A RETROSPECTIVE SURVIVAL ANALYSIS OF TOWNSEND'S BIG-EARED BAT (*CORYNORHINUS TOWNSENDII*) FROM WASHINGTON STATE

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ABSTRACT—Townsend's Big-eared Bat (*Corynorhinus townsendii*) is a species of conservation concern for many states and provinces. However, little is known about key demographic parameters, such as survival, for this species due to its sensitivity to human disturbance. This species can also be vulnerable to injuries from wing bands; the most commonly applied marking technique used in the past to estimate survival in bats. During the US Fish and Wildlife Service's Bat Banding Program (1932–1972), CM Senger banded 1,346 Townsend's Big-eared Bats at 3 major cave systems in Washington during 1964–1975, and continued to recapture banded bats until 1980. I applied current mark-recapture techniques to retrospectively estimate survival of hibernating Townsend's Big-Eared Bats banded by CM Senger. I also investigated sex, time, and trend effects on survival and capture probabilities of these 3 populations of bats using Cormack-Jolly-Seber (CJS) open models and the modeling capabilities of program MARK. For each location, estimates of annual survival and capture probabilities varied somewhat by sex and ranged from 0.54 to 0.68 for males and 0.60 to 0.67 for females. During the banding study, band injuries were noted and populations declined at all locations potentially violating assumptions of the CJS model. However, the dataset from which these estimates were derived is likely to be the most complete and well-maintained dataset in the Bat Banding Program files. Resulting annual survival estimates from these data were relatively precise and modeling provided evidence of time and trend effects and differences in survival between the sexes. These results provide historical, *post hoc* estimates of an important life-history parameter for this species of bat wintering in caves in 3 localized areas of Washington State.

Key words: bat banding, *Corynorhinus townsendii*, mark-recapture, survival analysis, Townsend's Big-eared Bat, Washington

Townsend's Big-eared Bat (*Corynorhinus townsendii*) occurs throughout much of western North America from British Columbia to Mexico and east to Texas, with relict populations in states further eastward (Kunz and Martin 1982; Pierson and others 1999). It is a species of special concern for many states and provinces within its geographic range and a federal species of concern in many US states (formerly Category II [C2]; US Fish and Wildlife Service 1994; Pierson and others 1999). However, little is known about key demographic parameters for this species, such as survival, and this is most likely due to its sensitivity to human disturbance. Research activities have been known to depress, break up colonies, or extirpate populations (Pearson and others 1952; Humphrey and Kunz 1976; Kunz and Martin 1982; Pierson and others 1999). Townsend's Big-eared Bats can also be especially vulnerable to injuries from wing bands, the most commonly applied marking technique used in the past to estimate survival in bats (Ellison 2008). The sensitivity to banding and other research activities documented by this species has resulted in difficulties in accurately estimating survival, and the inability to model environmental factors that may influence this important life-history parameter. Survival is a key life history characteristic important not only in understanding and predicting population dynamics, but also for managing populations.

From 1932–1972, the US Fish and Wildlife Service's (USFWS) Bat Banding Program (BBP) issued 2 million bands of which approximately 1.5 million were applied to 36 species of bats in North America and Central America. Throughout the program, banders noticed negative effects of the bands on bat health and survival (Trapido and Crowe 1946; Cockrum 1956;

Hitchcock 1957; Herreid and others 1960). Banding was also linked to significant declines in bat populations because of disturbance during critical periods such as hibernation (Mohr 1972; Tuttle 1979; Barclay and Bell 1988). The program also suffered from administrative problems (reviewed in Ellison 2008). For these reasons, a moratorium on bat banding was proposed by the USFWS in 1972, and a resolution to cease banding by the American Society of Mammalogists was later ratified in 1973. A history and evaluation of the BBP was provided by Ellison (2008).

Here I apply current mark-recapture theory to estimate survival of Townsend's Big-Eared Bats using information from the bands issued to CM Senger during the BBP. Most of Senger's banding took place in the fall and winter of October 1964 through December 1975 in 3 counties in the state of Washington: Klickitat, Skagit, and Skamania (Senger and others 1972, 1974). A small group of bats was also banded in Whatcom County, but these sites were not as consistently visited for evidence of resightings as the others. Resightings of banded bats continued through the winter of 1980. Senger and his associates banded 8 different bat species, but the majority of bands (61%) were applied to Townsend's Big-eared Bats. My objectives were the following: 1) to retrospectively estimate survival and capture probabilities of hibernating Townsend's Big-eared Bats by sex and location using Cormack-Jolly-Seber (CJS) open models; 2) to examine the effect of sex, time, and trend on survival and capture probabilities using model selection techniques; and 3) to discuss issues surrounding violation of assumptions of the CJS model, disturbance at hibernacula, and band injuries.

