

Survival and Cause-Specific Mortality of Coyotes on a Large Military Installation

Elizabeth R. Stevenson^{1,*}, M. Colter Chitwood^{1,2}, Marcus A. Lashley^{1,3},
Kenneth H. Pollock¹, Morgan B. Swingen¹, Christopher E. Moorman¹, and
Christopher S. DePerno¹

Abstract - *Canis latrans* (Coyote) recently expanded into the southeastern United States, creating ecologically novel interactions with other species. However, relatively few studies have examined vital rates of southeastern Coyotes or estimated vital rates where individuals are protected from hunting and trapping. In 2011, we captured and attached GPS radio-collars to 31 Coyotes at Fort Bragg Military Installation, NC, where Coyote harvest was restricted. We used a 12-month period (February 2011–January 2012) and known-fate modeling in Program MARK to estimate annual survival. Model-selection results indicated the time-varying model ($S[t]$) was the most parsimonious model, and annual survival was 0.80 (95% CI = 0.60–0.91). We documented 7 mortalities, including 2 from vehicles, 2 from off-site trapping, and 3 from unknown causes. Estimated Coyote survival rates at Fort Bragg were similar to most other estimates from the southeastern US. Anthropogenic causes of mortality were important even though hunting and trapping were restricted locally.

Introduction

Prior to the 1940s, *Canis latrans* Say (Coyote) was restricted to western North America (Nowak 1978). However, Coyotes now occur throughout the eastern United States (Parker 1995), including the most recent expansion into the southeastern United States (Hill et al. 1987). For example, Lovell et al. (1998) documented a 7.5-fold increase in Coyote population size since 1980 in Mississippi. Similarly, Main et al. (2000) reported that Coyote distribution continued to expand southward in Florida, and the rate of spread increased over the most recent decade. In North Carolina, Coyotes rarely were reported prior to the early 1980s but were documented in all counties by 1998 (DeBow et al. 1998). Other states in the southeastern US have reported similar trends in recent Coyote expansion and population growth (Houben 2004).

As Coyote populations continue to expand in range and abundance, wildlife managers have expressed concerns about the ecological impact of Coyotes, especially related to prey populations. Ample evidence suggests the effects of Coyotes on community structure may be far reaching (Gompper 2002); effects may be indirect (e.g., resource competition with species such as *Lynx rufus* Kerr

¹Fisheries, Wildlife, and Conservation Biology Program, North Carolina State University, Raleigh, NC 27606. ²Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO 65211. ³Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State, MS 39762. *Corresponding author - estevenson@al.umces.edu.

[Bobcat]; Litvaitis and Harrison 1989) or direct (e.g., predation). For example, numerous studies in the Southeast have documented direct effects of Coyotes on *Odocoileus virginianus* Zimmermann (White-Tailed Deer) (e.g., Chitwood et al. 2015, Kilgo et al. 2012). Though recent focus has been directed toward negative effects of expanding Coyote populations on prey species and competitors, other evidence suggests positive implications of Coyote presence. For instance, Brady (1994) reported eradication of *Canis familiaris* L. (Feral Dog) following Coyote establishment in southeastern New York. Similarly, because Coyotes compete with and depredate *Vulpes vulpes* L. (Red Fox) and *Procyon lotor* L. (Raccoon), Coyote presence has resulted in increased nesting success of *Anas* spp. (Duck) and *Melospiza melodia* Baird (Song Sparrow) (Rogers and Caro 1998, Sovada et al. 1995). Also, increases in songbird diversity have been associated with Coyote predation on *Felis catus* L. (Feral Cat; Crooks and Soulé 1999). The complex ecological effects of Coyotes highlight the need for a comprehensive understanding of Coyote vital rates throughout their new range.

