

PORTRAIT OF A SMALL POPULATION OF BOREAL TOADS (*ANAXYRUS BOREAS*)

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ABSTRACT: Much attention has been given to the conservation of small populations, those that are small because of decline, and those that are naturally small. Small populations are of particular interest because ecological theory suggests that they are vulnerable to the deleterious effects of environmental, demographic, and genetic stochasticity as well as natural and human-induced catastrophes. However, testing theory and developing applicable conservation measures for small populations is hampered by sparse data. This lack of information is frequently driven by computational issues with small data sets that can be confounded by the impacts of stressors. We present estimates of demographic parameters from a small population of Boreal Toads (*Anaxyrus boreas*) that has been surveyed since 2001 by using capture–recapture methods. Estimates of annual adult survival probability are high relative to other Boreal Toad populations, whereas estimates of recruitment rate are low. Despite using simple models, clear patterns emerged from the analyses, suggesting that population size is constrained by low recruitment of adults and is declining slowly. These patterns provide insights that are useful in developing management directions for this small population, and this study serves as an example of the potential for small populations to yield robust and useful information despite sample size constraints.

Key words: Decline; Demographics; Recruitment; Rocky Mountain National Park; Survival

UNDERSTANDING what it means to be a small population in ecological and conservation terms has long been a focus of conservation biology. Caughley (1994) presented a dichotomy within the study of small populations. He described the declining population paradigm, a paradigm that focuses on the cause of decline and how to remediate the effects of the decline (i.e., smallness), and contrasted that with the small population paradigm, a paradigm that focuses on the effect of smallness on persistence. Caughley (1994) called for more theory to define the declining population paradigm and for more practice focused on the small population paradigm. This paper promulgated much debate as to the validity of the proposed dichotomy and continued discussion about the paradigms (e.g., Asquith, 2001; Green, 2003; Hedrick et al., 1996; Norris, 2004). Nearly two decades later, we are still struggling with a balanced understanding of the interaction (or lack thereof) between population declines leading to smallness, the effect of smallness (natural or induced) on persistence, and how to manage populations that are small.

Smaller populations are more vulnerable to the deleterious effects of environmental, demographic, and genetic stochasticity as well as natural catastrophes (Purvis et al., 2000; Shaffer, 1987), and theory predicts that small populations are more likely to go extinct than large populations (Gilpin and Soule, 1986; Shaffer, 1987). Habitat alteration, invasive species, and disease can affect multiple aspects of population demography and interact with other stressors to exacerbate the risk to small populations (e.g., McCallum and Dobson, 1995; Smith et al., 2009).

Unfortunately, smallness, declining abundance, and limited persistence are often hallmarks of populations of conservation concern. Although small populations can provide opportunities for thorough data collection, inferences regarding population parameters can still be imprecise. One of the most serious problems in studying small populations is the difficulty in modeling demographic processes and providing parameter estimates when constrained by sparse data (Williams et al., 2002). In addition, a lack of historical data and thus the inability to categorize the target population as naturally small or small after a stressful event (*sensu* Caughley, 1994) also may

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constrain our ability to identify appropriate management actions.

Many amphibian populations are small (Green, 2003). They can be naturally small and isolated (e.g., isolated over geologic time, as with Wood Frogs, *Lithobates sylvaticus* [formerly *Rana sylvatica*]; Lee Yaw et al., 2008); artificially small due to habitat destruction (e.g., Arroyo Toad, *Anaxyrus californicus* [formerly *Bufo californicus*]; US Fish and Wildlife Service, 2009); or small as a result of a stressor such as disease (e.g., Boreal Toads, *Anaxyrus boreas* [formerly *Bufo boreas*]; Scherer et al., 2005). Smallness, in terms of population size, has been identified as a factor in global amphibian declines (e.g., De Castro and Bolker, 2005; Lips et al., 2003). Overcoming the difficulties of investigating and subsequently gaining reliable information about such small populations is critical in forecasting their likely fate and identifying appropriate management options (e.g., Blaustein et al., 1994).

