



Post-catastrophe patterns of abundance and survival reveal no evidence of population recovery in a long-lived animal

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Abstract. Population catastrophes are widespread, unpredictable phenomena occurring in natural populations that have important, yet frequently underappreciated, consequences for persistence. As human impacts on ecosystems increase globally, the frequency of catastrophes is likely to rise as increasingly fragmented and depleted populations become more vulnerable. Species with slow life histories are expected to recover slowly from catastrophes because of their longer generation times, and assessing their population recovery requires data spanning long periods. We report results from a long-term mark–recapture study of snapping turtles (*Chelydra serpentina*) in Algonquin Provincial Park, Ontario, that experienced a major mortality event from winter predation by river otters. We estimated abundance and survival of nesting females before, during, and 23 yr following the catastrophe. We built multistate mark–recapture models incorporating movement between sites, temporary emigration, and observation effects. We found that during the 3-yr mortality event, abundance of nesting females declined by 39% overall, and by 49% at our focal nesting area. Apparent survivorship of nesting females during these three years fell from 0.94 before the mortality event to 0.76 at the focal site and 0.86 at adjacent nest sites. Survivorship over the following 23-yr period averaged 0.972 and 0.940 at the two sampling areas. Despite high post-catastrophe survivorship and connectivity with other populations, the population failed to recover, displaying consistently reduced abundances across 23 post-catastrophe years. We discuss the relationship between life-history attributes and the causes and consequences of local catastrophes and their conservation implications.

Key words: *Chelydra serpentina*; density dependence; multinomial m-array; multistate mark–recapture model; parameter-expanded data augmentation; reproductive frequency; temporary emigration; trap-happiness.

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INTRODUCTION

The current global extinction crisis has resulted in an estimated one-thousand-fold increase in extinction above the baseline rate (Pimm et al. 2014). A recent assessment of vertebrate populations based on the Living Planet Index (Collen et al. 2009) estimates that average declines in abundance since 1970 have reached 52% (World Wildlife Fund 2014). The greatest single contributing factor to these observed declines is direct

exploitation (World Wildlife Fund 2014). Another emerging global threat is climate change (World Wildlife Fund 2014), which is increasing environmental variability, including the potential for increases in the frequency of extreme weather-related events, such as wildfires, droughts, and floods (IPCC 2014). Both classes of threats can produce catastrophes, resulting in sudden and severe declines in abundance of affected populations (Fey et al. 2015). A catastrophe may be defined as a short-term decline of over 50% of a

population, and the probability of catastrophes in vertebrate populations is estimated to be 14% per generation (Gerber and Hilborn 2001, Reed et al. 2003, Ward et al. 2007). Natural and anthropogenic population catastrophes can have a disproportionately large impact on population persistence and in many cases may be the dominant process causing extinctions (Menges 1990, Mangel and Tier 1994, but see Finkelstein et al. 2010). The risk that catastrophes pose to population persistence is expected to depend on their frequency relative to generation time (Frankham and Brook 2004, O'Grady et al. 2008). Thus, for long-lived species, catastrophes that are spaced far apart in time could still have important effects on abundance and persistence. Unfortunately, published reports of catastrophes often fail to quantify long-term consequences (Fey et al. 2015).

Life-history traits have important consequences for population responses to potentially catastrophic events. Populations with faster life histories are more vulnerable to perturbations in reproductive success, whereas those with slow life histories are most sensitive to adult survivorship (Jonsson and Ebenman 2001) and thus take longer to recover from depletion (Roff 2002, Hutchings and Reynolds 2004, Neubauer et al. 2013). Conversely, length of generation time is positively correlated with per-generation strength of density-dependent compensation in some groups such as birds (Sæther et al. 2005), marine fishes (Bjørkvoll et al. 2012), and freshwater fishes (Vélez-Espino and Koops 2012). Species with fast life histories also tend to be more sensitive to environmental stochasticity, which disproportionately impacts younger age classes, and show more variation in population growth rate (Jonsson and Ebenman 2001, Gaillard et al. 2005, Sæther et al. 2005, Bjørkvoll et al. 2012). Effective density-dependent compensation increases population growth rate following declines, eventually allowing for recovery from perturbations.

Among vertebrates, turtles are disproportionately imperiled (Gibbons et al. 2000, Böhm et al. 2013). Turtles typify the slow end of the life-history spectrum, exhibiting iteroparity, high adult survivorship, and low and variable juvenile recruitment. Populations of organisms with slow life-history strategies are vulnerable to even small decreases in adult survivorship, with as little as a 2–3% reduction in survivorship resulting in severe

population decline (Congdon et al. 1993, 1994, Cunnington and Brooks 1996, Enneson and Litzgus 2008). As with other long-lived organisms, much concern in chelonian conservation has been focused on anthropogenic increases in chronic mortality caused by threats such as road mortality (Steen et al. 2006), fishing gear entanglement (Steen et al. 2014, Midwood et al. 2015), hunting and collecting (Garber and Burger 1995, Nickerson and Pitt 2012, Colteaux and Johnson 2017), boat strikes (Bulté et al. 2010, Bennett and Litzgus 2014), and introduced or subsidized predators (Fordham et al. 2007). In addition to chronic threats, acute catastrophes have been observed in populations of multiple chelonian species in different ecological contexts. Catastrophic local declines have been caused by droughts (*Gopherus agassizii* [Longshore et al. 2003], *Chrysemys picta* [Christiansen and Bickham 1989]), fire (*Testudo hermanni* [Stubbs et al. 1985, Hailey and Willemssen 2000]), pathogens (*Terrapene carolina* [Johnson et al. 2008], *Myuchelys georgesi* [Spencer et al. 2018]), road mortality (Aresco 2005), and hunting (Nickerson and Pitt 2012). In some cases, the causes are mysterious (Sheppard 2014, Catrysse et al. 2015). Many ecologists and conservationists believe that turtles are likely to have only a weak ability to compensate for perturbations and that recovery of turtle populations after declines will be extremely slow, if they occur at all (Brooks et al. 1991, Congdon et al. 1993, 1994, Cunnington and Brooks 1996, Heppell 1998, Enneson and Litzgus 2008). However, some authors have suggested that some turtle populations show a more robust compensatory response (Stubbs et al. 1985, Bjørndal et al. 2000, Spencer et al. 2006, Fordham et al. 2009). For long-lived species, a better understanding of the long-term risks associated with short-term perturbations is needed to inform management decisions.

Snapping turtles (*Chelydra serpentina*) are near the northern limit of their distribution in Algonquin Park, Ontario, Canada, where a population in Lake Sasajewun has been the subject of a long-term life-history study since 1972. Snapping turtles in this population have very slow life histories with late age at maturity (16–19 yr for females), low and variable recruitment, and high adult survival (Galbraith et al. 1989, Brooks et al. 1991, Cunnington and Brooks 1996, Armstrong and Brooks 2013). During the winters of 1986–1989,

the study population experienced predation by river otters (*Lontra canadensis*) that amounted to an acute catastrophe in which approximately 50% of the adult population was killed (Brooks et al. 1991). Given the slow life history of turtles, and the climatic constraints experienced by northern populations, Brooks et al. (1991) predicted a very slow and limited recovery. Here, we present updated abundance and survival for this population to evaluate the recovery 23 yr after the catastrophe and in light of a second putative mortality event resulting from the blowout of the dam on the study lake. Abundance and survival of nesting females were analyzed using multistate models that allowed for survival and detection to vary with time and between sites and accounted for movement between sites and temporary emigration (TE). We assess evidence for density-dependent compensation in nesting female survivorship by comparing survival before and after the catastrophe using Bayesian variable selection and examining the trend in abundance. We also estimate recent abundance of adults in the study lake and compare it to previously reported pre- and post-catastrophe estimates.

METHODS

Study site and sampling methods

The long-term snapping turtle life-history project began in 1972 at the Algonquin Wildlife Research Station (WRS) in Algonquin Provincial Park, Ontario, Canada. Because of the combination of high latitude and cold regional climate, the study site is near the northern climatic limit of the distribution of snapping turtles (Boby and Brooks 1994). Annual capture–mark–recapture (CMR) sampling with baited hoop traps, opportunistic capturing from canoe, and nest site monitoring occurs at the WRS population within the North Madawaska River (NMR) drainage basin and at several alternate sites near the Highway 60 corridor within 10 km of the WRS. Lake Sasajewun, a 43.5-ha impoundment of the North Madawaska River, has received the majority of the trapping effort although surrounding water bodies have also been surveyed. Turtles are marked by notching the marginal scutes (Cagle 1939), and adults are tagged by wiring aluminum tags into holes drilled through the marginal scutes (Loncke and Obbard 1977).

Further details of the study site and field methods are described elsewhere (Obbard and Brooks 1981, Galbraith et al. 1988, Keevil et al. 2017).

Defining populations for analyses

We performed two separate mark–recapture analyses. First, we analyzed survivorship and abundance of females sampled during 34 yr of nesting surveys at sites within the NMR basin (Fig. 1). Second, we estimated recent abundance of the adult male and female residents of Lake Sasajewun sampled by trapping and canoe captures to assess recovery of both sexes using data that are independent of nest site selection.

The analysis of survival and abundance of nesting females was performed for the period from 1980 to 2013. Females were considered to have entered the population upon their first capture at a nesting site within the NMR, and only subsequent recaptures during nest site monitoring were included. Recaptures by aquatic sampling were excluded from this portion of the analysis as they would be biased toward the subset of females whose summer home ranges are in Lake Sasajewun. The embankment of the Sasajewun dam at the southeast end of the lake is the most intensively monitored and most important nest site for turtles residing within the lake and in water bodies upstream. Between the dam and the mouth of the river at Lake of Two Rivers are five other known nesting areas (Fig. 1). In addition, we also included nesting sites around Mew Lake, which is 200 m away from the North Madawaska River and is connected by a short tributary (700 m). The greatest straight-line distance between any two nesting sites is 2.3 km (Fig. 1).

