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POTENTIAL EFFECTS OF ENVIRONMENTAL CONTAMINATION ON YUMA MYOTIS DEMOGRAPHY AND POPULATION GROWTH

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Abstract. Unplanned natural and anthropogenic disasters provide unique opportunities for investigating the influence of perturbations on population vital rates and species recovery times. We investigated the potential effects of a major pesticide spill by comparing annual survival rates using mark–recapture techniques on a riparian bat species, Yuma Myotis (*Myotis yumanensis*). Demography and population dynamics for most bat species remain poorly understood despite advances in mark–recapture estimation and modeling techniques. We compared survival and population growth rates of two roost populations exposed to a large chemical (metam sodium) spill in the upper Sacramento River in Northern California with two roost populations outside the contaminated area from 1992 to 1996. Hypotheses about long-term effects of the spill on female juvenile and adult survival were tested using an information-theoretic approach (AIC). Working hypotheses included effects of age, chemical spill, and time trend on survival. Female adult survival was higher than female juvenile survival across all sites, suggesting stage-specific mortality risks. Model-averaged estimates of female juvenile survival in the contaminated area (0.50–0.74) were lower than in control roosts (0.60–0.78) for each year in the study, suggesting that the spill may have reduced juvenile survival for several years. Female adult survival (0.73–0.89) did not appear to be strongly affected by the spill during the years of the study. There was an increase in survival for both stage-classes across all populations during the study period, which may have been caused by the end of an extended drought in California in the winter of 1993. The spill-affected population was in decline for the first year of the study as indicated by an estimated growth rate (λ) < 1, but population growth rates increased during the four-year period.

Key words: bat demography; contamination; Cormack–Jolly–Seber; mark–recapture; metam sodium; *Myotis yumanensis*; pesticide spill; survival.

INTRODUCTION

Understanding how populations respond to variation in environmental conditions is fundamental to ecology, and is especially important for successful management and conservation of species. Specifically, conservation biologists are concerned with understanding how landscape perturbations may affect underlying population dynamics in order to assess risks to populations and species. Estimation of survival is critical for characterizing life history traits of species and evaluating population response to disturbance events (Lebreton et al. 1992). In particular, measuring stage- or age-specific survival rates can reveal differences among stage-specific mortality risks and thereby demonstrate the relative importance of certain life stages to overall population performance (Morris and Doak 2002).

Although bats make up a quarter of all mammals, ecologists know little about bat population dynamics (Barclay and Harder 2003). The nocturnal, volant, and

cryptic nature of bats makes it especially challenging to measure demographic parameters and evaluate population dynamics. Recapture rates of banded bats in foraging habitats are typically very low, rendering efforts to evaluate survival with extensive bat-banding efforts inefficient (Barclay and Bell 1988). As 51% of microchiropteran bats are considered either critically endangered, endangered, data-deficient, vulnerable, or near threatened (Hutson et al. 2001), understanding influences on survival is important for the conservation of these taxa and can provide valuable information about how bat populations respond to changing landscapes and habitat degradation, and thus inform conservation and management strategies (Pryde et al. 2005).

The development of mark–recapture models that allow separate estimation for groups and stage classes has improved survival estimation methodology and provided researchers with a powerful tool for investigating factors associated with population dynamics (Lebreton et al. 1992). Only a few researchers have taken advantage of these new tools to estimate bat survival (Keen and Hitchcock 1980, Hitchcock et al. 1984, Loery et al. 1987, Hoyle et al. 2001, Sendor and

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Simon 2003, Pryde et al. 2005). Early studies of bat survival (see Tuttle and Stevenson 1982 for a thorough review) relied on regression techniques, the percentage of known survivors, or cohort life table analyses, which do not provide reliable survival estimates because survival and recapture rates are often confounded and underlying assumptions are rarely met (Lebreton et al. 1992, Sendor and Simon 2003).

Our study estimates apparent survival for adult and juvenile female Yuma Myotis (*Myotis yumanensis*) to determine stage-specific survival rates and to investigate the effect of a major chemical spill in the Sacramento River on bat survival. In July 1991, a train derailment released 71 000 L of metam sodium solution into the upper Sacramento River at the Cantara Loop, north of Dunsmuir, California. The fumigant was responsible for killing and threatening aquatic and terrestrial organisms along 68 km of the Sacramento River north of Shasta Lake (Garrison 2000, Luke and Sterner 2000a, b). An estimated 10^6 or more fish were killed as a result of the Cantara spill (Hankin and McCanne 2000). Similarly, aquatic amphibian populations were severely reduced and had not recovered three years after the spill (Luke and Sterner 2000a).

Yuma Myotis are closely linked to riparian systems; they typically forage over open water for emerging aquatic insects (Brigham et al. 1992). Morphological specialization for aquatic trawling and reliance of this species on aquatic insects suggest it is particularly vulnerable to riparian contamination. Though there is no direct evidence, high levels of aquatic and volatilized toxicants shortly after the spill may have resulted in a significant mortality event for resident bat colonies located along the main stem of the river. In addition, the timing of the spill may have resulted in lactating adult females and recently volant young, both with high energy demands, searching for aquatic insects over a contaminated, largely defaunated river.

