to be a positive association between CPK in the serum and probability of mortality during the year

Table 3. Estimated annual probability of mortality (P_m) due to natural or human-induced factors for adult male white-tailed deer 1.5–2.5, 3.5–4.5, and ≥5.5 years old in a population from southeastern Oklahoma.

Mortality agent	At risk (n)	Mort. (n)	P_m	SE	95% C.I. Lower	95% C.I. Upper
1.5–2.5 years old	76					
Human-induced		5	0.133	0.055	0.024	0.241
Natural		1	0.027	0.026	0.000	0.078
3.5–4.5 years old	75					
Human-induced		13	0.209	0.051	0.108	0.310
Natural		8	0.129	0.042	0.046	0.212
≥5.5 years old	55					
Human-induced		6	0.133	0.050	0.034	0.231
Natural		6	0.133	0.050	0.034	0.231

Table 4. Estimated risk ratios of morphological and physiological parameters for mortality in 57 (21 mortalities) adult, male white-tailed deer from a population in southeastern Oklahoma.

Variable	Parameter estimate	SE	χ^2	P	Risk ratio[a]
Age	−1.0215	0.3962	6.7	0.001	0.360
Body length	0.0441	0.0406	1.2	0.277	1.045
Chest girth	0.0008	0.0057	0.0	0.892	1.001
Antler score	0.0240	0.0111	4.7	0.030	1.024
Ticks	0.1117	0.0562	4.0	0.047	1.118
Leukocytes	−0.0013	0.0120	0.0	0.912	0.999
Blood urea nitrogen	0.0502	0.0380	1.7	0.187	1.051
Total protein	−0.0304	0.0760	0.2	0.689	0.970
Albumin	−0.0697	0.2157	0.1	0.746	0.933
Creatinine phosphokinase	0.0031	0.0017	3.4	0.065	1.003

[a] Risk ratio is the predicted change in the probability of mortality due to a 1-unit increment increase in the variable of interest. A risk ratio <1.0 indicates that probability of mortality would decrease, and a risk ratio >1.0 indicates that probability of mortality would increase.

following capture. Measures of body size, white blood cell counts, and measures of serum protein were not associated ($P > 0.05$) with probability of mortality during the year following capture.

DISCUSSION

Kaplan-Meier survival estimates suggested that mortality rates in our study population of white-tailed deer were relatively constant among age classes of adults. These data are similar to results reported by DeYoung (1989), who noted that survival rates of white-tailed deer did not vary with age in Texas. Overall survival of deer in our population (0.68) was similar (0.71) to that reported by DeYoung (1989). Kie and White (1985) also found that survival rates of deer were independent of age between juvenile and senescent stages. In contrast, Klein and Olson (1960) reported that black-tailed deer (*O. hemionus sitkensis*) in Alaska had increased mortality at ages >5 years. Proportional hazard models seemed to contradict the results of Kaplan-Meier estimates by indicating there was a substantial decrease in likelihood of mortality during the year following capture with each 1-year increase in age. However, unlike Kaplan-Meier estimates, hazard models estimate effects that specific variables have on survival by calculating how each variable influences risk of mortality (risk ratio) during a defined time period (Allison 1995). Because most mortalities (90.5%) that occurred during the defined time period (1 yr) of the model were human-induced (most natural mortalities could not be included in this analysis because they occurred >1 yr after capture) and proportion of mortalities caused by human factors decreased with age (e.g., Table 3), the model actually supports results from our study.

While our data suggest that overall survival rates of male deer in our study population were consistent throughout adulthood, susceptibility to specific mortality agents changed with age. We found that deer ≥3.5 years old were more susceptible to natural mortality than younger adults (1.5–2.5 years old), and these mortalities usually followed the breeding season. In contrast, De Young (1989) did not detect changes in cause-specific mortality with age. In ungulate populations where a large proportion of mature males exist—such as on our study area (Ditchkoff et al. 2000)—competition for mates can be intense and energy expenditure great, and could result in increased levels of natural mortality (Robinette et al. 1957, Klein and Olson 1960, Clutton-Brock et al. 1982).

Owen-Smith (1993) and Byers (1997) described this elevated mortality as senescence, but it should be considered increased exposure to mortality due to behavioral factors (weakened condition resulting from rutting) rather than physiological deterioration caused by aging. We did not detect an increase in mortality during late adulthood that we could attribute to senescence.

Males that invest significant resources during competition for mates may increase their exposure to natural mortality agents (e.g., malnutrition, exhaustion). Although some natural mortality may not be linked directly to mate competition, most natural mortality can be attributed to physical exhaustion and poor nutritional intake, which are common in male cervids during and following the breeding season (Klein and Olson 1960). In populations where a large proportion of mature deer exist, young males do not fully participate in rut-related activities and thus are not as susceptible to natural mortality agents because they remain in good physical condition (Miller and Marchinton 1995). Although no data are available that directly assess impacts of breeding activity on subsequent survival following the breeding season in male deer, Whitlaw et al. (1998) reported that mortality rates of male deer in New Brunswick during winter were greater than mortality rates of females. Although they did not report data on physical condition or breeding effort of these deer, we can assume there was a difference in energy reserves of males and females following the breeding season. In contrast, Nelson and Mech (1986) and Van Deelen et al. (1997) did not detect intrasexual differences in mortality of adult deer following the breeding season.