METHODS

I chose 3 general areas in 3 counties in Washington to examine annual survival and capture probabilities for Townsend's Big-eared Bats banded from 1964 to 1975. Adult bats were banded in November or December in their hibernacula (all hibernacula were caves). In southwestern Washington, the 2 cave areas were the Mount St. Helens area and Klickitat County. The Mount St. Helens area consisted of bats hibernating in 2 main caves, Bat Cave and Spider Cave, both in Skamania County (hereafter Skamania). I considered these 2 caves as 1 population of wintering bats because they formed the main hibernating population and bats sometimes moved between them in the winter months (CM Senger, Bellingham, WA, pers. comm.). In Skamania, banding of bats occurred from December 1965 through November 1970 with recaptures noted until the winter of 1980 (16 years of capture occasions). The Klickitat County site (hereafter Klickitat) also consisted of bats hibernating mainly in 2 caves: Jug Cave and Poacher's Cave. I also considered colonies occupying the 2 main caves where banding took place in Klickitat as 1 population of wintering bats. For Klickitat, banding of bats occurred from November 1968 through October 1975 with recaptures noted until the winter of 1976 (9 years of capture occasions). In northwestern Washington, Skagit County (hereafter Skagit), most of the banding of Townsend's Big-eared Bats (90%) took place at Blanchard Mountain Cave (now called Senger's Talus Cave). For Skagit, banding took place from winter of 1965 through winter of 1973 with recaptures noted until the winter of 1977 (14 years of capture occasions). Each county was analyzed separately because banding efforts occurred over different time periods.

I used the "recaptures only" model in Program MARK (White and Burnham 1999) to estimate apparent survival (ϕ) and capture probability (p) of Townsend's Big-eared Bats. The "recaptures only" model in Program MARK is the open population model based on Cormack-Jolly-Seber (CJS; Cormack 1964; Jolly 1965; Seber 1965). The CJS model requires information on only the recaptures of the marked animals and assumes that marked animals are representative of the population (Amstrup and others 2005). Apparent survival (hereafter survival) is not equivalent to true survival but is the probability that the animal is alive and remains on the study area and is available for recapture. The CJS method cannot distinguish mortality from permanent emigration. I made the following specific assumptions based on the general assumptions in Williams and others (2001): (1) every banded bat present in the population at sampling period i has the same probability p_i of being recaptured; (2) every banded bat present in the population immediately following the sampling in period i

has the same probability ϕ_i of survival until sampling period $i + 1$; (3) bands were neither lost nor overlooked and were recorded correctly; (4) all emigration from the caves was permanent; and (5) the fate of each banded bat was independent of the fate of any other bat with respect to capture and survival probability.

I constructed a set of *a priori* candidate models to investigate survival and capture probabilities for the 3 wintering populations of bats. Candidate models examined the effects of time, trend, and sex on both survival and capture probabilities. For models incorporating time, each parameter was allowed to vary by year in a nonlinear, random pattern. I also examined whether there was an increasing or decreasing linear trend on survival and capture probabilities over the course of the winter banding activities. Evidence of a decreasing or increasing linear trend in survival rates could strongly affect long-term population viability. I also included in the set of candidate models a global model with sex and time-varying differences on both survival and capture probabilities. I ran the global model first, and then constrained survival and capture probabilities as either constant over time, different by sex, with a downward (or upward) trend, or with a combination of sex and trend effects. This exercise resulted in a total of 38 models built in Program MARK and applied to each of the 3 locations.

I used an information-theoretic approach to compare candidate models (Burnham and Anderson 2002). I assessed the goodness-of- fit (GOF) of the global model and whether the encounter data were overdispersed using the median $\hat{c}$ in Program MARK. The variance inflation factor ($\hat{c}$) was used as an estimate of GOF of the models with $\hat{c}$ values of 1.0 indicating good fit, and values of 1–3 acceptable fit of the data to the models (Lebreton et al. 1992). I estimated $\hat{c}$ using a lower bound of 1.0, an upper bound of 5.0, 10 intermediate points, and 10 replicates at each point (Cooch and White 2006). AIC_c values were then converted to $QAIC_c$ values to adjust for overdispersion. The most parsimonious set of models was selected using a combination of $QAIC_c$ (Akaike's Information Criterion corrected for overdispersed data and small sample sizes), $\Delta QAIC_c$, and $QAIC_c$ weights (Burnham and Anderson 2002).