Yuma Myotis form colonial roosts and can be found in large maternity and night aggregations in anthropogenic structures, such as buildings and bridges (Dalquest 1947, Nagorsen et al. 1993). From 1991 to 1996, we collected mark-recapture data at two roosts on the Sacramento River to assess the impacts of the spill on local bat populations. Radio tracking of sampled females from one roost site in the years following the spill indicated foraging occurred primarily over the Sacramento River (Rainey and Pierson 1996). Two roosts located in nearby drainages outside the contaminated region were used as controls. Fidelity to anthropogenic structures allowed for effective mark-recapture efforts for survival estimation, because bats could be reliably recaptured there.

By estimating survival rates of adults and juveniles at roosts within the contaminated area and in two separate control sites, we aimed to test for persistent effects on survival from altered habitat and prey availability in

years following the spill. We also explored how changes in survival affected overall population growth rates.

METHODS

Study site

The study was conducted at four bat roosts in Shasta and Siskiyou counties in Northern California. Two roosts occurred within the 68-km stretch of the upper Sacramento River contaminated by the Cantara spill. These sites were located at the confluences of Soda Creek (630 m elevation) and Shotgun Creek (475 m elevation) with the Sacramento River. Two sites were considered control sites and occurred outside the contaminated area. One of the control sites was located on Squaw Creek (420 m elevation) in Shasta County, a smaller tributary to Shasta Lake, an artificial impoundment. The other control site was located across a drainage divide in northern Siskiyou County on the Butte Valley Wildlife Refuge (1300 m elevation) (Fig. 1). All trapping sites were maternity and/or night roost structures. Three roosts were in buildings used for both maternity day and night roosting, whereas the Shotgun roost was a night roost bridge. An additional maternity roost control site along the river below Shasta Lake was not included in this analysis because the colony was not accessible after two years.

The study area consists predominantly of rugged, mountainous terrain dominated by montane hardwood/conifer vegetation managed for timber production. Dominant tree species at mid-elevations include ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and black oak (*Quercus kelloggii*) (Mayer and Laudenslayer 1988). Gray pine (*Pinus sabiniana*) and Pacific madrone (*Arbutus menziesii*) are common at lower elevations.

Field methods

Bats were captured with mist nets or hand-held hoop nets on telescoping poles (Pierson et al. 1996). In some cases, large fabric curtains were employed to increase probability of capture. Trapping was conducted at these sites from 1992 to 1996 during the maternity season, from late May to September. Because few males were encountered, we restricted our analysis to females.

Age, sex, and reproductive status were determined for each captured bat (Anthony 1988, Racey 1988). Each bat was assigned to one of two age classes, young of the year (hereafter referred to as juveniles) or adult, based on incomplete ossification of the epiphyseal finger joints (Anthony 1988). After their first winter, juveniles are not distinguishable from adults. Reproductive condition (pregnant, lactating, postlactating, nulliparous) was assessed by abdominal palpation and examination of the mammary region (Racey 1988). Each bat was fitted with 2.8-mm numbered, lipped, metal forearm bands (British Mammal Society or Lambournes Limited, Leominster, UK).

Survival rate estimation

We used program MARK (White and Burnham 1999) to estimate apparent survival and recapture probabilities using extensions of the Cormack-Jolly-Seber open-population capture-recapture models (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992). A set of a priori candidate models was developed to address hypotheses about factors affecting adult and juvenile bat survival. A priori models on apparent survival (ϕ) included constant survival (\cdot), yearly variation (t), time trend (T), and two different group effects: roost site (r), and chemical exposure (hereafter "treatment") (c). The roost site group effect (r) allowed separate estimation of survival rate at each of the four roost sites. The treatment group (c) constrained the model to estimation of apparent survival for the two contaminated roost sites and the two control sites separately, thus testing for a potential chemical-exposure "treatment" effect on survival. Models on ϕ included main effects, additive effects, and interactive effects between yearly variation, time trend, and the two different groupings. Since capture effort varied with year and capture probability may have varied with local conditions at each roost site, we modeled these two effects on the recapture probability parameter. For recapture (p), we developed five a priori models, including constant recapture (\cdot), roost group (r), yearly variation (t), parallel effects of roost by year ($r + t$), and interactive effects of roost by year ($r \times t$).

To simplify the model selection process, we added stage effects into the analysis for a subset of competing models on adult survival after finding the best model structure for recapture (p). The effects of year (t) and roost site (r) had no support and were dropped from the stage class analysis. Stage class models included comparisons of treatment effects based on a priori hypotheses that juvenile survival may be affected differently than adult survival by the contamination, due to a greater vulnerability to detrimental effects of habitat degradation. This resulted in 14 a priori models included in the final analysis (Table 2). Throughout this paper, we refer to juvenile and adult survival stage classes. Juvenile rates refer to the annual survival interval for the entire first year of life for bats banded as young of the year.

