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Among-Population Variation in Monthly and Annual Survival of the Baja California Treefrog, *Pseudacris hypochondriaca curta*, in Desert Oases of Baja California Sur, Mexico

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Abstract.—**Survival is an important component of the demography of an animal. We estimated monthly and annual survival probabilities of three populations of the Baja California Treefrog (*Pseudacris hypochondriaca curta*) inhabiting desert oases of Baja California Sur, Mexico. We used data from a two-year mark recapture study to estimate survival. Recapture probabilities varied widely among months and there was no clear temporal pattern underlying the fluctuations. Annual survival was 27 and 29% for two populations and 1% for the third population. This implies that the populations, particularly the third one, can persist only if there is steady and high recruitment. With annual survival as low as 1–29%, a lack of recruitment could quickly cause local extinction. Because immigration seems unlikely in these populations due to their isolation from other breeding populations, recruits must be produced locally. Non-native fish, crayfish, and frogs that prey on tadpoles may therefore be a threat for the persistence of the populations.**

Key Words.—amphibian; demography; *Pseudacris hypochondriaca curta*; survival; population.

Introduction

Knowledge of life-history traits and demography is of fundamental importance for the conservation of endemic or rare species. Lack of demographic information makes it difficult to assess extinction risk and to develop management strategies (Lebreton 2005, 2006). Survival is an important demographic trait because it often has a larger effect on population growth than other vital rates (Pfister 1998). Environmental heterogeneity can lead to spatial and temporal variation in survival and this variation can affect the dynamics and persistence of populations (Pulliam and Danielson 1991).

Estimates of spatial and temporal variation in survival can be used to learn about the mechanisms that determine population growth and fluctuations in abundance. Understanding the demographic drivers of population dynamics is particularly important for amphibians because this taxonomic group is undergoing declines at a global scale (Houlahan et al. 2000, 2001; Stuart et al. 2004; Wake and Vredenburg 2008). Spatial variation in survival can be used to identify the causes of population declines and can affect

management decisions for particular sites or regions (Schmidt et al. 2005; Johnson et al. 2010). Another source of information on the mechanisms that most likely drive population dynamics is temporal variation in survival, in particular temporal variation within the year. Within-year patterns of survival reveal when most mortality occurs (Schmidt et al. 2007, 2014). This knowledge may also inform conservation management.

Here, we studied temporal and spatial variation in survival among populations of an endemic frog. The Baja California Treefrog (*Pseudacris hypochondriaca curta*) (Fig. 1) is an endemic subspecies of Baja California Sur, Mexico, inhabiting exclusively isolated desert oases and mountain arroyos (Recuero et al. 2006). To date, approximately 45 isolated populations have been located across Baja California Sur and little is known about the ecology or conservation of the species (Grismer 2002). Unfortunately, several populations are under pressure because of human activities (e.g., habitat modification) and, more recently, invasive species. Several species of non-native fish and the American Bullfrog (*Lithobates catesbeianus*) are present in the oases (Luja and Rodríguez-Estrella 2010). More recently, the pathogenic Amphibian Chytrid Fungus (*Batrachochytrium dendrobatidis*) was detected in at least five populations (Luja et al. 2012). For species like the endemic Baja California Treefrog, knowledge of population size and survival probabilities are critical to assess long-term population viability. Detailed studies of demography are thus fundamental to understanding the life history of a species and are a necessary component of future conservation efforts. We use data from a two-year mark-recapture study of three populations of the Baja California Treefrog to estimate among-population variation in annual and monthly survival probabilities.

Materials and Methods

Study sites.—We monitored three Baja California Treefrog (*P. h. curta*) populations inhabiting three desert oases located in the Vizcaíno Biosphere Reserve in the central part of the Baja California peninsula, Mexico, from March 2007 to January 2009. These oases are located in the Sonoran Desert subprovince (Shreve and Wiggins 1964). The climate is hot and dry; the annual average temperature is 21.5° C and annual average precipitation of 96 mm (Coria 1997). The sites (oases) where we studied frogs were: El Sauzal (27°10'26.1"N, 112°52'52.0"W), San Zacarías (27°08'14.9"N, 112°54'18.2"W), and El Álamo (27°06'29.1"N, 112°55'38.3"W). The three oases are located along a 10 km stretch of road from the town of San Ignacio to the San Ignacio lagoon. The straight-line distance between the ponds in the oases is 5.7 km for El Sauzal - San Zacarías, 3.9 km for San Zacarías - El Álamo, and 9.6 km for El Sauzal - El Álamo (for a map, see Luja and Rodríguez-Estrella 2010). The vegetation in between the oases is Desert Scrub (Rzedowski 2006). There are no microhabitats (e.g., streams) that could facilitate frog dispersal.