We have been studying a small, isolated population of Boreal Toads at Spruce Lake in Rocky Mountain National Park (RMNP), Colorado, USA, for 21 yr, including capture–recapture data from 2001 to 2010. The Boreal Toad has suffered population declines in the Rocky Mountains since the mid-1990s (Carey et al., 2005; Muths et al., 2003), and the number of breeding sites in RMNP has decreased from 18 historic locations (Corn et al., 1997) to three sites, including Spruce Lake. Disease (i.e., *Batrachochytrium dendrobatidis*, Bd) is one contributor to population declines in the region (Muths et al., 2008). Our objectives were to estimate key demographic parameters for this small, wild population (annual survival, recruitment, and population growth rate) and to use these estimates to inform conservation efforts for this population and possibly other small populations.

MATERIALS AND METHODS

Study Area

Spruce Lake is a high-elevation lake (2707 m) just to the east of the continental divide in RMNP. The lake is embedded in coniferous forest including Engelmann Spruce (*Picea engelmannii*) and Subalpine Fir (*Abies lasio-*

carpa). The understory includes Willow (*Salix* sp.) and Bog Birch (*Betula pumila*), and the lakeshore has sedges (*Carex* spp.), mosses, and grasses leading up to undercut banks. Bd has been detected at Spruce Lake, but prevalence seems to be low. Spruce Lake was treated with antimycin in 1990 and was stocked with fingerling fish (Greenback Cutthroat, *Oncorhynchus clarkii stomias*) in 1991 and 1992 (US Fish and Wildlife Service, 1998; M. K. Watry, personal communication). The lake is a popular destination fishing spot in RMNP.

Data Collection

We conducted three to seven, night-time capture occasions, over approximately 1 mo during each breeding season, from 2001 to 2010. During each capture occasion, the site, including adjacent wetlands and terrestrial areas, was searched, and toads were captured by hand in individual plastic bags (Scherer et al., 2008). New captures received a passive integrated transponder (PIT) tag with a unique number, and recaptured animals' PIT tags were recorded. All captured animals were assessed noninvasively for the presence of Bd, measured (snout–vent length and mass), and released. We also compiled field observations collected before 2001 on this population (Corn et al., 1997; E. M. and M. K. Watry, personal communication).

Data Analysis

We used the Pradel model (Pradel, 1996) for data collected under Pollock's robust design (Kendall and Nichols, 1995; Pollock, 1982) and Program MARK (White and Burnham, 1999) to analyze the capture–recapture data for male toads only. Data collected under Pollock's robust design are characterized by two temporal scales (Kendall et al., 1997). Multiple capture occasions (i.e., secondary occasions) are conducted over a relatively short period during which individuals are assumed to be neither added to nor lost from the population (Kendall et al., 1997). The time period that includes one set of secondary occasions and lasts until the beginning of the next set of secondary occasions is referred to as a primary period (Kendall et al., 1997). In this study, primary periods lasted from the first secondary occasion during the breeding season in year t to the beginning

of the first secondary occasion in the breeding season of year $t + 1$ and were long enough to allow gains and losses in the population.

We used the closed population models of Otis et al. (1978) to model capture and recapture probabilities and estimate abundance, N , within each set of secondary occasions (Williams et al., 2002). Capture probability, p , is defined as the probability an individual is initially captured within a primary period, whereas recapture probability, c , is defined as the probability an individual is recaptured. The c value may be smaller than the p value if a toad avoids recapture (e.g., by diving to the bottom of the pond) after a negative experience during initial capture.