Model assumptions

The CJS model has several model assumptions (Pollock et al. 1990, Williams et al. 2002), which can be violated when emigration from the study site after initial capture is high, or marked populations exhibit strong trap dependence, or band loss occurs (Pollock et al. 1990, Williams et al. 2002, Hines et al. 2003). The CJS model cannot separate mortality from permanent emigration, so if significant permanent emigration occurs from the study area, estimates of survival rates will be biased low (Williams et al. 2002). Therefore, high site fidelity in bat species is critical for unbiased estimates of survival.

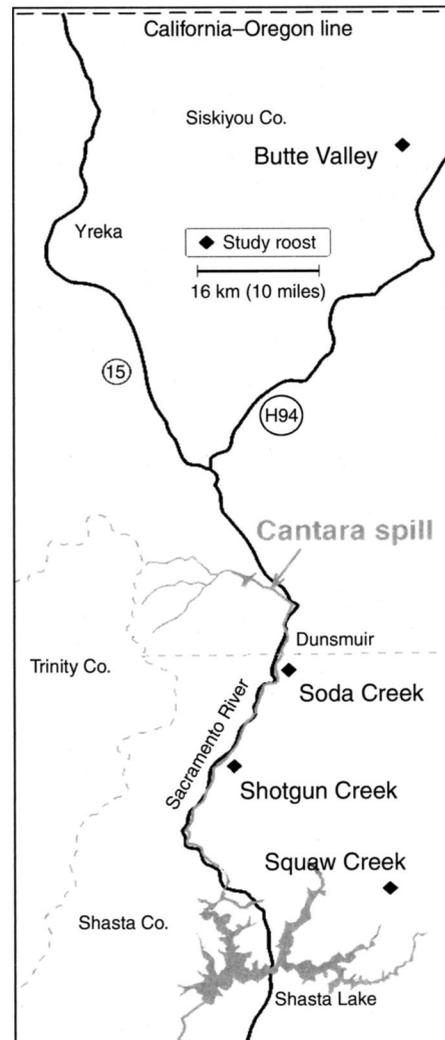


FIG. 1. Location of four Yuma Myotis roost sites where mark-recapture data were collected from 1992 to 1996. Soda Creek and Shotgun Creek roost sites are within the 68-km contaminated segment of the Sacramento River main stem in Shasta County, California, USA. Squaw Creek and Butte Valley roost sites served as controls. Squaw Creek is on an unaffected Sacramento River tributary also discharging into Shasta Lake, and Butte Valley is in a separate drainage basin in Siskiyou County, California, USA.

While there are no independent means to verify this, we infer that permanent emigration was not a significant issue in our study system, as site fidelity to maternity day roosts and night roosts for adult female and juvenile bats appears quite high in species that use permanent roost structures (Kunz 1982, Lewis 1994, 1995, O'Donnell 2002, Kunz and Lumsden 2003, Rivers et al. 2006). A comparison of recapture rates among all night roost structures used in the Cantara study area, which includes other night roost bridges within the study area not used in this analysis (see Rainey and Pierson 1996), demonstrated high night roost site fidelity (Pierson et al. 1996). For example, Pierson et al. (1996) reported that

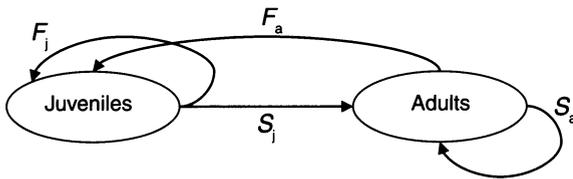


FIG. 2. Life cycle graph representing a stage-structured model for Yuma Myotis population dynamics. The juvenile stage includes the entire first year of life for bats initially captured as young of the year. Bats had a 42% probability of breeding their first year, based on a grand average of known age of first breeding at all four roosts. Mark-recapture occurred as a postbreeding census, so both stage classes contribute to fecundity. F_j = first-year fecundity; F_a = adult fecundity; S_j = juvenile survival; S_a = adult survival.

506 of 608 (83%) recaptured bats at the Shotgun Creek site were originally banded there.

There was no evidence that bats displayed a trap-response at our capture sites, as bats were unlikely to avoid recapture given our ability to enclose roost sites during capture events, and protocols were designed to avoid repeat sampling when bats may have exhibited temporary roost-switching behavior. Because of potential negative effects of cumulative band mass, no double-marking studies were conducted to assess mark loss rates. Some band loss did occur, which could create a negative bias in our survival rates. The types of bands used were the most reliable bands available for mass marking of bats (Keen 1988).

