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Comparing survival and cause-specific mortality between resident and transient bobcats *Lynx rufus*

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Numerous studies have analyzed bobcat *Lynx rufus* survival in temperate regions of North America. Our study compared survival and cause-specific mortality rates of resident and transient bobcats in a subtropical region of southern Texas in the United States. Our objectives were to estimate seasonal and annual survival rates and cause-specific mortality rates for resident and transient bobcats, and to evaluate differences between resident and transient bobcats. We conducted the study on the Welder Wildlife Foundation Refuge in San Patricio County, Texas. We radio-monitored 30 resident (15 F, 15 M) and 23 transient (9 F, 14 M) bobcats from 31 December 1993 through 1 January 2004, with 19 transients being subadult bobcats and 26 residents being adult bobcats. Annual ($P = 0.09$) and seasonal ($P > 0.53$) survival rates did not differ significantly between male and female resident bobcats. Seasonal survival did not differ for resident ($P = 0.64$) and transient ($P = 0.72$) bobcats. Resident bobcats had a higher ($P < 0.01$) annual survival rate ($\hat{S} = 0.88$, $SE = 0.04$) than transient bobcats ($\hat{S} = 0.26$, $SE = 0.14$). Resident bobcats had a higher rate ($P = 0.04$) of harvest mortalities, whereas transient bobcats had a higher rate ($P = 0.01$) of vehicle-caused mortalities. Other forms of mortality did not differ between resident and transient bobcats ($P \geq 0.15$). Survival rates for bobcats seem to be lower outside the refuge environment. Data presented in this study will be helpful in assessing the viability of bobcat populations through population modeling.

Key words: bobcat, *Lynx rufus*, mortality, resident, survival, Texas, transient

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Estimates of survival and cause-specific mortality rates provide important information to wildlife biologists to identify major sources of mortality, and allow researchers to model populations under different management

scenarios to predict population response. Fuller et al. (1995) stated that decisions on how to manage bobcat *Lynx rufus* populations are often guided by population models that are based on bobcat survival and cause-spe-

cific mortality rates. Numerous studies have calculated survival and cause-specific mortality rates for bobcats within temperate regions of North America (Fuller et al. 1985, 1995, Knick 1990, Chamberlain et al. 1999, Kamler & Gipson 2000, Nielsen & Woolf 2002).

In contrast, our study occurred in a subtropical environment of southern Texas in the United States (U.S.) and was the first to compare survival and cause-specific mortality rates between resident and transient bobcats. Resident bobcats are usually adults with stable home ranges, whereas transient bobcats are usually juvenile or subadult individuals that have dispersed from a natal home range.

Kamler & Gipson (2000) stated that transient bobcats had < 50% survival of resident bobcats because transients were likely to be more vulnerable when traveling in unfamiliar areas. However, Kamler & Gipson (2000) only monitored 10 bobcats during a 2.5-year period. Haines et al. (2005) conducted the only known study that statistically compared survival rates of resident and transient mid-sized felids. Haines et al. (2005) monitored 80 ocelots *Leopardus pardalis* over 20 years and found that survival of transient ocelots was significantly lower than that of resident ocelots. Haines et al. (2005) believed most transients were roaming juveniles or subadults attempting to establish a breeding range, and thus were more susceptible to multiple sources of mortality, including intraspecific mortality. In addition, studies analyzing the survival of wolves *Canis lupus* and wolverines *Gulo gulo* found that mortality increased during dispersal (Hayes & Harestad 2000, Krebs et al. 2004)

Our objectives were to 1) estimate seasonal and annual survival rates for resident and transient bobcats, 2) estimate seasonal and annual cause-specific mortality rates for resident and transient bobcats, and 3) evaluate differences between resident and transient bobcats. We hypothesized that 1) annual bobcat survival would be similar between male and female resident bobcats (Fuller et al. 1995, Chamberlain et al. 1999, Nielsen & Woolf 2002), and 2) survival of transient bobcats would be significantly lower than that of resident bobcats because transients will be more susceptible to mortality (e.g. vehicle collisions, intraspecific mortality or natural mortality) in unfamiliar environments (Kamler & Gipson 2000, Haines et al. 2005).