The El Sauzal study site has a permanent pond with invasive fish Tilapia, *Tilapia cf. zilli*; Swordtail, *Xiphophorus hellerii*, Guppy, *Poecilia reticulata*), Red Swamp Crayfish (*Procambarus clarkii*), and American Bullfrogs (*Lithobates catesbeianus*). Treefrogs were usually found in smaller fishless, temporary ponds adjacent to the permanent pond. At the El Álamo study site, a spring feeds a small stream that in turn feeds a small pond. While the pond is drained once or twice a week because ranchers use the water for irrigation purposes, the spring and the stream are never dry. Guppies occur at the site. The San Zacarías study site has a permanent pond with Guppies and Swordtails.

Field methods.—We collected mark-recapture data at each site (i.e., oasis) on a monthly basis (except for the months of July and December) during three consecutive nights. We used identical sampling protocols during the three nights in each of the three sites, and spent a total of 62 nights in each oasis with a total of 124 man-hours

Figure 1. Baja California Treefrogs (*Pseudacris hypochondriaca curta*) from Baja California Sur, Mexico. Photographed by Victor H. Luja.

at each. Usually, we started the sampling 30 min after sunset. Every day we randomly selected the order in which oases were sampled to avoid time-of-day bias in the sampling. Two observers captured by hand all treefrogs that were detected while walking slowly along fixed transects along the edge vegetation of each water body. Frogs were placed in sealable plastic bags (maximum of five frogs/bag). Transects were 2.5-m wide and 130 m, 100 m, and 90 m long at El Sauzal, San Zacarías, and El Álamo, respectively. The area covered by transects was 325, 250, and 225 m^2, respectively, and proportional to the area of the water bodies.

Capture and marking protocol.—Because of the passive behavior of treefrogs, we captured approximately 90% of the individuals seen at each site. Upon first capture, we assigned a permanent individual number to each treefrog by implanting Visible Implant Alphanumeric Tags (Northwest Marine Technology, Inc., Shaw Island, Washington, USA). We used standard size (1.0 mm × 2.5 mm) orange tags. We implemented the insertion procedure as follows: we anesthetized frogs in groups of five in dilute solution of tricaine (MS-222; dilution was 1 g / 1 L of water). Once anesthetized, in this and every subsequent recapture, we measured snout-urostyle length (SUL) in mm with digital callipers and body mass (g) with a Pesola scale (Pesola AG, Baar, Switzerland) for every individual. We also determined sex of every individual. At our study sites, average SUL of males was 33.1 mm (SE = 0.1 mm, n = 197) and female length was 38.4 mm (SE = 0.3 mm, n = 62). Males can be distinguished from females by the color of the throat. Females have a smooth, white throat whereas males have dark brown or yellow throat.

We inserted alphanumeric marks subcutaneously into the ventral surface of the back leg of the frog using a special injector provided by the company. We dipped the injector into ethanol to disinfect it and wiped off the excess ethanol between frogs. The frogs were then allowed to recover in captivity; frogs were kept in the sealable plastic bags. We retained the frogs collected during each sampling period (three days) and released them on the last night of sampling in the same place they were found. Marking, handling, and keeping frogs in captivity did not cause mortality during the process.

Mark-recapture statistical analysis.—We used R (R Development Core Team 2012) and the package RMark to fit Cormack-Jolly-Seber (CJS) models to find a model that describes the data best (Lebreton et al. 1992; White and Burnham 1999; Laake and Rexstad 2012). The analysis accounted for unequal time intervals between capture events (which occurred because no field work was done in July and December). The goal of the mark-recapture analysis was to test whether survival was best explained by the additive effects of site, sex, variation among capture occasions, or a combination thereof. We estimated monthly survival probabilities. A goodness-of-fit test in program U-CARE (Choquet et al. 2009) showed that the model with site, sex, and time-specific survival and recapture probabilities (p(site*sex*t), p(site*sex*t)) fitted the data well (χ^2 = 59.8, df = 92, P = 0.996).

We fitted a small set of candidate models for recapture probability to the data and selected the one with the lowest AICc value (Burnham and Anderson 2002) for further analysis. While doing so, we kept the model for survival probability at the greatest complexity (i.e., Φ(t + site + sex); initial analyses showed that there was not enough information in our dataset to allow for interactive effects. We fitted eight candidate models to the data with constant recapture probabilities (Φ(.)); with recapture probabilities varying among months (capture occasions; Φ(t)); with recapture probabilities showing a linear trend (Φ(trend)); with recapture probabilities differing between the sexes (Φ(sex) and among sites (Φ(site)); with the additive effects of site and sex (Φ(site + sex)); the additive effects of site, sex and time (Φ(site + sex + time)); and the interac-

tive effects of site, sex, and time (Φ(site * sex * t)).