The long recapture period (late May to September) potentially violates model assumptions of a short recapture period relative to the survival interval. Long recapture periods relative to the survival interval can bias survival rates, because the actual interval an individual must survive may be either shorter or longer than the interval of estimation, depending on whether the individual was caught early or late in the recapture period (Williams et al. 2002). However, this bias can be mediated if survival rates are high during the recapture period (Smith and Anderson 1987, Williams et al. 2002). A conventional assumption is that the primary period of mortality for temperate bat species is over winter; thus we suspect that our lengthy trapping period generated only minimal error in our survival estimation (but see Sendor and Simon 2003).

We used two different goodness-of-fit tests to assess the fit of our data to the CJS model and estimate the variance inflation factor (\hat{c}) to determine whether our data were overdispersed (Burnham and Anderson 2002, Williams et al. 2002, Cooch and White 2006). First, using a fully time-dependent global model for adults we used Tests 2 and 3 in Program RELEASE (Burnham et al. 1987). But because program RELEASE does not incorporate age effects, the estimate of extra-binomial variation may be negatively biased (Burnham and Anderson 2002). Therefore, we used a relatively new method to assess goodness-of-fit for the most parame-

terized model ($K = 22$) in the final model group that included both age and group effects, using the median \hat{c} method (Cooch and White 2006).

Model selection

We used small-sample corrected Akaike Information Criteria (AIC_c) for model selection (Burnham and Anderson 2002). Models were ranked by AIC_c value (lowest AIC_c has the most support from the data) and were compared using both ΔAIC_c and AIC_c weights (w_i).

The ΔAIC_c values represent the relative support between the best approximating model ($AIC_{c, \min}$) and each competing model ($AIC_{c,i}$). Models with $\Delta AIC_c \leq 2$ were considered to have competing support from the data, and models with $\Delta AIC_c > 10$ were considered to have no support (Burnham and Anderson 2002).

AIC_c weights were calculated for R models as

$$\hat{w}_i = \frac{\exp\left(-\frac{1}{2} \Delta AIC_i\right)}{\sum_{i=1}^R \exp\left(-\frac{1}{2} \Delta AIC_i\right)}$$

to measure the relative weight of support for any given model (Burnham and Anderson 2002).

Parameter estimates were model-averaged across all 14 models to account for model selection uncertainty (Burnham and Anderson 2002). Model-averaged estimates were computed as

$$\bar{(\hat{\phi})} = \sum_{i=1}^{11} w_i (\hat{\phi}_i)$$

where w_i is the Akaike weight and $(\hat{\phi}_i)$ is the apparent survival estimate for model i . The unconditional sampling variance for the model-averaged parameter estimates was estimated as (Burnham and Anderson 2002):

$$\text{var}(\hat{\phi}) = \left[\sum_{i=1}^{11} \hat{w}_i \sqrt{\text{var}(\hat{\phi}_i | \text{Model}_i) + (\hat{\phi}_i - \bar{(\hat{\phi})})^2} \right]^2$$

Population growth rate estimation

We used a stage-based matrix model (Caswell 2001, Morris and Doak 2002) to assess the effects of the chemical spill on population performance by comparing the population growth rate (λ) among contaminated and control populations. Matrix models use stage-specific survival rates and fecundity estimates to estimate a long-term population growth rate (λ , the dominant eigenvalue [Caswell 2001]).

The matrix model incorporated two stages, juvenile and adult stages (Fig. 2). Fecundity rates were based on previously published reproductive rates of one young per year for Yuma Myotis (Nagorsen et al. 1993). Both stage classes contributed to fecundity because mark-recapture efforts occurred as a postbreeding census, and some juvenile Yuma Myotis breed in the summer

TABLE 1. Banding data summary for juvenile and adult Yuma Myotis (*Myotis yumanensis*) at each sampled roost location in Northern California, from 1992 to 1996.

Moths	Contaminated sites		Control sites		Totals
	Shotgun	Soda	Squaw	Butte	
Juveniles					
Total individuals	276	269	126	133	804
Total recaptures	138	77	37	38	290
Adults					
Total individuals	488	519	291	353	1651
Total recaptures	389	230	106	111	836

following their birth year. Fecundity contributions of juveniles were calculated given a 42% probability of breeding their first year, based on a grand-average of known age at first breeding from all four roosts (Rainey and Pierson 1996).

We calculated the annual population growth rate (λ) for contaminated and control populations separately for each year of the study using MATLAB, Version 5.3 (Mathworks, Incorporated, Natick, Massachusetts, USA) code from Morris and Doak (2002). We estimated λ using results from the survival analysis for year-specific adult and juvenile survival rates to compare population dynamics in the contaminated vs. control populations.

RESULTS

Mark-recapture results

A total of 2455 female bats (1651 adults and 804 juvenile bats) were captured during the five capture occasions. There were 1552 bats captured at contaminated sites, compared to 903 bats captured at control

sites. We captured 788 individuals at Soda, 764 at Shotgun, 417 at Squaw, and 486 at Butte Valley (Table 1).