We used the f -parameterization of the Pradel model (Pradel, 1996; Williams et al., 2002) to estimate apparent survival probability (Φ) and recruitment rate over primary periods. Φ is the probability of surviving and remaining on the study area over a primary period. Because Φ is the product of surviving and remaining on the study area, it can represent a negatively biased estimate of true survival in the presence of emigration. Toads in general have high site fidelity (Olson, 1992), and we have shown previously that temporary emigration in male Boreal Toads tends to be very low, with males seldom absent from the breeding site in consecutive years (Muths et al., 2006); therefore, we assume minimal bias in Φ as an estimate of true survival. Recruitment rate, f , is the per capita number of individuals added to a breeding population each year. Despite intensive surveys in the area around Spruce Lake, no other Boreal Toad population or breeding activity has been observed. Therefore, we suspect that in situ reproduction is the sole source of recruits into this adult population. Within Program MARK, we used annual estimates of Φ and f to derive estimates of the finite population growth rate, λ , and standard errors using the equation $\lambda_t = \Phi_t + f_t$, where t indexes year. Concerns about confounded parameters led us to report a subset of the estimated λ values (Williams et al., 2002).

During capture occasions, two attributes of the population became apparent. First, the population was small. Despite multiple secondary occasions each breeding season,

few individuals were captured (Table 1). Second, we tended to capture the same individuals across secondary occasions within a primary period and across primary periods, and captures of new individuals were rare (Table 1). Given that the population had persisted for 10 yr and the individuals captured each year tended to be recaptures from previous years, we hypothesized that the population was persisting primarily because adult survival was high, a supposition supported by Biek et al. (2002) who show that the elasticity of λ (population persistence) is highest for adult survival, that is, changes in adult survival result in the greatest proportional change in λ . Because we rarely captured new individuals, we hypothesized that recruitment was low and a factor contributing to the smallness of the population.

Our primary interest was to determine annual estimates of Φ , f , and λ ; thus, we evaluated only a few relatively simple structures for each parameter in the model. Furthermore, the consideration of models with many parameters, and the potential identification of factors (covariates) that might lead to variation in our target parameters, was precluded by the smallness of the data set. We specified three hypotheses (and thus model structures) for the variation in p and c within each primary period: (i) c is equal to p and varies across secondary occasions within a primary period ($p[t] = c[t]$), (ii) c is smaller than p but neither parameter varies across secondary occasions ($p[.]$, $c[.]$), and (iii) c is equal to p and does not vary across secondary occasions within a primary period ($p[.] = c[.]$). We also specified three hypotheses for the temporal variation in both Φ and f : (i) Φ and f vary across primary periods (i.e., time), where primary period is a categorical variable ($\Phi[t]$ and $f[t]$); (ii) Φ and f are declining or increasing linearly (i.e., a trend; $\Phi[T]$ and $f[T]$); and (iii) Φ and f do not vary across primary periods ($\Phi[.]$ and $f[.]$). We built models by assembling the structures mentioned above in every possible combination (three structures on p and c times three structures on Φ times three structures on f , for a total of 27 models; Table 2). We used change in Akaike's Information Criterion adjusted for small sample size (ΔAIC_c) values, Δ_i , and Akaike

TABLE 1.—Male Boreal Toads (*Anaxyrus boreas*) captured at Spruce Lake, Rocky Mountain National Park (passive integrated transponder tag numbers) and total number of new toads (not caught previously). Numbers in the body of the table indicate the number of times each toad was captured within each year and bold type indicates the first year of capture.

