

ESTIMATING SURVIVAL AND BREEDING PROBABILITY FOR POND-BREEDING AMPHIBIANS: A MODIFIED ROBUST DESIGN

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Abstract. Many studies of pond-breeding amphibians involve sampling individuals during migration to and from breeding habitats. Interpreting population processes and dynamics from these studies is difficult because (1) only a proportion of the population is observable each season, while an unknown proportion remains unobservable (e.g., non-breeding adults) and (2) not all observable animals are captured. Imperfect capture probability can be easily accommodated in capture–recapture models, but temporary transitions between observable and unobservable states, often referred to as temporary emigration, is known to cause problems in both open- and closed-population models.

We develop a multistate mark–recapture (MSMR) model, using an open-robust design that permits one entry and one exit from the study area per season. Our method extends previous temporary emigration models (MSMR with an unobservable state) in two ways. First, we relax the assumption of demographic closure (no mortality) between consecutive (secondary) samples, allowing estimation of within-pond survival. Also, we add the flexibility to express survival probability of unobservable individuals (e.g., “non-breeders”) as a function of the survival probability of observable animals while in the same, terrestrial habitat. This allows for potentially different annual survival probabilities for observable and unobservable animals.

We apply our model to a relictual population of eastern tiger salamanders (*Ambystoma tigrinum tigrinum*). Despite small sample sizes, demographic parameters were estimated with reasonable precision. We tested several a priori biological hypotheses and found evidence for seasonal differences in pond survival. Our methods could be applied to a variety of pond-breeding species and other taxa where individuals are captured entering or exiting a common area (e.g., spawning or roosting area, hibernacula).

Key words: *Ambystoma tigrinum*; capture–recapture; detection probability; multistate models; pond-breeding amphibians; survival probability; temporary emigration; unobservable state.

INTRODUCTION

Concerns about global amphibian declines have accelerated research efforts to improve current population assessment methods and understand the processes governing population trends. Most amphibian declines have involved aquatic-breeding species, and this group is believed to be especially at risk (Semlitsch 2000). Interpreting population fluctuations of pond-breeding amphibians is difficult because only a proportion of the population of many species is observable; namely, breeding adults, larvae, and metamorphs (Pechmann et al. 1991). Adults and juveniles are often unobservable because they are fossorial or otherwise not exposed to capture except when adults migrate to ponds during the breeding season.

Traditional capture–recapture models provide a means for estimating a variety of demographic parameters in the face of imperfect detection, provided that all individuals in the population have a nonzero probability of detection. Transition to an unobservable state and then back to an observable state is generally referred to as temporary emigration, a process that violates key assumptions for both open and closed-population capture–recapture models (Burnham 1993, Kendall et al. 1997, Kendall 1999). Violations of these assumptions can result in biased estimates of population parameters. The presence, severity, and direction of the bias depend on the proportion of unobservable individuals and whether movement to and from the observable state is completely random or Markovian (Burnham 1993, Kendall et al. 1997, Kendall 1999).

Recently, multistate, mark–recapture (MSMR) methods have been employed to address temporary emigration (Kendall et al. 1995, Lebreton et al. 1999, 2003, Kendall and Nichols 2002, Schaub et al. 2004). MSMR methods were originally developed to estimate movement probabilities among spatial locations (Arnason

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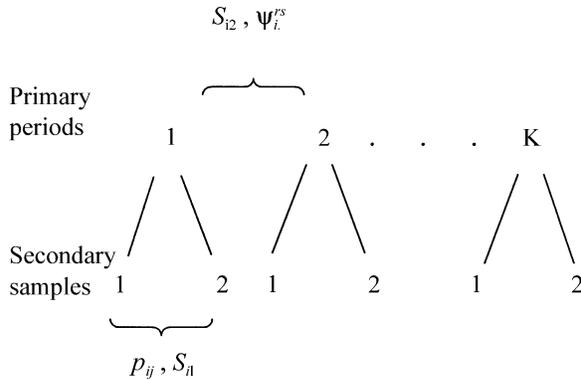


FIG. 1. Modified “open” robust design for a K -period study. Each primary period i contains two secondary samples, representing capture occasions when the animal enters ($j = 1$) and exits a common area such as a breeding pond ($j = 2$). Capture probability, p_{ij} , and survival probability in the pond, S_{i1} , are estimated over secondary samples. Transition probabilities, ψ_i^{rs} , and survival probability outside the pond, S_{i2} , are estimated between primary periods.

1972, 1973, Brownie et al. 1993, Schwarz et al. 1993), but more general MSMR models estimate transitions between “stages” such as those defined by age, size, or other life history states, such as juvenile, immature, adult (Nichols et al. 1992, 1994, Fujiwara and Caswell 2002a). State or movement transitions are generally treated as a Markov process, a type of stochastic process in which the future state of the process depends only on the present state, but not past states. Normally, state transitions are treated as a first-order Markov process, where the probability that an animal is alive and in state s at time $t + 1$ depends only on the state of the animal at time t (i.e., one previous time step). Second-order or “memory models” also exist (Brownie et al. 1993), where the probability of transitioning between states in t to $t + 1$ depends on the state at time t and $t - 1$. A standard assumption in both cases is that all states are observable; transitions to unobservable states are assumed to be permanent and are confounded with survival probability estimates (Kendall et al. 1997, Kendall 1999, Kendall and Nichols 2002). Nevertheless, transition to an unobservable state is often a temporary condition for many species. Fujiwara and Caswell (2002b) outline several situations where these transitions are deterministic. They note that transitions to unobservable states are expected for immature stages or between successive reproductive events.

Conceptually, the presence of an unobservable state can be accommodated in MSMR models, where the simplest case involves two states: one observable, one unobservable. Nevertheless, estimation of demographic parameters requires various model constraints (Kendall and Nichols 2002, Schaub et al. 2004) or extra information to estimate detection probability, either from an independent source or via Pollock’s

robust design (Pollock 1982). Under a standard open-population design (one sample per season), parameter estimation is possible only if one or more of the following types of constraints are made: reduce the order of Markovian transition probabilities (e.g., assume transitions are a completely random process) that permits estimation of survival probabilities; impose partial determinism on transition probabilities; assume parameters are constant over time (Kendall and Nichols 2002); or impose equality in some parameters between groups, such as sex (Schaub et al. 2004). In almost all cases, survival probabilities for observable and unobservable states must be assumed equal (Fujiwara and Caswell 2002b, Kendall and Nichols 2002, Schaub et al. 2004).