Abundance of adult females at monitored nesting sites might not track abundance of adults in aquatic habitat. To assess this possibility, we estimated the recent adult population size at Lake Sasajewun, our focal aquatic sampling site, and assessed similarity to historical abundance estimates before and during the 1986–1989 mortality event reported by Brooks et al. (1991). Adult turtles (females with straight-line carapace lengths [SCL] >24 cm; males SCL >30 cm) captured by baited hoop trap or by canoe in Lake Sasajewun from 2009 to 2013 were included in survival and abundance estimates of the lake population. During this period, data on secondary (within-season) captures were available. Juveniles and sub-adult

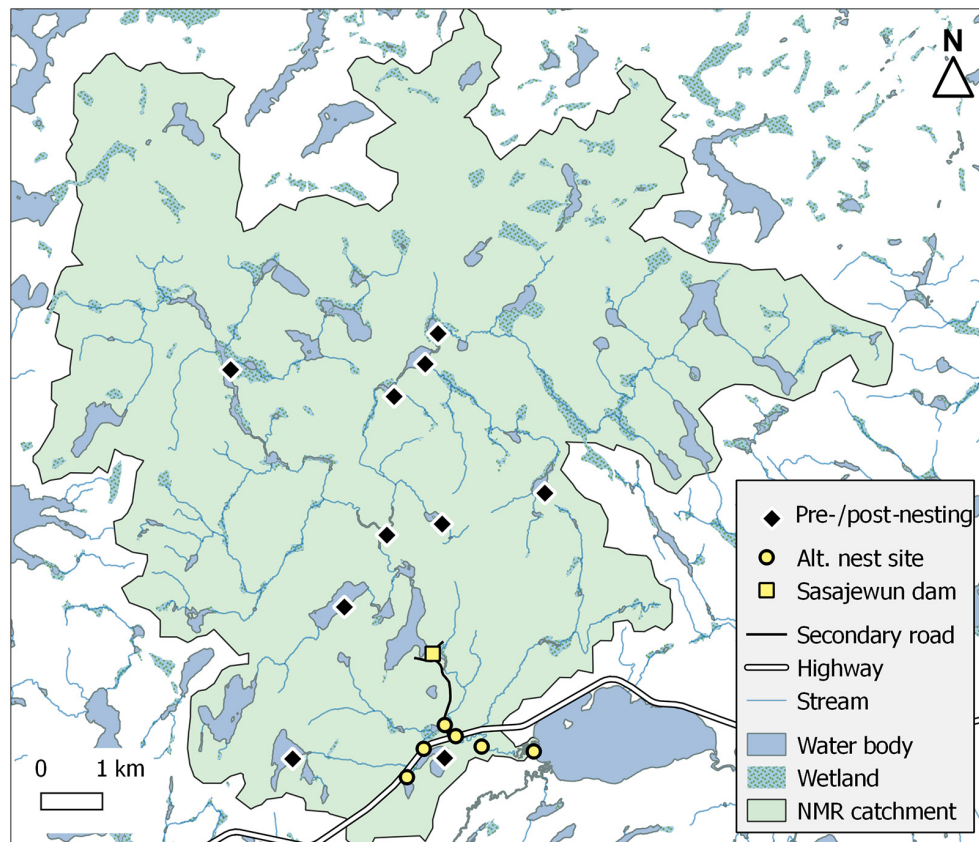


Fig. 1. The North Madawaska River basin in Algonquin Park, Ontario. The Sasajewun dam snapping turtle (*Chelydra serpentina*) nesting site (yellow square) and alternate nesting sites (yellow circles) are indicated, as well as selected distant observations of dam-nesting females outside of nesting season (black diamonds; Obbard and Brooks 1980, previously *unpublished data*).

turtles were excluded from the analysis because of their substantially lower recapture rate (Keevil et al., *unpublished data*). The criterion for minimum female size reflects the known threshold for maturity in our study area (Armstrong and Brooks 2013), whereas that for males is based on our observation that smaller males are less likely to be recaptured within the same water body and less likely to show sex-specific behaviors such as eversion of the penis and wounding from conspecific aggression (Keevil et al. 2017).

Mark–recapture analysis I: Nesting females (1980–2013)

To estimate abundance and survival of nesting females, we developed CMR models that treated nesting on the Sasajewun dam as a state and nesting on the other sampled sites within the NMR

basin (“alternate sites”) as a second state to allow for possible differences in survival and detection among sites. Population analysis of nesting females was therefore done in a multistate framework (Brownie et al. 1993). Development of models proceeded in four steps: (1) Goodness-of-fit (GOF) testing for standard, initial multistate models was performed in Programs MARK and U-CARE; (2) Incorporating observation effects (OE) and TE to create candidate base models using the multistate m-array parameterization (Burnham et al. 1987, Lebreton et al. 2009) implemented in Program JAGS (Plummer 2003) to account for lack of fit. Fit was then reassessed using posterior predictive checks. (3) After selecting a base model, further model selection was done for recapture and survivorship parameters using Gibbs variable selection (GVS; Dellaportas et al. 2000, O’Hara

and Sillanpää 2009) to assess support for hypotheses of survival differences between periods (before, during, and after mortality events) and states (dam and alternate sites) and to select an appropriate structure with which to assess abundance; (4) Abundance was assessed using a state-space model with parameter-expanded data augmentation implemented in WinBUGS (Lunn et al. 2000, Royle and Dorazio 2012). Each of these steps is described in the following sections, and further details are given in Appendix S1.

Initial model construction and GOF.—The CMR data of nesting females were analyzed using multistate models with nesting on the Sasajewun dam as one state and nesting at pooled alternate sites as another state to allow for transitions and differential survival and detection probability between sites (Brownie et al. 1993). We included *period* as a categorical time effect on survival and movement to reflect a priori hypotheses about the effects of the otter predation event (before, during = otter, after) and the temporary failure of the Sasajewun dam during the spring of 1998 (blowout; Appendix S1: Table S1). Program U-CARE (Choquet et al. 2005) was used to test GOF of the fully parameterized multistate model (Pradel et al. 2003). Goodness-of-fit of a reduced-parameter model was tested using the parametric bootstrap GOF procedure implemented in Program MARK (White and Burnham 1999, White et al. 2006).

Construction of candidate general models.—Three candidate general models were implemented in Program JAGS (Plummer 2003) and assessed for adequate fit to the data before further model selection: constrained conditional Arnason–Schwarz (CAS), CAS modified for TE, and CAS with immediate OE. Because of sparseness of the data, and informed by a preliminary exploration in MARK that indicated that many parameters were not identifiable in models with fixed time effects on survival and transitions, we started with a constrained, reduced-parameter model:

$$S_{\text{site} \times \text{period} + E(t)} p_{\text{site} \times t} \Psi_{E(t)}^{S-}$$

which has fixed effects of period, site, and their interaction as well as random year effects ($E(t)$) on survivorship, S ; fixed period and site effects on recapture probability p ; and random time effects on state transitions Ψ . Treating year as a

random effect requires far fewer parameters than fixed time effects while avoiding the potentially unrealistic constraint of identical parameters across multiple years. Using random effects leverages the large number of sampled occasions to estimate time variation and to share data across years despite relatively low numbers of observations per occasion. We treated year as a fixed effect on p because our initial data exploration indicated multiyear trends and because a priori knowledge of long-term fluctuations in recapture effort suggested that separate parameters for each year would be more appropriate.

We chose the m-array parameterization for model selection and GOF analysis because it was better-suited than state-space models for posterior predictive checking and comparing among candidate models (Kéry and Schaub 2012). See Appendix S1 for details of multistate m-array model construction.

Temporary emigration.—We modified the CAS framework to account for TE by adding unobservable states (Fig. 2; Fujiwara and Caswell 2002, Kendall and Nichols 2002, Schaub et al. 2004). We used two unobservable states: C1 for individuals that became temporarily unavailable for capture from the Sasajewun dam (A) and C2 for individuals temporarily unavailable from the alternate sites (B). Under this model, individuals could not transition between C1 and C2, B and C1, or A and C2. Survival in C1 was the same for A, and C2 survival was the same as B. Because our dataset is relatively sparse, we modeled transition probabilities involving unobservable states as time-invariant fixed effects. See Appendix S1 for multistate m-array model modifications for TE.

Observation effects.—Observation effects occur when the probability of detection varies depending on whether an individual was observed on a previous occasion, and are often called behavioral response or trap dependence (Otis et al. 1978, Pradel 1993), although such effects can result from observer behavior rather than behavioral responses of animals (Schaub et al. 2005, Kéry and Schaub 2012, Papadatou et al. 2012). Observation effects can be modeled using a separate, individually indexed recapture matrix (Kéry and Schaub 2012, Pradel and Sanz-Aguilar 2012) or multiple states can be used to model immediate OE in the state-space framework (Gimenez et al. 2003, Schaub et al. 2009, Pradel and Sanz-

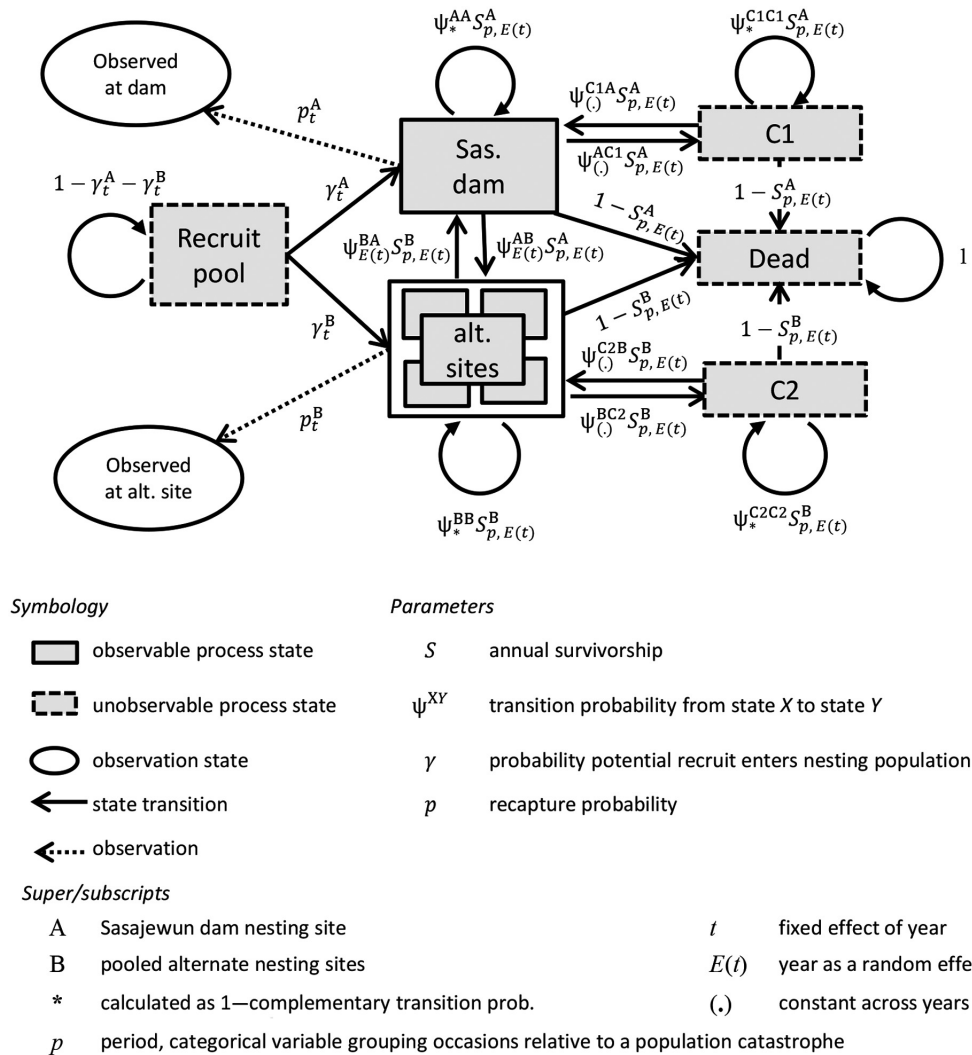


Fig. 2. Structure of the general multistate mark–recapture model with temporary emigration for nesting female snapping turtles (*Chelydra serpentina*) in Algonquin Park. The recruit pool and associated transitions occur in the state-space model of abundance but not in the multinomial m-array parameterization used for model selection.

