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Female White-tailed Deer Survival Across Ecoregions in Minnesota and South Dakota

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ABSTRACT.—Survival and cause-specific mortality of female white-tailed deer (*Odocoileus virginianus*) have been well documented in forested and agricultural landscapes, but limited information has been collected in grassland habitats typical of the Northern Great Plains. Our objectives were to document and compare survival and cause-specific mortality of adult female white-tailed deer in four distinct ecoregions. We captured and radiocollared 190 (159 adult, 31 yearling) female white-tailed deer and monitored (including deer from a previous study) a total of 246 (215 adult, 31 yearling) deer from Jan. 2000 to Dec. 2007. We documented 113 mortalities; hunting (including wounding loss) accounted for 69.9% of all mortalities and vehicle collisions accounted for an additional 15.0%. Natural causes (*e.g.*, disease, predation) of mortality were minor compared to human-related causes (*e.g.*, hunting, vehicle collisions). We used known fate modeling in program MARK to estimate survival rates and compare ecoregions and seasons. Model $\{S_{\text{season (winter=summer)}}\}$ had the lowest AIC_c value suggesting that survival differed only between seasons where winter and summer survival was equal and differed with fall season. Annual and seasonal (summer, fall, winter) survival rates using the top model $\{S_{\text{season (summer=winter)}}\}$ were 0.76 (95% CI = 0.70–0.80), 0.97 (95% CI = 0.96–0.98), 0.80 (95% CI = 0.76–0.83) and 0.97 (95% CI = 0.96–0.98), respectively. High human-related mortality was likely associated with limited permanent cover, extensive road networks and high hunter density. Deer management in four distinct ecoregions relies on hunter harvest to maintain deer populations within state management goals.

INTRODUCTION

Knowledge of survival rates, cause-specific mortality, and temporal and spatial patterns of survival is essential to understanding white-tailed deer (*Odocoileus virginianus*) population dynamics (Dusek *et al.*, 1992; DePerno *et al.*, 2000; Brinkman *et al.*, 2004). Survival rates vary regionally with sex, age and density of deer (Gavin *et al.*, 1984; Dusek *et al.*, 1992; Whitlaw *et*

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TABLE 1.—Landcover and environmental characteristics for four ecoregions in South Dakota and Minnesota, USA, 2000–2007 (Smith *et al.*, 2002; Midwest Regional Climate Center, 2009; Minnesota Department of Natural Resources, 2009; South Dakota Office of Climatology, 2009)

	Ecoregion			
Landcover (%)	Driftless Area	Western Corn Belt Plains	Northern Glaciated Plains	Northwestern Glaciated Plains
Forested cover	7.7–20.0	1.5–7.3	1.6–2.5	1.9–2.8
Wetland	0.0	0.2–0.4	3.5–4.4	9.4–11.9
Pasture and grassland	14.2–23.6	2.4–14.6	31.5–41.8	30.6–55.6
Cultivated land	55.4–62.8	81.1–93.4	51.7–58.3	32.1–56.7
Water	0.2–0.4	0.5–0.9	0.8–2.3	0.0
$\bar{x}$ winter temperature (°C)	−6.3	−9.8	−8.7	−9.4
$\bar{x}$ summer temperature (°C)	20.1	23.1	21.3	20.9
$\bar{x}$ annual precipitation (cm)	83.5	65.4	55.3	49.1

al., 1998; DelGiudice *et al.*, 2002). Common causes of mortality include human-related factors (*e.g.,* legal and illegal hunting, vehicle collisions; Fuller, 1990; Nixon *et al.*, 1991; Brinkman *et al.*, 2004), weather (*e.g.,* winter severity; DePerno *et al.*, 2000; DelGiudice *et al.*, 2002), predation (Mech, 1984), and disease (Matschke *et al.*, 1984). In most areas, hunter harvest is the primary cause of deer mortality and is the factor most amenable to management efforts (DelGiudice *et al.*, 2002). Hunter harvest accounted for 43% of mortality in southwestern Minnesota (Brinkman *et al.*, 2004), 60% in Illinois (Nixon *et al.*, 2001), 43% in north-central Minnesota (DelGiudice *et al.*, 2002) and 74% in eastern Montana (Dusek *et al.*, 1992). Conversely, harvest accounted for only 23% of mortality in the central Black Hills of South Dakota (DePerno *et al.*, 2000).