Alternatively, investigators have exploited aspects of Pollock’s robust design to estimate transitions to and from an unobservable state (Kendall and Nichols 1995, Kendall et al. 1997). Pollock’s robust design consists of two or more secondary samples within each primary period (e.g., year or breeding season; Fig. 1). Pollock’s original design assumed complete closure over secondary samples, but more recent models relax the geographic closure assumption, allowing individuals to enter and leave the study area once during the primary period. Schwarz and Stobo (1997) and Kendall and Bjorkland (2001) developed two such open-robust design models for situations when only adult breeders are observable, applying them to grey seals (*Halichoerus grypus*) and hawksbill sea turtles (*Eretmochelys imbricata*), respectively. In both cases, the geographic closure assumption is relaxed, allowing individuals to enter and exit breeding or nesting areas in a staggered fashion. Implicit in this approach is the need to model arrival times within a season; however, the demographic closure assumption of no mortality or true recruitment over secondary samples is retained. To our knowledge, no method exists that relaxes demographic closure over secondary samples.

In this paper, we present a general method for addressing questions about population processes in situations where individuals are captured (or “resighted”) entering and leaving a common location (e.g., breeding area, spawning area, hibernaculum, upstream migration, movement through a road underpass). This design is common in studies of pond-breeding amphibians (Gill 1978, 1985, Semlitsch et al. 1996, Trenham et al. 2000, Hels 2002). Demographic closure may not be reasonable in these cases. Thus, we extend open-robust design models (Schwarz and Stobo 1997, Kendall and Bjorkland 2001), permitting one entry and one exit from the study area each primary period, such as a breeding season, and permit mortality between secondary samples within a breeding season. A key feature of this design is that directly monitoring the arrival process removes the need to model arrival times.

STUDY DESIGN AND DATA

We begin with a standard capture–recapture study where individuals can be uniquely identified. We assume a special case of Pollock’s robust design (Pollock 1982) where the population is sampled for K primary periods ($i = 1, 2, \dots, K$), each with two secondary samples representing entering and leaving the common area (Fig. 1, total number of sample occasions = $2K$). For example, drift fences provide an effective tool for sampling pond-breeding amphibians. Adult individuals are captured in pitfall traps outside the fence migrating to the breeding pond, representing the first secondary sample ($j = 1$). Upon initial capture, animals are uniquely identified by marking, tagging, or photographing individually unique characteristics (e.g., spot pattern). Investigators may also record covariates such as sex, size or age, and reproductive condition. Animals are then released on the inside of the drift fence and enter the breeding area. Animals are not at risk of capture again until they encounter the drift fence as they exit the breeding area. The “exit” represents the second and last secondary sample ($j = 2$). Previously unmarked individuals captured upon exit represent animals that were present but not captured entering the breeding area (i.e., missed by the drift fence). Notice that the “state” of the animal (e.g., breeder, nonbreeders) is maintained over secondary samples; there are no transitions between “states” within primary periods. In this sense, “geographic” or “state” closure is maintained over secondary samples, while demographic closure is relaxed (animals may die while in the breeding pond). This maintenance of geographic closure assumes animals enter and exit simultaneously, but it is robust if survival probability is independent of entry and exit times within the sampling season (i.e., if breeding individuals spend approximately equal amounts of time in the pond where their survival probability is relatively constant within a given breeding season).

Capture records for each individual are summarized in a single matrix, commonly referred to as the “capture history form.” Each row of the matrix represents an individual, and the columns represent all sampling occasions. The individual entries in the matrix are either “1”s corresponding to sample occasions when the individual was caught or seen and “0”s if it was not seen. For example, 00 10 00 11 represents a possible capture history from a breeding area sampled for four seasons ($K = 4$). The animal(s) was first caught coming into the breeding area in the second season, not captured exiting the area that season, not seen the third season, and then captured both entering and exiting the breeding area in the fourth season. A single matrix containing capture histories from all individuals is the basis for the MSMR analyses discussed in this paper.

STATISTICAL MODELS AND ESTIMATION

Parameter definition and notation

We consider a multinomial model with two states: $r =$ observable (denoted as O) or unobservable (U). We assume transitions are a first-order Markov process, but also test models with completely random transitions. We maintain notation of previous MSMR models that includes four parameters: p_{ij}^r (probability that an animal is captured or detected during secondary sample j in primary period i in state r , given it is alive, $i = 1, 2, \dots, K$; $j = 1, 2$); S_{i1}^r (probability that an animal in state r at sampling time $i = i$, $j = 1$ [entering the common area] survives until the next sampling time $i = i$, $j = 2$ for $i = 1, 2, \dots, K$); S_{i2}^r (probability that an animal in state r at sampling time $j = 2$ [leaving the common area] survives until the next sampling time $i + 1$, $j = 1$ for $i = 1, 2, \dots, K$; excluding $i = K$, $j = 2$); and ψ_i^{rs} (probability that an animal in state r at time i is in state s at time $i + 1$, given the animal survived from i to $i + 1$, $i = 1, 2, \dots, K - 1$).

For our model, where we include an unobservable state and condition on first capture, $p_{ij}^U = 0$ for all ij , and p_{i1}^r , S_{k2}^r , and ψ_1^{UO} are never used (the latter because no animals are released from the unobservable state). Unbiased estimation of population parameters is based on the following summary statistics obtained from individual capture histories: R_{ij}^r (the number of marked animals released in state r during sampling occasion j of primary period i [this is the number of animals caught minus any animals that died during handling or animals that were otherwise removed from the population]) and $m_{hl,ij}^r$ (the number of marked animals recaptured in state s at period i sample j that were last captured in state r at period h sample l).

For our simple situation, only one state is observable, so the superscripts on the above statistics are omitted. Furthermore, unobservable animals have no probability of detection, p_{ij}^U , so we use p_{ij} to denote time-specific detection probability for observable animals (e.g., breeders). Finally, transitions between observable and unobservable states are possible between primary periods only, after an individual exits the common area. Individuals maintain their “state” within primary periods (e.g., during the breeding, spawning, or nesting season).