Despite increased interest in the community-level effects of Coyote expansion, relatively few studies have examined vital rates of Coyotes in the southeastern US. Because Coyote vital rates vary considerably across their range (Gompper 2002), estimation of population-specific vital rates is needed to construct accurate Coyote demographic models and inform management practices in the southeastern US. Therefore, we quantified survival and determined causes of mortality for a population of Coyotes at Fort Bragg Military Installation, NC. Specifically, our objectives were to (1) estimate annual survival, (2) determine potential effects of sex and age on survival, and (3) determine causes of mortality.

Field-Site Description

Fort Bragg Military Installation (hereafter Fort Bragg) is located in south-central North Carolina, in the Sandhills ecoregion. At the time of the study, Fort Bragg consisted of 73,469 ha and was one of the largest contiguous blocks of the threatened *Pinus palustris* Mill (Longleaf Pine) ecosystem in the southeastern United States. The Pine/Scrub Oak sandhill community described by Sorrie et al. (2006) was widespread and abundant within Fort Bragg and was dominated by Longleaf Pine, *Quercus laevis* Walter (Turkey Oak), and *Aristida stricta* Michx (Wiregrass). Upland forests were managed with growing-season prescribed fire on a 3-year fire-return interval (Lashley et al. 2014). Coyotes were first documented at Fort Bragg in 1989 and were considered well established by the mid-1990s (Chitwood et al. 2015). Historically, Fort Bragg allowed Coyote hunting when other game seasons were open; however, trapping never has been permitted on the base. According to Fort Bragg estimates, <10 Coyotes were removed each year through hunter harvest (J. Jones, Fort Bragg Wildlife Branch, Fort Bragg, NC, pers. comm.). During our study period, Fort Bragg suspended Coyote hunting.

Methods

Coyote capture and monitoring

We captured Coyotes throughout Fort Bragg using MB-550 foothold traps (Minnesota Trapline Products Inc., Pennock, MN) from February–May 2011. We manually restrained trapped Coyotes and recorded sex and weight for each. We determined age (juvenile [≤ 1 year], subadult [between 1 and 2 years], adult [≥ 2 years]; Gier 1968) based on tooth wear. We fitted each with a Wildcell SG global positioning system (GPS) radiocollar (Lotek Wireless Inc., Newmarket, ON, Canada) and programmed radiocollars to obtain relocation data at 3-hour intervals and to transmit all data to a remote site until a collar was no longer being monitored due to Coyote mortality, loss of signal, or pre-programmed collar release (70 weeks following deployment). To determine cause of death, we located collars that were transmitting a mortality signal and subsequently performed a field necropsy. We classified mortalities as unknown when field evidence was not sufficient to identify cause. All Coyote trapping and handling methods were approved by the North Carolina Wildlife Resources Commission and the North Carolina State University Institutional Animal Care and Use Committee (Protocol: 11-005-O) (Elfelt 2014).

Data analysis

We used a Kaplan-Meier known-fate model (Kaplan and Meier 1958) in Program MARK version 8.0 (White and Burnham 1999) following a staggered-entry procedure (Pollock et al. 1989) to estimate monthly survival for the 21-month study period. We estimated annual survival for February 2011 through January 2012 by truncating the 21-month study period.

To determine the importance of sex and age on survival, we used an information theoretic approach to select from a priori models (Burnham and Anderson 2013). We first compared time-varying ($S[t]$) and time-constant ($S[.]$) survival models. We then determined the relationship of survival estimates to age and sex covariates by using the best time-predicted model. We used Akaike's Information Criterion adjusted for small sample size (AIC_c) and compared ΔAIC_c values and model weights (w_i) to determine the most parsimonious model. We considered models with ΔAIC_c values ≤ 2 units from the top model as best-supported models (Burnham and Anderson 2013); however, we used model deviance to omit best-supported models that contained uninformative parameters (Arnold 2010).