Deer have readily adapted to the mosaic of habitats that characterize the Midwest and Northern Great Plains (Nixon *et al.*, 2001; Brinkman *et al.*, 2004) and high deer densities commonly occur in this intensively farmed region despite limited patches of permanent cover (Naugle *et al.*, 1996). Survival rates and cause-specific mortality of white-tailed deer have been well documented in forested habitats (Van Deelen *et al.*, 1997; Whitlaw *et al.*, 1998; DePerno *et al.*, 2000; DelGiudice *et al.*, 2002) and intensively farmed areas (Nixon *et al.*, 2001; Brinkman *et al.*, 2004); however, information in grassland habitats with limited forested cover is lacking. Region specific practical data is important to predict spatial and temporal changes in deer populations (Brinkman *et al.*, 2004). Therefore, our primary objectives were to quantify survival and cause-specific mortality rates of adult female white-tailed deer. Additionally, our secondary objective was to compare survival rates between ecoregions with differences in land cover characteristics.

MATERIALS AND METHODS

Our study encompassed four ecoregions (Omernick and Gallant, 1988) from southeastern Minnesota to north-central South Dakota. The Driftless Area Ecoregion (DAE) differed from the other three ecoregions by being characterized by steeply sloped topography and greater percent of forested cover. The Western Corn Belt Plains (WCBPE), Northern Glaciated Plains (NGPE) and Northwestern Glaciated Plains (NWGPE) ecoregions graduated from one to another; cultivated land decreased and grassland and pasture increased from east to west (Table 1; Smith *et al.*, 2002; Minnesota Department of Natural Resources, 2009).

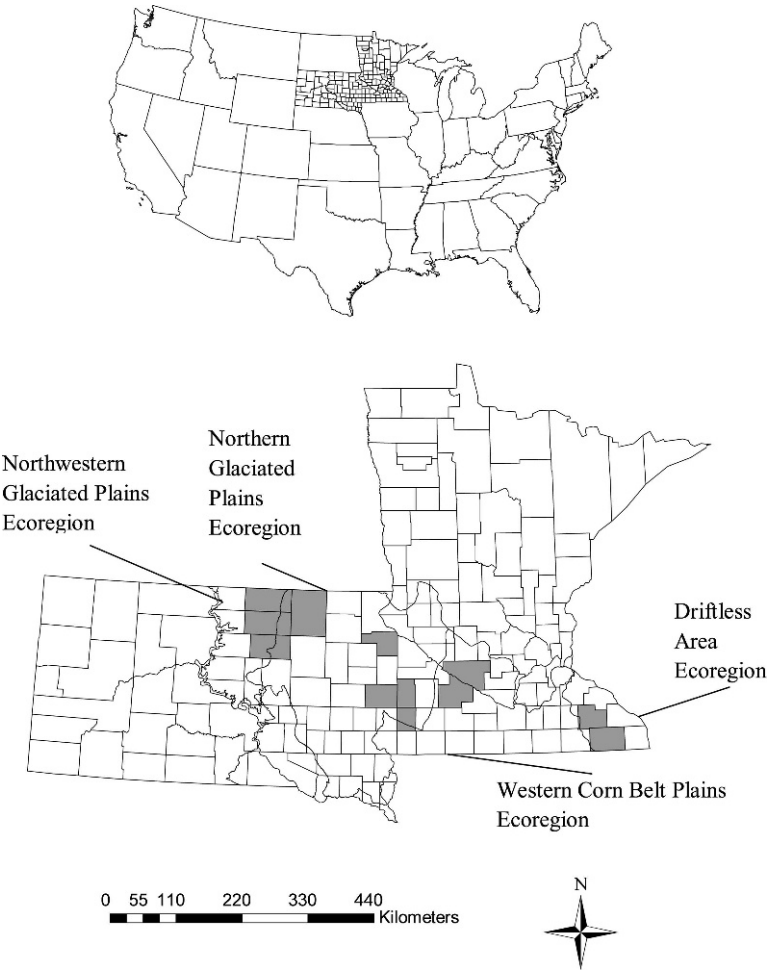

FIG. 1.—White-tailed deer (*Odocoileus virginianus*) study areas (shaded in gray) in southeastern Minnesota (Fillmore and Olmsted counties), southwestern Minnesota (Lincoln, Pipestone, Renville and Redwood counties), eastern South Dakota (Brookings and Grant counties) and north-central South Dakota (Brown, Edmunds, Faulk and McPherson counties), 2000–2007