General model

We begin with a general model that includes time- and state-specific parameters (S_{ij}^O , S_{ij}^U , ψ_i^{OO} , ψ_i^{UO} , p_{ij}). To illustrate the structure of the model, we give a subset of expected cell frequencies ($m_{11,ij}$) for recaptures of marked animals released after the first capture occasion (R_{11}) of a three-season study:

$$\begin{aligned}
E(m_{11,12} | R_{11}) &= R_{11} S_{11}^O p_{12} \\
E(m_{11,21} | R_{11}) &= R_{11} S_{11}^O (1 - p_{12}) S_{12}^O \psi_1^{OO} p_{21} \\
E(m_{11,22} | R_{11}) &= R_{11} S_{11}^O (1 - p_{12}) S_{12}^O \psi_1^{OO} \\
&\quad \times (1 - p_{21}) S_{21}^O p_{22} \\
E(m_{11,31} | R_{11}) &= R_{11} S_{11}^O (1 - p_{12}) S_{12}^O \\
&\quad \times [\psi_1^{OO} (1 - p_{21}) S_{21}^O (1 - p_{22}) S_{22}^O \psi_2^{OO} \\
&\quad + (1 - \psi_1^{OO}) S_{21}^U S_{22}^U \psi_2^{UO}] p_{31} \\
E(m_{11,32} | R_{11}) &= R_{11} S_{11}^O (1 - p_{12}) S_{12}^O \\
&\quad \times [\psi_1^{OO} (1 - p_{21}) S_{21}^O (1 - p_{22}) S_{22}^O \psi_2^{OO} \\
&\quad + (1 - \psi_1^{OO}) S_{21}^U S_{22}^U \psi_2^{UO}] \\
&\quad \times (1 - p_{31}) S_{31}^O p_{32}
\end{aligned}$$

We assume that transitions occur between primary periods only and that survival probability S_{ij}^r is dependent only on the state (r) the animal is in during primary period i . Survival probabilities for unobservable animals, S_{ij}^U , cannot be directly estimated unless transition probabilities are partially deterministic and modeled as a second-order Markov process (Kendall and Nichols 2002). Specifically, if observable animals in season/primary period i become obligate unobservable in periods $i + 1$ and $i + 2$, then state-specific survival probabilities are estimable. This is the case for some large marine mammals, such as right whales, when females do not return to calving grounds for at least two years after breeding (Fujiwara and Caswell 2002a). This special case, however, only applies to a limited number of populations. When populations do not exhibit this type of partial determinism in their life history strategy, then state-specific survival estimation is not possible.

Previous MSMR models simply assume that time-specific survival probabilities are equal for observable and unobservable animals, $S_{ij}^U = S_{ij}^O$. This assumption may be violated in situations where mortality is higher inside a common area, such as a breeding pond or colony, or lower inside some common refuge. In the case of pond-breeding amphibians, survival for non-breeders likely resembles that of breeders outside the pond, where they face the same mortality risks in the terrestrial habitat. Here, we describe a model with the same basic requirement that survival probability for unobservable animals must be derived from survival probability of observable animals, but it has more flexibility. Because there are two survival probabilities for the observable state corresponding to different habitats (S_{11}^O and S_{22}^O), S_{ij}^U can be based on either of them. For example, assume breeding amphibians spend 14 wk in a pond and 38 wk in terrestrial habitat, whereas non-breeding amphibians spend the entire year in terrestrial habitat. We assume that both groups face the same mortality risks during the time spent in the terrestrial habitat. A logical approach would be to base the estimate of both S_{11}^U and S_{22}^U on S_{22}^O , the survival probability for breeders during the terrestrial part of their life cycle. This is straightforward for the part of the season that

all amphibians are in the terrestrial habitat (i.e., set $S_{22}^U = S_{22}^O$), but for the other part of the season the temporal scales have to be resolved. We set $S_{11}^U = (S_{22}^O)^a$, where a is the ratio of time spent in the pond to the time spent in the terrestrial habitat (e.g., $a = 14/38$ in the above example). A modified version of the program MSSURVIV permits the practitioner to specify the amount of time spent in and out of the common area for each primary period (Jim Hines, *unpublished program* [available online]).⁵ Resulting survival estimates are reported as annual probabilities and must to be adjusted for direct comparison to models where time-specific survival probabilities are equal for observable and unobservable animals. For example, assume that survival probability for breeders inside and outside of the pond was $S_{11}^O = 0.80$ and $S_{22}^O = 0.80$, respectively. Under the assumption of equal survival for each component of the annual cycle, including $S_{11}^U = S_{11}^O$, annual survival probability is 0.64 regardless of breeding status. Conversely, if we set $S_{11}^U = (S_{22}^O)^a$, where $a = 14/38$, then annual survival probability for breeders is 0.64 and nonbreeders is 0.74. The modified version of the MSSURVIV program would report two annual survival probabilities $S_{11}^* = 0.44$ and $S_{22}^* = 0.74$ where $S_{11}^* = (0.44)^{14/52}$, $S_{11}^U = (0.74)^{14/52}$, $S_{22}^O = S_{22}^U = (0.74)^{38/52}$. These annual rates can be interpreted as the probability of surviving an entire year if the specified seasonal survival corresponded to the entire year.

Methods: analytical–numerical approach

We explored whether model parameters were uniquely estimable or confounded in the likelihood function, using the analytic–numeric method described by Burnham et al. (1987; also see Kendall and Nichols 2002, Schaub et al. 2004). Large-sample expected cell frequencies for the $m_{hl,ij}$ summary statistics were computed with known parameter values and initial marked sample sizes R_{ij} . The frequencies were used as “actual” data for the program MSSURVIV, under an appropriately parameterized model. The conditional maximum-likelihood estimates and standard errors produced represent the approximate expected values of the estimators and their standard errors. Models were determined to be without structural problems when all estimators (except some parameters at the end of the study) were unbiased to the fifth decimal place and had coefficients of variation <100% (Kendall and Nichols 2002). We considered scenarios with four seasons ($K = 4$) and modeled survival probability for unobservable animals in two ways. First, we assumed equal time-specific survival probabilities for unobservable and observable animals. Next, we modeled survival probability of unobservable animals as an exponential function of survival probability for observable animals outside of the common area (see *Statistical models and estimation: General model*).