Individuals (males)	No. of times captured (no. of capture occasions) by year									
	2001 (5)	2002 (4)	2003 (7)	2004 (5)	2005 (5)	2006 (4)	2007 (3)	2008 (3)	2009 (5)	2010 (5)
23355893	0	1	0	0	0	0	0	0	0	0
23359895	0	3	3	2	1	2	3	2	3	3
23563589	1	0	1	2	0	0	1	0	1	2
23598107	3	2	3	2	1	3	0	0	3	0
23611633	3	2	5	1	1	1	1	2	3	0
23616521	2	2	1	2	0	0	0	0	0	0
23774083	2	0	0	0	0	0	0	0	0	0
23792357	1	2	0	1	0	0	0	0	2	1
23805052	0	3	3	1	2	2	1	1	0	0
23807332	2	0	2	2	1	2	1	1	2	4
23818079	0	0	0	0	0	0	0	0	1	2
23818321	0	0	2	2	1	2	1	2	1	2
23867020	3	2	1	1	1	2	2	0	3	2
23876013	1	2	2	1	0	1	2	0	1	3
23876020	0	0	0	0	0	0	1	0	0	0
24032593	3	2	2	2	0	0	0	0	0	0
24033074	2	2	2	4	1	0	3	0	1	1
24039341	0	0	2	0	1	3	1	1	1	2
24052071	2	1	0	0	0	0	0	0	0	0
24072538	1	2	1	4	1	2	0	0	0	0
24082547	0	0	2	2	1	1	1	0	0	2
24333525	2	1	4	2	1	3	0	0	0	0
24345610	0	2	2	2	0	0	0	0	0	0
24353013	2	0	4	0	1	0	2	1	2	3
24383102	1	0	0	0	0	0	0	0	0	0
Total no. of new captures	16	4	3	0	0	0	1	0	1	0

weights, w_i , to quantify the support for each model i in the data. Both Δ_i and w_i quantify the strength of evidence in support of a particular model as the best model in the candidate set of models (Burnham and Anderson, 2002). Finally, we used model-averaging (Burnham and Anderson, 2002) to derive estimates of each parameter. Due to the small number of captures, numerical convergence was not

always reached or some parameters were not estimated. Models where this occurred had little to no support in the data (i.e., $\Delta AIC > 11$) and were removed from the model set before model-averaging.

RESULTS

Boreal Toads have inhabited Spruce Lake since at least 1979 (Corn et al., 1997). Adult

TABLE 2.—Model selection results (using the Pradel model under Pollock’s robust design) for Boreal Toads (*Anaxyrus boreas*) captured at Spruce Lake, Rocky Mountain National Park (2001–2010). Parameters modeled included survival probability (Φ), capture probability (p), recapture probability (c), and recruitment rate (f). Models including a linear time trend are denoted by (T). K = number of parameters in the model.

Model	AIC _c	ΔAIC_c	w_i	Model likelihood	K	Deviance
{ Φ (.), f (.), p (.)= c (.)}	657.415	0.000	0.468	1.000	22	609.052
{ Φ (.), f (T), p (.)= c (.)}	658.520	1.106	0.269	0.575	23	607.741
{ Φ (T), f (.), p (.)= c (.)}	659.815	2.400	0.141	0.301	23	609.035
{ Φ (T), f (T), p (.)= c (.)}	660.909	3.495	0.082	0.174	24	607.692
{ Φ (.), f (.), p (.), c (.)}	663.436	6.021	0.023	0.049	33	587.282
{ Φ (T), f (.), p (.), c (.)}	665.929	8.515	0.007	0.014	34	587.111
{ Φ (.), f (T), p (.), c (.)}	666.054	8.639	0.006	0.013	34	587.236
{ Φ (T), f (T), p (.), c (.)}	668.544	11.130	0.002	0.004	35	587.037

TABLE 3.—Visual encounter surveys (two or fewer site visits, 1979–2000) and systematic (three or more site visits using standard capture–recapture protocols, 2001–2010) observations for Boreal Toads (*Anaxyrus boreas*) at Spruce Lake, Rocky Mountain National Park. y, yes (numbers unreported); u, unknown.