In contrast to older adults, young adults (1.5–2.5 years of age) were more susceptible to human-induced than to natural mortality agents. Elevated susceptibility of young adults to human-induced mortality agents may be due to lack of experience. These data are not without precedence because young adults commonly are over-represented in hunter–harvest data due to differential mortality (Dasmann and Taber 1956, Roseberry and Klimstra 1974, McCullough 1979, Ditchkoff et al. 2000). Holzenbein and Marchinton (1992) attributed elevated mortality in dispersing yearlings to inexperience and unfamiliarity with new areas and noted that human-induced mortality factors were very important. In contrast to young males, mature deer have substantially more experience in eluding hunters and safely

traversing roads and are thus less susceptible to human-induced mortality agents.

Proportional hazard models also suggested that antler size and an index of tick infestation may influence likelihood of mortality during the year following capture. In addition, there tended to be a low positive association between CPK and probability of mortality during the year following capture, although the relationship was not significant. Because hazard models calculate risk ratios for each variable while controlling for all other variables (Allison 1995) and age was included as a variable in the model, theoretically we could draw inferences to how antler size, parasites, and CPK affect survival within an age class. We would expect large-antlered deer to participate more in breeding activities (Klein and Olson 1960, Clutton-Brock et al. 1982), parasites to negatively influence condition and survival (Davidson 1981), and CPK could be used as an index of ability to cope with stress (Seal et al. 1981, Seal and Bush 1987, DelGiudice et al. 1990). However, because 90.8% of the mortalities used in this analysis were human-induced, it is almost impossible to form a clear interpretation of how these factors would influence survival because they would likely have a greater influence on natural mortality than human-induced mortality in this population.

Contrary to our original expectations, we did not detect an association between body size and mortality. Indices of body size normally are associated positively with antler development in cervids (Harmel 1983, Ditchkoff et al. 2001), and antler development positively influenced probability of mortality when controlling for age in our study. Additionally, body size has been found to be important during establishment of dominance hierarchies in white-tailed deer (Townsend and Bailey 1981) and other cervids (Espmark 1964, Suttie 1979, Clutton-Brock et al. 1982). We expected body size to be positively associated with probability of mortality because previous research suggests that large, dominant males exhibit more effort toward breeding activity than smaller subordinates (Miller et al. 1987). However, it is possible that body size may be a phenotypic expression of genetic quality, and large males within an age class may have a greater capacity to cope with rut-induced stresses because of superior genetics (Ditchkoff et al. 2001).

Unlike many populations of free-ranging cervids, deer in our study were not exposed to predation levels that may occur in the presence of large predators. Although coyotes (*Canis latrans*) and bobcats (*Felis rufus*)—the only predators of deer on our study area—can occasionally capture healthy adults, most of their predation is upon fawns (Litvaitis and Shaw 1980, Caire et al. 1989). As a result, their impact on survival rates of adult male deer is negligible, which is illustrated by low annual mortality (0.02) due to predation in our study. In contrast, Nelson and Mech (1986) found that annual mortality rates due to wolf (*Canis lupus*) predation approached 0.20 for adults. Deer populations that are exposed to large predators such as wolves or puma (*Felis concolor*) can be strongly influenced by predation and may demonstrate differences in age-specific rates of mortality during adulthood that support mate competition theory. Previous studies have observed that mature deer are more vulnerable to predation by wolves (Fritts and Mech 1981, Nelson and Mech 1981), possibly because of diminished energy reserves from breeding and energetic stresses of elevated social rank (Nelson and Mech 1986).

We found that young male white-tailed deer from a population with a large proportion of mature males had cause-specific rates of mortality that differed from mature males. Young males (<3.5 years old) were more susceptible to human-induced than natural mortality agents, while older males (≥3.5 years old) were more likely to succumb to natural mortality agents than young males. The increase in mortality due to natural factors that we found among older age classes is consistent with mate-competition theory. In a population that contains a substantial proportion of mature males, young males may not fully participate in the rut and hence may not be as susceptible to natural mortality agents as are older deer following the breeding season. We acknowledge that participation in breeding activities does not imply probable death, only that probability of mortality in males following the breeding season likely increases as energy expenditure during the breeding season increases.

MANAGEMENT IMPLICATIONS

Until recently, management of deer herds has typically been aimed at maximizing harvest rates, resulting in male segments composed primarily of immature adults (1.5 to 2.5 years old) in most herds (Miller and Marchinton 1995). However, with increasing popularity of quality deer management, demographic models need to consider differential mortality of immature and mature

adult males. In addition, further work is needed to clarify effects that breeding activity can have on survival and future reproductive success of male white-tailed deer.

ACKNOWLEDGMENTS

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