⁵ www.mbr-pwrc.usgs.gov/software.html

We generated expected cell frequencies based on 1000 unmarked animals entering the common area the first season, $i = 1$, and 500 every season thereafter ($i = 2, 3, 4$). Capture probabilities were $p_{i1} \equiv 0.90$ and $p_{i2} \equiv 0.95$. The two sets of survival and transition probabilities were: $S_{i1}^U = S_{i1}^O \equiv 0.90$, $S_{i2}^U = S_{i2}^O \equiv 0.78$, $\psi_{i=1,2,3}^{OO} \equiv 0.40$, $\psi_{i=1,2,3}^{UO} \equiv 0.60$, and $S_{i1}^O \equiv 0.84$, $S_{i2}^U = S_{i2}^O \equiv 0.83$ and $S_{i1}^U = (S_{i2}^O)^a$, $a = 14/38$, $\psi_{i=1,2,3}^{OO} \equiv 0.60$, $\psi_{i=1,2,3}^{UO} \equiv 0.40$. These values were chosen to be representative of drift fence studies of pond-breeding amphibians. We analyzed the generated expected frequencies using the modified version of the program MSSURVIV.

Results: analytical- numerical approach

In a four-season study, our most general model ($S_{ij}^O, S_{ij}^U, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$) contains 28 potential parameters, but this model is overparameterized. As mentioned above, there is no information in the data to estimate p_{11} , S_{k2}^O , or ψ_1^{UO} . Parameters of reduced models become estimable if survival probabilities of unobservable animals are modeled as a function of survival probability for observable animals, such as the two survival situations discussed in the preceding section. In addition, there is some confounding between the last transition and survival probabilities. To avoid this confounding, we either set the last two transition probabilities equal, $\psi_{k-1}^{OO} = \psi_{k-2}^{OO}$ and $\psi_{k-1}^{UO} = \psi_{k-2}^{UO}$, or made survival or transition parameters constant over time. The last time-specific survival and detection probabilities are also confounded. Thus the most general models where parameters are fully estimable are ($S_{ij}^U = S_{ij}^O, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$) and ($S_{i1}^O, S_{i2}^O = S_{i2}^U, S_{i1}^U = (S_{i2}^O)^a, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$). Notice that four seasons of sampling are necessary to estimate ψ_1^{UO} , unless constant survival is assumed. Resulting maximum likelihood estimates and standard errors represent approximate expected values and standard errors of the estimators, provided R_{ij} is large. There is no bias in the estimators and coefficients of variation (estimated standard error/estimate $\times 100$) are well below 100% for all estimators (Table 1).

EXAMPLE

We use the methods described above to estimate survival, capture, and breeding probabilities for a population of male eastern tiger salamanders (*Ambystoma tigrinum tigrinum*) from a single pond in Augusta County, Virginia, USA. This species is listed as endangered in Virginia. Males migrate to the pond in the fall or early winter and remain in the pond for several months before returning to the forest in March or April (D. Church, unpublished data). The pond is ephemeral, usually drying in the summer, thus no salamanders remain at the breeding site year-round. Males of this population are known to skip breeding seasons and the length of time spent in the pond varies among seasons. Therefore, it is unreasonable to assume demographic

TABLE 1. Large-sample properties of conditional maximum-likelihood estimators from models $S_{ij}^O = S_{ij}^U, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$ and $S_{i1}^O, S_{i2}^O = S_{i2}^U, S_{i1}^U = (S_{i2}^O)^a, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$, where the true models are: $S_{ij}^O = S_{ij}^U, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$, and $S_{i1}^O, S_{i2}^O = S_{i2}^U, S_{i1}^U = (S_{i2}^O)^a, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$.

Parameter	$S_{ij}^O = S_{ij}^U, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$		$S_{i1}^O, S_{i2}^O = S_{i2}^U, S_{i1}^U = (S_{i2}^O)^a, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$	
	Parameter value†	CV (%)	Parameter value‡	CV (%)
S_{11}^O, S_{11}^U	0.90, 0.90	11.69	0.84, 0.93	33.81, 21.78
S_{21}^O, S_{21}^U	0.78, 0.78	19.77	0.83, 0.83	21.78, 21.78
S_{22}^O, S_{22}^U	0.90, 0.90	12.52	0.84, 0.93	34.88, 23.39
S_{31}^O, S_{31}^U	0.78, 0.78	22.24	0.83, 0.83	23.39, 23.39
S_{32}^O, S_{32}^U	0.90, 0.90	12.28	0.84, 0.93	35.19, 31.68
S_{41}^O, S_{41}^U	0.78, 0.78	26.59	0.83, 0.83	31.68, 31.68
S_{42}^O, S_{42}^U	0.90, 0.90	12.55	0.84, 0.93	34.51, 31.68
ψ_1^{OO}	0.40	24.54	0.60	39.50
$\psi_{2&3}^{OO}$	0.40	22.6§	0.60	36.40§
$\psi_{2&3}^{UO}$	0.60	35.99§	0.40	54.04§
P_{12}	0.95	10.60	0.95	10.35
P_{21}	0.90	15.42	0.90	14.21
P_{22}	0.95	11.57	0.95	10.74
P_{31}	0.90	14.14	0.90	13.81
P_{32}	0.95	12.58	0.95	10.94
P_{41}	0.90	13.78	0.90	13.49

Notes: Properties are based on 1000 unmarked animals entering the area in $i = 1$ and 500 every season thereafter ($i = 2, 3, 4$); a is the proportion of time spent inside the common area to outside the common area, $a = 14/38$. All estimators are unbiased to at least the fifth decimal place. Parameters are defined as follows: S_r^i = probability that an animal in state r at sampling time i , j survives until the next sampling time (S_{i1}^O corresponds to the time that animals may be within the common area, S_{i2}^O corresponds to the time that animals are not in the common area); ψ_r^s are transition probabilities, defined as the probability that an animal in state r at time i is in state s at time $i + 1$, given that the animal survived from i to $i + 1$; states, r , are either observable (O) or unobservable (U); p_{ij} is the probability that an animal is captured or detected during secondary sample j in primary period i .