Effort (no. of known visits):	1980–										1980–														
	1979	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
Observations:	1	0	2	1	1	0	2	0	1	1	0	1	1	1	1	20	8	9	7	5	4	3	3	5	5
Egg masses	0	u	0	0	y	u	0	u	0	1	u	0	1	1	3	2	2	3	2	5	2	15	0	1	7
Tadpoles	0	u	0	0	0	u	0	u	0	y	u	0	0	0	>500	150	0	200	0	3000	250	375	100	0	y
Metamorphs	0	u	0	0	0	u	0	u	0	0	u	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Juveniles	0	u	3	0	0	u	1	u	0	0	u	1	0	0	3	3	0	0	0	0	0	0	0	0	0
Adults	y	u	y	y	y	u	y	u	y	y	u	y	y	y	y	y	y	y	y	y	y	y	y	y	y
Females	u	u	1	1	0	u	0	u	0	0	u	1	3	0	4	2	1	2	0	4	2	3	1	3	6
Males	u	u	3	0	0	u	0	u	2	0	u	3	9	1	10	16	15	18	17	13	12	13	7	13	12
Unknown	u	u	0	0	2	u	5	u	0	7	u	0	0	0	2	0	0	0	0	0	0	0	0	0	0

toads were observed in each of the years ($n = 14$) that the site was surveyed between 1979 and 2000, but only eight juveniles, one metamorph, and seven egg masses were reported between 1988 and 2000 (Table 3).

From 2001 to 2010, we captured 25 individual male toads 255 times over 46 secondary occasions. The probability of capturing an individual at least once within a primary period was high (2005 and 2008, 0.54–0.61; other years, 0.83–0.93). Of these animals, 23 were captured in the first 3 yr of the study. Therefore, only two individuals were newly captured from 2004 to 2010, suggesting recruitment of adult males was low over this period. The fact that 13 (56%) of the 23 individuals captured by 2003 were observed alive in 2009 or 2010 also suggests high survival of adult males. Seven toads have not been captured in at least 5 yr, and we expect that these individuals are dead.

We tested 27 individuals (males and females) for Bd (70 swabs). Three individuals, from three separate years, yielded weak positive results (<0.27 zoospore equivalents): one individual in 2004, which tested negative in 2008 and 2009; one individual in 2009, which tested negative in 2010; and one individual in 2010. During our study, there were no mass mortalities, and only one toad was found dead (apparently from predation, the carcass tested negative for Bd).

Survival was relatively constant over time and recruitment declined during the study. Specifically, model selection results (1) indicated that c was equal to p and did not vary across secondary occasions within a primary period ($p[.] = c[.]$), (2) provided moderate to strong support for four models, and (3) reflected a preference for models with the fewest parameters (Table 2). Models that included linear temporal trends in Φ and f were among the highest ranked models, but examination of regression coefficients supported only a declining linear trend in f ($\beta_{Trend,f} = -0.30$; 95% CI, -0.78 to 0.18). Model-averaged estimates of f were small relative to estimates from other populations of Boreal Toads (Muths et al., 2011) and also showed a declining trend (Table 4).

Model-averaged estimates of population size ranged from 21 individuals (95% CI, 11–31 individuals) in 2005 to 12 individuals

TABLE 4.—Model averaged estimates for population size (N), survival probability (Φ), recruitment rate (f), and rate of change in population size (λ ; 2001–2010) from data collected on male Boreal Toads (*Anaxyrus boreas*) at Spruce Lake, Rocky Mountain National Park.

	Estimate	SE	LCI ^a	UCI ^b
N				
2001	18	2.333	14	23
2002	17	2.116	13	21
2003	19	1.392	16	22
2004	19	1.801	15	22
2005	21	5.164	11	31
2006	14	1.979	10	18
2007	15	2.252	11	20
2008	12	4.270	4	21
2009	14	1.655	11	17
2010	12	1.270	10	15
Φ				
2001	0.918	0.030	0.839	0.961
2002	0.919	0.026	0.850	0.958
2003	0.919	0.024	0.857	0.956
2004	0.920	0.023	0.861	0.955
2005	0.920	0.023	0.861	0.955
2006	0.921	0.024	0.859	0.957
2007	0.921	0.026	0.853	0.959
2008	0.921	0.028	0.846	0.961
2009	0.922	0.031	0.837	0.964
f				
2001	0.055	0.062	0.006	0.377
2002	0.046	0.039	0.008	0.214
2003	0.039	0.025	0.011	0.133
2004	0.034	0.019	0.011	0.100
2005	0.030	0.017	0.010	0.091
2006	0.027	0.018	0.008	0.093
2007	0.025	0.018	0.006	0.099
2008	0.024	0.019	0.005	0.105
2009	0.023	0.019	0.004	0.111
λ				
2002	0.965	0.045	0.675	0.997
2003	0.958	0.032	0.824	0.991
2004	0.954	0.027	0.861	0.986
2005	0.950	0.026	0.866	0.983
2006	0.948	0.027	0.861	0.982
2007	0.946	0.029	0.852	0.982
2008	0.945	0.031	0.840	0.983