Results

We attached GPS collars to 31 Coyotes, including 19 males (4 juveniles, 3 subadults, and 12 adults) and 12 females (4 juveniles, 5 subadults, and 3 adults). We monitored Coyotes from February 2011–October 2012. Three Coyotes (1 subadult male, 1 subadult female, and 1 juvenile female) dispersed from the study area, established home ranges elsewhere, and were excluded from analyses. We documented 7 mortalities, including 2 from vehicle collisions, 2 from off-site trapping,

and 3 from unknown causes (Table 1). Vehicle collisions occurred in March and April, whereas both trapping mortalities occurred in January.

The best model indicated survival varied monthly (i.e., $S[t]$; Table 2). The time-varying models that included age and sex separately received some support (i.e., these models fell within $2 \Delta AIC_c$ of the $S[t]$ model); however, model deviance was not markedly different from the $S(t)$ model, indicating the addition of age or sex to the $S(t)$ model was uninformative. Thus, using the $S(t)$ model, monthly survival for our 21-month study period ranged from 0.86 (January 2012) to 1.00 (most months) (Fig. 1), and annual survival from February 2011 through January 2012 was 0.80 (95% CI = 0.60–0.91).

Discussion

Annual Coyote survival rates at Fort Bragg were greater than those reported in Georgia (0.50; Holzman et al. 1992), but other estimates from the southeastern US were similar (i.e., included within our 95% confidence interval [South Carolina: 0.67 (Schrecengost et al. 2009); Mississippi; 0.73 (Chamberlain and Leopold 2001)]). Known mortality causes within the boundaries of Fort Bragg were limited to vehicle collisions; however, 2 Coyotes that left Fort Bragg were legally trapped, highlighting the influence of anthropogenic effects (i.e., hunting, trapping, vehicles) on Coyote survival. The proportion of Coyote mortalities that are anthropogenic vary throughout the Southeast and range from 22% in Georgia (Holzman et al. 1992) to 60% in South Carolina (Schrecengost et al. 2009). We provide evidence that anthropogenic sources of mortality appear to be important even where Coyote hunting and trapping are prohibited.

Table 1. Causes of mortality among 28 Coyotes captured at Fort Bragg Military Installation, NC, February 2011–October 2012.

Age at mortality	Trapping		Vehicle		Unknown	
	Male	Female	Male	Female	Male	Female
Juvenile (<1 year)	0	0	0	0	0	0
Subadult (1–2 years)	0	1	0	2	1	0
Adult (>2 years)	1	0	0	0	2	0

Table 2. Full set of candidate models, including number of parameters (k), Akaike's Information Criterion values corrected for small sample size (AIC_c), ΔAIC_c , AIC weights (w_i), and model deviance for estimating Coyote monthly survival ($n = 28$), Fort Bragg Military Installation, NC, February 2011–October 2012.

Model	k	AIC_c	ΔAIC_c	w_i	Deviance
$S(t)$	5	59.4209	0.0000	0.51853	49.2514
$S(t + \text{age})$	6	61.2196	1.7987	0.21096	48.9816
$S(t + \text{sex})$	6	61.3897	1.9688	0.19376	49.1517
$S(t + \text{age} + \text{sex})$	7	63.2825	3.8616	0.07520	48.9643
$S(.)$	1	71.0369	11.6160	0.00156	69.0257

Despite Fort Bragg being protected from hunting and trapping, 2 Coyotes were trapped during the study period; this result was likely due to wide-ranging movement, as both trapping events occurred in January on private lands just outside the boundary of Fort Bragg. Elfelt (2014) documented large home ranges and high numbers of transient Coyotes at Fort Bragg, a phenomenon possibly attributed to high Coyote population density, increased territoriality among older adults, and low resource availability (Conner et al. 2008, Gese et al. 1996). During our study, 15 Coyotes left the boundaries of Fort Bragg at least once, which predisposed them to hunting and trapping on adjacent private land. Proportions of Coyote populations that are transient or dispersers are high (e.g., Chamberlain et al. 2000, Hickman et al. 2015, Hinton et al. 2012). Therefore, Coyote populations in the southeastern US may remain vulnerable to hunting and trapping mortality despite localized protected status because wide-ranging individuals are common and frequently move into unprotected areas.