† Values of parameters not estimated are: $p_{11} = 0.90$; $p_{42} = 0.95$; $\psi_1^{UO} = 0.60$; $\psi_3^{UO} = 0.60$; $\psi_3^{OO} = 0.40$.

‡ Values of parameters not estimated are: $p_{11} = 0.90$; $p_{42} = 0.95$; $\psi_1^{UO} = 0.40$; $\psi_3^{UO} = 0.40$; $\psi_3^{OO} = 0.60$.

§ Based on setting $\psi_2^{OO} = \psi_3^{OO}$ and $\psi_2^{UO} = \psi_3^{UO}$.

closure or that breeding probabilities are completely random or constant across time.

Field methods

Data were collected from August 1999 through April 2003 using drift fences constructed with aluminum flashing buried 10 cm into the soil and extending 50 cm above the ground. Pitfall traps (19-L plastic buckets) were buried every 10 m on both sides of the fence. Traps were opened and monitored daily throughout the breeding season. Adults were digitally photographed at each capture as a method of identification. Males are easily distinguished by swollen cloacae and have proportionately longer tails than females (Petranka 1998). All individual capture events were stored electronically according to the date of capture, and capture histories were constructed by matching an adult's unique color pattern (see D. Church [2003] for more details).

TABLE 2. Summary of the fit and selection statistics for the top 10 models for eastern tiger salamander (*Ambystoma tigrinum tigrinum*) data.

Model	Log-likelihood	<i>K</i>	AIC _c	ΔAIC _c	<i>w</i>
$S_{11}^O = S_{11}^U, S_2^O = S_{22}^U, \psi_i^{OO} = \psi_i^{UO}, p_{ij}$	-27.576	8	71.721	0	0.206
$S_{11}^O = S_{11}^U, S_2^O = S_{22}^U, \psi_i^{OO} = \psi_i^{UO}, p_{ij}$	-22.843	13	73.154	1.433	0.101
$S_{11}^O = S_{11}^U, S_2^O = S_{22}^U, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$	-27.355	9	73.424	1.703	0.088
$S_{11}^O = S_{11}^U, S_2^O = S_{22}^U, \psi_i^{OO} = \psi_i^{UO}, p_{ij}$	-29.680	7	73.801	2.080	0.073
$S_{11}^O = S_{11}^U, S_2^O = S_{22}^U, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$	-23.245	13	73.958	2.237	0.067
$S_{11}^O = S_{11}^U, S_2^O = S_{22}^U, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$	-28.765	8	74.099	2.378	0.063
$S_{11}^O = S_{11}^U, S_2^O = S_{22}^U, \psi_i^{OO} = \psi_i^{UO}, p_{ij}$	-24.430	12	74.113	2.392	0.062
$S_{11}^O = S_{11}^U, S_2^O = S_{22}^U, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$	-22.3587	14	74.418	2.697	0.053
$S_{11}^O = S_{11}^U, S_2^O = S_{22}^U, \psi_i^{OO} = \psi_i^{UO}, p_{ij}$	-27.066	10	75.008	3.287	0.040
$S_{11}^O, S_{12}^O, S_{22}^O = f(S_{22}^U), \psi_i^{OO}, \psi_i^{UO}, p_{ij}$	-27.094	10	75.03	3.344	0.039

Notes: Model selection was based on second-order Akaike Information Criteria (AIC_c); the model with the lowest AIC_c value is considered “best.” ΔAIC_c is the difference in AIC_c values between each model and the low-AIC_c model; *K* is the number of estimated parameters; *w* is the Akaike model weight. *S*₁₁ is the probability that an animal in state *r* survives the period corresponding to the time that animals may be within the pond (*S*₂ corresponds to the time that no animals are in the pond). *S*_{ij}^U = *f*(*S*₂^U) indicates that survival probabilities for nonbreeders are a function of the breeder’s terrestrial survival probability only. Transition probabilities, ψ_i^{rs} , are defined as the probability that an animal in state *r* at time *i* is in state *s* at time *i* + 1, given that the animal survived from *i* to *i* + 1. States, *r*, are either observable (O) or unobservable (U); *p*_{ij} is the probability that an animal is captured during secondary sample *j* in primary period *i*.

Analysis methods

We restricted this analysis to adult males only and we tested several a priori hypotheses about salamander population parameters using the program MSSURVIV. First, we expected survival within the pond to vary among breeding seasons probably due to changes in hydroperiod; however, we expected survival probabilities in the terrestrial habitat to remain relatively constant. Damages to fences were repaired rapidly during the study so we expect capture probabilities to be common over all sampling occasions. We believe that male breeding probability is <1 and largely governed by environmental factors (Semlitsch et al. 1996), thus we expected time-specific transition probabilities, but random rather than Markovian movement. With these a priori hypotheses in mind, we constructed 24 candidate models with the following levels of factors: three levels of survival probability for breeders (time-specific in the pond and time-constant in the terrestrial habitat, time-specific in both habitats, time-constant in both habitats); four levels of movement probabilities (time-specific Markovian, time-specific random, time-constant Markovian, time-constant random); and two levels of capture probabilities (time-specific, time-constant).

We also tested whether the data were modeled better by expressing annual survival probability for nonbreeders as a function of breeder’s terrestrial survival probability only or by including the breeder’s survival probabilities in both terrestrial and pond habitats. We determined the median day salamanders entered and exited the pond each season and based on those dates, calculated the number of 2-wk intervals between sampling occasions. These intervals were rounded to the nearest whole number and inputted into the modified

MSSURVIV program. We fit eight additional models encompassing the same levels of movement and capture probabilities listed above, but we set annual survival probability for nonbreeders as a function of breeder’s terrestrial survival probability only. These eight models assume that biweekly survival probabilities are different between habitats, but constant over breeding seasons. They suggest that survival probabilities in both habitats are time-specific because the median amount of time spent in each habitat varied over breeding seasons, but the biweekly survival probability experienced in the respective habitats is constant over seasons. With these eight additional models, our complete model set consisted of 32 models. We compared the candidate models based on Akaike Information Criteria (AIC_c) adjusted for small sample sizes (Burnham and Anderson 2002). Akaike weights, *w*_{*p*}, are given for each model and are interpreted as a measure of evidence that the model is the “best” model in the candidate model set (Burnham and Anderson 2002). We assessed the relative importance of each parameter (e.g., time-specific pond survival) by summing Akaike weights across all models containing the given parameter. We also report evidence ratios (the relative support of one model compared to another) for relevant a priori hypotheses (Burnham and Anderson 2002).