Southeastern Minnesota lies within the DAE and was distinguished by hilly uplands deeply dissected by streams, and loess-capped and bedrock dominated plateaus (Omernik and Gallant, 1988). The DAE contained forested cover on steep slopes and in woodlots with the majority of grasslands converted to agriculture (Omernik and Gallant, 1998). Study sites in the DAE were in Olmstead and Fillmore counties, Minnesota (Fig. 1). The WCBPE in southwestern Minnesota was characterized by nearly level to gently rolling dissected glacial till plains, hilly loess plains and broad morainal hills with smooth ridgetops (Omernik and Gallant, 1988; Bryce *et al.*, 1998). Land cover in the WCBPE was dominated by lands converted to cropland [*i.e.*, corn (*Zea mays*), soybeans (*Glycine max*)] and those used for

livestock production (Omernik and Gallant, 1998). Study sites in the WCBPE were located in Redwood and Renville counties, Minnesota (Fig. 1).

Landscape in the NGPE historically contained numerous wetlands, many of which were converted into farmland because of fertile soils (Johnson and Larson, 1999). Throughout the NGPE, numerous lakes, reservoirs and wetlands were common and dry-farming and livestock production were the most common forms of land use (Omernik and Gallant, 1998). Study sites in the NGPE were located in Brookings and Grant counties in eastern South Dakota, and Lincoln and Pipestone counties in Minnesota (Fig. 1). The NWGPE was the westernmost extent of continental glaciations and the landscape had significant surface irregularity with a high concentration of wetlands. Land use was transitional between intensive dry farming to the east and a predominance of cattle ranching to the west (Bryce *et al.*, 1998). Terrain was characterized by flat to gently rolling terrain mixed with numerous pothole wetlands between mounds of glacial till (Bryce *et al.*, 1998). Study sites in the NWGPE were located in Brown, Edmunds, Faulk and McPherson counties in north-central South Dakota (Fig. 1).

We captured adult (≥18 mo at capture) and yearling (6–18 mo at capture) female white-tailed deer using helicopter net-guns (Jacques *et al.*, 2009) in DAE during Jan. 2000–2003, in WCBPE during Jan. 2003 and in NWGPE during Apr. 2005 and Jan. 2006. We captured deer using modified Clover traps (Clover, 1956) in NGPE during winter 2003–2004 and in NWGPE during winter 2005. Additionally, we captured deer in NWGPE using immobilizing drugs (4.4 mg/kg Telezol™ and 2.2 mg/kg Xylazine™) delivered via a Pneu-Dart (Pneu-Dart, Inc., Williamsport, PA, USA) with flight stabilizers from a Dan-Inject CO_2 Rifle, model JM Standard (Dan-Inject of North America, Ft. Collins, CO, USA; Haulton *et al.*, 2001) and administered Yohimbine™ (0.2 mg/kg) intravenously as an antagonist. We fitted captured deer with VHF radiocollars (Advanced Telemetry Systems, Isanti, MN, USA) equipped with a mortality sensor that switched to mortality mode after the transmitter remained stationary for ≥8 h. Furthermore, we monitored deer captured and radiocollared in WCBPE that remained from a previous study (20 Redwood County, 12 Renville County, 24 Lincoln County; Brinkman *et al.*, 2004). Animal handling protocols used in this research were approved by the Institutional Animal Care and Use Committee at South Dakota State University (SDSU; Approval numbers 02-A043, 02-A037 and 04-A009) and followed guidelines for the care and use of animals approved by the American Society of Mammalogists (Gannon *et al.*, 2007).

We monitored radiocollared deer for mortality 2–3 times per week from Jan. 2000 to Dec. 2007. We conducted field necropsies and recorded evidence at the site of the mortality to determine cause of death (White *et al.*, 1987). If we could not determine cause of death in the field, we transported carcasses to the SDSU Animal Disease Research Diagnostic Laboratory for further investigation. We classified mortalities as unknown if cause of death could not be determined.