Two mortalities during the study period were caused by vehicles. The majority of roads at Fort Bragg are low-traffic sandy roads that are used for military training and function as firebreaks for prescribed fire. However, several paved and gravel roads experience greater amounts of military and civilian vehicle traffic. During our study, 1 Coyote was killed on a paved high-traffic road, while another was killed on a relatively low-traffic gravel road. Coyote mortality rates due to vehicle fatalities vary throughout their range and are dependent on level of urbanization and road density (Gehrt 2007). No other Coyote survival studies in the southeastern United States have reported vehicle-related mortalities (Chamberlain and Leopold 2001, Holzman et al. 1992, Schrecengost et al. 2009), but those studies had small numbers of Coyote mortalities, low road density, or few paved roads.

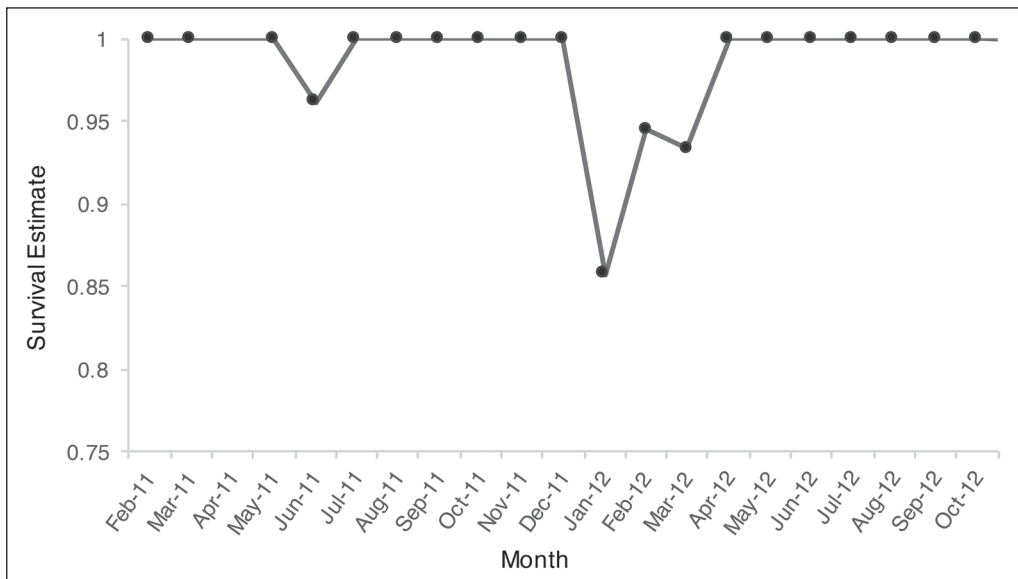


Figure 1. Monthly Coyote survival estimates ($n = 28$) for a 21-month period at Fort Bragg Military Installation, NC, February 2011–October 2012.

Our results indicated little support for age and sex effects on Coyote survival, which is similar to other studies in the region (age: Holzman et al. 1992; sex: Chamberlain and Leopold 2001, Schrecengost et al. 2009). These studies and ours may have been limited by small sample sizes that precluded the ability to make inferences regarding the role of sex and age. Studies from elsewhere in North America have indicated that age is a significant source of variation in survival, with juveniles reportedly having lower survival relative to adults (e.g., Parker 1995, Van Deelen and Gosselink 2006, Windberg 1995). However, sex does not appear to be a significant source of variation in Coyote survival elsewhere in the United States (e.g., Van Deelen and Gosselink 2006, Windberg et al. 1985). Future studies with larger sample sizes may be better equipped to assess the effects of age and sex on Coyote survival in the southeastern United States.