Material and methods

Our study was conducted on the 3,160-ha Welder Wildlife Foundation Refuge (WWFR) in San Patricio County, Texas, USA (Fig. 1). Legal harvest of bobcats was pro-

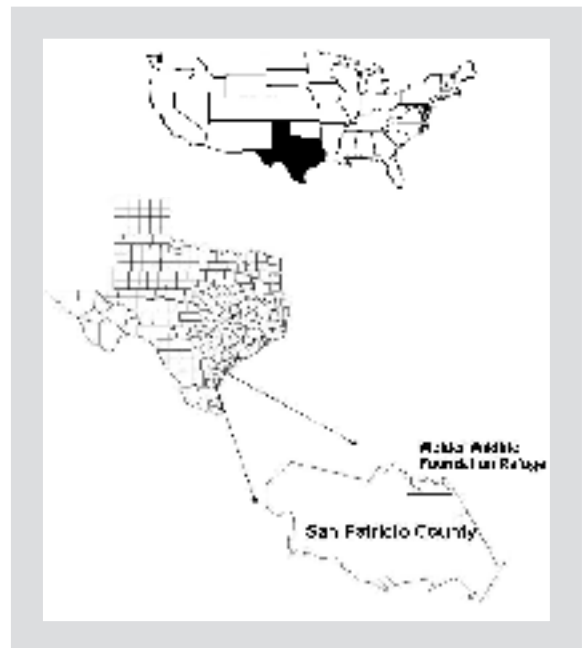


Figure 1. Location of the Welder Wildlife Foundation Refuge in San Patricio County, Texas, USA.

hibited on the refuge. The WWFR lies in a transitional zone between the South Texas Plains and the Gulf Prairies and Marshes vegetational regions (Drawe et al. 1978). The climate is humid and subtropical with hot summers and cool winters, with an average maximum temperature of 34°C in July and an average low temperature of 6°C in January (www.caller2.com/caliente/cityinfo/index_ingleside.html). The 48-year average annual rainfall is 91.8 cm. Mean monthly rainfall showed a bimodal annual distribution with peaks in May-June and September. The topography is flat with elevations ranging within 3-16 m a.s.l. The Aransas River forms the northern boundary of the WWFR (Drawe et al. 1978).

We captured bobcats with modified Tomahawk (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) live traps (107 × 38 × 51 cm). A 51 × 38 × 51 cm extension was added to the trap and covered with hardware cloth to hold and protect domestic live chickens *Gallus* spp. used for bait. Live chickens were provided food and water *ad libitum*. We immobilized trapped bobcats with an intramuscular injection of 10-15 mg/kg body weight of ketamine hydrochloride and 0.05 mg/kg body weight of promazine hydrochloride. Bobcats were sexed, weighed, measured, fitted with a small numbered metal tag placed in each ear, and depending on age, each bobcat was fitted with a radio-collar (Advanced Telemetry Systems® [ATS], Isanti, Minnesota, USA). We classified collared bobcats as subadults (≤ 2 years old) and

adults (> 2 years old) based on dental stage of replacement, weight and physical characteristics (Crowe 1975, Knick 1990).

We used a large 2-element null-peak antenna mounted on a vehicle and an ATS R2100 receiver to locate radio-collared bobcats. We estimated animal locations using the homing-in technique described by White & Garrott (1990), and collected telemetry data on roads, fence lines, pipelines and power lines. We conducted aerial radio-tracking (Gilmer et al. 1981) periodically to locate bobcats outside the boundaries of the WWFR. We attempted to collect > 10 locations monthly for each collared bobcat on the WWFR. We obtained locations during the day from 05:00 to 20:00 to determine activity and resting periods.

Bobcats were classified as residents or transients. Transient bobcats exhibited a nomadic movement pattern with temporary activity areas and eventually moved away from the WWFR. Bobcats were residents if they used a defined range for at least six months. We used ground and aerial searches for bobcats that dispersed from the WWFR, and checked bobcats found in the same location for 2-3 days to determine condition. Bobcat mortality was classified as vehicle collision, natural causes (i.e. starvation), harvest or unknown factors. If date of death was unknown, we designated date of death as the last known live telemetry or visual location.

