SURVIVAL OF WESTERN COTTONMOUTHS (*AGKISTRODON PISCIVORUS LEUCOSTOMA*) IN A PULSING ENVIRONMENT

FRANCIS L. ROSE,* THOMAS R. SIMPSON, JAMES R. OTT, RICHARD W. MANNING, AND JULIEN MARTIN

Department of Biology, Texas State University–San Marcos, San Marcos, TX 78666 (FLR, TRS, JRO, RWM)
Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville, FL 32611 and Patuxent Wildlife Research Center, United States Geological Survey, Laurel, MD 20708 (JM)
Present address of RWM: 107 LBJ Cove, San Marcos, TX 78666
**Correspondent: fr02@txstate.edu*

ABSTRACT—We present the first robust estimates of apparent survival of western cottonmouths (*Agkistrodon piscivorus leucostoma*) in central Texas. Estimates presented were obtained using the Cormack–Jolly-Seber Model that accounts for detectability. Apparent annual probability of survival of western cottonmouths located at Honey Creek, Comal County, Texas, a spring-fed stream flowing 3.2 km to its confluence with the Guadalupe River, was 0.81 and was consistent with estimates for similar species of snakes. Despite low probability of detection (0.12) and relatively small sample ($n = 51$), the estimate of survival was reasonably precise (coefficient of variation was 4%). One benefit of our study is that we used a long-term dataset (11 years) that encompassed multiple floods and droughts, and therefore, represents a relatively wide range of conditions to which western cottonmouths are exposed at this locality.

RESUMEN—Presentamos las primeras estimaciones robustas de supervivencia aparente de la mocasín de boca de algodón (*Agkistrodon piscivorus leucostoma*) en Texas central. Las estimaciones presentadas fueron obtenidas utilizando el modelo de Cormack-Jolly-Seber que se ajusta por la detectabilidad. La probabilidad anual aparente de supervivencia de la mocasín de boca de algodón localizada en Honey Creek, condado de Comal, Texas, una corriente alimentada por un manantial que fluye 3.2 km a su confluencia con el río Guadalupe, fue 0.81 y fue consistente con estimaciones para especies semejantes de serpientes. A pesar de la probabilidad baja del descubrimiento (0.12) y la muestra relativamente pequeña ($n = 51$), la estimación de supervivencia fue razonablemente precisa (coeficiente de variación de 4%). Un beneficio de nuestro estudio es que utilizamos un conjunto de datos a largo plazo (11 años) que abarcó inundaciones y sequías múltiples, y por lo tanto, representa una relativamente gran variedad de condiciones a las que las mocasines de boca de algodón están expuestas en esta localidad.

The western cottonmouth, *Agkistrodon piscivorus leucostoma*, is an iteroparous pit viper that inhabits a wide variety of habitats (Gloyd and Conant, 1990; Werler and Dixon, 2000). In Texas, the species is ubiquitous in the eastern one-half of the state and is found from coastal marshes to inland streams (Werler and Dixon, 2000). In north-central Texas, it is associated with mesic habitats, where it migrates seasonally between woodlands and river bottoms (Tennant, 1984; Ford, 2002). Because of its wide distribution and abundance, the western cottonmouth might be an important predator of fish, amphibians, birds, and small mammals (Savitzky, 1992). Furthermore, many habitats occupied by western cottonmouths, particularly the ones characterized by pulsing environments (e.g., streams and rivers) are largely influenced by activities of humans. Little is known, however, about demography of this important species, and estimates of survival based on robust statistical methods are lacking. The objective of our study was to provide estimates of survival for western cottonmouths in central Texas, based on robust approaches to statistical estimation.