Aguilar 2012). Instead, we devised another method that was more straightforward to implement in the multistate m-array formulation (see Appendix S1 for details).

Comparing candidate general models.—We assessed the fit of our three candidate general models, CAS, TE, and OE, using posterior predictive checks (Gelman et al. 2004). We compared model discrepancy, calculated as the Freeman-Tukey statistic, between the observed data and data simulated using the model (Brooks et al. 2000, Kéry

and Schaub 2012). Fit statistics were computed within the JAGS model code and assessed visually using scatterplots and Bayesian P -values (Gelman et al. 2004). Deviance information criterion (Spiegelhalter et al. 2002) was computed in JAGS and used to compare TE and OE models.

Variable selection.—We used a generalized linear model (GLM) parameterization for S and p to examine effects of individual parameters and for variable selection. The general model for survivorship is

$$\text{logit}(S) = \beta_0 + \beta_1 + \beta_2 + \beta_3 + \beta_4 + \beta_5 + \beta_6 + \beta_7 + \varepsilon_t$$

where β_0 = intercept, $\beta_{1..3}$ are the effects for three of the four levels of *period* (the first level is the intercept), β_4 is the effect of site, and $\beta_{5..7}$ are the interactions of site and period, and ε_t is the random time effect. To induce a minimally informative prior for mean survivorship on the probability scale, we used a $\mu_i = 0$ for the mean and an inverse gamma hyperprior (King et al. 2010) for the variance, $\sigma_i^2 \sim \Gamma^{-1}(4, 5)$, as β_i priors. This produces an approximately flat prior for sums of three parameters (Appendix S1: Fig. S1). We used the same prior for each parameter in our general model of recapture probability p :

$$\text{logit}(p) = \beta_{\text{site}} + \beta_{T(1)} + \dots + \beta_{T(T)} + \beta_{\text{site} \times T(1)} + \dots + \beta_{\text{site} \times T(T)}$$

or

$$\text{logit}(p_{\text{site},t}) = \beta_{\text{site}} + \beta_{T(t)} + \beta_{\text{site} \times T(t)}$$

where β_{site} are the fixed site effects, $\beta_{T(t)}$ are the fixed effects of occasion t , and $\beta_{\text{site} \times T(t)}$ are the interactions of site and occasion t .

We used GVS (Dellaportas et al. 2000) to assess support for the inclusion of parameters affecting S and p . To assess effects of site, occasion, and their interaction on recapture probability, the 33 occasion parameters were assigned a single inclusion parameter, as were the 33 interaction parameters, with the result that these variables were selected (or not) as single blocks. We only considered nested sub-models so that models with an interaction always included both occasion and site main effects. This resulted in five possible sub-models: $p(\cdot)$, $p(t)$, $p(\text{site})$, $p(\text{site} + t)$, and $p(\text{site} \times t)$ (notation adapted from Lebreton et al. [1992]).

In order to apply GVS to survivorship parameters, we used dam = 1, alternate sites = 0 dummy coding in the design matrix of the survivorship GLM so that the interaction site \times period _{i} without one or both of the corresponding main effects parameters implies a model in which the effect of period _{i} applies only to the dam-nesting females. We view such non-nested candidate models as meaningful hypotheses in which survival changed at the Sasajewun dam but not at the alternate sites which were farther from the observed mortality. Further details

about our implementation of GVS are available in Appendix S1.

Estimation of abundance of nesting females using data augmentation.—In the CAS family of models, individuals are excluded from the likelihood before first capture, and therefore, abundance cannot be directly estimated. To estimate abundance, we modified our preferred model, TE, identified using the procedure described above (and see *Results*), to implement it in a state-space formulation with parameter-expanded data augmentation (Fig. 2). This model was implemented in Program WinBUGS (Lunn et al. 2000) through the R package R2WinBUGS (Sturtz et al. 2005, R Development Core Team 2014). While not a focus of our analysis, a consequence of the abundance model with TE is that it produces an estimate of the number of females that are unavailable during nesting which has bearing on reproductive frequency, an important but difficult-to-estimate life-history parameter. State-space CMR models separate the observation (captured in A, captured in B, not captured) and population processes (entry, survival, and site transitions; Gimenez et al. 2007, Royle and Dorazio 2008), and are convenient to implement in WinBUGS. In the multistate formulation described in Royle and Dorazio (2012), the removal entry probability, $\gamma_{t,sr}$ is the probability that an individual M_i in the pre-entry state will be recruited into an alive state s (in our case, one of two nesting areas: A = dam and B = alternate) on occasion t . This parameter is required to implement data augmentation but does not have direct biological meaning (Kéry and Schaub 2012, Royle and Dorazio 2012). A dummy occasion was added before the first occasion (so that indexing differs between m-array and state-space models, see Appendix S1: Table S1), and thus, $\gamma_{1,s}$ becomes the proportions of individuals present on the first real occasion at each site and the multistate model becomes conditional on individuals being present rather than conditional on initial capture, allowing abundance and time-dependent recruitment of adults at nesting sites to be estimated (Kéry and Schaub 2012). Details of our implementation of the data-augmented state-space model are provided in the Appendix S1.

To quantify the effect of the single dam blow-out event in early spring 1998, we estimated the number of nesting female turtles that died

during that 1997–1998 interval by subtracting the number expected to die in a typical post-catastrophe interval (mean survivorship during 1989/1990–2012/2013, subscript pc) from the estimated number of actual deaths:

$$\begin{aligned} \text{deaths} = & \sum_{i=1}^M \mathbb{I}(z_{i,19} \neq 6 \text{ AND } z_{i,20} = 6) \\ & - \text{Bin}\left(\left(N_{97}^A + N_{97}^{C1}\right), \left(1 - \bar{S}_{pc}^A\right)\right) \\ & - \text{Bin}\left(\left(N_{97}^B + N_{97}^{C2}\right), \left(1 - \bar{S}_{pc}^B\right)\right) \end{aligned}$$

where z_{ij} is the latent state matrix that contains information on the known or estimated state of each individual i on each occasion j (see Appendix S1 for details).

Mark–recapture analysis II: Abundance of males and females (2009–2013)

We performed a simple robust design analysis to estimate mean adult male and female abundance in Lake Sasajewun using trap and canoe captures over five years (primary occasions). We consolidated trapping and canoe surveys within each year into one to three secondary occasions (Table 1) and counted the number secondary occasions in which each individual was captured in each year. We analyzed these data using a state-space formulation with data augmentation

Table 1. Timing and duration, trap days, and number of captures of snapping turtles (*Chelydra serpentina*) for secondary (within a season) sampling occasions using baited hoop traps and dip nets in Lake Sasajewun, Algonquin Park, Ontario.

Survey period		Trap days	Captures	
Start	End		Male	Female
1 May 2009	1 June 2009	0	4	5
1 July 2009	1 October 2009	113	5	4
1 June 2010	1 July 2010	0	3	3
1 July 2010	15 September 2010	32	2	2
1 May 2011	25 May 2011	0	3	5
26 May 2011	1 July 2011	45	9	8
1 May 2012	1 July 2012	0	5	7
1 July 2012	15 September 2012	276	13	14
14 April 2013	21 May 2013	2.5	3	3
21 May 2013	1 July 2013	72.5	3	4
1 July 2013	15 September 2013	61	4	3

Note: Juveniles and sub-adults (females straight-line carapace length [SCL] <24 cm, males SCL <30 cm), which were not used in our analyses, are excluded from counts.

similar to that described above for abundance of nesting females. We assumed that the number of observed encounters of each individual in each occasion was a binomial random variable with the total equal to the number of secondary occasions, and probability as the product of recapture probability $p_{i,t}$ and the latent state $z_{i,t}$ (Royle and Dorazio 2012). Because of the small sample of individuals and occasions, and our limited objectives for this analysis (mean abundance), we did not use formal model selection to rank a large number of models, and instead chose a reasonable reduced-parameter fixed-effects model ($\varphi_{\text{sex}} p_{\text{sex}} + t \gamma_t \times \text{sex}$) that assumed apparent survival φ varied only by sex, recapture probability varied by primary occasion with a constant additive effect of sex on the logit scale, and removal entry probability varied by time and sex. This analysis was carried out in Program WinBUGS (v.1.4; Lunn et al. 2000) through the R2WinBUGS package in Program R (Sturtz et al. 2005, R Development Core Team 2014).

RESULTS

Mark–recapture analysis I: Nesting females (1980–2013)

Between 1980 and 2013, 140 individual female snapping turtles were observed at the NMB nesting sites. Fifty-eight females were observed nesting across sites on the first occasion, but only 22 were confirmed on the last occasion. Seven turtles were observed on both the first and last occasions, and another two females were known to be alive but not observed on one of those occasions. One female that nested in 2013 had been recorded nesting in 1972, which was the first year the population was studied. Three others observed in 2013 were first observed nesting in 1973. All four had already been nesting for some years, based on size at initial capture (Armstrong and Brooks 2014).