We estimated annual and seasonal survival rates and cause-specific mortality rates of resident and transient bobcats using number of transmitter-days and total number of deaths within a defined time interval (Trent & Rongstad 1974, Heisey & Fuller 1985a) in the program MICROMORT (Heisey & Fuller 1985b) which is based on the Mayfield methodology (Mayfield 1961, 1975). In addition, we estimated annual and seasonal survival rates of subadult and adult bobcats. Bobcat survival may be influenced by parental care responsibilities to kittens (Chamberlain et al. 1999). Thus, to meet the assumptions of the Mayfield method, we assumed that constant survival occurred during the breeding (1 December - 31 May) and kitten-rearing (1 June - 30 November) seasons in the study area, based on reproductive observations from Blankenship (2000).

Study assumptions included 1) newly collared bobcats had the same survival rate as previously collared bobcats, 2) sampled bobcats were random and independent, 3) working collars were always located, 4) censoring was random, and 5) trapping, handling and radio-collaring did not affect bobcat survival (Winterstein et al. 2001). We used bobcats with transmitter failure in the data analysis for survival probabilities until signal loss occurred (Burger et al. 1995). These individuals were

censored from the survival analysis, but were not considered mortalities (Pollock et al. 1989).

We pooled data across years because low annual sample sizes would have resulted in low statistical power for tests (Fuller et al. 1985, Cunningham et al. 2001, Nielsen & Woolf 2002, Haines et al. 2005). Nielsen & Woolf (2002) stated that testing for differences in annual survival rates over years would have been biased because different number of radio-days occurred each year. Hence, Nielsen & Woolf (2002) believed that testing for differences in survival between years is unfounded and biologically meaningless (Yoccoz 1991, Cherry 1998). However, the ratio of total radio-days to number of mortalities should produce a relatively constant survival rate. We believed bias would occur if sample size (number of radio-days) was extremely low. This was our main justification for pooling data across years.

We used chi-square tests in the program CONTRAST (Hines & Sauer 1989, Sauer & Williams 1989) to test for differences in annual and seasonal survival rates and cause-specific mortality rates between resident and transient bobcats. In addition, we tested for differences in annual and seasonal survival rates and mortality rates between male and female resident bobcats. Experiment-wise error rate was maintained during associated multiple comparisons by adjusting α with a Bonferroni correction factor (α /number of comparisons; Neter et al. 1990). Statistical significance was inferred at $P \leq 0.05$.

Results

From 31 December 1993 to 1 January 2004, we monitored 30 resident (15 F, 15 M) and 23 transient (9 F, 14 M) bobcats for 27,738 radio-days (\bar{x} days/bobcat = 523, SD = 430 days) for survival and cause-specific mortality analyses. We monitored resident bobcats for 26,094 radio-days (\bar{x} = 870 days/bobcat, SD = 410 days) and transient bobcats were monitored for 1,644 radio-days (\bar{x} = 72 days/bobcat, SD = 60 days). We monitored resident female bobcats for more radio-days (14,569) than male residents (11,524), and male transient bobcats for more radio-days (1,213) than female transients (431). Our study found fewer female transient bobcats ($N = 9$) than males ($N = 14$). In addition, female bobcats spent more time (\bar{x} = 971 radio-days) as residents than males (\bar{x} = 768 radio-days), and male bobcats spent more time as transients (\bar{x} = 87 radio-days) than females (\bar{x} = 48 radio-days). Most transient bobcats were subadults with only four adult transient bobcats, and most resident bobcats were adults with only four subadult resident bobcats.

Table 1. Seasonal and annual survival rates (\hat{S}) of male and female resident bobcats during the breeding (1 December - 31 May) and kitten-rearing seasons (1 June - 30 November) in San Patricio County, Texas, for the period 31 December 1993 - 1 January 2004.