In the research reported herein we used results of an 11-year mark-recapture study to investigate apparent survivorship (1—mortality and permanent emigration) and probabilities of detection within a population of western cottonmouths resident in Honey Creek, a typical small, highly variable, and low-productivity stream in central Texas. Two published estimates of apparent annual survival for North American pit vipers based on robust estimators for timber rattlesnakes *Crotalus horridus* (Brown et al., 2007) and western rattlesnakes *Crotalus viridis oreganos* (Diller and Wallace, 2002) suggest high annual rates of survival (0.820–0.958) for adult terrestrial pit vipers. However, because the environment occupied by the semi-aquatic western cottonmouth at Honey Creek is extremely variable with oscillations ranging from extreme drought to flood, we hypothesized a lower apparent annual rate of survival in this population of western cottonmouths in comparison to the above estimates. We envisioned that apparent annual survivorship might be directly affected by variable stream flow via attendant effects on abundance and distribution of resources, indirectly as a consequence of flow-dependent emigration from the system, or both. We also predicted that apparent survival would be lower in male than in female western cottonmouths in this system because dispersal in snakes is hypothesized to be greater in males than females (Keogh et al., 2007) and because our own studies at Honey Creek showed that males move significantly greater distances between successive captures (unpublished data). We expected, therefore, that males would have higher probabilities of permanent emigration from the study area. Finally, we predicted that expansion of the search area would increase estimates of apparent survivorship because of higher probabilities of recapturing marked snakes that dispersed from the initial study area, or were displaced downstream during floods.

Materials and Methods—Honey Creek emanates from Honey Creek Cave (UTM coordinates 549681 Easting and 3303260 Northing) located in Comal County, Texas, and is contained within the protected Honey Creek State Natural Area. The stream is enhanced along its 3.2-km course to the Guadalupe River by secondary springs. General habitat of Honey Creek is a limestone spring-fed stream running in a rocky bed (typically 3–5 m in width), bounded by high-walled cliffs. The streambed alternates between four deep pools and shallow riffles meandering in channels among roots of baldcypresses (*Taxodium distichum*) and exposed rocks and gravel beds. The riparian habitat is dominated by baldcypresses, sycamores (*Platanus occidentalis*), and dwarf palmettos (*Sabal minor*) growing along the banks and on exposed soils and gravel bars in the streambed. Steep rock walls up to 17 m high occur within meters of the border along parts of the stream, while at other points the stream broadens and banks slope upward at 15–25° to arid uplands of rocky soils with oak (*Quercus fusiformis*)-juniper (*Juniperus ashei*) woodlands and a Texas persimmon (*Diospyros texana*) understory. Rain events in the Honey Creek watershed generate large-amplitude variation in hydrologic conditions. Nine periods of high flow (floods) were visually confirmed at Honey Creek during our study, wherein water levels were ≥15 m above base level. There was a period in 1999 of no flow between pools, and a severe drought occurred in 2000 when flow from the cave ceased during May–September.

A 684-m segment of stream (Area 1), beginning at the opening of Honey Creek Cave, was selected in 1992 to survey snakes. This headwater section of the stream represented the first 21% of the 3.2-km length of the stream measured from origin to confluence with the Guadalupe River. In 1995, we extended the search area an additional 880 m downstream (Area 2). Expansion of the study area had the potential to increase apparent survival by permitting recaptures of snakes that moved but would have been permanent emigrants in a smaller study area.

The expanded search area totaled 1,564 m and encompassed 49% of the entire stream. We surveyed for snakes on average 4.4 times (range 2–8) during May–September each year in 1992–2003. For each survey, two to five individuals (mean = 3.2) methodically searched the length of the study area and its margins (0–3 m) and on the return leg searches were made up to the shear vertical cliffs. A total of 53 surveys were conducted with an average of 2.3 h expended/survey for a search effort of 418.3 h.

Capture points were the number of meters downstream from the cave. Snakes were captured with tongs, and sex, snout–vent length, and weight were recorded. Snakes were injected subcutaneously with a PIT-tag, scale-clipped, and released at site of capture. For data analyses, 51 adult and subadult snakes were used. Individuals identified as juveniles, based on morphological features (Neill, 1960), were excluded from our study.