Model selection.—A multistate model with TE emerged as our preferred model (see Appendix S1 for detailed results of GOF analysis and initial model selection). Apparent survival beta parameters, posterior means, and 95% credible interval (CRI) of the general model (Fig. 3) compared with those of the OE model (see Appendix S1 for OE model results). Temporary emigration model-averaged apparent survival, state transition, and recapture probabilities are shown in Fig. 4. Marginal posterior probabilities of each parameter

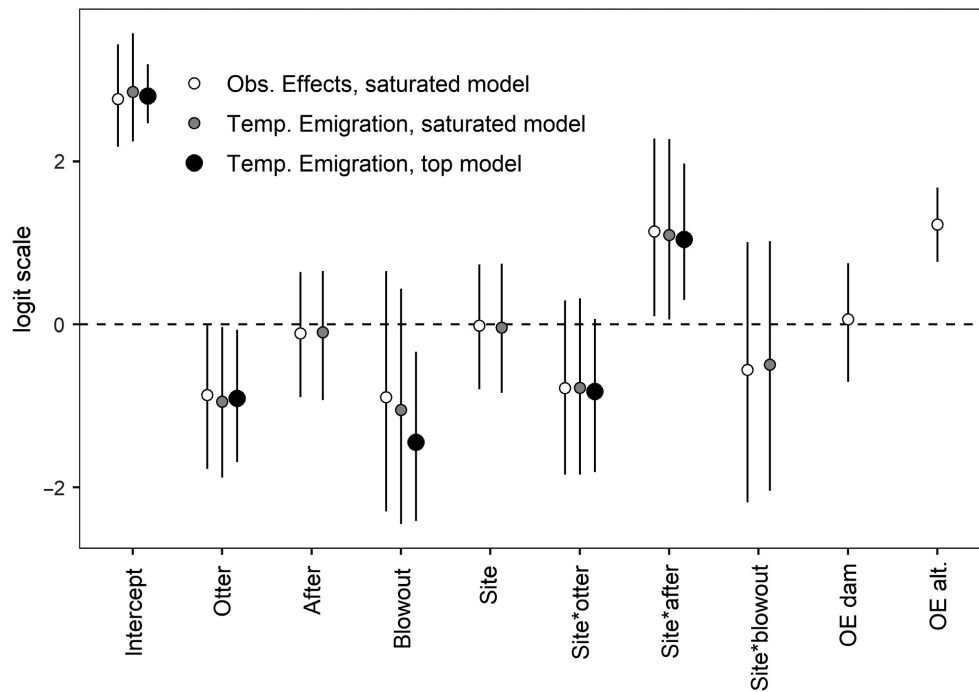


Fig. 3. Relative strength and uncertainty (means and 95% CRIs) of period and site effects on survival, and observation effects (OE) on detection, compared among three multistate models of nesting female snapping turtles (*Chelydra serpentina*). Positive effects are associated with increases in survival or in recapture probability. Models shown are the temporary emigration (TE) and OE models before Gibbs variable selection (GVS) and the top TE model after GVS. The first eight parameters are effects of four periods (the first is the intercept), site (dam or alternate), and interactions on apparent survival. Because of the design matrix coding, site interactions without corresponding main effects apply to the dam, but not to alternate sites. The final two parameters are the immediate observation effect on recapture probability of dam (*OE dam*) and alternate site (*OE alt.*) nesters. There was good agreement on survivorship parameters between the TE and OE models. Within the OE model, there was a “trap-happy” response at the alternate sites but not at the dam site.

were averaged across models for survivorship parameters and recapture sub-models to assess their relative support (Tables 2, 3). Support for an effect of otter predation on apparent survival was very high, with 99.8% posterior probability of effects of otter or otter \times site (Table 2). Likewise, pooling main and interaction effects, there were >90% posterior probabilities for a change in survival during the post-otter low abundance period (after) and for the blowout effect. Only after had higher support for the interaction term alone than for the main effects or main effects and interaction, which indicates that the after- effect primarily affected individuals nesting on the dam. There was little support for excluding any of the period effects (Table 2). Out of a model space of 635, no single combination of survival and recapture

parameters achieved >10% posterior probability following GVS, indicating that no single model received unambiguous support and therefore we selected the highest probability combination of main and site interaction effects for each period resulting in the following model used to estimate abundance:

$$\text{logit}(S_{i,t}) = \beta_0 + \beta_{\text{otter}} + \beta_{\text{otter} \times \text{site}} + \beta_{\text{after} \times \text{site}} + \beta_{\text{blowout}} + \varepsilon_t$$

A time-dependent model of recapture probabilities ($p(t)$, 72% posterior probability) was highly supported while a model with additive site effects was the second most supported ($p(\text{site} + t)$, 23% posterior probability; Table 3).

Survivorship, transition, and recapture probability.— Apparent survival, taking into account model

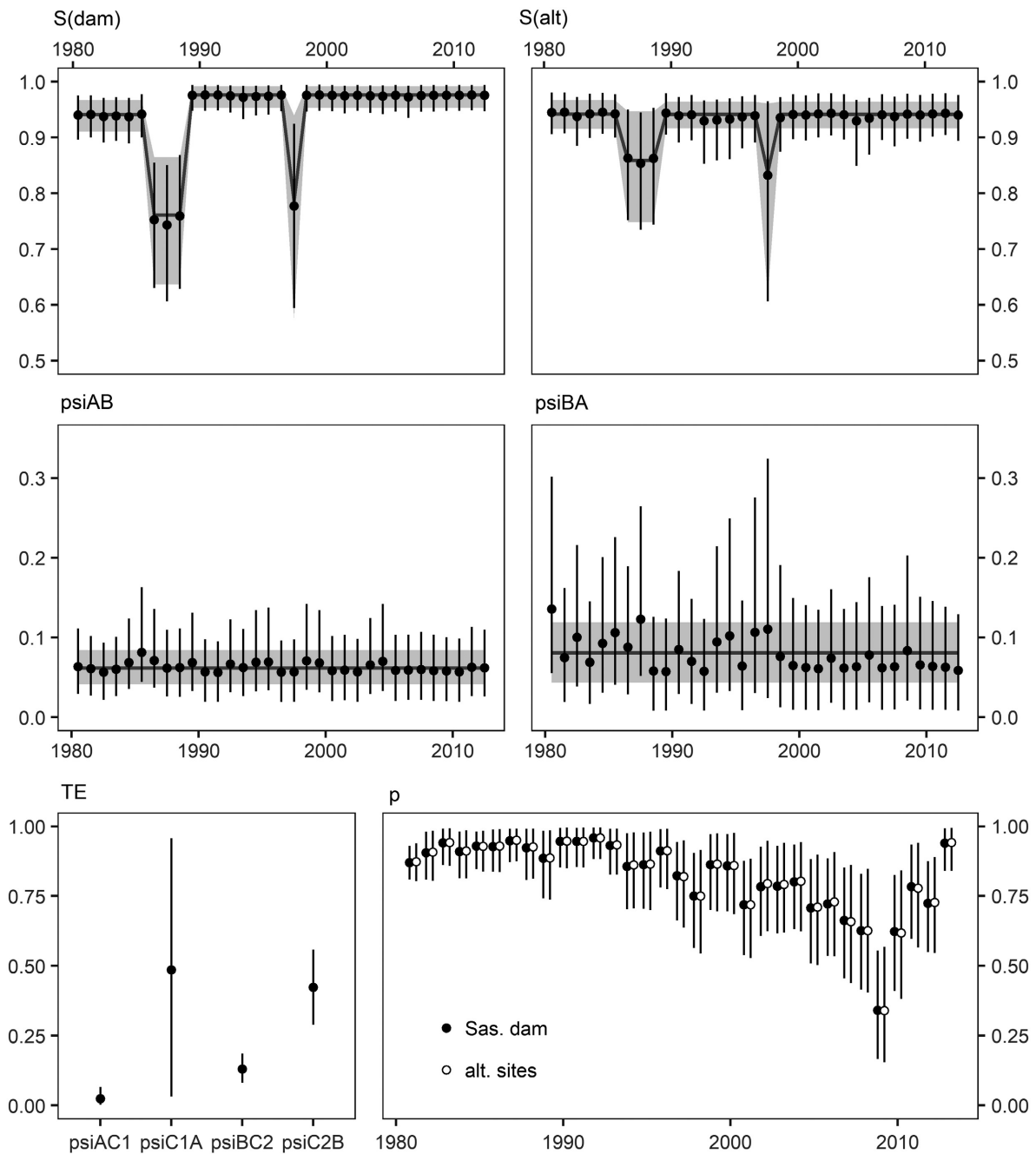


Fig. 4. Model-averaged estimates of survival, transition, and recapture parameters from multistate mark–recapture models of nesting female snapping turtles (*Chelydra serpentina*) in Algonquin Park. Models were averaged using Gibbs variable selection on apparent survival (S) and recapture (p) effects. Hyperparameter means are shown by solid lines with shaded 95% CRIs. $S(\text{dam})$ and $S(\text{alt})$ show estimates of survival for females nesting at dam and alternate sites, respectively. psiAB is transition from dam to alternate sites, while psiBA is the reverse. Temporary emigration (TE) shows constant (no time variation) transition probabilities to (psiAC1 , psiBC2) and from (psiC1A , psiC2B) unobservable states (i.e., TE). Parameter psiC1A was not identifiable (Appendix S1: Fig. S4).

Table 2. Results of Gibbs variable selection for main effects and site interactions of apparent survival parameters of nesting female snapping turtles (*Chelydra serpentina*) in Algonquin Park over 33 occasions with two observable states (dam and alternate nesting sites) and two unobservable states to account for temporary emigration.

Effect	Probabilities of main effect and interaction with site						
	Marg. main	Marg. ixn	Both	Either	Main only	Ixn only	Neither
Otter	0.82	0.68	0.50	1.00	0.32	0.18	0.00
After	0.23	0.91	0.21	0.93	0.03	0.70	0.07
Blowout	0.76	0.51	0.31	0.96	0.45	0.20	0.04
Site	0.25	NA	NA	NA	NA	NA	NA

Note: Models with only an interaction effect ("ixn only") have a period effect for dam-nesting females but not alternate site females.

Table 3. Support for recapture probability sub-model structure assessed using marginal posterior probabilities from Gibbs variable selection within a multi-state model of nesting female snapping turtles (*Chelydra serpentina*) in Algonquin Park over 33 occasions with two observable states (dam and alternate nesting sites) and temporary emigration.

Model	Marginal probability
$p(\cdot)$	0.00
$p(t)$	0.72
$p(\text{site})$	0.00
$p(t + \text{site})$	0.23
$p(t \times \text{site})$	0.05

uncertainty, varied across site and period (Figs. 4, 5). Mean apparent survivorship estimates of the abundance model over the four periods (before, otter, after, blowout) are shown with credible intervals in Fig. 5. Survival at the alternate sites was mostly constant across years except for the otter predation and dam blowout events (Fig. 4). The impact of the otter mortality event was more severe for dam-nesting turtles. After the mortality event, apparent survivorship of dam-nesting females was higher than at the alternate sites and higher than during the before period.