	Mortalities	Radio-days	\hat{S}	S.E.
Male				
Breeding	1	5669	0.97	0.03
Kitten	1	5885	0.97	0.03
Annual	2	11524	0.94	0.04
Female				
Breeding	3	7240	0.93	0.04
Kitten	4	7330	0.91	0.09
Annual	7	14569	0.84	0.05
Pooled				
Breeding	4	12909	0.95	0.03
Kitten	6	13185	0.93	0.03
Annual	9	26094	0.88	0.04

During the study, 15 mortalities occurred with nine residents (7 F, 2 M) and six transients (3 F, 3 M). Mortalities within resident bobcats included four (44%) harvested, two (22%) natural (starvation), two (22%) vehicle-collisions, and one (11%) unknown mortality. Mortalities for transient bobcats included four (67%) vehicle-collisions, and two (33%) natural mortalities (starvation). Overall, mortalities for all radio-monitored bobcats did not differ dramatically between the breeding ($N = 7$, 47%) and kitten-rearing ($N = 8$, 53%) seasons. In addition, vehicle-collision caused mortality was the highest source of mortality (40%) for bobcats radio-monitored on the WWFR, followed by harvest (27%), natural (27%) and unknown (7%) mortalities.

From 31 December 1993 to 1 January 2004, annual survival rates did not differ significantly ($\chi^2_1 = 2.94$, $P = 0.09$) between male and female resident bobcats (Table 1). Survival did not differ between male and female resident bobcats during the breeding ($\chi^2_1 = 0.64$, $P = 0.42$) and kitten-rearing seasons ($\chi^2_1 = 0.40$, $P = 0.53$; see Table 1). This supported the hypothesis that survival between sexes would be similar for resident bobcats. In addition, survival did not differ between the breeding and kitten-rearing seasons for resident ($\chi^2_1 = 0.22$, $P = 0.64$) and transient ($\chi^2_1 = 0.13$, $P = 0.72$) bobcats (see Table 1 & 2).

Table 2. Seasonal and annual survival rates (\hat{S}) of transient bobcats during the breeding (1 December - 31 May) and kitten-rearing seasons (1 June - 30 November) in San Patricio County, Texas, for the period 31 December 1993 - 1 January 2004.

	Mortalities	Radio-days	\hat{S}	S.E.
Breeding	3	943	0.56	0.19
Kitten	3	701	0.46	0.20
Annual	6	1644	0.26	0.14

Table 3. Seasonal and annual survival rates (\hat{S}) of subadult and adult bobcats during the breeding (1 December - 31 May) and kitten-rearing seasons (1 June - 30 November) in San Patricio County, Texas, for the period 31 December 1993 - 1 January 2004.

	Mortalities	Radio-days	\hat{S}	S.E.
Subadult				
Breeding	3	1990	0.75	0.12
Kitten	1	1898	0.91	0.09
Annual	4	3888	0.68	0.13
Adult				
Breeding	4	11866	0.94	0.03
Kitten	7	11984	0.90	0.04
Annual	11	23850	0.85	0.04

We combined male and female transient bobcat radio-days for survival and cause-specific mortality analysis because of the low number of radio-days for transients (see Table 2). Resident bobcats had a significantly higher ($\chi^2_1 = 18.13$, $P < 0.01$) annual survival ($\hat{S} = 0.88$, $SE = 0.04$) rate than transient bobcats ($\hat{S} = 0.26$, $SE = 0.14$; see Table 1 & 2). This supported the hypothesis that annual survival of resident bobcats would be significantly higher than that of transient bobcats. In addition, we combined male and female radio-days to compare annual survival rates between subadult and adult bobcats (Table 3). Adult bobcats had a higher annual survival rate ($\hat{S} = 0.85$, $SE = 0.04$) than subadult bobcats ($\hat{S} = 0.68$, $SE = 0.13$). However, there was no significant difference ($\chi^2_1 = 1.56$, $P = 0.21$) between adult and subadult bobcat annual survival rates.

Cause-specific mortality of male and female resident

Table 4. Pooled seasonal and annual cause-specific mortality rates (M) of male and female resident and transient bobcats during the breeding (1 December - 31 May) and kitten-rearing seasons (1 June - 30 November) in San Patricio County, Texas, for the period 31 December 1993 - 1 January 2004.