^a LCI, lower confidence interval.

^b UCI, upper confidence interval.

(95% CI, 10–15 individuals) in 2008 and 2010 (Table 4). Like other demographic analyses of Boreal Toad populations (Pilliod et al., 2010; Scherer et al., 2008), estimates of Φ showed little temporal variation. However, estimates of Φ in this population (Table 4) were considerably higher than estimates from previous analyses (Pilliod et al., 2010; Scherer et al., 2008).

Finally, all estimates of λ were <1 and indicate that the population is declining by approximately 2–6% per year.

DISCUSSION

Survival at Spruce Lake is higher than reported for other Boreal Toad populations in Colorado (46–80%; Scherer et al., 2008) and seems to have allowed the population to persist in the short term. However, recruitment is substantially lower than values reported previously for toads (e.g., 24–41%, Boreal Toads; Muths et al., 2011; 44–56%, common toads [*Bufo bufo*]; Gittins, 1983). Furthermore, estimates of population growth rate clearly show a declining population ($\lambda < 1$). Without increased recruitment, the outlook for long-term persistence is grim. This scenario is consistent with the observation of Franklin et al. (2000) that the high and temporally consistent survival probability in populations of long-lived species sets the baseline for annual population growth rate. Recruitment rates, alternatively, tend to be temporally variable and are the primary driver of variation in population growth rates across years. In a simulation study, Biek et al. (2002) found that population growth rate was most sensitive to changes in postmetamorphic survival probability in Boreal Toads, but a higher proportion of the temporal variation in population growth rate was explained by changes in embryo and metamorph survival. These relationships are particularly important when considering management actions, and this study quantifies the contribution of recruitment as well as survival in this particular population.

The Spruce Lake population of Boreal Toads is small by most metrics. It is also small relative to other toad populations in similar habitat in Colorado that have been studied recently (e.g., 121 [SE = 40]–249 [SE = 17]; Corn et al., 1997; 55–100 [count data]; Pilliod et al., 2010). Because we lack quantitative long-term data, we are unable to determine whether this population is a small population “naturally” and conservation efforts should focus on ensuring its persistence or whether it is a declining population and is small as a result of some environmental or anthropogenic stressor that should be identified and removed. For example, Bd has been shown to be lethal to

Boreal Toads in the laboratory (Carey et al., 2006) and has been identified as a stressor and a contributing factor in the decline of Boreal Toad populations in RMNP (Muths et al., 2003) and in the region (Carey et al., 2005; Muths et al., 2008). Although there is evidence for survival with Bd by Boreal Toads (Pilliod et al., 2010) and other amphibians (e.g., Briggs et al., 2010), Southern Rocky Mountain Boreal Toads (southern Wyoming, eastern Utah, Colorado, and northern New Mexico; Goebel et al., 2009) seem to be more susceptible to the disease than other closely related Boreal Toads (Murphy et al., 2009).