Mean annual probability of a female switching nest sites from the dam to an alternate site was 0.062 (95% CRI 0.041, 0.084) with variance 0.3 (0.0, 0.8), whereas switching from an alternate site to the dam was 0.081 (0.043, 0.12) with variance 0.6 (0.0, 1.4; Figs. 4, 5). The estimate of constant transition probability from the dam to an unobservable state (ψ_{AC1}) was 0.024 (0.002, 0.066) and that from alternate (ψ_{BC2}) sites was 0.13 (0.08, 0.18). Females returned to the alternate sites from an unobserved state (ψ_{C2B}) with

probability 0.42 (0.29, 0.56). The probability of returning to the dam from an unobserved state was 0.49 (0.030, 0.96), which is essentially the same mean and CRI as the $U[0, 1]$ prior, strongly suggesting that this parameter was not identifiable (Appendix S1: Fig. S4; Gimenez et al. 2009).

Estimated recapture probability varied with occasion but was essentially the same between sites when differences in TE were accounted for (Fig. 4), reflecting the high averaged posterior probability obtained for the $p(t)$ sub-model (Table 3). Recapture probabilities declined after about 2000, reached the lowest point in 2009, and increased after that, matching our expectations based on trends in sampling effort. In general, estimated recapture probability was high, with a median of 0.86 across years and sites.

Patterns of abundance of nesting females.—Total median abundance estimates in the NMB varied from 57 to 69 females (mean = 65.1) between 1980 and 1986 and then dropped rapidly to 41 during the subsequent three winters of high mortality (Fig. 6). Mean total abundance was 41.6 over the five years following the catastrophe between 1989 and 1993, and 40.4 over the most recent five years (2009–2013). The decline was more severe for the subset of turtles nesting on the dam whose abundance decreased from a mean estimate of 34.7 (0.4 unobservable) in 1986 to 17.9 in 1989 (0.3 unobservable) and then 16.0 (0.01 unobservable) the following year. Mean abundance over the most recent five years was estimated at 18.8 (0.44 unobservable). Abundance in 2013, the last occasion, was 18.8 (0.18 unobservable) and 20.3 (3.3 unobservable) for the dam and alternate sites, respectively. A graphical comparison of parameter estimates between the state-space abundance model and the conditional multinomial m-array

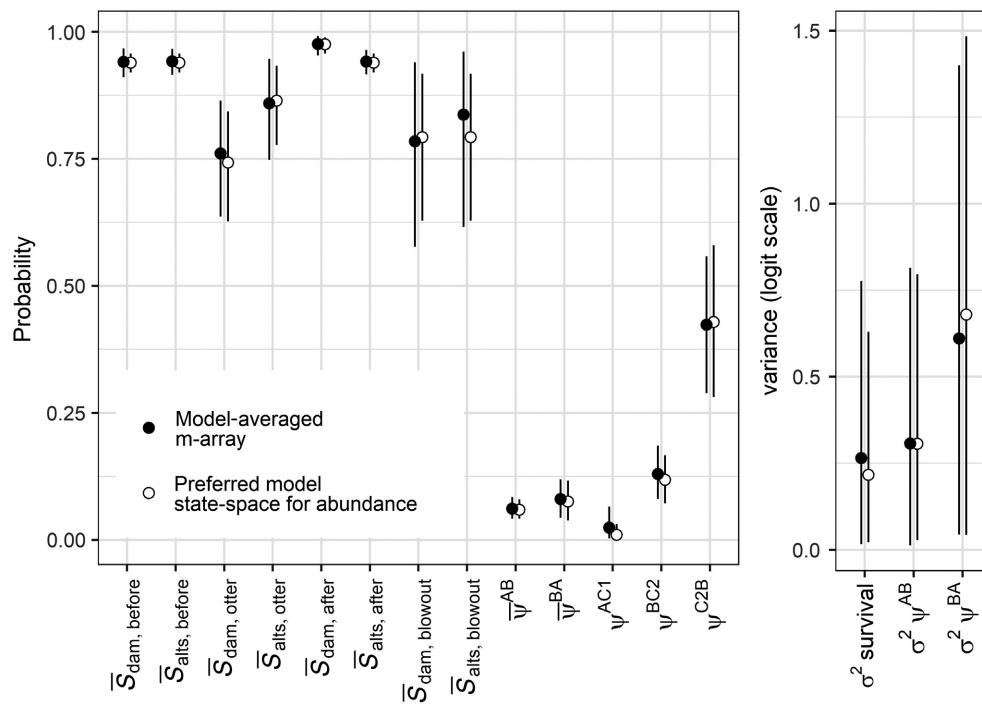


Fig. 5. Comparison of nesting female snapping turtle (*Chelydra serpentina*) survival and transition parameters (means with 95% CRIs) among models, sites (dam, alternate sites), and periods. Models shown are the multinomial m-array with model averaging using Gibbs variable selection (GVS) and a state-space model constructed using the most supported parameter structure from GVS. Subscript before denotes mean annual survival from 1980 to 1986, before the otter predation event; otter denotes three years (1986–1989) of elevated mortality from predation by otters; after is mean post-catastrophe survivorship from 1989 to 2013. During the 1997–1998 interval (blowout), the Sasajewun dam failed. Mean apparent survivorship estimates of the abundance model over the four periods (before, otter, after, blowout) at the dam were 0.941, 0.761, 0.976, 0.785, and at alternate sites were 0.942, 0.860, 0.942, and 0.837, respectively. Parameters ψ^{YZ} are annual transition probabilities from Y to Z where superscript A is the Sasajewun dam, C1 is its corresponding unobservable state, B is the alternate sites, and C2 is the corresponding unobservable state. Transitions involving unobservable states were modeled without time variation, while other transitions and survival were random-effects means with corresponding variances $\sigma^2\psi^{AB}$, $\sigma^2\psi^{BA}$, and σ^2 survival.

showed estimates were very similar (Fig. 5) with slightly higher precision of apparent survivorship in the state-space model, likely because it did not include model uncertainty. Over all occasions included in this analysis (excluding the first when no estimate is available), the proportion of individuals estimated to be temporarily unobservable during a nesting season was 0.016 (95% CRI = 0.00, 0.050) for dam-nesting females and 0.19 (0.15, 0.24) at alternate sites. The relative abundance of the temporarily unavailable fraction of the nesting populations averaged 1.6% (95% CRI, 0–5.0%) at the dam and 19% (95% CRI, 15–24%) at the alternate sites across all occasions.

The estimated number of individuals recruited (individuals newly maturing and nesting in situ or new immigrants) annually is shown in Fig. 7. A median of 57 individual nesting females was estimated to be present at the NMB on the first occasion, and a further 82 entered the population from 1981 to 2013. Annual recruitment (entry of new adults) was higher over the first seven intervals (median = 5) than over the remaining 26 intervals (median = 2). The median estimated number of individuals killed during the blowout was 8 (mean 7.5, 95% CRI = 3, 12). One individual, an adult female, was found dead in 1998 on the occasion following the blowout.

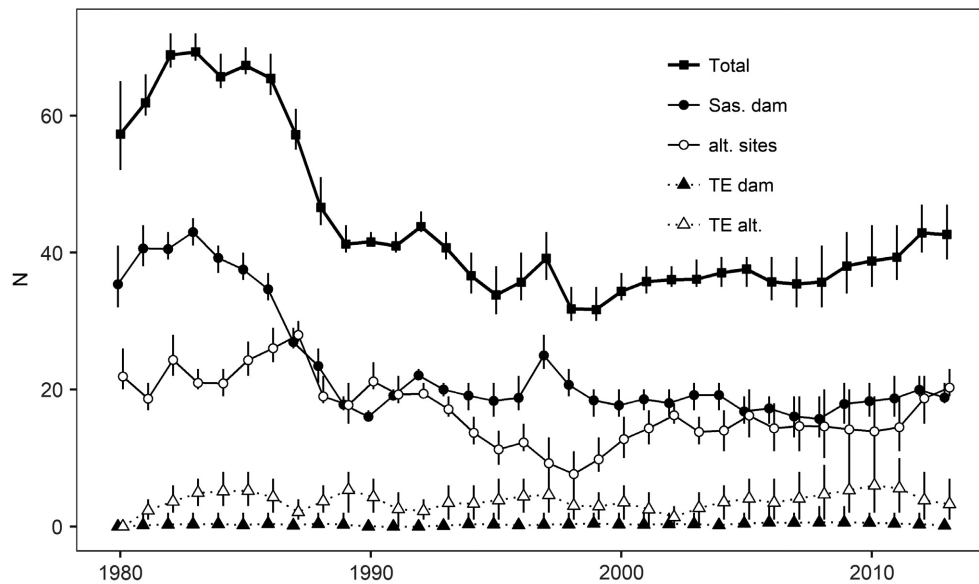


Fig. 6. Abundance estimates for female snapping turtles (*Chelydra serpentina*) nesting at monitored sites in Algonquin Park from 1980 to 2013. States are as follows: available for detection at the Sasajewun dam (Sas. dam) or the alternate sites (alt. sites), or temporarily unavailable from either of those sites (temporary emigration [TE] dam, TE alt., respectively). Filled squares indicate total abundance across all four states. Error bars are 95% CRIs.

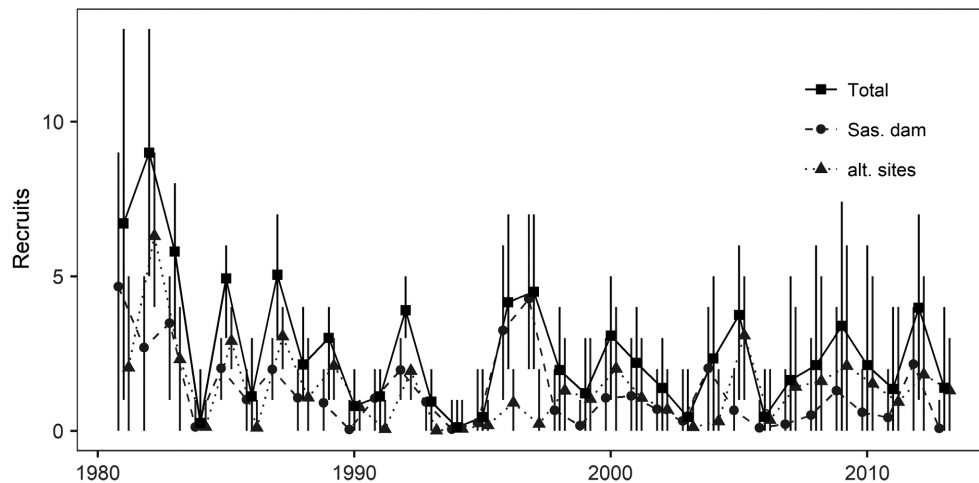


Fig. 7. Estimated recruitment (medians and 95% CRIs) of new nesting female snapping turtles (*Chelydra serpentina*) to two nesting areas, the Sasajewun dam and alternate sites, in Algonquin Park from 1981 to 2013. We attribute the relatively high recruitment estimates over the first three intervals to returning temporary emigrants.