Model selection results

Both goodness-of-fit tests demonstrated that the data fit the assumptions of the CJS model and overdispersion was not a problem. Results from Tests 2 and 3 from program RELEASE indicated a good fit to the adults-only, time-dependent global model ($\chi^2 = 8.24$, $df = 16$, $P = 0.94$) and the variance inflation factor (\hat{c}) was < 1 . The estimate of \hat{c} was 1.14 ± 0.007 (mean \pm SE) using the median \hat{c} method on the most parameterized model in the final model set. Therefore, we did not account for extra-binomial variation, as it was deemed unnecessary (Burnham and Anderson 2002, Cooch and White 2006).

Juvenile bats experienced differences in survival in contaminated and control sites, and survival of both stage classes increased linearly during the study period, according to the best-fit model [$\phi(\text{ad}(T), \text{juv}(c + T))$] (Table 2). The second-ranked model, which had competing support from the data ($\Delta\text{AIC} \leq 2$), included parallel linear time trends for stage-specific survival with no contamination effect [$\phi(\text{age} + T)$]. Of the top five ranked models, which accounted for 80% of the cumulative AIC_c weights, all included stage-specific survival and a linear time trend, but only three had a chemical spill effect included (Table 2). A ranking of relative variable importance (Burnham and Anderson 2002) indicates that age (0.99) is the most important variable relative to others, time trend (0.87) is second in importance, and chemical spill (0.68) is third.

These results suggest that contamination may have affected juvenile survival for a few years after the spill, but not adult survival, and both stage classes experienced a linear increase in survival during the study period across all sites. To account for model uncertainty,

TABLE 2. Final model selection results for the stage-specific analysis for Yuma Myotis. Models are ranked by ascending ΔAIC_c .

Survival (ϕ) model	AIC_c	ΔAIC_c	AIC_c weights	No. of parameters	Deviance
$\text{ad}(T), \text{juv}(c + T)$	5678.08	0.00	0.31	20	221.60
$\text{age} + T$	5679.00	0.93	0.20	19	224.55
$\text{age} \times c + T$	5680.10	2.02	0.11	21	221.60
$\text{age} + c + T$	5680.25	2.17	0.11	20	223.77
$\text{age} \times T$	5681.02	2.95	0.07	20	224.55
$\text{age} \times c \times T$	5682.00	3.92	0.04	22	221.47
$\text{ad}(\cdot), \text{juv}(c)$	5682.07	3.99	0.04	19	227.61
age	5682.18	4.10	0.04	18	229.74
$\text{ad}(\cdot), \text{juv}(c + T)$	5682.62	4.55	0.03	20	226.14
$\text{age} + c$	5683.43	5.36	0.02	19	228.98
$\text{age} \times c$	5684.03	5.95	0.02	20	227.55
T	5700.35	22.28	0.00	18	247.92
(\cdot)	5705.08	27.00	0.00	17	254.66
c	5706.61	28.54	0.00	18	254.18

Notes: All models shown had roost by year effects ($r \times t$) on the recapture parameter (p). Model notation: T = time trend; c = chemical spill "treatment" effect; age = stage-specific survival for adults and juveniles; (\cdot) = constant survival. Models with different parameter structure for adults and juveniles are indicated by noting separately the effects on ad (= adults) and juv (= juveniles), respectively. Multiplication symbols (\times) indicate interactive effects; plus symbols ($+$) indicate additive models.

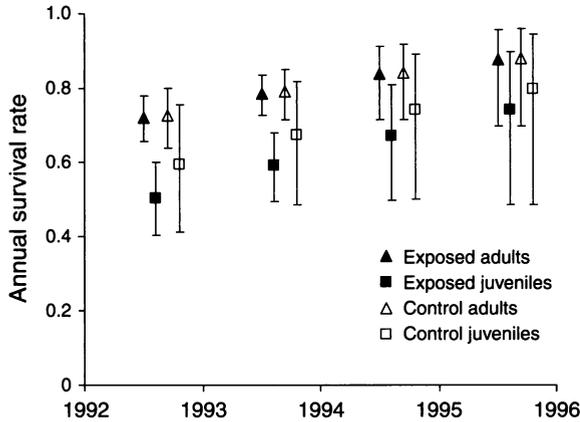


FIG. 3. Annual stage-specific apparent survival rates and 95% confidence intervals for Yuma Myotis in Northern California, 1992–1996. Estimates are from model-averaged estimates showing year-specific survival for adult and juveniles bats for contaminate-exposed and control groups.

reported survival estimates were model averaged (Burnham and Anderson 2002). All models considered with both stage classes had roost by year effects on recapture rate because of the overwhelming support for this structure on the recapture parameter (99% of the support of the data according to AIC weights) when compared among adult-only models.