I derived maximum likelihood estimates of survival and capture probabilities by sex for each location using a model with sex as the group effect on both parameters (ϕ (sex) p (sex)). To investigate time, trend, and sex on parameters, I used model averaging techniques to calculate the real estimates of survival and capture probabilities for each location. Model averaging computes the average of a parameter from all models in the model set and therefore includes model selection uncertainty in the estimate of precision of the parameter. Model averaging produces unconditional estimates of variances and standard errors (Burnham and Anderson 2002). I examined the confidence intervals around the beta (β) estimate for evidence of any significance for a trend on survival and capture probabilities.

Results

A total of 1123 Townsend's Big-eared Bats banded in the 3 counties was used in the analyses. More female bats were banded than males, with an overall sex composition of 57.7% females (Table 1). Most bats (36.1%; n = 405) were banded at Spider Cave, and 53.3% of these were females. A total of 378 bats were banded at Bat Cave, 58.5% of them female. Sex ratios were more skewed toward females in Klickitat. Of 110 banded bats at Jug Cave, 66.4% were female, and 67.3% of 98 banded at Poacher's Cave during 6 winters were female. Farther north in Skagit, at Blanchard Mountain Cave, 54.5% of the 132 bats banded during the 8 winters were female. All banded bats used for these analyses were considered adults of unknown age but likely included some young-of-the-year.

For each location, maximum likelihood estimates of annual survival and capture probabilities varied somewhat by sex (Table 2). Survival for male Townsend's Big-eared Bats ranged from a low of 0.54 for Klickitat County to a high of 0.68 for Skagit County. Survival for adult female Townsend's Big-eared Bats ranged from a low of 0.60 for Skamania to a high of 0.67 for Skagit. Adult male bats tended to have lower capture probabilities than females, ranging from a low of 0.30 in Klickitat to a high of 0.46 for Skamania. Capture probabilities for females ranged from 0.49 in both Klickitat and Skamania to 0.61 in Skamania. There were no significant differences between the sexes and among the

TABLE 1. Number of Townsend's Big-eared Bats used in survival analyses, by county, cave, year of banding, sex, and number of recaptures by sex in subsequent years. All bats were banded in the winter from 1964 to 1975 by CM Senger and associates with recaptures noted until winter of 1980.

County	Cave name	Year of banding	Reports of adult males banded (# of recaptures)	Reports of adult females banded (# of recaptures)	Total bats banded (# of recaptures)
Skamania	Bat Cave	1966	91 (72)	137 (127)	228 (199)
		1967	13 (2)	18 (7)	31 (9)
		1968	6 (2)	18 (3)	24 (5)
		1969	26 (21)	26 (25)	52 (46)
		1970	21 (24)	22 (13)	43 (37)
	Spider Cave	1965	133 (103)	135 (228)	268 (331)
		1966	32 (16)	52 (81)	84 (97)
		1967	10 (4)	12 (14)	22 (18)
		1968	3 (0)	2 (0)	5 (0)
		1969	9 (6)	11 (11)	20 (17)
		1970	2 (0)	4 (7)	6 (7)
Klickitat	Jug Cave	1968	6 (0)	26 (38)	32 (38)
		1969	20 (5)	27 (21)	47 (26)
		1970	7 (0)	4 (0)	11 (0)
		1971	4 (0)	9 (1)	13 (1)
		1972	0 (0)	3 (1)	3 (1)
		1973	0 (0)	2 (0)	1 (0)
		1975	0 (0)	3 (0)	3 (0)
	Poacher's Cave	1968	0 (0)	8 (10)	8 (10)
		1969	6 (8)	25 (50)	31 (58)
		1970	19 (8)	30 (44)	49 (52)
		1971	5 (5)	2 (1)	7 (6)
		1972	1 (0)	1 (0)	2 (0)
		1973	1 (0)	0 (0)	1 (0)
Skagit	Blanchard Mountain Cave (Senger's Talus Cave)	1965	20 (27)	29 (29)	49 (56)
		1966	8 (11)	10 (18)	18 (29)
		1967	7 (4)	6 (3)	13 (7)
		1968	9 (11)	10 (6)	19 (17)
		1969	5 (4)	8 (6)	13 (10)
		1970	5 (2)	3 (6)	8 (8)
		1971	2 (0)	3 (3)	5 (3)
		1972	0 (0)	1 (0)	1 (0)
		1973	4 (1)	2 (0)	6 (1)
Totals			475	648	1123

locations in the survival estimates; all 95% confidence intervals (CI) were broadly overlapping. Capture probabilities also did not differ significantly between sexes and among locations (95% CI also overlapped).