We calculated annual and seasonal survival rates using known fate models in Program MARK (White and Burnham, 1999). We constructed 8 *a priori* models from various combinations of variables to determine differences in survival between ecoregions, states, study sites, seasons and years (Table 2). Because deer management strategies (*i.e.*, harvest) differ between Minnesota and South Dakota, we chose to include the variable state in our models to determine survival differences between management regimes. Additionally, because ecoregions contained >1 study site, we modeled study site as an explanatory survival variable. We used Akaike's Information Criterion (AIC_c) corrected for small sample sizes to select models that best described the data. We compared AIC_c values to select the

TABLE 2.—*A priori* models used to determine adult female white-tailed deer survival in four ecoregions[a] in South Dakota and Minnesota, USA, 2000–2007

Model	No. parameters	Description
$\{S_{season\ (summer=winter)}\}$	2	Survival varies between seasons with summer and winter equal
$\{S_{state*season\ (summer=winter)}\}$	4	Survival varies between states and seasons, with summer and winter equal
$\{S_{eco\ (WCBPE=NGPE=NWGPE,\ DAE)\ *season\ (summer=winter)}\}$	4	Survival varies between ecoregions, with WCBPE, NGPE, and NWGPE equal and between seasons with summer and winter equal
$\{S_{eco\ (WCBPE,\ NGPE,\ DAE,\ NWGPE)\ *season\ (summer=winter)}\}$	8	Survival varies between ecoregions and seasons with summer and winter equal
$\{S_{study\ site*season\ (summer=winter)}\}$	20	Survival varies between study sites and seasons, with summer and winter equal
$\{S_{study\ site*season}\}$	30	Survival varies between study sites and seasons
$\{S_{study\ site*year*season}\}$	78	Survival varies between study sites, years, and seasons
$\{S_{full\ Kaplain\ Meier}\}$	396	Survival was best explained by the fully saturated Kaplain Meier model (Kaplain and Meier, 1958)

[a] WCBPE = Western Corn Belt Plains Ecoregion, NGPE = Northern Glaciated Plains Ecoregion, NWGPE = Northwestern Glaciated Plains Ecoregion, DAE = Driftless Area Ecoregion

most parsimonious model and considered models differing by $\leq 2\ \Delta AIC_c$ from the selected model as potential alternatives (Burnham and Anderson, 2002). We used Akaike weights (w_i) as an indication of support for each model and used multi-model inference to average parameters across potential models. We calculated seasonal survival rates for three time seasons: May–Aug. (summer), Sept.–Dec. (fall) and Jan.–Apr. (winter). We classified yearlings as adults following the hunting interval. We performed statistical analyses using SAS version 9.1 (SAS Institute, 2000) with an experiment-wide error rate of 0.05.

RESULTS

We captured and radiocollared 190 (159 adult, 31 yearling) female white-tailed deer and monitored (including deer from a previous study) a total of 246 (215 adult, 31 yearling)

TABLE 3.—Cause-specific mortality (percent) for radiocollared female white-tailed deer at study sites in Minnesota and South Dakota, 2000–2007

	Ecoregion			
Mortality	Driftless Area	Western Corn Belt Plains	Northern Glaciated Plains	Northwestern Glaciated Plains
Hunting	25 (58.1%)	7 (46.7%)	22 (66.7%)	16 (72.7%)
Vehicle Collision	5 (11.6%)	4 (26.7%)	5 (15.2%)	3 (13.6%)
Predation	2 (4.7%)	1 (6.7%)	1 (3.0%)	0
Disease	1 (2.3%)	0	1 (3.0%)	0
Unknown	1 (2.3%)	2 (13.3%)	4 (12.1%)	2 (9.1%)
Wounding loss	7 (16.3%)	1 (6.7%)	0	1 (4.5%)
Poaching	1 (2.3%)	0	0	0
Other	1 (2.3%)	0	0	0
Total	43	15	33	22

deer (90 DAE, 73 WCBPE, 41 NGPE, 42 NWGP) from Jan. 2000 to Dec. 2007. We documented 113 mortalities (Table 3); hunting (including wounding loss; defined as exhibiting wounds from bullets or arrows at time of death) accounted for 69.9% of all mortalities and vehicle collisions accounted for an additional 15.0% of mortalities. Mean age at death was 4.5 y (SE = 0.3, n = 77, range 1.0–14.5 y) and was similar ($F_{3,73} = 0.76$, $P = 0.520$) between ecoregions. Annual yearling survival was similar to adult survival across ecoregions ($\chi^2_1 \leq 2.78$, $P \geq 0.428$), thus, we pooled survival across age classes.