Survival estimates

Juvenile female Yuma Myotis survival estimates were lower in the contaminated population throughout the study period, increasing from 0.50 in 1992 to 0.74 by 1995, compared to juvenile survival in the control population, which increased from 0.60 in 1992 to 0.80 by 1995, according to model-averaged estimates. Adult survival was constant across sites, but increased from 0.72 in 1992 to 0.88 by 1995 (Fig. 3). The slope coefficient for the contamination treatment effect on juveniles was estimated (mean \pm SE) at -0.63 ± 0.40 (95% CL = $-1.41, 0.16$) on a logit scale, suggesting that contamination may have had a negative effect on juvenile survival. The slope coefficient for the time trend was estimated at 0.43 ± 0.19 (95% CL = $0.05, 0.81$) on a logit scale, demonstrating support for an increasing time trend in age-specific survival.

Recapture rates generally ranged from 0.11–0.58, depending on roost and year. There were two exceptionally low recapture years, 0.03 ± 0.01 , 95% CL = $0.02, 0.07$) in 1994 at the Squaw Creek roost, and 0.09 (SE = 0.02 , 95% CL = $0.06, 0.14$) in 1996 at the Soda Creek roost. The low recapture rate at the Squaw Creek roost reflects an interesting biological phenomenon; the bats were absent during the sampling period, perhaps from delayed reproduction from a late spring (Grindal et al. 1992), but returned the following year. The low recapture rate in 1996 reflected logistical difficulties in gaining similar access to the building roost.

Population growth rate estimates

The population was in decline in 1992 for the sites exposed to the chemical spill ($\lambda = 0.92$), based on estimates using year-specific juvenile and adult survival rates (Fig. 4). By 1993, the population had recovered and growth was positive ($\lambda > 1$). The population growth rate continued to increase as survival rates increased during the study period. By 1995, population growth was 1.2 in the spill-exposed population. Population growth rates steadily increased in the control population as well, due to the increasing survival time trend, but population growth in 1992 for the control population was close to equilibrium ($\lambda = 0.98$).

DISCUSSION

Stage-specific survival rates

High female adult survival for the Yuma Myotis was consistent with predictions based on life history theory (Racey and Entwistle 2002) and similar to the few other published survival estimates for vespertilionid bats (Keen and Hitchcock 1980, Hitchcock et al. 1984, Sendor and Simon 2003, Pryde et al. 2005) (Table 3). Bats are notably long lived when compared to other small mammals; individual longevity determined by mark–recapture exceeds 30 years for several species (Wilkinson and South 2002). Given a life history characterized by unusual longevity and low fecundity, high adult and juvenile survival likely play an important role in maintaining stable populations. Results from our population modeling suggest that variation in juvenile and adult survival rates did influence population performance during the four-year study period.

The ability to fly may positively influence survival by increasing avoidance of terrestrial predators (Pomeroy 1990). In general, predation rates for bat species appear to be quite low (Barclay and Harder 2003). Other factors believed to affect adult bat survival include roost site

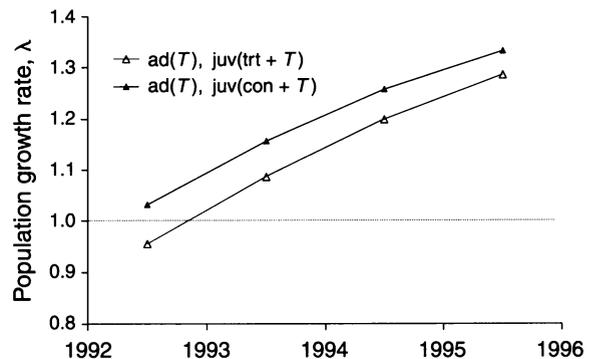


FIG. 4. Annual population growth rates for Yuma Myotis under different survival conditions. Model $ad(T), juv(trt + T)$ estimates λ using yearly estimates for all adults and yearly estimates of juvenile survival from the contaminated group. Model $ad(T), juv(con + T)$ used the same adult survival rates and yearly estimates of juvenile survival rates from the control group. Yearly estimates are based on the best-fit model in the stage-specific survival analysis: $\phi(ad(T), juv(c + T))$.

TABLE 3. Comparison of published bat survival rates from studies where survival was estimated using Cormack-Jolly-Seber methods.

Source	Species	Survival			
		Females		Males	
		Juvenile	Adults	Juveniles	Adults
This study	<i>Myotis yumanensis</i>	0.60–0.80	0.73–0.89		
Keen and Hitchcock (1980)	<i>Myotis lucifugus</i> †		0.71 ± 0.02		0.82 ± 0.01
Hitchcock et al. (1984)	<i>Myotis leibii</i> †		0.42 ± 0.07		0.76 ± 0.11
Hitchcock et al. (1984)	<i>Eptesicus fuscus</i> †		0.70 ± 0.06		0.47 ± 0.06
Hoyle et al. (2001)	<i>Macroderma gigas</i>	0.35–0.46	0.57–0.77	0.29–0.42	0.43–0.66
Sendor and Simon (2003)	<i>Pipistrellus pipistrellus</i>	0.53 ± 0.10	0.80 ± 0.05	0.53 ± 0.10	0.80 ± 0.05
Pryde et al. (2005)	<i>Chalinolobus tuberculatus</i>	0.47–0.72	0.52–0.83	0.47–0.72	0.34–0.69

Notes: Yuma Myotis juvenile survival rates are presented from control sites, using model-averaged estimates for the control population.