We then fitted a small set of candidate models for survival probability to the data while using the previously identified best model for recapture probability. We fitted seven candidate models to the data with constant survival probabilities (Φ(.)); with survival probabilities varying among months (capture occasions, (Φ(t)); with survival probabilities showing a linear trend (Φ(trend)); with survival probabilities differing between the sexes (Φ(sex) and among sites (Φ(site)); with the additive effects of site and sex (Φ(site + sex)); and the additive effects of site, sex and time (Φ(site + sex + time)). After selecting a best model, we fitted the model in the Bayesian software JAGS (version 3.4; Plummer 2003) to estimate parameters. We specified diffuse priors for all parameters to be as uninformative as possible. The JAGS code for the CJS model can be found in Kéry and Schaub (2012). Annual survival was computed in JAGS as the product of monthly survival probabilities.

Table 1. Modelling monthly survival (Φ) of the Baja California Treefrog (*Pseudacris hypochondriaca curta*). The AICc of the top-ranking model was 1161.381. Model notation follows Lebreton et al. (1992). The variable time refers to time dependence (i.e., monthly variation), site refers to variation among populations, sex refers to variation between males and females, and Time refers to a temporal trend in survival. Table entries are the number of estimated parameters (K), the difference of the AICc value of the current model and of the best model (ΔAICc), and the Akaike weight. The model for recapture probability was p(time + sex + site) for all models listed in the table.

Model	K	ΔAICc	Akaike weight
Φ(time + site)	41	0.00	0.435
Φ(site)	24	0.740	0.301
Φ(time + site + sex)	42	1.954	0.164
Φ(sex + site)	25	2.928	0.101
Φ(Time)	23	21.568	0.000
Φ(.)	22	25.703	0.000
Φ(sex)	23	27.912	0.000

Results

We captured 30 females and 68 males at El Álamo, 10 females and 34 males at El Sauzal, and 19 females and 68 males at San Zacarías. Individuals were captured on average 2.1 times (range: 1–11). The model selection analysis showed that recapture probability was best described by a model with additive effects of site, sex, and time (Akaike weight = 1.0; detailed model selection results not shown). Recapture probability of females was only about half of the recapture probability of males at all sites (Fig. 2). Recapture probability of males and females at El Sauzal averaged about 0.05 and 0.02, respectively. This contrasts with the other two sites, which averaged around 0.45 for males and 0.15 for females (Fig. 2).

The model selection analysis showed that survival was best described by a model that included the additive effects of site and time, but excluded sex effects (Table 1). Monthly survival probability was similar and high at El Álamo and El Sauzal and averaged about 0.9, and lowest at San Zacarías (average about 0.73; Fig. 3). Survival probability varied among months but cycles were not regular such that there were no months when survival was always high or low. Annual survival in both years was 0.27 for the population at El Alamo, 0.29 and 0.31 for the two years at El Sauzal, and 1% for both years in the third population, San Zacarías (Table 2).

Discussion

The analysis of mark-recapture data of Baja California Treefrogs inhabiting three desert oases revealed that there was substantial variation in recapture and survival probabilities among months and among sites. Annual survival varied among the three sites. Even though capture effort was similar at all sites and across months, recapture

Table 2. Estimates (and 95% credible intervals) of annual survival probability in three populations of the Baja California Treefrog (*Pseudacris hypochondriaca curta*). Estimates are based on monthly estimates of model Φ(time + site), Φ(Time + sex + site). The first annual survival refers to the time period from March 2007 to March 2008, the second annual survival from January 2008 to January 2009.

Population	Annual survival probability (95% credible interval) for first year	Annual survival probability (95% credible interval) for second year
El Álamo	0.273 (0.172, 0.391)	0.271 (0.110, 0.545)
El Sauzal	0.288 (0.034, 0.853)	0.311 (0.022, 0.871)
San Zacarías	0.009 (0.001, 0.032)	0.010 (0.000, 0.053)