This study demonstrates that anthropogenic activities are a primary cause of mortality for Coyotes, even in areas with low hunting and trapping effort. Transient individuals likely will be susceptible to anthropogenic mortality sources even on large public land bases like Fort Bragg, where hunting effort was low. Interestingly, the survival rate in our study was greater than all other reported estimates in the region, so local policies that restrict hunting and trapping may confer greater Coyote survival, potentially yielding an age structure different than surrounding populations where hunting or trapping efforts are more substantial. This result has implications on potential management strategies that employ Coyote removal as a tool to mitigate undesired effects on other taxa (e.g., depredation of White-Tailed Deer). Future research could explore the population-level effects of anthropogenic mortality on Coyote age structure in the Southeast and how Coyote age structure contributes to direct or indirect effects on prey species and community structure.

Acknowledgments

Funding for this project was provided by the United States Department of Defense, the Fort Bragg Wildlife Branch, and the Fisheries, Wildlife, and Conservation Biology Program at North Carolina State University. We thank USDA APHIS Wildlife Services, especially T. Menke and S. Thompson, for assistance with Coyote trapping. We thank A. Schultz, J. Jones, C. Brown, J. Heisinger, and the Fort Bragg Wildlife Branch for logistical support. We thank E. Kilburg, M. Nunnery, A. Prince, A. Schaich Borg, B. Sherrill, and many other volunteers for assistance in the field. We thank R. Meentemeyer, A. Edelman, and 2 anonymous reviewers for providing constructive comments that improved the manuscript.

Literature Cited

- Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- Brady, J.F. 1994. Black Rock Forest deer population management report 1984–1994, unpublished report, Black Rock Forest, Cornwall, NY. 58 pp.
- Burnham, K.P., and D.R. Anderson. 2013. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer, New York, NY. 488 pp.
- Chamberlain, M.J., and B.D. Leopold. 2001. Survival and cause-specific mortality of adult Coyotes (*Canis latrans*) in Central Mississippi. *American Midland Naturalist* 145:414–418.

- Chamberlain, M.J., C.D. Lovell, and B.D. Leopold. 2000. Spatial-use patterns, movements, and interactions among adult Coyotes in central Mississippi. *Canadian Journal of Zoology* 78:2087–2095.
- Chitwood, M.C., M.A. Lashley, J.C. Kilgo, C.E. Moorman, and C.S. DePerno. 2015. White-Tailed Deer population dynamics and adult female survival in the presence of a novel predator. *Journal of Wildlife Management* 79:211–219.
- Conner, M.M., M.R. Ebinger, and F.F. Knowlton. 2008. Evaluating Coyote management strategies using a spatially explicit, individual-based, socially structured population model. *Ecological Modelling* 219:234–247.
- Crooks, K.R., and M.E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–566.
- DeBow, T.M., W.D. Webster, and P.W. Sumner. 1998. Range expansion of the Coyote, *Canis latrans* (Carnivora: Canidae), into North Carolina, with comments on some management implications. *Journal of the Elisha Mitchell Scientific Society* 114:113–118.
- Elfelt, M.B. 2014. Coyote movement ecology and food habits at Fort Bragg Military Installation. M.Sc. Thesis. North Carolina State University, Raleigh, NC. 63 pp.
- Gehrt, S.D. 2007. Ecology of Coyotes in urban landscapes. *Wildlife Damage Management Conferences Proceedings*. 63:303–311.
- Gese, E.M., R.L. Ruff, and R.L. Crabtree. 1996. Social and nutritional factors influencing the dispersal of resident Coyotes. *Animal Behavior* 52:1025–1043.
- Gier, H.T. 1968. Coyotes in Kansas (revised). *Agricultural Experiment Station Bulletin* 393, Kansas State University, Manhattan, KS. 118 pp.
- Gompper, M.E. 2002. Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of northeastern North America by Coyotes. *BioScience* 52:185.
- Hickman, J.E., W.D. Gulsby, C.H. Killmaster, J.W. Bowers, M.E. Byrne, M.J. Chamberlain, and K.V. Miller. 2015. Home range, habitat use, and movement patterns of female Coyotes in Georgia: Implications for fawn predation. *Journal of the Southeastern Association of Fish and Wildlife Agencies* 2:144–150.
- Hill, E.P., P.W. Sumner, and J.B. Wooding. 1987. Human influences on range expansion of Coyotes in the Southeast. *Wildlife Society Bulletin* 15:521–524.
- Hinton, J.W., M.J. Chamberlain, and F.T. van Manen. 2012. Long-distance movements of transient Coyotes in eastern North Carolina. *American Midland Naturalist* 168:281–288.
- Holzman, S., M.J. Conroy, and W.R. Davidson. 1992. Diseases, parasites, and survival of Coyotes in south-central Georgia. *Journal of Wildlife Diseases* 28:572–580.
- Houben, J.M. 2004. Status and management of Coyote depredation in the eastern United States. *Sheep and Goat Research Journal* 19:16–22.
- Kaplan, E.L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53:457–481.
- Kilgo, J.C., H.S. Ray, M. Vukovich, M.J. Goode, and C. Ruth. 2012. Predation by Coyotes on White-Tailed Deer neonates in South Carolina. *Journal of Wildlife Management* 76:1420–1430.
- Lashley, M.A., M.C. Chitwood, A. Prince, M.B. Elfelt, E.L. Kilburg, C.S. DePerno, and C.E. Moorman. 2014. Subtle effects of a managed-fire regime: A case study in the Longleaf Pine ecosystem. *Ecological Indicators* 38:212–217.
- Litvaitis, J.A., and D.J. Harrison. 1989. Bobcat–Coyote niche relationships during a period of Coyote population increase. *Canadian Journal of Zoology* 67:1180–1188.
- Lovell, C.D., B.D. Leopold, and C.C. Shropshire. 1998. Trends in Mississippi predator populations, 1980–1995. *Wildlife Society Bulletin* 26:552–556.
- Main, M.B., S.F. Coates, and G.M. Allen. 2000. Coyote distribution in Florida extends southward. *Florida Field Naturalist* 28:201–203.