Mark–recapture analysis II: Abundance of males and females (2009–2013)

Estimates of adult male and female abundance using a simple robust model of trapping and canoe observations in Lake Sasajewun from 2009 to 2013 are shown in Fig. 8. The mean

abundance over all five occasions was 12.5 for females and 9.5 males, respectively. Apparent survivorship was substantially lower at 0.84 than survivorship estimated from nest site surveys and likely indicates lower fidelity or higher transience or TE. Mean recapture probabilities were

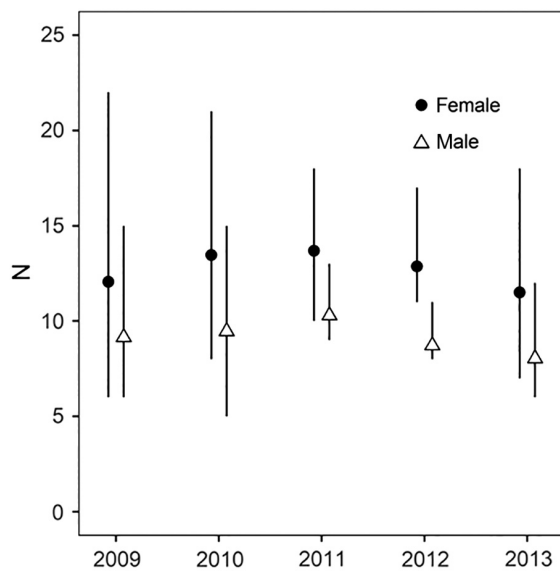


Fig. 8. Abundance estimates and 95% CRIs of Lake Sasajewun resident adult snapping turtles (*Chelydra serpentina*; females >24 cm straight-line carapace length [SCL], males >30 cm SCL) estimated using a robust design model of trap captures and canoe observations.

0.40 (range 0.32–0.61) for males and 0.31 (range 0.24–0.51) for females over the five occasions.

DISCUSSION

Our analyses show that despite a return to pre-catastrophe survivorship, abundances of snapping turtles 23 yr after a major decline (i.e., long enough for offspring born after the catastrophe to begin to be recruited) are essentially the same as they were in the years immediately after the catastrophe. Such a limited population response is consistent with constraints imposed by the life-history traits of snapping turtles. There has been limited evidence of population recovery.

Abundance and survival of nesting females

Our analysis of the nesting female population produced similar estimates of declining abundance as those reported in the earlier analysis by Brooks et al. (1991). Three winters of elevated predation during which survivorship fell from 0.94 to 0.76 (dam) and 0.86 (alternate sites) was enough to reduce the population by approximately 39% (Fig. 6). The abundance trend was

nearly flat over the subsequent 23 yr, indicating that recovery has been very slow to non-existent. There was some evidence that the early spring flood followed by failure of the Sasajewun dam in 1998 resulted in further excess mortality, also contributing to lack of recovery. Furthermore, annual recruitment (entry of new adults) to the nesting population was essentially flat over most of the study (Fig. 7) and was balanced by mortality except during the catastrophes.

A density-dependent response in survival would be expected to have a substantial positive impact on population recovery. There was some evidence for an increase in survivorship of adult females nesting at the dam after the catastrophe, but not for females nesting at the alternate sites who may be subjected to road mortality insofar as some of the alternate sites are adjacent to a two-lane highway. It is also possible that predation by otters began, but was undetected, prior to the three intervals of high mortality that we observed. This would lower the relative survival during the pre-catastrophe period and could contribute to the pattern we observed. Another possibility, conditional on survival heterogeneity among individual adults, is that turtles surviving the mortality event have higher survivorship in general and made up a higher proportion of the post-mortality event population. Adult survival heterogeneity based on size has been detected in our population (Armstrong et al. 2017), but no size bias was detected for predated turtles (Brooks et al. 1991). The lack of recovery suggests that any possible density-dependent compensatory responses of other life-history traits, such as immigration, juvenile growth, and fecundity, have not affected abundance at the observed timescale. Further, direct assessment of these vital rates may reveal weak density-dependent effects that are not yet detectable from abundance series, even at the present timescale (Brook and Bradshaw 2006, Lebreton 2009); future work will examine responses in these vital rates.

Temporary emigration and inferences about reproductive frequency

Annual TE was much lower for females nesting at the dam (2.4%) compared to those at the alternate sites (12%). The difference in TE can be interpreted as differences in two processes, biological and observational. It is possible that

observers were more likely to detect individuals that they had seen on the previous occasion because of increased vigilance at a particular sub-site and time-of-day on the subsequent occasion. This may have been a factor at the alternate sites, which were scattered and heterogeneous, but not at the dam. This difference could appear as a difference in TE between sites. The biological process is TE to nest at other sites. Transitions away from the dam are usually downstream to the alternate sites and so are already accounted for by the observed state transitions in our analysis. In contrast, temporary transitions from alternate sites to nest at downstream sites take individuals outside of the NMR watershed which delineates the study area (i.e., to an unobservable state).

The lower influence of observer effects and transitions by females at the Sasajewun dam to unmonitored nesting areas means that TE from the dam is likely to be a reasonable estimate of the upper boundary of the annual frequency of skipped reproductive events. The relative abundance of the temporarily unavailable fraction of the dam-nesting population was low across all occasions (Fig. 6). This is a maximum estimate because the proportion of TE that is due to nesting at unmonitored upstream sites is unknown, so true frequency of skipped reproduction is likely to be somewhat lower. Our estimated reproductive frequency is higher than previously estimated in Michigan (85%, Congdon et al. 1994). The high reproductive frequency we observed is notable given the cool climate and low productivity of this habitat (Galbraith et al. 1988). Among iteroparous taxa, reproductive frequency is one of the most difficult life-history traits to estimate (Gibbons 1982, Moll and Iverson 2008); analyses of mark-recapture data using models that include TE have potential to allow inferences of this important parameter.

Abundance of males and females

Our recent (2009–2013) abundance estimates (males = 9.5, females = 12.5; Fig. 8) of adults in Lake Sasajewun are similar to those reported by Brooks et al. (1991) for the years at the end of the catastrophe caused by otter predation (1988–1989; males and females combined = 20.5, minimum alive = 16). This concordance indicates that the lack of recovery is not limited to females at

particular nest sites, but applies to the population as a whole.

Conservation and management implications

An important feature of our study population is high connectivity with adjacent habitats. The slow recovery is notable because our study area is open to immigration from an abundance of surrounding patches and does not only rely on in situ recruitment. Our observations confirm that individuals do occasionally immigrate from, and emigrate to, distant sites. For example, one female that was recruited to an alternate site in 2013 had previously only been observed nesting 9.3 km away by water. However, the frequency of immigration events to nesting areas and to Lake Sasajewun has apparently not sufficiently increased relative to mortality and emigration to compensate for decreased abundance during a catastrophe. This suggests that movement between patches is not sensitive to density and so contributes little to any compensatory response following a catastrophe. In contrast, managers often assume that localized depletion will be compensated for by ex situ recruitment from less exploited patches (Cain 2010). Such an assumption, made without provisions for follow-up empirical validation, is an explicit feature of the management of some exploited turtle populations (Cain 2010).

More generally, our results demonstrate an absence of effective recovery indicating an absence of a substantial contribution of density-dependent compensation to this point. This is consistent with other analyses of turtle life history which emphasize the limited ability of many populations to compensate for chronic or catastrophic mortality (Brooks et al. 1991, Congdon et al. 1993, 1994, Cunningham and Brooks 1996, Heppell 1998). Our study provided a unique opportunity to empirically test these principles over a long time series following a perturbation. The lack of recovery at management-relevant timescales, and the manifest risk of further, unanticipated catastrophes, strongly supports prioritizing protection of existing populations rather than relying on recovery after declines have already occurred.

For conservation biologists, it is important to consider both human-centric and generation timescales when evaluating factors impacting

population persistence. Intrinsic population processes such as population growth rate and density dependence are best understood on the scale of generation time (Sæther et al. 2005), but many extrinsic processes, such as frequency of catastrophes, aspects of community dynamics, and management actions and policy, scale more or less independently. Anthropogenic and environmental impacts on long-term viability must be related back to the scale of population processes to be understood in that context. In a meta-analysis of extinction risk and temporal scaling, O'Grady et al. (2008) found that generation time was the appropriate frame of reference despite the lack of direct connection to extrinsic processes. Using estimated age at first reproduction (AFR) of 17 yr (Galbraith et al. 1989) and adult survivorship (S) in typical (non-catastrophe) periods as 0.942–0.976 (this study), we can calculate a crude estimate of generation time for our population as $AFR + (1 - S)^{-1} = 34.2\text{--}58.7$ yr, indicating that perhaps we should not expect to see signs of population recovery for at least 59 yr post-catastrophe.

Slow life histories entail not only vulnerabilities to certain demographic perturbations but also robustness in the face of many kinds of environmental stochasticity (Jonsson and Ebenman 2001). We suggest that definitions of catastrophes should incorporate differences in relative sensitivity of different life-history parameters among taxa. In a study of catastrophes in pinniped populations (Gerber and Hilborn 2001), most natural catastrophes were characterized by nearly complete reproductive failure or very high pup mortality and resulted in abrupt population declines. In contrast, the life history of turtles is typified by low and variable reproductive success and their strategy of constant, high adult survivorship insulates the population from routine environmental stochasticity which primarily affects the youngest age classes (Congdon et al. 1994, Cunningham and Brooks 1996, Jonsson and Ebenman 2001). In some years, reproductive success in turtle populations may be essentially nil (Bobyne and Brooks 1994), and although chronic reproductive failure has obvious consequences, even drastic short-term fluctuations in reproductive success are unlikely to impact abundance severely enough to warrant naming them a catastrophe. Taking into account the elasticity of different life-history stages (Cunningham and

Brooks 1996, Enneson and Litzgus 2008), catastrophes in turtles and other organisms with similar life histories can be characterized solely by abrupt increases in adult and older juvenile mortality. The extended lack of recovery that we have observed suggests that perturbations to adult survivorship of long-lived species will be potentially catastrophic even when short-term mortality is substantially lower than the commonly used 50% threshold used to evaluate catastrophic events.