Results

One hundred and thirty-nine adult male salamanders were caught and released over the four-year study. The most general model fits the data well based on Pearson’s goodness-of-fit test after pooling cells with small expected values ($S_{ij}^O = S_{ij}^U, \psi_i^{OO}, \psi_i^{UO}, p_{ij}; \chi^2 = 0.108, df = 2, P = 0.948$) (White 1983). Model selection procedures suggested that survival within the pond varied

TABLE 3. Summary of parameter estimates from the top 10 models for the male eastern tiger salamander (*Ambystoma tigrinum tigrinum*) example.

Model	\hat{S}_{11}^O	\hat{S}_{21}^O	\hat{S}_{31}^O	\hat{S}_{41}^O	\hat{S}_{11}^U
$S_{11}^O = S_{11}^U, S_{21}^O = S_{21}^U, \psi_i^{OO} = \psi_i^{UO}, p.$	0.850	1.000	0.384	0.906	0.850
$S_{11}^O = S_{11}^U, S_{21}^O = S_{21}^U, \psi_i^{OO} = \psi_i^{UO}, p_{ij}$	0.867	1.000	0.478	0.905	0.867
$S_{11}^O = S_{11}^U, S_{21}^O = S_{21}^U, \psi_i^{OO}, \psi_i^{UO}, p.$	0.850	1.000	0.392	0.906	0.850
$S_{11}^O = S_{11}^U, S_{21}^O = S_{21}^U, \psi_i^{OO} = \psi_i^{UO}, p.$	0.847	1.000	0.389	0.906	0.847
$S_{11}^O = S_{11}^U, S_{21}^O = S_{21}^U, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$	0.859	1.000	0.558	0.905	0.859
$S_{11}^O = S_{11}^U, S_{21}^O = S_{21}^U, \psi_i^{OO}, \psi_i^{UO}, p.$	0.847	1.000	0.393	0.906	0.847
$S_{11}^O = S_{11}^U, S_{21}^O = S_{21}^U, \psi_i^{OO} = \psi_i^{UO}, p_{ij}$	0.859	1.000	0.507	0.905	0.859
$S_{11}^O = S_{11}^U, S_{21}^O = S_{21}^U, \psi_i^{OO}, \psi_i^{UO}, p_{ij}$	0.865	1.000	0.518	0.905	0.865
$S_{11}^O = S_{11}^U, S_{21}^O = S_{21}^U, \psi_i^{OO} = \psi_i^{UO}, p.$	0.850	1.000	0.338	0.906	0.850
$S_{11}^O, S_{21}^O, S_{ij}^U = f(S_{ij}^O), \psi_i^{OO}, \psi_i^{UO}, p_{ij}$	0.921	0.931	0.912	0.921	0.839
Model-averaged estimates	0.863	0.990	0.502	0.908	0.859
(Standard error)	(0.060)	(0.172)	(0.183)	(0.043)	(0.058)

Notes: Model-averaged estimates and unconditional standard errors are reported for survival and transition probabilities based on the full set of candidate models. S_r^c is the probability that an animal in state r survives the time period corresponding to the time that animals may be within the pond (S_r^c corresponds to the time that no animals are in the pond). $S_{ij}^U = f(S_{ij}^O)$ indicates that survival probabilities for nonbreeders are a function of breeder's terrestrial survival probability only; ψ_i^r are transition probabilities, defined as the probability that an animal in state r at time i is in state s at time $i + 1$, given the animal survived from i to $i + 1$. States, r , are either observable (O) or unobservable (U); p_{ij} is the probability that an animal is captured or detected during secondary sample j in primary period i . Estimates of detection probability are: $\{\hat{p}_{12}, \hat{p}_{21}, \hat{p}_{22}, \hat{p}_{31}, \hat{p}_{32}, \hat{p}_{41}\} = \{0.915, 0.964, 0.964, 0.964, 0.764, 0.923\}$.

among breeding seasons (S_{11}^O), but survival probability in the terrestrial habitat was more consistent (Tables 2 and 3). The top model ($S_{11}^O = S_{11}^U, S_{21}^O = S_{21}^U, \psi_i^{OO} = \psi_i^{UO}, p.$) was twice as likely as any of the competing models (Table 2); however, its AIC_c weight was only 0.206, indicating considerable model selection uncertainty. Consequently, we chose to base our inferences on the entire set of candidate models and used model averaging to calculate a weighted estimate and standard errors that reflect model uncertainty for all parameters (multi-model inference; Burnham and Anderson 2002).

Realized survival probabilities within the pond were highly variable, ranging from 0.502 (SE = 0.183) during the 2002 breeding season (\hat{S}_{31}^O) to 0.990 (SE = 0.172) in 2001 (\hat{S}_{21}^O). All of the top 10 models contained year-specific pond survival probabilities (S_{11}^O). Akaike weights for models with year-specific pond survival and constant terrestrial survival totaled 0.788, indicating that these models constitute 79% of the weight. The sum of Akaike weights for models with year-specific survival in both habitats, including models where $S_{11}^U = f(S_{11}^O)$, was 0.157, while weight sums for models with time-constant survival in both habitats was only 0.055 (Table 2).

Estimates of capture probabilities were high (>0.90) for all but one sample occasion (Table 3). Consistent with our a priori prediction, evidence ratios favored constant capture probabilities (Table 4) despite one seemingly low estimate during the third sampling season. Akaike weights for models with constant capture probabilities ($p.$) totaled 0.544, but there was also considerable weight for models with time-specific capture probabilities (p_{ij} , weight totaled 0.456).