- Nowak, R.M. 1978. Evolution and taxonomy of Coyotes and related *Canis*. Pp. 210–227, *In* M. Bekoff (Ed.). *Coyotes: Biology, Behavior, and Management*. Academic Press, New York, NY. 384 pp.
- Parker, G.R. 1995. *Eastern Coyote*. Nimbus Publishing, Halifax, NS, Canada. 264 pp.
- Pollock, K.H., S.R. Winterstein, C.M. Bunck, and P.D. Curtis. 1989. Survival analysis in telemetry studies: The staggered-entry design. *Journal of Wildlife Management* 53:7–15.
- Rogers, C.M., and M.J. Caro. 1998. Song sparrows, top carnivores, and nest predation: A test of the mesopredator-release hypothesis. *Oecologia* 116:227–233.
- Schrecengost, J.D., J.C. Kilgo, H.S. Ray, and K.V. Miller. 2009. Home range, habitat use and survival of Coyotes in western South Carolina. *American Midland Naturalist* 162:346–355.
- Sorrie, B.A., J.B. Gray, and P.J. Crutchfield. 2006. The vascular flora of the Longleaf Pine ecosystem of Fort Bragg and Weymouth Woods, North Carolina. *Castanea* 71:129–161.
- Sovada, M.A., A.B. Sargeant, and J.W. Grier. 1995. Differential effects of Coyotes and Red Foxes on duck nest success. *Journal of Wildlife Management* 59:1–9.
- Van Deelen, T.R., and T.E. Gosselink. 2006. Coyote survival in a row-crop agricultural landscape. *Canadian Journal of Zoology* 84:1630–1636.
- White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Windberg, L.A. 1995. Demography of a high-density Coyote population. *Canadian Journal of Zoology* 73:942–954.
- Windberg, L.A., H.L. Anderson, and R.M. Engeman. 1985. Survival of Coyotes in southern Texas. *Journal of Wildlife Management* 49:301–307.