Mortality cause	Residents			Transients		
	Mortalities	M	S.E.	Mortalities	M	S.E.
Breeding						
Vehicle	1	0.014	0.013	2	0.291	0.172
Natural	1	0.014	0.013	1	0.146	0.134
Harvest	2	0.027	0.019	0	0	-
Unknown	0	0	-	0	0	-
Kitten						
Vehicle	1	0.013	0.013	2	0.359	0.200
Natural	1	0.013	0.013	1	0.179	0.161
Harvest	2	0.026	0.018	0	0	-
Unknown	1	0.013	0.013	0	0	-
Annual						
Vehicle	2	0.026	0.018	4	0.493	0.173
Natural	2	0.026	0.018	2	0.247	0.152
Harvest	4	0.052	0.025	0	0	-
Unknown	1	0.012	0.012	0	0	-

bobcats did not differ during the breeding season ($\chi^2_1 \leq 1.09$, $P \geq 0.30$) and the kitten-rearing season ($\chi^2_1 \leq 1.00$, $P \geq 0.32$). In addition, cause-specific mortality did not differ for resident ($\chi^2_1 \leq 1.52$, $P \geq 0.22$) and transient bobcats ($\chi^2_1 \leq 0.66$, $P \geq 0.80$) during the breeding and kitten-rearing seasons (Table 4). However, transient bobcats had a higher rate ($\chi^2_1 = 7.21$, $P = 0.01$) of vehicle-caused mortalities ($M = 0.49$, $SE = 0.17$) than resident bobcats ($M = 0.03$, $SE = 0.02$), and resident bobcats had a higher rate ($\chi^2_1 = 4.33$, $P = 0.04$) of harvest mortalities ($M = 0.05$, $SE = 0.03$) than transient bobcats ($M = 0$). Other mortality causes did not significantly differ between resident and transient bobcats ($\chi^2_1 \leq 2.09$, $P \geq 0.15$; see Table 4).

Our study violated one of the assumptions of the Mayfield method. Not all bobcats with working collars were located. Of the 23 transient bobcats, 12 traveled off the refuge for a considerable distance and contact was lost (censored). In addition, four of 30 resident bobcats also traveled off the refuge for a considerable distance and contact was lost (censored). However, no bobcats suffered mortality shortly after being radio-collared, and the shortest time interval from when a bobcat was collared until mortality was 43 days.

Discussion

Our study provides the first results comparing survival and cause-specific mortality rates of resident and transient bobcats, and bobcats in a subtropical environment. Resident bobcats exhibited > 60% higher survival than transients. Most transient bobcats were young individuals probably attempting to identify a breeding range, whereas four were adult individuals probably attempting to reestablish a breeding range. Our results concur with Kamler & Gipson (2000) who found that transient bobcats in Kansas had a substantially lower survival rate than resident bobcats. Kamler & Gipson (2000) attributed this difference to resident bobcats occupying a military base that served as a refuge, and transient bobcats being more susceptible to hunting and trapping and vulnerable within unfamiliar areas. In addition, Sunquist & Sunquist (2002) stated that long movements made by cats over a large area, typical of transients, increases encounters with highways and humans, the two primary sources of mortality for wild cats. Furthermore, studies that have analyzed survival rates for other carnivore species have found that mortality increases during dispersal (Hayes & Harestad 2000, Krebs et al. 2004, Haines et al. 2005).

We found that transient bobcats were more suscepti-

ble to vehicle collisions, thus concurring with Kamler & Gipson (2000) and Sunquist & Sunquist (2002). In addition, Chamberlain et al. (1999) stated that greater bobcat movement rates would increase mortality from harvest. However, resident bobcats within our study were more susceptible to harvest than transient bobcats. There are two possible explanations for this finding. Transient bobcats were more likely to move long distances and mortalities were never found. In addition, the northern boundary of the WWFR is a river and this provides access to poachers who illegally shot bobcats on WWFR property.

We found that the largest sources of mortality for resident and transient bobcats were human-related (67%), with residents more susceptible to human harvest and transients more susceptible to vehicle-collisions. Knick (1990) found that 50% of bobcat mortalities in an unexploited population in Idaho were human-related. Chamberlain et al. (1999) found that 18 of 31 (58%) bobcat mortalities were from harvest and vehicle-collisions. Nielsen & Woolf (2002) identified 19 mortalities with 52% caused by automobiles and human activities linked to 79% of the cumulative mortality.