Model-averaged estimates suggest the probability a male tiger salamander returns to breed at the same pond in successive years is only 20–30% ($\hat{\psi}_1^{OO}, \hat{\psi}_{2\&3}^{OO}$, Table

3). The probability of breeding was higher for nonbreeders in the previous season ($\hat{\psi}_{2\&3}^{UO} = 0.451$, $s_{\hat{E}} = 0.251$) than for breeders ($\hat{\psi}_1^{OO} = 0.205$, $s_{\hat{E}} = 0.106$; $\hat{\psi}_{2\&3}^{OO} = 0.286$, $s_{\hat{E}} = 0.103$), but precision of these estimates was poor. Small sample sizes likely accounted for this poor precision and affected our ability to clearly distinguish between Markovian and random breeding processes and between time-specific and constant breeding probabilities (Tables 2 and 4). Total Akaike weights for models with the four levels of movement probabilities were: 0.208 for year-specific Markovian breeding probability (ψ_i^{OO}, ψ_i^{UO}), 0.247 for constant Markovian breeding probability (ψ_i^{OO}, ψ_i^{UO}), 0.376 for year-specific random breeding probability ($\psi_i^{OO} = \psi_i^{UO}$) and 0.169 for constant random breeding probability ($\psi_i^{OO} = \psi_i^{UO}$).

DISCUSSION

Motivated by practical situations where animals are captured entering and exiting a common location, we extended previous temporary emigration models (multistate mark-recapture models with an unobservable state) in two ways. First, our model permits estimation of parameters when state closure within a season can be assumed, but assumptions of demographic and geographic closure within a season are relaxed. Previous open-robust designs assumed demographic closure over secondary samples (no mortality or true recruitment), but they relaxed the geographic closure assumption allowing for staggered entry and exit from the common sampling area (Schwarz and Stobo 1997, Kendall and Bjorkland 2001). Our method relaxes the assumption of demographic closure by permitting mortality between all sampling occasions. It relaxes geographic closure to the extent that staggered entry and exit are permitted, as long as survival probability while

TABLE 3. Extended.

\hat{S}_{31}^U	\hat{S}_{31}^O	\hat{S}_{41}^U	\hat{S}_2^O	ψ^{OO}	$\psi_{2&3}^{OO}$	$\psi_{2&3}^{UO}$
1.000	0.384	0.906	0.914	0.151	0.328	0.328
1.000	0.478	0.905	0.885	0.152	0.309	0.309
1.000	0.392	0.906	0.792	0.175	0.353	0.497
1.000	0.389	0.906	1.000	0.231	0.231	0.231
1.000	0.558	0.905	0.715	0.258	0.258	0.574
1.000	0.393	0.906	0.790	0.258	0.258	0.511
1.000	0.507	0.905	1.00	0.209	0.209	0.209
1.000	0.518	0.905	0.722	0.188	0.335	0.556
1.000	0.388	0.906		0.138	0.384	0.384
0.857	0.821	0.839		0.235	0.235	0.637
0.987	0.498	0.904		0.195	0.294	0.423
(0.177)	(0.177)	(0.046)		(0.106)	(0.114)	(0.239)

in the common area remains similar for each individual. This can be achieved if survival probability in the common area is approximately constant for the duration of the season, and if each individual spends approximately the same amount of time in the common area. The key feature common to all forms of the robust design, Pollock’s original design (1982), the open-robust design (Schwarz and Stobo 1997), or the modified open-robust design presented here, is state closure within primary periods. Ultimately, the ability to estimate time-specific parameters, including transitions to an unobservable state, comes from exposing each individual in an observable state to sampling effort at least twice while it is in the observable state.

The second useful feature of our model is the added flexibility to express survival probability for individuals in the unobservable state as a function of the survival probability of observable animals while both are in the same habitat. This method is intuitively appealing as it is likely that unobservable animals experience the same mortality risks as observable animals outside the common area, but they do not experience the mortality risks encountered by the observable animals inside the common area. This is particularly important if predation risks differ between the two habitats, or if activities within the common area, such as breeding, have fitness consequences that affect survival. If observable animals incur additional mortality during migration to and from the common area, or if activities in the common area have residual effects on survival, then survival probabilities of unobservable animals could be still be underestimated. At this time, survival differences among “observable” and “unobservable” populations can only be tested effectively if individuals are sampled outside of the common area (Cam et al. 1998, Kendall and Nichols 2002). Limited simulations suggest several scenarios where parameter estimation is robust to violations of the assumption of equal survival probabilities for observable and unobservable animals, but a more comprehensive investigation is still needed to draw meaningful generalizations (W. L. Kendall and C. S. Jennelle, unpublished data). Parameter estimates in our salamander example (excluding sur-

vival) were similar for models that assumed equal survival probabilities in all time periods in contrast to models where unobservable survival probabilities were expressed as a function of only the observable survival probability outside the pond.

Capture–recapture models are rarely used to analyze drift-fence data and use of the sampling technique is often discouraged because of varying capture efficiency among individuals and species (Dodd 1991, Dodd and Scott 1994). Imperfect capture probability, together with the presence of “non-breeding” or “skipped breeding seasons” can bias commonly used *ad hoc* estimators for survival and breeding probabilities (Anderson et al. 1981, Martin et al. 1995). The few capture–recapture analyses that do exist for pond-breeding amphibians utilized classic open-population models (i.e., one sample occasion per season). These analyses either ignored transitions to unobservable states (Gill 1985, Nichols et al. 1987), or accounted for the transitions but assumed that some parameters were constant across time (B. R. Schmidt, O. Gimenez, R. Pradel, and M. Schaub, unpublished manuscript). Schaub et al. (2004) revealed an unusual exception where time-specificity in all parameters can be maintained if more than one group (e.g., sex) is considered (Models 17 and 18 in their paper), but precision of parameter estimates is likely poor. Both Kendall and Nichols (2002) and Schaub et al. (2004) strongly recommend Pollock’s robust design for studies involving unobservable states, but no previous study has exploited the unique sample design (drift fence) common to many pond-breeding amphibian studies.

Our purpose was to create a model whose assumptions matched both our biological understanding of the system and the sampling design. For pond-breeding amphibians sampled using a drift fence we felt that (1) survival within the pond is likely <1.0 for most species and sexes and may differ among breeding seasons due to variation in time spent in the pond and the pond’s hydrology; (2) capture probability is likely <1.0 for most species and could vary among sampling occasions due to factors such as fence condition; and (3) temporary emigration, or conversely breeding probability,

TABLE 4. AIC_c values and evidence ratios for a priori hypothesis involving capture and transition probabilities.