Predator-induced catastrophes

It is startling to consider that the dominant environmental influence on the study population over 41 yr of monitoring is the predilections of one or at most a few individual river otters. This dramatically underscores both the importance and unpredictability of catastrophes. Population dynamics of cyclic species such as small mammals and clupeid fishes are often mediated by predation, but we suggest that it is not productive to lump catastrophes, which are defined partly by their unpredictability, within these regular phenomena. Excluding such cyclic predator–prey dynamics, population catastrophes due to predation by native predators are rare compared to other causes such as extreme environmental events, starvation, and disease (Young 1994). Predator-mediated catastrophes have been reported in some circumstances, usually commensurate with one or more other abiotic factors (Young 1994). Another instance of mass mortality of turtles (*Emys orbicularis*) resulting from otter (*Lutra lutra*) predation was attributed to reduced availability of prey fish (Lanszki et al. 2006). Human-subsidized native predators have also been implicated in acute mortality events that may affect chelonians (Fincham and Lambrechts 2014).

Because syntopic predators are a constant, predictable, feature of populations on which they prey, it is surprising that these predators can occasionally induce sudden, unpredictable catastrophes. One potential explanation is that individual specialization to depredate adult snapping turtles may be a rare realization of a heterogeneous suite of potential foraging personalities. Individual specialization in foraging strategy is widespread in many animals, and many predators will adopt strategies that are unique among a sample of their conspecifics (Araujo

et al. 2011, Wolf and Weissing 2012). Snapping turtles themselves exhibit individual specialization in habitat selection during the active season and hibernation (Brown and Brooks 1994, Paterson et al. 2012), and heterogeneity of overwintering sites may have protected a proportion of the population that used refugia inaccessible to otters (Brooks et al. 1991).

CONCLUSIONS

Although natural catastrophes are unpredictable in their timing, evidence is accumulating that they do happen and represent a real threat, and this risk must be appreciated by population ecologists and conservation planners (Lande 1993, Mangel and Tier 1994, Reed et al. 2003). Increasing rates of habitat fragmentation, direct exploitation, and increasing climate variability mean that in many ecosystems, the frequency of both natural and anthropogenic catastrophes may also be expected to increase. Organisms with slow life histories are somewhat insulated from typical environmental variation but may be extremely vulnerable to any catastrophes that result in substantial adult female mortality. Following such a catastrophe, our study population of snapping turtles has been unable to substantially recover, despite a return to high survivorship and continued connectivity with neighboring populations. The lack of recovery suggests that density-dependent compensation is limited. This aligns with the prediction of Brooks et al. (1991) who suggested that intrinsic environmental constraints on vital rates would impose limits on snapping turtle populations to compensate for declines. Our analyses at two spatial scales, basin level nest surveys and local aquatic habitat surveys, demonstrate population impacts persisting over more than two decades. We strongly support a risk-averse, precautionary approach to conservation and management of long-lived animals given their limited ability to compensate for declines and the unpredictable continuing risk that catastrophes pose to depleted populations.

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LITERATURE CITED

- Araujo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. *Ecology Letters* 14:948–958.
- Aresco, M. J. 2005. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. *Journal of Wildlife Management* 69:549–560.
- Armstrong, D. P., and R. J. Brooks. 2013. Application of hierarchical biphasic growth models to long-term data for Snapping Turtles. *Ecological Modelling* 250:119–125.
- Armstrong, D. P., and R. J. Brooks. 2014. Estimating ages of turtles from growth data. *Chelonian Conservation and Biology* 13:9–15.
- Armstrong, D. P., M. G. Keevil, N. Rollinson, and R. J. Brooks. 2017. Subtle individual variation in indeterminate growth leads to major variation in survival and lifetime reproductive output in a long-lived reptile. *Functional Ecology* 32:752–761.
- Bennett, A. M., and J. D. Litzgus. 2014. Injury rates of freshwater turtles on a recreational waterway in Ontario, Canada. *Journal of Herpetology* 48:262–266.
- Bjørkvoll, E., V. Grøtan, S. Aanes, B.-E. Sæther, S. Engen, and R. Aanes. 2012. Stochastic population dynamics and life-history variation in marine fish species. *American Naturalist* 180:372–387.
- Bjorndal, K. A., A. B. Bolten, and M. Y. Chaloupka. 2000. Green turtle somatic growth model: evidence for density dependence. *Ecological Applications* 10:269–282.
- Boby, M. L., and R. J. Brooks. 1994. Incubation conditions as potential factors limiting the northern distribution of snapping turtles, *Chelydra serpentina*. *Canadian Journal of Zoology* 72:28–37.
- Böhm, M., et al. 2013. The conservation status of the world's reptiles. *Biological Conservation* 157:372–385.

- Brook, B. W., and C. J. A. Bradshaw. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* 87:1445–1451.
- Brooks, R. J., G. P. Brown, and D. A. Galbraith. 1991. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). *Canadian Journal of Zoology* 69:1314–1320.
- Brooks, S. P., E. A. Catchpole, B. J. T. Morgan, and S. C. Barry. 2000. On the Bayesian analysis of ring-recovery data. *Biometrics* 56:951–956.
- Brown, G. P., and R. J. Brooks. 1994. Characteristics of and fidelity to hibernacula in a northern population of snapping turtles, *Chelydra serpentina*. *Copeia* 1994:222–226.
- Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173–1187.
- Bulté, G., M.-A. Carrière, and G. Blouin-Demers. 2010. Impact of recreational power boating on two populations of northern map turtles (*Graptemys geographica*). *Aquatic Conservation: Marine and Freshwater Ecosystems* 20:31–38.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monographs* 5:1–437.
- Cagle, F. R. 1939. A system of marking turtles for future identification. *Copeia* 1939:170–183.
- Cain, P. W. 2010. The cost of soup: an assessment of the commercial harvest of snapping turtles (*Chelydra serpentina*) in Maryland. Townsend University, Townsend, Maryland, USA.
- Catrysse, J., E. Slavik, J. Choquette, A. E. Leifso, and C. M. Davy. 2015. Mass mortality of northern map turtles (*Graptemys geographica*). *Canadian Field Naturalist* 129:80–83.
- Choquet, R., A. M. Reboulet, J.-D. Lebreton, O. Gimenez, and R. Pradel. 2005. U-Care 2.2 user's manual. Cefe, Montpellier, France.
- Christiansen, J. L., and J. W. Bickham. 1989. Possible historic effects of pond drying and winterkill on the behavior of *Kinosternon flavescens* and *Chrysemys picta*. *Journal of Herpetology* 23:91–94.
- Collen, B., J. Loh, S. Whitmee, L. McRae, R. Amin, and J. E. M. Baillie. 2009. Monitoring change in vertebrate abundance: the Living Planet Index. *Conservation Biology* 23:317–327.
- Colteaux, B. C., and D. M. Johnson. 2017. Commercial harvest and export of snapping turtles (*Chelydra serpentina*) in the United States: trends and the efficacy of size limits at reducing harvest. *Journal for Nature Conservation* 35:13–19.
- Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conservation Biology* 7: 826–833.
- Congdon, J. D., A. E. Dunham, and R. C. V. van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. *American Zoologist* 34:397–408.
- Cunnington, D. C., and R. J. Brooks. 1996. Bet-hedging theory and eigenelasticity: a comparison of the life histories of loggerhead sea turtles (*Caretta caretta*) and snapping turtles (*Chelydra serpentina*). *Canadian Journal of Zoology* 74:291–296.
- Dellaportas, P., J. Forster, and I. Ntzoufras. 2000. Bayesian variable selection using the Gibbs sampler. Pages 273–286 in D. Dey, S. Ghosh, and B. Mallick, editors. *Generalized linear models: a Bayesian perspective*. Volume 5. CRC Press, New York, New York, USA.
- Enneson, J. J., and J. D. Litzgus. 2008. Using long-term survey data and a stage-classified matrix to assess conservation strategies for an endangered turtle (*Clemmys guttata*). *Biological Conservation* 141: 1560–1568.
- Fey, S. B., A. M. Siepielski, S. Nusslé, K. Cervantes-Yoshida, J. L. Hwan, E. R. Huber, M. J. Fey, A. Catenazzi, and S. M. Carlson. 2015. Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proceedings of the National Academy of Sciences of the USA* 112:1083–1088.
- Fincham, J. E., and N. Lambrechts. 2014. How many tortoises do a pair of pied crows *Corvus alba* need to kill to feed their chicks? *Ornithological Observations* 5:135–138.
- Finkelstein, M. E., S. Wolf, M. Goldman, D. F. Doak, P. R. Sievert, G. Balogh, and H. Hasegawa. 2010. The anatomy of a (potential) disaster: volcanoes, behavior, and population viability of the short-tailed albatross (*Phoebastria albatrus*). *Biological Conservation* 143:321–331.
- Fordham, D. A., A. Georges, and B. W. Brook. 2007. Demographic response of snake-necked turtles correlates with indigenous harvest and feral pig predation in tropical northern Australia. *Journal of Animal Ecology* 76:1231–1243.
- Fordham, D. A., A. Georges, and B. W. Brook. 2009. Experimental evidence for density-dependent responses to mortality of snake-necked turtles. *Oecologia* 159:271–281.
- Frankham, R., and B. W. Brook. 2004. The importance of time scale in conservation biology and ecology. *Annales Zoologici Fennici* 41:459–463.