We used the Cormack-Jolly-Seber Model implemented in program MARK to simultaneously estimate probabilities of apparent survival (ϕ) and detection (p; White and Burnham, 1999; E. G. Cooch and G. C. White, http://phidot.org/software/docs/book/). Parameter ϕ_t is the probability of not dying and not permanently emigrating between survey t and t + 1. Parameter p_t is the probability of capturing a western cottonmouth given that it was alive and present in the study area during survey t. We developed a series of models to evaluate our hypotheses. We compared these models using the Akaike Information Criterion (AIC; Akaike, 1973). We identified the most-parsimonious models by selecting models with the lowest AIC (Burnham and Anderson, 2002). Change in AIC for the i^{th} model was computed as $AIC_i - \min(AIC)$. Models with a change in AIC < 2 were considered to have received similar support and could not be rejected based on AIC (Burnham and Anderson, 2002). As suggested by Burnham and Anderson (2002), we used model averaging to compute overall estimates of ϕ and p.

Model notation followed Lebreton et al. (1992) and time dependency was denoted as ''t'' and no time

TABLE 1—Cormack–Jolly-Seber models of probabilities of apparent survival (ϕ) and detection (*p*) of western cottonmouths (*Agkistrodon piscivorus leucostoma*) in central Texas during 1992–2003. Factors incorporated in the models included time effect (t), no time effect (.), study area effect (AREA), sex effect (SEX), and time of study area expansion effect (TESA). Change in AIC (Akaike information criterion) for the i^{th} model was computed as AIC_i – min (AIC). K was the number of parameters.

Model	AIC	ΔAIC	K
ϕ(.) *p*(AREA)	609.9	0.0	3
ϕ(AREA)*p*(.)	610.4	0.5	3
ϕ(.) *p*(.)	610.5	0.6	4
ϕ(AREA)*p*(AREA)	610.7	0.8	4
ϕ(TESA)*p*(AREA)	612.0	2.1	4
ϕ(SEX)*p*(AREA)	612.0	2.1	4
ϕ(AREA)*p*(SEX)	612.1	2.2	4
ϕ(.)*p*(SEX)	612.3	2.4	3
ϕ(TESA)*p*(.)	612.4	2.5	3
ϕ(SEX)*p*(.)	612.6	2.7	3
ϕ(TESA)*p*(SEX)	614.2	4.3	4
ϕ(SEX)*p*(SEX)	614.4	4.5	4

TABLE 2—Model-averaged estimates (based on all models) of probability of apparent survival (ϕ) and detection (*p*) of male and female western cottonmouths (*Agkistrodon piscivorus leucostoma*) in two study areas (areas 1 and 2) before and after expansion of the study area.

Parameter	Estimate	*SE*	95% CI
ϕ: Area 1, before, male	0.791	0.058	0.656–0.882
ϕ: Area 1, after, male	0.796	0.048	0.687–0.874
ϕ: Area 1, before, female	0.791	0.055	0.664–0.878
ϕ: Area 1, after, female	0.796	0.045	0.695–0.870
ϕ: Area 2, before, male	0.824	0.064	0.663–0.917
ϕ: Area 2, after, male	0.829	0.053	0.700–0.909
ϕ: Area 2, before, female	0.824	0.061	0.671–0.914
ϕ: Area 2, after, female	0.829	0.050	0.708–0.906
Model averaged ϕ	0.810	0.019	0.771–0.848
p: Area 1, male	0.110	0.019	0.077–0.153
p: Area 1, female	0.113	0.018	0.082–0.153
p: Area 1, male	0.130	0.026	0.087–0.189
p: Area 1, female	0.133	0.023	0.094–0.185
Modeled average *p*	0.121	0.011	0.099–0.143

variation was denoted ''.''. For instance, model: ϕ(t)*p*(.), assumed that ϕ varied over time but that *p* remained constant over time. We also developed several models that assumed the effect of factors of particular interest on ϕ and *p*: SEX, study area (denoted AREA) and time when the study area was extended (denoted TESA). Because the initial study area was extended in 1995, we predicted that ϕ would increase after 1995.