Only models $\{S_{season\ (summer=winter)}\}$ and $\{S_{state*season\ (summer=winter)}\}$ were supported by the data; these models were ≤2 AIC_c units from each other (Table 4). Of the eight models tested, the top five models all included the variable survival varied by season with summer survival equal to winter survival. Ninety-five percent confidence intervals of parameter estimates did not overlap, indicating that survival differed between seasons. Model $\{S_{season\ (summer=winter)}\}$ had the lowest AIC_c value and the weight of evidence supporting this model was 1.3 times greater than the second best model and >4.7 times greater than remaining models (Table 4). Model $\{S_{state*season\ (summer=winter)}\}$ indicated that

TABLE 4.—Top-ranked survival models of adult female white-tailed deer in four ecoregions[a] in South Dakota and Minnesota, USA, 2000–2007

Model[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	K[f]	Deviance
$\{S_{season\ (summer=winter)}\}$	1283.75	0.00	0.47	2	547.16
$\{S_{state*season\ (summer=winter)}\}$	1284.26	0.51	0.37	4	543.67
$\{S_{eco\ (WCBPE=NGPE=NWGPE,\ DAE)}\ *season\ (summer=winter)\}$	1286.79	3.03	0.10	4	564.20
$\{S_{eco\ (WCBPE,\ NGPE,\ DAE,\ NWGPE)}\ *season\ (summer=winter)\}$	1288.16	4.51	0.05	8	539.57

[a] WCBPE = Western Corn Belt Plains Ecoregion, NGPE = Northern Glaciated Plains Ecoregion, NWGPE = Northwestern Glaciated Plains Ecoregion, DAE = Driftless Area Ecoregion

[b] Description of models are listed in Table 2

[c] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson, 2002)

[d] Difference in AIC_c relative to minimum AIC

[e] Akaike weight (Burnham and Anderson, 2002)

[f] Number of parameters

survival varied between states and among seasons, where winter and summer survival was equal and differed with fall season. However, 95% confidence intervals for parameter estimates overlapped, indicating there was no difference in survival between states. Therefore, we excluded this model from consideration. Annual survival rate using the top model {$S_{season\ (summer=winter)}$} was 0.76 (95% CI = 0.70–0.80) and seasonal survival rates (summer, fall, winter) were 0.97 (95% CI = 0.96–0.98), 0.80 (95% CI = 0.76–0.83) and 0.97 (95% CI = 0.96–0.98), respectively.

DISCUSSION

Survival of female white-tailed deer did not vary regionally throughout Minnesota and South Dakota study areas. Annual survival was similar to survival rates reported elsewhere for northern populations (65–80%; Gavin *et al.*, 1984; Fuller, 1990; Nixon *et al.*, 1991; DePerno *et al.*, 2000; Brinkman *et al.*, 2004). Interestingly, we documented no difference in survival between regions as forested cover decreased from eastern Minnesota (20%) westward to north-central South Dakota (1.9%). In the central Black Hills, survivorship on winter range was related to differential habitat use; survival increased with basal area per hectare of trees and average diameter at breast height of trees (Klaver *et al.*, 2008). However, survival rates for female deer in the central Black Hills were lower (50–62%; DePerno *et al.*, 2000) than those observed during our study. Contrary to our results, natural mortality (*i.e.*, canid predation, malnutrition, sickness and unknown causes) was the primary cause (71%) of mortality in the central Black Hills; hunting accounted for 22.6% of mortality (DePerno *et al.*, 2000). Because natural predators such as coyotes (*Canis latrans*) hunt by visual and olfactory searching (Wells and Lehner, 1978; Hyde *et al.*, 1987), we suspect the influence of forested cover on survival of female deer would be greater in areas with greater density of predators.