Parameter used in hypothesis	Models tested (H_0 vs. H_a)	Model AIC _c values		Model weights		Evidence ratio
		H_0	H_a	w_0	w_a	
Capture probability	$(S_{11}^O = S_{11}^U, S_{22}^O = S_{22}^U, \psi_i^{OO} = \psi_i^{UO}, p.)$ vs.	71.721	73.154	0.206	0.101	2.040
Transition probability (Time-sp)	$(S_{11}^O = S_{11}^U, S_{22}^O = S_{22}^U, \psi_i^{OO} = \psi_{ij}^{UO}, p_{ij})$ vs.	73.801	71.721	0.073	0.206	0.354
Transition probability (Random vs. Markovian)	$(S_{11}^O = S_{11}^U, S_{22}^O = S_{22}^U, \psi_i^{OO} = \psi_i^{UO}, p.)$ vs. $(S_{11}^O = S_{11}^U, S_{22}^O = S_{22}^U, \psi_i^{OO}, \psi_i^{UO}, p.)$	71.721	73.424	0.206	0.088	2.341

Notes: We report evidence ratios for each hypothesis using the lowest AIC_c model ($S_{11}^O = S_{11}^U, S_{22}^O = S_{22}^U, \psi_i^{OO} = \psi_i^{UO}, p.$). Evidence ratios, calculated as w_0/w_a , represent the relative likelihood of the reduced model, representing the null hypothesis (H_0) vs. the more general model, representing the alternative hypotheses (H_a).

is likely time specific for populations of most species and could be either a random process possibly governed by environmental factors or a first-order Markovian process, where an individual’s probability of breeding depends on whether it bred in the previous season.

The data we analyzed for the eastern tiger salamander were obtained from a small, relictual population of conservation concern in Virginia (Church et al. 2003). We had relatively few captured individuals compared to many pond-breeding amphibian studies, where hundreds or thousands of individuals are captured and marked (Gill 1978, 1985, Semlitsch et al. 1996, Trenham et al. 2000). Despite small sample sizes, we were able to estimate important demographic parameters with reasonable precision. Male survival probabilities within the pond were <1.0 and varied considerably among breeding seasons, probably due to variation in the pond’s hydrology and duration of freezing weather. Well-maintained fences successfully captured most individuals, but capture probabilities were not perfect (1.0) and there was some evidence that capture probabilities varied among sampling occasions. This emphasizes the importance of estimating rather than ignoring this “nuisance” parameter. Model-averaged estimates of breeding probabilities suggest that males of this population often “skip” breeding opportunities. Males that are currently absent from the breeding pond tend to have a higher probability of returning in the next season than males that are currently breeders (a pattern that might suggest a cost of breeding for males). Our estimates of breeding probabilities should be interpreted cautiously because (1) they were the least precise of all model parameter estimates and (2) only a single estimate of the transition probability from non-breeder to breeder ($\psi_{2&3}^{UO}$) is possible with only four seasons of data. Church (2003) presents an extended analysis of these data, including both sexes of salamanders and movements among three ponds.

Robust design MSMR models presented in this paper provide several advantages compared to traditional ad hoc approaches, such as life table methods that depend on untested assumptions. First, it is possible to test hypotheses and assumptions in a common statistical framework. Model selection using Akaike’s Information Criterion allow for comparison among non-nested

competing models with varying biological interpretations. Basic demographic parameters are estimated directly and can be compared among studies with different levels of sampling effort. Furthermore, parameter estimates obtained from MSMR models can be employed by population matrix models to assess population viability and parameter sensitivity or evaluate possible management actions (Nichols et al. 1992, Biek et al. 2002, Fujiwara and Caswell 2002a, Vonesh and Cruz 2002). For these reasons, we recommend using MSMR models to analyze drift-fence data with marked individuals.

In this paper, we develop a modified open-robust design for use when records are kept of animals entering and exiting a pond or common area. Several other authors (Fujiwara and Caswell 2002b and citations within, Kendall and Nichols 2002, Schaub et al. 2004) have explored models useful in situations with only one sample occasion per season (standard open-population design). Obtaining mark-recapture information via drift fence sampling is laborious, thus data should be analyzed as completely as possible.

Our model assumes no heterogeneity among individuals that cannot be attributed to variations among groups (e.g., age, sex) or to covariates (e.g., size). If such attributes are relevant, then the number of states is increased to incorporate the additional source(s) of variation (Nichols et al. 1994). The MARK program (White and Burnham 1999) accommodates group and covariate information easily, thus we recommend using it when exploring more complicated relationships involving several groups or covariates. Problems may also arise if there is considerable heterogeneity in time spent in the common area, if survival probability within the common area changes radically within the sampling season, or if individuals stay within the common area for multiple seasons (e.g., over winter). Investigators should use prior knowledge about the natural history of the system as well as arrival and departure dates of individuals to determine the appropriateness of these model assumptions. If necessary, sampling design changes (e.g., sampling within the breeding pond) could accommodate within-season variation in survival probability within the common area.

The flexibility of our modeling approach has several practical implications for studies of pond-breeding species. Because our methods allow estimation of p , the probability of capture (or resighting), rather than assuming that $p = 1.0$ or is constant across time or species, drift fences would not need to completely encircle the pond. If necessary, gaps in fences could even be left open and traps closed at times during the breeding season to minimize mortality risk when they cannot be checked regularly, provided this act does not introduce heterogeneity in capture probabilities.

We believe that the MSMR methods presented here could be applied to a variety of different taxa where individuals are captured or detected entering and exiting a common area. Possible applications include bats entering roosts or hibernacula (O'Shea et al. 2003 and citations within), snakes overwintering in common hibernacula (Prior et al. 2001), and anadromous fish migrating to spawning grounds (Sulak and Clugston 1999, Fox et al. 2000). MSMR methods could also be employed in studies of pond turtles, but simultaneous radiotelemetry would be necessary to separate breeding and movement probabilities since both processes occur outside the pond (i.e., between primary periods; Wilbur 1975, Congdon and Gibbons 1996).

We are in the process of extending theory presented here to accommodate systems with more than one pond or site. We envision MSMR models that estimate between-pond movement probabilities as well as pond-specific capture and breeding probabilities. We believe these models hold great promise for exploring and testing hypotheses about metapopulation dynamics as well as studies of selection on life histories.

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