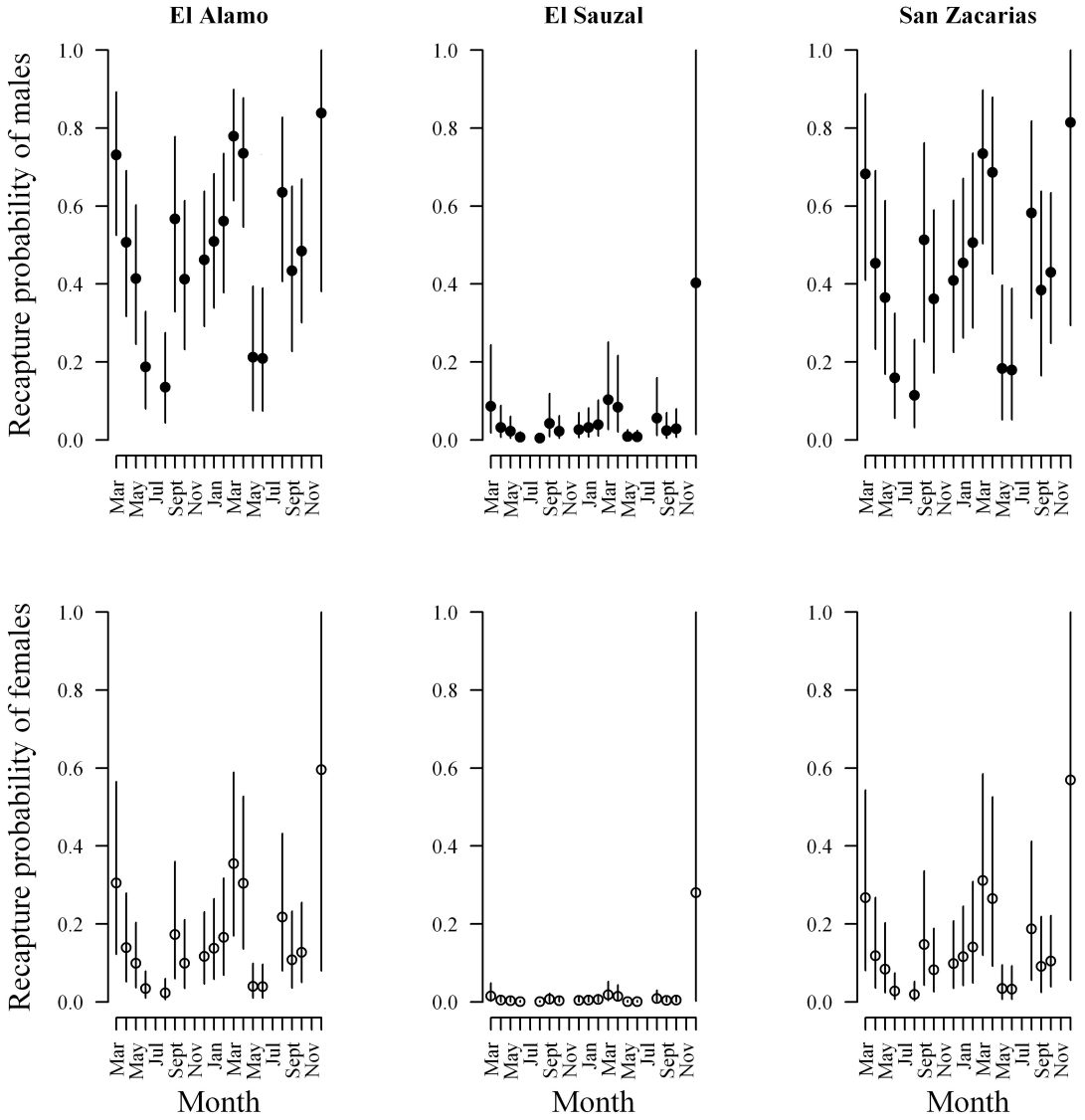

Figure 2. Estimates (mean and 95% credible interval, based on best model in Table 1) of monthly recapture probabilities of males (closed symbols) and females (open symbols) in three populations of the Baja California Treefrog (*Pseudacris hypochondriaca curta*). The first month is March 2007.