† Juvenile and adult survival were confounded because banding was conducted at hibernacula.

selection, human disturbance, weather patterns, predation, and spatial proximity of available foraging habitat and hibernating sites (Tuttle and Stevenson 1982). For the most part, however, effects of these factors on survival have not been empirically tested (but see Hoyle et al. 2001, Sendor and Simon 2003, Pryde et al. 2005).

Higher mortality for juveniles is common in mammals and birds (Pearson et al. 1952, Caughley 1966, Loery et al. 1987, Hoyle et al. 2001, Kauffman et al. 2003, Sendor and Simon 2003). Many factors may contribute to reduced survival in juvenile bats. Amount of maternal care and investment are important for juvenile survival (Kunz and Hood 2002) as well as natal condition and location (Tuttle and Stevenson 1982). Inexperience may negatively affect survival by increasing vulnerability to predation and reducing foraging efficiency, which could affect valuable over-wintering fat stores (Tuttle and Stevenson 1982, Pryde et al. 2005).

Female juvenile Yuma Myotis experienced higher survival than three other available estimates of first-year female bat survival (Hoyle et al. 2001, Sendor and Simon 2003, Pryde et al. 2005) (Table 3). The estimates of Pryde et al. (2005) for *Chalinolobus tuberculatus* were the most similar to our estimates, during low-predator years, when average female juvenile survival was reported as high as 0.72. The estimates for *Pipistrellus pipistrellus* (Sendor and Simon 2003) are lower than the estimates for Yuma Myotis, but the authors reported problems with negative bias due to strong transience in juvenile females. The estimates for *Macroderma gigas* (Hoyle et al. 2001) are the lowest reported juvenile survival rates, but these estimates may have been negatively affected by trap-shyness, and this species is a large carnivorous bat with a different ecology than the small, insectivorous species studied here. The paucity of comparable estimates demonstrates the need for future studies on age-specific survival studies for this group of mammals.

Estimates of mortality during the preweaning period, which includes prevolancy and early volancy for young bats, are available for a few vespertilionid species and range from 4% to 11.8% (Foster et al. 1978). Our

juvenile survival estimates should be interpreted as survival from volancy to one year old, and do not incorporate the “preweaning” period. Juvenile survival was still significantly lower than adult survival, indicating risks associated with being an inexperienced flyer, increased risk of predation, or lack of foraging efficiency to store fat for over-wintering, which may cause decreased survival chances for bats in their first year of life (Adams 1996, Adams 1997, Pryde et al. 2005).

Many bat banding studies have been conducted at winter hibernacula (Keen and Hitchcock 1980, Hitchcock et al. 1984) because of ease of capture and fidelity at these sites. When banding is conducted at hibernacula, stage-specific survival rates usually cannot be modeled because juvenile bats are normally indistinguishable from adults after their first summer. Combining adults and juveniles into a single group for survival estimation could produce a negative bias in adult survival if juveniles experience a considerably lower survival rate than adults, as has been shown in this study and others (Hoyle et al. 2001, Sendor and Simon 2003, Pryde et al. 2005).

Potential contamination effects on juvenile survival

A clear interpretation of an effect on juvenile survival is difficult given the lack of precision in the model-averaged estimates and the equivocal model selection results (Table 2). Using model-averaged estimates helps our interpretation by accounting for the uncertainty in the model selection, which is particularly useful when real-world situations are difficult to approximate with a single best model (Burnham and Anderson 2002).

Our findings suggest that juvenile bats may be more vulnerable than adults to mortality risks associated with habitat degradation. While the environmental contamination caused by the metam sodium spill in the Sacramento River did not appear to have strong lingering effects on adult survival, there was a general trend of lower juvenile survival in the contaminated area compared to control sites, although the precision of these estimates was poor.

This potential impact on juvenile survival is especially interesting considering that the first survival interval occurred well after immediate toxic impacts. At the time of the spill, bats within the spill-exposed area were likely directly exposed to the fumigant; the roosts were located in the river canyon where the fumigant persisted as a toxic cloud over the river for days (Pruett et al. 2001). In this study bats banded as juveniles were born after the toxic spill, and therefore reflect changes in first-year survival associated with longer-term habitat degradation than factors associated with direct toxicant exposure. We suspect that reduced juvenile survival may be linked to altered prey availability coupled with inexperienced foraging.

Yuma *Myotis* are highly dependent on aquatic insect prey (Brigham et al. 1992), and aquatic invertebrate populations may take a significant time to recover from contamination events (Lytle and Peckarsky 2001). For example, Lytle and Peckarsky (2001) found stream invertebrate community composition was still altered 15 months after a diesel oil spill. If the aquatic invertebrate community in the Sacramento River experienced a similar time to recover, the aquatic prey base of Yuma *Myotis* may have been altered for several years.