Most studies on bobcat survival did not differentiate between residents or transients. Thus, we combined data on resident and transients to more accurately compare bobcat survival rates between studies. Survival of transient bobcats on the WWFR was low, but when resident and transient annual survival rates were combined the annual survival rate was ($\hat{S} = 0.82$). This survival rate was similar to that of a harvested population of bobcats in Mississippi ($\hat{S} = 0.80$; Chamberlain et al. 1999) and a non-exploited population of bobcats in Illinois ($\hat{S} = 0.84$; Nielsen & Woolf 2002). However, our survival rates were high compared to harvested bobcat populations in Minnesota ($\hat{S} = 0.19$ and 0.61 ; Fuller et al. 1985), Idaho ($\hat{S} = 0.67$; Knick 1990), and Massachusetts ($\hat{S} = 0.62$; Fuller et al. 1995), with illegal harvest of radio-monitored bobcats also incorporated into the latter survival estimates. Bobcat harvest was not permitted on the WWFR. However, harvest of adult residents occurred along the refuge boundary. Resident and transient bobcat survival may be substantially lower outside the WWFR because there are no limitations on bobcat harvest occurring in Texas (Texas Parks and Wildlife 2004).

Kamler & Gipson (2000) conducted the only other study that differentiated survival between transient and resident bobcats. Annual survival rate of transient bobcats radio-monitored on the WWFR ($\hat{S} = 0.26$) was low when compared to transient bobcats in Kansas ($\hat{S} = 0.46$; Kamler & Gipson 2000). In addition, annual survival rate of resident bobcats in southern Texas was nearly

identical to annual survival rate of resident ocelots in southern Texas ($\hat{S} = 0.87$; Haines et al. 2005).

We found similar annual and seasonal survival between male and female resident bobcats. However, annual survival of male resident bobcats approached being significantly higher than annual survival of resident females ($P = 0.09$). We do not have an explanation for this, and believe this warrants further investigation. Chamberlain et al. (1999) found that female bobcat survival was lower than male bobcat survival during the parturition-young-rearing period (1 June - 30 September) in central Mississippi. Chamberlain et al. (1999) attributed this increased mortality to parental care responsibilities influencing female survival. In addition, Chamberlain et al. (1999) also found that male bobcats were more susceptible to harvest than females. However, Knick (1990) and Nielsen & Woolf (2002) found that the annual survival rates were similar between male and female adult bobcats. In addition, Nielsen & Woolf (2002) found no difference in seasonal survival between male and female adult bobcats. Furthermore, unlike Chamberlain et al. (1999) we found no difference in the harvest mortality rates between resident male and female bobcats. However, this may be due to no legal harvest allowed on WWFR.

We did not find a significant difference in annual survival rates between adult and subadult bobcats. This may be the result of some subadult bobcats never becoming transient individuals and some adult bobcats exhibiting transient behaviour. Thus, the results of our study suggest that transient behaviour is more detrimental to bobcat survival than age. Hence, any events that may cause a bobcat to disperse (i.e. destruction of habitat, translocation of individuals and low prey populations) may significantly increase bobcat mortality.

More male than female transient bobcats were radio-monitored. In addition, individual female bobcats spent more time as residents and less time as transients than males. There are usually fewer female transients than male transients in populations of solitary cats, because females often settle adjacent to or within their natal range to breed (Sunquist & Sunquist 2002). This same pattern of behaviour has been documented for tiger *Panthera tigris*, leopard *Panthera pardus*, Iberian lynx *Lynx pardinus*, puma *Puma concolor*, and ocelot (Smith et al. 1987, Lindzey et al. 1988, Bailey 1993, Ferreras et al. 1997, Haines et al. 2005).

In our study, the highest source of cause-specific mortality for bobcats was vehicle-collisions (40%). In addition, Nielsen & Woolf (2002) and Haines et al. (2005) identified vehicle-collisions as the primary anthropogenic factor causing deaths in wild felids. Thus, future

management considerations should include the placement of culverts under highways in relation to habitat features and travel corridors, with barrier fences guiding bobcats to the culverts to reduce bobcat-vehicle collisions (Tewes & Hughes 2001, Cain et al. 2003). Bobcats have been found to successfully use travel culverts (Cain et al. 2003). Furthermore, information from our study will be helpful in assessing bobcat population status through population modeling. Population models that include other factors such as prey abundance and habitat composition can be used to assess potential effects of bobcat harvest rates, disease, drought, vegetation changes, and fragmentation of habitat on the viability of local bobcat populations.

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