No clear top model was chosen with model selection techniques for each of the 3 counties. However, a trend on either survival or capture probabilities was always in at least 1 of the 3 top models (Tables 3, 4, and 5). The 3 top models in all analyses explained >60% of model variation. Although 38 models were constructed for each analysis, I report only the models $\Delta QAIC_c$ <10 and the global model for reference (Tables 3, 4, and 5).

The highest ranking model selected for Skamania was a model with an upward trend on survival and sex-specific capture probabilities (Table 3). The CI around the β estimate for a trend on survival did not include 0, indicating a significant upward trend ($\hat{\beta}$ = 0.07 ± 0.03 SE [0.004–0.14 CI]). Female Townsend's Big-eared Bats had a higher capture probability than males ($\hat{p}$= 0.62 ± 0.04 SE [0.54–0.71 CI]; $\hat{p}$= 0.46 ± 0.05 SE [0.36–0.57 CI]; respectively). The 3 top models were within $\Delta QAIC_c$ <2 and explained 67% of the model variation. Survival and capture probability estimates from the model-averaged results are presented in Figures. 1 and 2.

The highest ranking model selected for Klickitat was the model with a constant survival and a downward trend in capture probabilities (Table 3). The CI around the β estimate for the

TABLE 2. Maximum likelihood estimates of apparent survival ($\hat{\phi}$) and capture probabilities ($\hat{p}$) with associated standard errors (SE) and 95% confidence intervals (CI) for Townsend's Big-eared Bats by county and sex. All bats were banded in the winter from 1964 to 1975 by CM Senger and associates with recaptures noted until winter of 1980. Estimates were calculated from the model {ϕ (sex) p (sex)}.

County	Sex	$\hat{\phi}$ ± SE (95% CI)	$\hat{p}$ ± SE (95% CI)
Skamania	Male	0.58 ± 0.04 (0.51–0.65)	0.46 ± 0.06 (0.35–0.56)
	Female	0.60 ± 0.03 (0.54–0.65)	0.61 ± 0.04 (0.52–0.69)
Klickitat	Male	0.54 ± 0.11 (0.33–0.75)	0.30 ± 0.12 (0.12–0.57)
	Female	0.65 ± 0.05 (0.54–0.74)	0.49 ± 0.07 (0.35–0.63)
Skagit	Male	0.67 ± 0.06 (0.56–0.77)	0.44 ± 0.08 (0.28–0.60)
	Female	0.67 ± 0.05 (0.56–0.77)	0.46 ± 0.08 (0.31–0.62)

trend on capture probabilities did not include 0, indicating a significant, downward trend ($\hat{\beta}$ = −0.43 ± 0.11 SE [−0.66 to −0.20 CI]). The estimate for survival was 0.69 ± 0.06 SE (0.56–0.79 CI). As with Skamania analysis, there was substantial model selection uncertainty, with 5 of the top models having a $\Delta QAIC_c$ <2 and explaining 70 percent of the variation. Estimates of survival and capture probabilities for Klickitat County are presented in Figures 1 and 2.

The highest ranking model selected for Skagit had constant survival and capture probabilities differing by year (not a linear trend) (Table 3). However, the confidence intervals around the β estimate for the trend on capture probabilities did not include 0, indicating a significant downward trend on capture probabilities ($\hat{\beta}$ = −0.12 ± 0.05 SE [−0.22 to −0.01 CI]). The estimate for survival was 0.68 ± 0.03 SE (0.62–0.74 CI). As with the other two analyses, there was substantial model selection uncertainty with the 3 top models having a $\Delta QAIC_c$ <2 and explaining 60% of the variation. Estimates of survival and capture probabilities for Skagit County are presented in Figures 1 and 2.

DISCUSSION

Estimates of annual survival of wintering Townsend's big-eared bats in 3 locations in Washington ranged from 53.5 to 76.0% and varied by location, time or trends, and sex. Estimates of capture probability ranged widely from 8.1 to 75.0%. In this current analysis, I used model selection techniques and the capabilities of program MARK to examine trends, time effects, and sex differences in survival as well as capture probabilities at each of the three locations where banding took place. Survival and capture probabilities had a tendency to be lower for males than for females and this pattern was consistent across all 3 locations. There was also evidence of a positive trend on survival at the Skamania location and a negative trend on capture probabilities at all 3 locations.