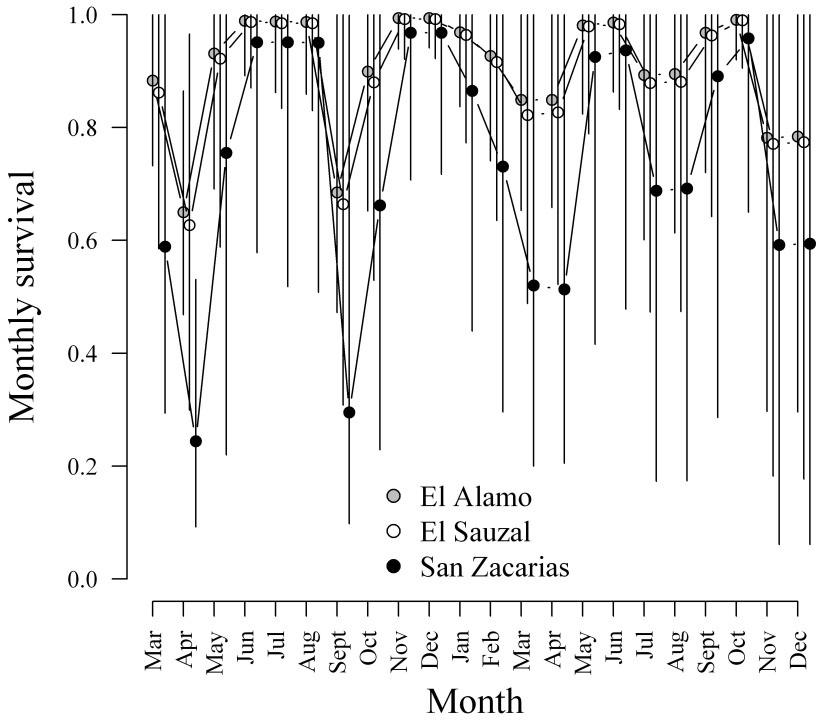

FIGURE 3. Estimates (mean and 95% credible interval, based on best model in Table 1) of monthly survival probabilities in three populations of the Baja California Treefrog (*Pseudacris hypochondriaca curta*). The first month is March 2007.

probabilities varied. This supports earlier assertions that it may be unwise to assume constant recapture probabilities. Instead, recapture probabilities have to be estimated (Nichols 1992; Schmidt et al. 2002). There is no obvious explanation for temporal variation in recapture probabilities. At El Sauzal recapture probabilities were very low. Low recapture probabilities can lead to imprecise survival estimates. Nevertheless, the credible intervals for survival probability for frogs at El Sauzal are not much different from the two other sites. This is probably the case because in our analysis information on recapture and survival was shared across sites (i.e., the models for survival were additive and had no interaction between site and time).

Monthly variation in survival probabilities was marked but there was no clear pattern that could easily be explained (Fig. 3). Estimates of monthly survival were similar to the ones reported for the European Treefrog *Hyla arborea* (0.83 to 1.0; Wagner et al. 2011). Previous studies revealed either a strong effect of winter weather on amphibian survival or they demonstrated that survival did not vary among seasons (Anholt et al. 2003; Lowe 2003; Reading 2007; Schmidt et al. 2014). Annual survival probability in the El Álamo and El Sauzal populations was as low as in other tree frogs, e.g., *Hyla arborea* (approximately 0.29; Pellet et al. 2007). At San Zacarías, annual survival was estimated to be almost zero.

Because our study included only three sites, we could not test which factors might have caused

the pattern of variation among sites. Prevalence of the Amphibian Chytrid Fungus varied among the three sites (Luja et al. 2012), but there was no obvious correlation between pathogen prevalence and annual survival. This may not be surprising because other species of *Pseudacris* are known to be tolerant of the pathogenic Amphibian Chytrid Fungus (Reeder et al. 2012). Because mark-recapture estimates of survival cannot distinguish between survival and permanent emigration (Sandercock 2004), the low survival probability at San Zacarías might be the result of permanent emigration. However, because San Zacarías is an isolated oasis in the desert, permanent emigration seems an unlikely explanation as there are no other oases where the frogs might go.

Population growth rate can be estimated as the sum of survival and recruitment (Nichols et al. 2000; Schmidt et al. 2005). The low survival probabilities of the Baja California Tree frog imply that recruitment must be high for population persistence (i.e., given survival of 0.3, roughly 0.7 recruits per female per year are required for a growth rate of 1.0). With annual survival probabilities of 0.27 to 0.31 at two sites (or even only 0.01 as at San Zacarias), these frogs are highly sensitive to variation in recruitment because a series of years without recruitment may cause the local extirpation of the populations. Desert oases are subject to natural stochasticity (e.g., prolonged droughts and torrential rains resulting from hurricanes), which could induce variation in reproduction and recruitment. Moreover, the oases are also affected by human activities such as the introduction of exotic species. Because there are invasive fish, crayfish, and bullfrogs in the oases that may prey on the different life stages of the native treefrog (Kats and Ferrer 2003; Cruz et al. 2006), removal of these species may be an important management action to increase population viability.

The survival analysis presented in this paper showed that the estimation of demographic parameters can inform conservation management. We recommend that conservation management in short-lived frogs should focus on improving recruitment. Amphibian ecologists should try to build a database of amphibian life-history traits such that species may be arranged along a slow-fast continuum of life histories (as it was done for birds and mammals; Sæther and Bakke 2000; Bielby et al. 2007). Such a data base may help to make general recommendations for amphibian conservation.

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