Time intervals were specified between each occasion in program MARK because time intervals between consecutive sampling occasions were uneven. Time intervals varied 4–290 days, but duration of sampling occasions remained short relative to time intervals between occasions. To make estimates of ϕ comparable among intervals we converted each estimate of ϕ for each time interval into annual estimates. These annual estimates were easily back transformed for any desired time duration (e.g., $\sqrt[12]{\hat{\phi}}$ yields monthly estimates; see E. G. Cooch and G. C. White, http://phidot.org/software/docs/book/, for more details). We computed three measures of precision: standard error (*SE*), 95% confidence intervals (95% CI), and coefficient of variation (*CV*). We computed *CV* of an estimate as the ratio of the standard error of the estimate to the value of the estimate (Burnham and Anderson, 2002) and multiplied this value by 100 to get a % *CV*. We tested goodness-of-fit of the fully time-dependent model (i.e., $\phi(t)p(t)$) using program RELEASE (Burnham et al., 1987). Choquet et al. (ftep://ftp.cefe.cnrs-mop.fr/biom/U-CARE) recommend a correction for over dispersion for cases where the goodness-of-fit was significant (i.e., $P < 0.05$).

RESULTS—The goodness-of-fit test was not statistically significant ($P > 0.05$); therefore, there was no need to correct for over dispersion. Model ϕ(.) *p*(AREA) was the most-parsimonious model (i.e., lowest AIC; Table 1). Three additional models, ϕ(AREA) *p*(.), ϕ(.) p(.), and ϕ(AREA) *p*(AREA), also were supported by the data and could not be rejected (ΔAIC < 2; Table 1). Estimates of ϕ and *p* averaged over all models (Table 2) were 0.81 ($SE(\phi) = 0.02$) and 0.12 $SE(P) = 0.01$). Estimate of ϕ after the expansion of the study area was slightly greater, but the difference was negligible based on estimates shown in Table 2. The model-selection technique suggested little support (ΔAIC > 2) for models that contained SEX, TESA, and time (t).

DISCUSSION—Because our study was done in a linear system and the habitat away from Honey Creek lacked life-sustaining resources for semi-aquatic snakes, and because during the driest periods water remained in the four pools, we theorized that movements of western cottonmouths away from Area 1 would be downstream. The model-averaged estimate of apparent annual probability of survival for western cottonmouths inhabiting Honey Creek was 0.81 ($SE(\phi) = 0.02$).

Models that hypothesized a sex effect, and an effect of study area (Area 1 versus 2) on apparent survival were not supported by the data. In addition, we included a model that accounted for the effect of expansion of the study area on survival, but this model did not receive support from the data. Therefore, our predictions that apparent survival within our study system would vary between sexes, and would increase with increasing size of the study area received no support from our data. Our estimate of apparent survival was consistent with estimates obtained for timber rattlesnakes *Crotalus horridus* (Brown et al., 2007) and western rattlesnakes, *Crotalus viridis oreganos* (Diller and Wallace, 2002). All of the above estimates were based on robust estimators of apparent survival (i.e., the probability of not dying and not permanently emigrating from the study area) and account for detectability (i.e., the probability of detecting an individual given that it is alive and present in the study area). Ford (2002) estimated survivorship by mark-recapture of 12 and 6 neonate western cottonmouths released at his study site at 30 and 50% for the first year. He attributed these relatively high estimates to the fact that the young were venomous.

Despite a low probability of detection (0.12), we were able to obtain estimates of survival with a reasonable precision (the coefficient of variation in percentage of the estimate of apparent survival for the most-parsimonious model was 4%). The substantial increase in size of the study area that occurred in 1995 did not affect substantially the estimates of apparent survival.

Brown et al. (2007) pointed out that robust estimates of important demographic parameters for wild populations of snakes remain scarce. Our study provides the first estimates of apparent survival for western cottonmouths based on robust estimators. One additional benefit of our study is that it is based on a relatively long-term dataset (11 years); therefore, the population had time to be exposed to a wide range of natural conditions (floods and droughts). These types of estimates are critical for additional modeling of population dynamics and management models (Caswell, 2001; Williams et al., 2002).

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