TABLE 3. Results from Program MARK for modeling survival (ϕ) and capture probabilities (p) of adult female and male Townsend's Big-eared Bats roosting in hibernacula in Skamania County, Washington, from band-recapture data collected from 1964 to 1980. For each model, the model name, the Akaike Information Criterion corrected for overdispersion ($QAIC_c$), the $\Delta QAIC_c$, $QAIC_c$ weight, and number of parameters (K) [($\hat{c}$ = 1.72)], are listed. The model with the lowest $QAIC_c$ is in the 1st row. Data were collected by CM Senger and associates.

Model name	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$weight	K
ϕ (trend) p (sex)	992.43	0.00	0.29	4
ϕ (trend) p (sex + trend)	992.59	0.16	0.26	5
ϕ (sex + trend) p (sex + trend)	994.13	1.69	0.12	6
ϕ (.) p (sex)	994.85	2.42	0.08	3
ϕ (trend) p (trend)	995.28	2.85	0.07	4
ϕ (sex + trend) p (trend)	995.30	2.87	0.07	5
ϕ (trend) p (.)	996.16	3.72	0.04	3
ϕ (sex) p (sex)	996.71	4.28	0.03	4
ϕ (trend) p (.)	996.16	4.43	0.03	3
ϕ (.) p (.)	998.92	6.49	0.01	2
ϕ (sex) p (.)	999.32	6.89	0.01	3
ϕ (.) p (trend)	1000.37	7.94	0.01	3
ϕ (sex × time) p (sex × time)	1063.78	71.35	0.00	58

TABLE 4. Results from Program MARK for modeling survival (ϕ) and capture probabilities (p) of adult female and male Townsend's Big-eared Bats roosting in hibernacula in Klickitat County, Washington, from band-recapture data collected from 1964 to 1980. For each model, the model name, the Akaike Information Criterion corrected for overdispersion ($QAIC_c$), the $\Delta QAIC_c$, $QAIC_c$ weight, and number of parameters (K) [($\hat{c}$ = 1.34)], are listed. The model with the lowest $QAIC_c$ is in the 1st row. Data were collected by C.M. Senger and associates.

Model name	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	K
ϕ (.) p (trend)	270.56	0.00	0.24	3
ϕ (sex + trend) p (trend)	270.59	0.03	0.24	5
ϕ (trend) p (sex + trend)	270.69	0.13	0.22	5
ϕ (sex + trend) p (sex + trend)	272.18	1.62	0.11	6
ϕ (trend) p (trend)	272.28	1.72	0.10	4
ϕ (.) p (time)	273.56	3.00	0.05	9
ϕ (trend) p (sex)	276.48	5.92	0.01	4
ϕ (time) p (time)	277.25	6.70	0.01	12
ϕ (trend) p (.)	279.06	8.50	0.00	3
ϕ (.) p (sex)	279.65	9.09	0.00	3
ϕ (time) p (sex)	279.80	9.25	0.00	9
ϕ (.) p (sex × time)	280.03	9.47	0.00	15
ϕ (sex) p (.)	280.47	9.92	0.00	3
ϕ (sex × time) p (sex * time)	288.80	18.24	0.00	21

Sex-related difference in survival of hibernating Townsend's Big-eared Bats was also found in a California population studied by Pearson and others (1952). They investigated natural history and reproduction of Townsend's big-eared bats from 1947 to 1951 and reported similar sex-related differences in return rates for wintering bats in caves in the Mt. Lassen area as compared to the differences found in this study. They used the percentage of recaptured banded bats to calculate annual return rates and recovered 53% of the males and 58% of the females in 2 subsequent years. Males and females of this species approached the hibernation period very differently. Pearson and others (1952) reported that males tended to waken at night and even fly around in hibernation caves. They observed that for females, the "inclination to hibernate is stronger." If male bats tend to move more often during hibernation than females, this could potentially explain the sex-related differences found in survival and capture probabilities in the Washington populations.

TABLE 5. Results from Program MARK for modeling survival (ϕ) and capture probabilities (p) of adult female and male Townsend's Big-eared Bats roosting in hibernacula in Blanchard Mountain Cave (Senger's Talus Cave), Skagit County, Washington, from band-recapture data collected from 1964 to 1980. For each model, the model name, the Akaike Information Criterion corrected for overdispersion ($QAIC_c$), the $\Delta QAIC_c$, $QAIC_c$ weight, and number of parameters (K) [($\hat{c}$ = 1.36)], are listed. The model with the lowest $QAIC_c$ is in the 1st row. Data were collected by C.M. Senger and associates.