Although there have been no observed mass mortalities or sick toads, environmental sampling for Bd at Spruce Lake indicated that Bd is present (although very low zoospore equivalents were measured; Kirshtein et al., 2007). Results from animal swabs also indicate a low incidence of infection (three individuals in three separate years) with extremely low zoospore loads. Based on this information and the documented impacts of the disease on toads in the region, it is clear that Bd has the potential to extirpate the toad population at Spruce Lake. Currently, Bd prevalence seems to be so low that the disease is not debilitating, but increases in prevalence could be disastrous for this small population that consists of mostly adult toads. Prevalence of Bd could increase if additional zoospores are transported to the site by anthropogenic or natural means. In addition, the dynamics of the host–pathogen relationship could change (vis a vis changes in the toad population or changes in climate); potentially favoring Bd and allowing for increased prevalence, infection rate, and death in the host (sensu Briggs et al., 2010), or, conversely, influencing host survival positively (e.g., McCaffery and Maxell, 2010) and thus generating a density-dependent response to disease.

At Spruce Lake, stressors, both potential (disease) and realized (anthropogenic impacts of fishing) are probably influencing the trajectory of the population. We present two plausible scenarios that, if realized, could lead to the extirpation of Boreal Toads at this site. First, if recruitment remains the same or decreases there will be few toads producing offspring; as adult toads senesce, the population will

gradually go extinct. Second, if prevalence of Bd increases, this population is likely to be extirpated within 1–2 yr, following the pattern documented for other Boreal Toad populations elsewhere in RMNP (Muths et al., 2003). Briggs et al. (2010) present hypotheses on host–pathogen interactions that allow the persistence of amphibian populations challenged by disease, but such response is predicated on a reasonably large population, unlike that at Spruce. Recolonization of Spruce is unlikely because of the isolation of the site and the paucity of Boreal Toad populations nearby (Corn et al., 1997).

Although it is clear that recruitment is not adequate to sustain the population at Spruce Lake, we do not know why it is low. The presence of fish may limit recruitment. Observed spawning sites, used by toads over the last 10 yr, are accessible to fish. Numerous studies indicate that fish prey on ranid frog eggs and tadpoles (e.g., Knapp and Matthews, 2000; Pilliod and Peterson, 2001) and that in the absence of fish, frog density and young adult frog survival increase (Pope, 2008). However, Yosemite Toads (*Anaxyrus canorus*; and probably other bufonids) are not palatable to Brook Trout (*Salvelinus fontinalis*; Grasso et al., 2010), suggesting that direct predation by fish on Boreal Toads at Spruce Lake is not important. Although the occasional ingestion of eggs by a naïve fish may impact a population producing few egg masses, it is more likely that the presence of fish has an indirect impact on toads. The marshy areas surrounding the spawning site—habitat used by recently metamorphed toads—is trampled throughout the summer by anglers as they move around the lake (E. Muths and R. D. Scherer, personal observation). This activity has the potential for direct mortality of metamorphs and for indirect mortality associated with habitat alteration (i.e., drying and destruction of refugia; e.g., Browne, 2010), thus limiting recruitment. These possibilities are clearly speculative but could be tested by excluding fish from spawning areas in the lake and protecting metamorph habitat in the late spring and summer.

Although challenging to acquire, reliable estimates of demographic parameters in small populations are critical in (1) developing theory about small populations, specifically

how naturally small populations persist over time (i.e., the small population paradigm); (2) understanding the demographic response of declining (and perhaps small) populations when challenged by stressors (i.e., the declining population paradigm); and (3) formulating management options. We suggest that defensible estimates of parameters allow a better understanding of the target population and may yield clues to enable assignment of the population to one branch of the Caughley (1994) dichotomy or the other and better direct conservation measures. High probability of capturing toads (multiple site visits per year) and using capture–recapture models for data collected under Pollock’s robust design (Kendall and Nichols, 1995) has facilitated our ability to estimate key demographic parameters at Spruce Lake despite small sample sizes and represents a step toward accurate assessment of population demographics for use in the identification and design of management options. This study illustrates that tracking the behavior of populations through time, especially those in a landscape that harbors identified threats (i.e., disease), contributes to our understanding of potential interactions between population declines leading to smallness and the effect of smallness (natural or induced) on persistence.

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