- Fujiwara, M., and H. Caswell. 2002. A general approach to temporary emigration in mark–recapture analysis. *Ecology* 83:3266–3275.
- Gaillard, J.-M., N. G. Yoccoz, J.-D. Lebreton, C. Bonenfant, S. Devillard, A. Loison, D. Pontier, and D. Allaine. 2005. Generation time: a reliable metric to measure life-history variation among mammalian populations. *American Naturalist* 166:119–123.
- Galbraith, D. A., C. A. Bishop, R. J. Brooks, W. L. Simser, and K. P. Lampman. 1988. Factors affecting the density of populations of common snapping turtles (*Chelydra serpentina serpentina*). *Canadian Journal of Zoology* 66:1233–1240.
- Galbraith, D. A., R. J. Brooks, and M. E. Obbard. 1989. The influence of growth rate on age and body size at maturity in female snapping turtles (*Chelydra serpentina*). *Copeia* 1989:896–904.
- Garber, S. D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. *Ecological Applications* 5:1151–1162.
- Gelman, A., J. P. Carlin, H. S. Stern, and D. B. Rubin. 2004. *Bayesian data analysis*. CRC/Chapman & Hall, Boca Raton, Florida, USA.
- Gerber, L. R., and R. Hilborn. 2001. Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. *Mammal Review* 31:131–150.
- Gibbons, J. W. 1982. Reproductive patterns in freshwater turtles. *Herpetologica* 38:222–227.
- Gibbons, J. W., et al. 2000. The global decline of reptiles, déjà vu amphibians. *BioScience* 50:653–666.
- Gimenez, O., R. Choquet, and J.-D. Lebreton. 2003. Parameter redundancy in multistate capture–recapture models. *Biometrical Journal* 45:704–722.
- Gimenez, O., B. J. T. Morgan, and S. P. Brooks. 2009. Weak identifiability in models for mark–recapture–recovery data. Pages 1055–1067 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. *Modeling demographic processes in marked populations*. Springer, New York, New York, USA.
- Gimenez, O., V. Rossi, R. Choquet, C. Dehais, B. Doris, H. Varella, J.-P. Vila, and R. Pradel. 2007. State-space modelling of data on marked individuals. *Ecological Modelling* 206:431–438.
- Hailey, A., and R. E. Willemsen. 2000. Population density and adult sex ratio of the tortoise *Testudo hermanni* in Greece: evidence for intrinsic population regulation. *Journal of Zoology* 251:325–338.
- Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. *Copeia* 1998:367–375.
- Hutchings, J. A., and J. D. Reynolds. 2004. Marine fish population collapses: consequences for recovery and extinction risk. *BioScience* 54:297–309.
- IPCC. 2014. *Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland.
- Johnson, A. J., et al. 2008. Ranavirus infection of free-ranging and captive box turtles and tortoises in the United States. *Journal of Wildlife Diseases* 44:851–863.
- Jonsson, A., and B. Ebenman. 2001. Are certain life histories particularly prone to local extinction? *Journal of Theoretical Biology* 209:455–463.
- Keevil, M. G., B. S. Hewitt, R. J. Brooks, and J. D. Litzgus. 2017. Patterns of intraspecific aggression inferred from injuries in an aquatic turtle with male-biased size dimorphism. *Canadian Journal of Zoology* 95:393–403.
- Kendall, W. L., and J. D. Nichols. 2002. Estimating state-transition probabilities for unobservable states using capture–recapture/resighting data. *Ecology* 83:3276–3284.
- Kéry, M., and M. Schaub. 2012. *Bayesian population analysis using WinBUGS: a hierarchical perspective*. Academic Press, Waltham, Massachusetts, USA.
- King, R., B. J. T. Morgan, O. Gimenez, and S. P. Brooks. 2010. *Bayesian analysis for population ecology*. CRC Press, Boca Raton, Florida, USA.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- Lanszki, J., M. Molnár, and T. Molnár. 2006. Factors affecting the predation of otter (*Lutra lutra*) on European pond turtle (*Emys orbicularis*). *Journal of Zoology* 270:219–226.
- Lebreton, J.-D. 2009. Assessing density dependence: Where are we left? Pages 19–42 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. *Modeling demographic processes in marked populations*. Springer, New York, New York, USA.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lebreton, J.-D., J. D. Nichols, R. J. Barker, R. Pradel, and J. A. Spindel. 2009. Modeling individual animal histories with multistate capture–recapture models. Pages 87–173 in H. Caswell, editor. *Advances in ecological research*. Elsevier, San Diego, California, USA.
- Loncke, D. J., and M. E. Obbard. 1977. Tag success, dimensions, clutch size and nesting site fidelity for the snapping turtle, *Chelydra serpentina* (Reptilia,

- Testudines, Chelydridae) in Algonquin Park, Ontario, Canada. *Journal of Herpetology* 11:243–244.
- Longshore, K. M., J. R. Jaeger, and J. M. Sappington. 2003. Desert tortoise (*Gopherus agassizii*) survival at two eastern Mojave Desert sites: Death by short-term drought? *Journal of Herpetology* 37:169–177.
- Lunn, D. J., A. Thomas, N. Best, and D. J. Spiegelhalter. 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* 10:325–337.
- Mangel, M., and C. Tier. 1994. Four facts every conservation biologist should know about persistence. *Ecology* 75:607–614.
- Menges, E. S. 1990. Population viability analysis for an endangered plant. *Conservation Biology* 4:52–62.
- Midwood, J. D., N. A. Cairns, L. J. Stoot, S. J. Cooke, and G. Blouin-Demers. 2015. Bycatch mortality can cause extirpation in four freshwater turtle species. *Aquatic Conservation: Marine and Freshwater Ecosystems* 25:71–80.
- Moll, D., and J. B. Iverson. 2008. Geographic variation in life-history traits. Pages 181–192 in R. J. Brooks, A. C. Steyermark, and M. S. Finkler, editors. *The biology of the snapping turtle*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Neubauer, P., O. P. Jensen, J. A. Hutchings, and J. K. Baum. 2013. Resilience and recovery of overexploited marine populations. *Science* 340:347–349.
- Nickerson, M. A., and A. L. Pitt. 2012. Historical turtle population decline and community changes in an Ozark river. *Bulletin of the Florida Museum of Natural History* 51:257–267.
- Obbard, M. E., and R. J. Brooks. 1981. A radio-telemetry and mark–recapture study of activity in the common snapping turtle, *Chelydra serpentina*. *Copeia* 1981:630–637.
- O’Grady, J. J., D. H. Reed, B. W. Brook, and R. Frankham. 2008. Extinction risk scales better to generations than to years. *Animal Conservation* 11:442–451.
- O’Hara, R. B., and M. J. Sillanpää. 2009. A review of Bayesian selection methods: What, how, and which? *Bayesian Analysis* 4:85–118.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:3–135.
- Papadatou, E., et al. 2012. Comparing survival among species with imperfect detection using multilevel analysis of mark–recapture data: a case study on bats. *Ecography* 35:153–161.
- Paterson, J. E., B. D. Steinberg, and J. D. Litzgus. 2012. Generally specialized or especially general? Habitat selection by snapping turtles (*Chelydra serpentina*) in central Ontario. *Canadian Journal of Zoology* 90:139–149.
- Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344:1246752.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Pages 1–10 in K. Hornik, F. Leisch, and A. Zeileis, editors. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, Vienna, Austria, March 20–22, 2003. Austrian Association for Statistical Computing (AASC) and the R Foundation for Statistical Computing, Vienna, Austria.
- Pradel, R. 1993. Flexibility in survival analysis from recapture data: handling trap-dependence. Pages 29–37 in J. D. Lebreton and P. M. North, editors. *Marked individuals in the study of bird populations*. Birkhaeuser Verlag, Montpellier, France.
- Pradel, R., and A. Sanz-Aguilar. 2012. Modeling trap-awareness and related phenomena in capture–recapture studies. *PLoS ONE* 7:e32666.
- Pradel, R., C. M. A. Wintrebert, and O. Gimenez. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture–recapture model. *Biometrics* 59:43–53.
- R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reed, D. H., J. J. O’Grady, J. D. Ballou, and R. Frankham. 2003. The frequency and severity of catastrophic die-offs in vertebrates. *Animal Conservation* 6: 109–114.
- Roff, D. A. 2002. *Life history evolution*. Sinauer, Sunderland, Massachusetts, USA.
- Royle, J. A., and R. M. Dorazio. 2008. *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. Academic Press, New York, New York, USA.
- Royle, J. A., and R. M. Dorazio. 2012. Parameter-expanded data augmentation for Bayesian analysis of capture–recapture models. *Journal of Ornithology* 152:S521–S537.
- Sæther, B.-E., et al. 2005. Generation time and temporal scaling of bird population dynamics. *Nature* 436:99–102.
- Schaub, M., O. Gimenez, B. R. Schmidt, and R. Pradel. 2004. Estimating survival and temporary emigration in the multistate capture–recapture framework. *Ecology* 85:2107–2113.
- Schaub, M., W. Kania, and U. Koeppen. 2005. Variation of primary production during winter induces synchrony in survival rates in migratory white storks

- Ciconia ciconia*. *Journal of Animal Ecology* 74:656–666.
- Schaub, M., R. Zink, H. Beissmann, F. Sarrazin, and R. Arlettaz. 2009. When to end releases in reintroduction programmes: demographic rates and population viability analysis of bearded vultures in the Alps. *Journal of Applied Ecology* 46:92–100.
- Sheppard, A. C. 2014. *Emydoidea blandingii* (Blanding's turtle) mass mortality. *Herpetological Review* 45:312–313.
- Spencer, R.-J., F. J. Janzen, and M. B. Thompson. 2006. Counterintuitive density-dependent growth in a long-lived vertebrate after removal of nest predators. *Ecology* 87:3109–3118.
- Spencer, R.-J., J. Van Dyke, K. Petrov, B. Ferronato, F. McDougall, M. Austin, C. Keitel, and A. Georges. 2018. Profiling a possible rapid extinction event in a long-lived species. *Biological Conservation* 221:190–197.
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. Van Der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society. Series B, Statistical Methodology* 64:583–639.
- Steen, D. A., B. C. Hopkins, J. U. Van Dyke, and W. A. Hopkins. 2014. Prevalence of ingested fish hooks in freshwater turtles from five rivers in the southeastern United States. *PLoS ONE* 9:e91368.
- Steen, D. A., et al. 2006. Relative vulnerability of female turtles to road mortality. *Animal Conservation* 9:269–273.
- Stubbs, D., I. R. Swingland, A. Hailey, and E. Pulford. 1985. The ecology of the Mediterranean tortoise *Testudo hermanni* in Northern Greece: the effects of a catastrophe on population structure and density. *Biological Conservation* 31:125–152.
- Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: a package for running WinBUGS. *Journal of Statistical Software* 12:1–16.
- Vélez-Espino, L. A., and M. A. Koops. 2012. Capacity for increase, compensatory reserves, and catastrophes as determinants of minimum viable population in freshwater fishes. *Ecological Modelling* 247:319–326.
- Ward, E. J., R. Hilborn, R. G. Towell, and L. R. Gerber. 2007. A state-space mixture approach for estimating catastrophic events in time series data. *Canadian Journal of Fisheries and Aquatic Sciences* 64:899–910.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- White, G. C., W. L. Kendall, and R. J. Barker. 2006. Multistate survival models and their extensions in Program MARK. *Journal of Wildlife Management* 70:1521–1529.
- Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution* 27:452–461.
- World Wildlife Fund. 2014. Living planet report 2014: species and spaces, people and places. World Wildlife Fund, Gland, Switzerland.
- Young, T. P. 1994. Natural die-offs of large mammals: implications for conservation. *Conservation Biology* 8:410–418.

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