Model name	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	K
ϕ (.) p (time)	602.66	0.00	0.26	13
ϕ (.) p (trend)	602.73	0.07	0.25	3
ϕ (trend) p (trend)	604.64	1.98	0.09	4
ϕ (sex) p (time)	604.78	2.12	0.09	14
ϕ (.) p (.)	605.49	2.83	0.06	2
ϕ (trend) p (sex + trend)	605.94	3.28	0.05	5
ϕ (.) p (sex)	606.06	3.39	0.05	3
ϕ (sex + trend) p (trend)	606.59	3.94	0.04	5
ϕ (trend) p (.)	607.68	4.43	0.03	3
ϕ (sex) p (.)	607.42	4.76	0.02	3
ϕ (trend) p (sex)	607.68	5.02	0.02	4
ϕ (sex + trend) p (sex + trend)	608.04	5.38	0.02	6
ϕ (sex) p (sex)	608.11	5.45	0.02	4
ϕ (time) p (time)	612.65	9.98	0.00	21
ϕ (sex × time) p (sex × time)	668.49	65.83	0.00	49

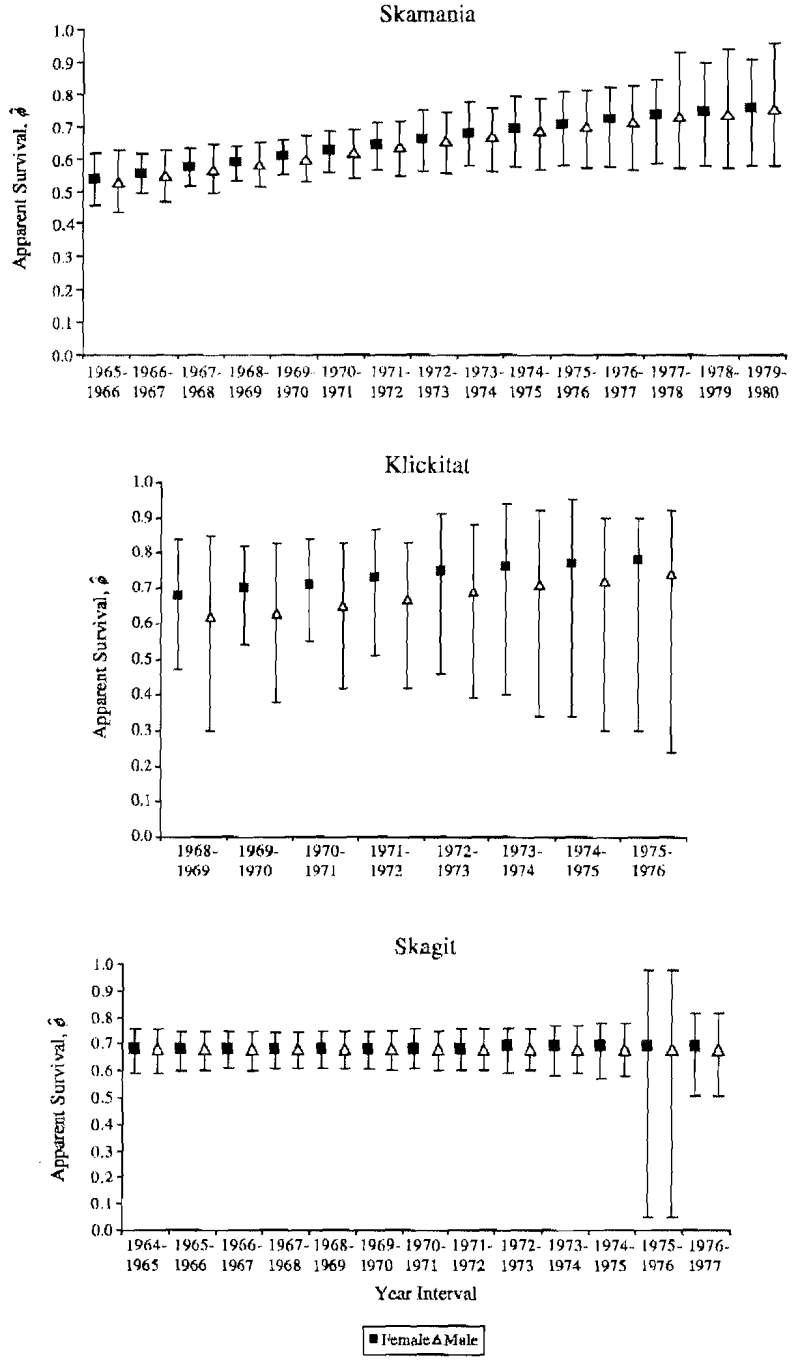

FIGURE 1. Model averaged estimates of apparent survival for Townsend's Big-eared Bats hibernating in Skamania, Klickitat, and Skagit Counties, Washington, from 1964 to 1981. Error bars are 95% confidence intervals.