Juvenile bats must successfully forage to gain sufficient fat stores for winter survival. Reduced prey availability (or altered taxonomic composition and size spectrum) in the Sacramento River could have reduced the foraging efficiency of juveniles, decreasing fat stores below a critical threshold for over-winter survival. Lower body masses and foraging inexperience may have increased mortality risks of juveniles compared with adult bats (Pryde et al. 2005). Greater foraging efficiency in more structurally complex habitat away from open water may have permitted adult bats to avoid energy or key nutrient intake deficits that increased mortality (Adams 1996, 1997). However, stressed adult condition during the summer breeding months may have also contributed to juvenile mortality.

Increasing survival time trend

The increase in adult survival at all roost locations during the course of the study period suggests adult survival may be influenced by regional factors, such as weather patterns. Since this increase occurred at both contaminated and control sites, a regional environmental trend is likely responsible rather than ameliorating conditions after the spill. Potential region-wide influences on bat survival may contribute to the equivocal model results in terms of a contamination effect. This highlights the usefulness of an information-theoretic approach and the advantage of using model-averaged estimates, which incorporate the uncertainty in model selection and permit biological interpretations of potentially complex patterns (Burnham and Anderson 2002).

The period 1987 to 1992 was the most recent severe drought in California, ending with considerably higher than normal precipitation in the winter of 1992–1993

(Keyantash and Dracup 2004). Winter floods in California rivers reset invertebrate communities and provide more prey in the subsequent warm season (Power 1995). Increased late-season surface water improves primary and secondary production in streams and could positively influence survival of bats via greater prey availability during the reproductive season, as well as allowing increased fat storage in preparation for winter. Grindal et al. (1992) showed that elevated precipitation in spring delayed or decreased Yuma *Myotis* reproduction in British Columbia. Longer-term survival studies that can compare survival among drought periods and years with ample precipitation would greatly increase our understanding of the explicit relationship between bat population dynamics and local and regional conditions.

Population growth rates

The population exposed to the spill was in decline in 1992, suggesting that the contamination negatively impacted the population for at least two years following the perturbation. Population growth recovered by 1993 and continued to increase during the course of the study. However, population growth remained lower in the contaminated population than in the control population for the duration of the study. The linear time trend increase in survival resulted in substantial increases in population growth rate over the four-year study period (range of λ was 0.92–1.22), suggesting that changes in adult and juvenile survival result in variation in population-level parameters. Pryde et al. (2005) recently reported fluctuations from 0.79 to 1.03 in population growth in the New Zealand long-tailed bat, *Chalinolobus tuberculatus*, due to changes in adult and juvenile survival from high and low introduced predator years.

The region-wide time trend in adult survival was surprising, given expectations that survival should be fairly constant because of low extrinsic mortality risk associated with high longevity (Barclay and Harder 2003). The fact that population growth was near equilibrium in the control populations and increased during the four-year study period in accordance with increasing survival rates, provides evidence that these bat population dynamics may be more susceptible to broad spatial patterns than previously realized.

Our survival analysis and population modeling results offer one of the first opportunities to demonstrate how observed variation in both juvenile and adult bat survival, influenced by both habitat perturbation as well as broad spatial patterns, influenced population performance in bats. Constraints on fecundity increase the importance of survival in maintaining stable populations (Sæther and Øyvind 2000). Therefore, as reproductive output is constrained in bat populations by body size limitations for flight (Barclay and Harder 2003), understanding factors related to bat survival and their subsequent influence on population growth may have particular importance for bat population dynamics.

Conservation and management implications

Using mark–recapture techniques at bat maternity roosts can provide reliable estimates of stage-specific survival in colonial bat species, allowing informed management decisions about conservation of sensitive species. Only recently have robust studies of bat demography been attempted (Hoyle et al. 2001, Sendor and Simon 2003, Pryde et al. 2005), and our knowledge of potential influences on population dynamics of this diverse group of mammals remains impressively deficient (Barclay and Harder 2003). Inferences from our research are restricted to one regional population, but our results suggest that adult female Yuma Myotis may be resilient to some types of habitat degradation; however, juvenile bats may be more sensitive. More research is needed on factors influencing species vital rates and population-level parameters for a variety of species and habitat types for effective management of bat populations.

Disasters offer unique opportunities to conduct natural experiments that may not be ethical or feasible to carry out as manipulated experiments. The research presented here offers an example of using a major anthropogenic disturbance to study the effects of a landscape perturbation on population dynamics and learn more about basic demography of a poorly studied taxonomic group. Management recommendations to prevent disasters are hollow, as disasters are rarely planned, and even in situations where preventative steps may be possible, they are often beyond the political or bureaucratic scope of land managers. However, managers can take advantage of catastrophic events by employing “scientific mitigation,” whereby postdisaster funding is allocated, not just to restoration, but to studies designed to assess how a disaster affected natural populations in a natural or quasi-experimental design context.

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