Our top-ranked model {$S_{season\ (summer=winter)}$} indicated that survival varied only between seasons, with summer and winter survival similar to one another and different from hunting season (fall) survival. Hunting (including wounding loss) was the greatest cause of mortality and natural causes of mortality (*e.g.,* disease and predation) were low relative to human-related causes, which were similar to results in other northern regions (Fuller, 1990; Dusek *et al.*, 1992; Whitlaw *et al.*, 1998; Nixon *et al.*, 2001; Brinkman *et al.*, 2004). High human-related mortality may be influenced by several factors. In grassland regions, permanent escape cover (*i.e.*, forested cover) often is limited and highly fragmented (Smith *et al.*, 2002). Deer are forced to make longer movements (Grovenburg *et al.*, 2009) across open areas, possibly leaving them vulnerable to hunters. In intensively farmed areas, well-established road networks and high hunter density may help explain greater human-related mortality (Hansen *et al.*, 1997; Brinkman *et al.*, 2004; Grovenburg *et al.*, 2008).

Relatively low coyote densities may have contributed to minimal predation. Because opportunistic scavenging is more common (Berg and Chesness, 1978; Bekoff and Wells, 1986), deer in southeast Minnesota had a 5% chance of mortality due to coyote predation (DePerno *et al.*, 2003; Turner *et al.*, 2011). Similarly, in southwestern Minnesota, Brinkman *et al.* (2004) reported low coyote densities, with only a single coyote captured during 1350 trap nights; low coyote densities may have been partially explained by a mange epizootic that reduced predator density (Brinkman *et al.*, 2004; Chronert *et al.*, 2007). In South Dakota, aerial shooting was conducted to control coyote densities (Jacques *et al.*, 2007). Aerial shooting consistently harvested 80–85% of the estimated coyote population in eastern South Dakota (South Dakota Department of Game, Fish and Parks, unpublished data) and we suspect that intensive predator control contributed to low predator related mortality.

The limited range of winter severity in our study did not provide an opportunity to assess the relationship between weather extremes and natural causes of deer mortality. Annual variation in winter severity has previously been documented as an important factor influencing winter survival. For instance, DelGiudice *et al.* (2002) reported the maximum risk of mortality occurred during winters with the highest deer winter severity index values. In north central Minnesota, effects of winter severity on the risk of natural mortality was greater than the risk of death from all causes (DelGiudice *et al.*, 2002). However, only a single winter (2001) during our study could be categorized as moderately severe. We speculate that limited availability of forested cover in grassland regions of the Northern Great Plains may interact with severe winter weather and subsequently increase natural mortality (Brinkman *et al.*, 2004). Deer in these habitats initiate long-distance migrations to locate suitable cover and forage habitats (Grovenburg *et al.*, 2009), presumably increasing energy expenditure for maintenance and locomotion (Parker *et al.*, 1984; DePerno *et al.*, 2000).

Our top-ranked model $\{S_{\text{season (summer=winter)}}\}$ indicated that survival was similar during summer and winter, and differed only during the hunting season. Thus, current management policy for predators (*i.e.*, aerial shooting harvesting 80–85% of the coyote population) and disease epizootics (*i.e.*, mange; Chronert *et al.*, 2007) along with climate change (Jacques *et al.*, 2007) have contributed to conditions that maximize survival of deer with concomitant anthropogenic effects necessary to control populations. Our study provided region-specific practical survival data and documented that survival did not vary regionally across ecoregions. State management goals included protecting future potential of stock, optimal utilization, equitable distribution of benefits to hunters and minimizing depredation (Huxol, 2006). Hunting was the primary cause of mortality in all study areas, thereby confirming the continued use of annual harvest as the primary management tool for maintaining deer populations. Severe winter weather, while not present during this study, has the potential to increase natural mortality. Therefore, we recommend further research on survival be conducted during severe winters in the grassland regions of the Northern Great Plains. While not part of this study, land use changes in the region have the potential to impact deer populations. As Conservation Reserve Program grasslands are converted to agricultural production, continued reduction and fragmentation of permanent cover is imminent (Grovenburg *et al.*, 2010). Research that documents potential impacts of these land use changes on survival of white-tailed deer is warranted.

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