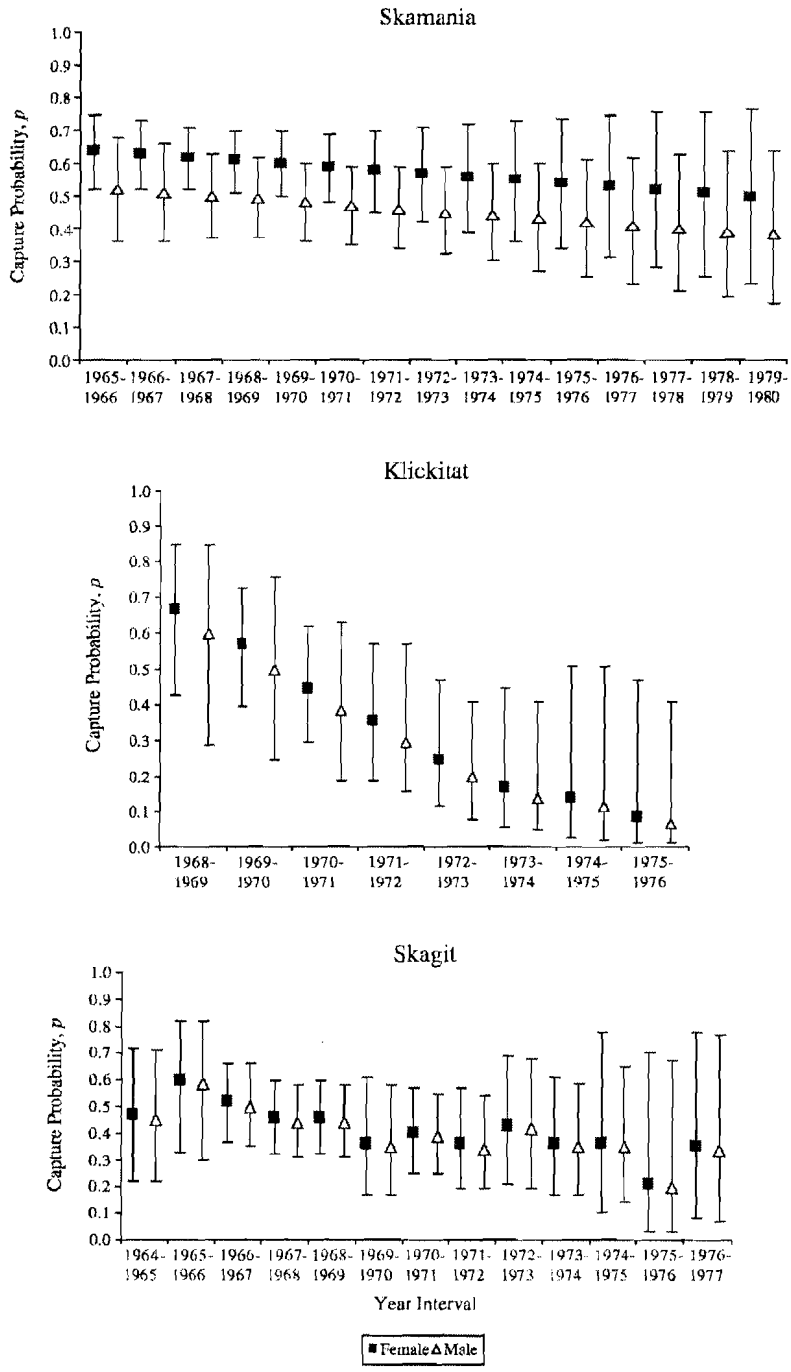

FIGURE 2. Model averaged estimates of capture probabilities, p, for Townsend's Big-eared Bats hibernating in Skamania, Klickitat, and Skagit Counties, Washington, from 1964 to 1981. Error bars are 95% confidence intervals.

There was evidence of an upward trend in survival from 1965 to 1980 on Townsend's Big-eared Bats, notably at the Skamania location. An increase in survival could be indicative of population growth during that time, but this is only speculative without additional biological information about this population such as recruitment during the maternity season. The decreasing trend on capture probabilities at all 3 locations could be a reflection of population declines observed at the banding sites during the course of the study resulting from a possible "trap response." Trap responses are thought to occur commonly in capture-recapture studies of vertebrate populations (Nichols and others 1984). The total number of bats in Spider Cave was approximately 300 in 1965 when banding efforts began. However, this population declined markedly with only 67 bats found in 1967–68 (a decline of 22.3%). A similar pattern of population decline was also noted for Bat Cave, but specific numbers were not provided (Senger 1969). Senger felt strongly that his study had been a serious disturbance to the bats, and he planned to reduce his visits for the next several years to preserve the remaining populations (Senger 1969). Disturbance of the hibernating population at Spider Cave may have come from other sources as well. Spider Cave was relatively unknown by the public in the late 1960s but was located near a road and was accessible to the public (CM Senger, Bellingham, WA, pers. comm.). About 100 acres of virgin timber were logged on the hillside just to the west of the mouth of Spider Cave in 1967, which may have had an effect on the use of the cave by bats. The hibernating populations of bats at Bat and Spider Caves appeared to recover somewhat from the drastic declines observed after the first few years of the banding efforts. Senger and Crawford (1984) reported that the hibernating populations at both Bat and Spider Caves had recovered somewhat, but to overall lower numbers than the original 250 to 300 counted. However, the observed population levels were consistent in the 6 years prior to 1984 (Senger and Crawford 1984).

Although this analysis applied current mark-recapture theory successfully to historical data on bats banded from 1964 to 1975, there are several caveats that need to be addressed when interpreting the results from this analysis. The two critical concerns include band injuries and population declines. Observed population declines at all three hibernacula could be due to permanent emigration of the bats after disturbance by banding. Banding and research was observed to negatively affect Townsend's Big-eared Bats hibernating in these areas in several different ways (CM Senger, Bellingham, WA, pers. comm.; Senger 1969, 1973, 1985; Senger and Crawford 1984). Senger noted band injuries to Townsend's Big-eared Bats over the course of his banding efforts regardless of the type of band used. Of 278 bats he had banded in 1966 with No. 2 bands, 1 of 21 recaptures had a cut through the wing membrane from the band, and another had some swelling. On the other hand, nearly half of the 28 recaptures from 210 bats banded in 1967 with the "BAT series" bands had cuts through the wing membranes, although without significant swelling or scar tissue formation (CM Senger, Bellingham, WA, pers. comm.). Humphrey and Kunz (1976) also documented band injuries in this species. They studied Townsend's Big-eared Bats in the southern Great Plains (western Oklahoma and Kansas) and examined population ecology of the bats using 827 banded individuals. They found evidence of in-grown bands, chewed bands, and infected arms 1 and 2 years after banding. Some bats would exhibit all 3 of these conditions simultaneously. Of 66 bats recaptured, 50 (75.8%) showed some evidence of damage from the bands.

Sometimes banding would cause bats to move to another cave most notably in Skamania County. Although none of the bats used in this particular analysis moved to other known caves besides Bat or Spider Caves, I cannot assume they did not permanently leave the area due to disturbance because not all possible cave locations were known (CM Senger, Bellingham, WA, pers. comm.). The number of bats that appeared to move among the Bat and Spider Caves was low, and if they did move, they were often seen at both caves during a single winter season. Only 8 of the 377 individuals banded from Bat Cave were recaptured at Spider Cave, and 19 of the 407 from Spider Cave were recaptured at Bat Cave. However low these numbers appear, additional movements most likely occurred that were not detected and could explain the declines in populations over

the time of banding. Davis (1968) reported that Senger did not think that the recapture ratios were indicative of survival because bats seem to readily move from 1 cave to another when disturbed and he did not think he was sampling all of the caves in the area.

The examples of injuries due to banding and the potential for bats to move permanently out of the study area (or among caves not sampled within the study area) violated 2 of the assumptions of the CJS model. Direct injuries from bands and disturbance from banding violates the basic rule that the sampled population is representative of the population at large. Movement of bats in response to banding activities could also violate the assumption of permanent emigration. However, violation of the assumption of permanent emigration does not always result in biased estimates of survival, especially if the emigration is random (that is, every individual within an age-sex category has the same probability of being in the area exposed to sampling efforts; Williams and others 2001).

To my knowledge, this retrospective analysis provides the 1st published CJS-based estimates of survival for Townsend's Big-eared Bat. The dataset from which these estimates were derived is likely to be the most complete and well-maintained dataset in the USFWS Bat Banding Program files that has not been published elsewhere. Resulting annual survival estimates from these data were relatively precise and modeling provided evidence of trends in survival, time effects, and differences in survival between the sexes. These results provide historical, *post hoc* estimates of an important life-history parameter for this species of bat wintering in caves in three localized areas of Washington State. Additionally, these estimates could potentially provide an historical baseline for future research and management issues concerning this species.

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