

2013

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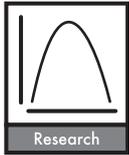
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Otto, Clint R.V.; Bailey, Larissa L.; and Roloff, Gary J., "Improving species occupancy estimation when sampling violates the closure assumption" (2013). *USGS Northern Prairie Wildlife Research Center*. 294.
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Improving species occupancy estimation when sampling violates the closure assumption

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Site occupancy models that account for imperfect detection of species are increasingly utilized in ecological research and wildlife monitoring. Occupancy models require replicate surveys to estimate detection probability over a time period where the occupancy status at sampled sites is assumed closed. Unlike mark–recapture models, few studies have examined how violations of closure can bias occupancy estimates. Our study design allowed us to differentiate among two processes that violate the closure assumption during a sampling season: 1) repeated destructive sampling events that result in either short- or long-term site avoidance by the target species and 2) sampling occurring over a time period during which non-random movements of the target species result in variable occupancy status. We used dynamic occupancy models to quantify the potential bias in occupancy estimation associated with these processes for a terrestrial salamander system. Our results provide strong evidence of a systematic decrease in salamander occupancy within a field season. Chronic disturbance due to repeated searches of natural cover objects accelerated natural declines in species occurrence on the forest surface as summer progressed. We also observed a strong but temporary disturbance effect on salamander detection probability associated with repeated sampling within a 24-h. period. We generalized our findings by conducting a simulation to evaluate how violations of closure can bias occupancy estimates when local extinction occurs within a sampling season. Our simulation study revealed general sensitivity of estimates from single-season occupancy models to violations of closure, with the strength and direction of bias varying between scenarios. Bias was minimal when extinction probability or the number of sample occasions was relatively low. Our research highlights the importance of addressing closure in occupancy studies and we provide multiple solutions, using both design- and model-based frameworks, for minimizing bias associated with non-random changes in occupancy and repeated sampling disturbances.

Site occupancy models that account for imperfect detection of species are increasingly utilized in ecological research and conservation planning (Marsh and Trenham 2008). For example, occupancy models have been used to assess the effects of anthropogenic disturbances on species distributions (Ferraz et al. 2007, Kroll et al. 2008, Zuckerberg et al. 2011), determine the efficacy of wildlife monitoring programs (Weller 2008, Mattfeldt et al. 2009, Collier et al. 2010), and investigate species habitat relationships (Seamans and Gutierrez 2007, Otto and Roloff 2012). Occupancy models are generally preferred over traditional logistic regression or incidence function models because of their ability to account for false-absences caused by imperfect species detection (Mazerolle et al. 2005, MacKenzie et al. 2006, Rota et al. 2011). Although a number of occupancy models have been developed to account for imperfect detection (Geissler and Fuller 1987, MacKenzie et al. 2002, Nichols and Karanth 2002, Tyre et al. 2003), the model developed by MacKenzie et al.

(2002) has been the most readily adopted and numerous extensions of this model are available for use (reviewed by MacKenzie et al. 2006, Nichols et al. 2008, Martin et al. 2010).

To account for false absences, the MacKenzie et al. (2002) occupancy model uses detection and non-detection data collected during multiple site surveys to estimate species detection probability. These repeated surveys are typically performed within a time period where sites are assumed to be closed to changes in occupancy (i.e. ‘closure’ implies no local extinction or colonization; MacKenzie et al. 2002). If the species is detected during a survey within a period where closure is assumed, the site is considered occupied. Hence, surveys at occupied sites that did not result in positive detection within a closed period can only be caused by imperfect detection (i.e. false absences, false zeros). Failure to detect the target species at a site within a closed period could result from true species absence or the species was present, but undetected during all sampling events.

Investigators must use knowledge of the species biology to inform the study design with respect to the 'closure assumption' (MacKenzie et al. 2006, pp. 104–106). In this regard occupancy studies share a similar sampling framework with mark–recapture research, which require repeated samples to estimate detectability of individual organisms within a closed period (Williams et al. 2002). Past research has highlighted the importance of accounting for violations of closure in mark–recapture research (Schwarz and Stobo 1997, Kendall 1999, Kendall and Bjorkland 2001); however, relatively little work has investigated occupancy bias resulting from violations of closure within a single sampling season (but see Kendall and White 2009, Rota et al. 2009, Kendall et al. 2013). Here we evaluate how the physical act of repeated sampling and seasonal changes in occupancy status result in bias if closure is assumed within a field season.

The physical act of sampling may bias occupancy or detection estimates if destructive techniques are used or if sampling alters the behavior of the target species during subsequent sampling events. Altered organism behavior as a consequence of sampling is typically referred to as a 'trap-response' in mark–recapture literature and multiple models have been developed to account for its potential bias (Zippin 1956, Otis et al. 1978). However, bias resulting from a 'trap-shy' response has not been tested in occupancy research. Furthermore, it is unknown to what degree invasive sampling techniques, which are often utilized for sampling cryptic species such as amphibians, reptiles and birds, can bias occupancy and detection estimates if not properly accounted for (Marsh and Goicochea 2003, Pike et al. 2010, Manning and Kaler 2011). Here, sampling can be viewed as an anthropogenic disturbance where the organism's habitat or behavior is altered as a byproduct of investigators gathering species detection information. Examples of commonly used invasive sampling techniques include natural (i.e. rocks, logs, leaf-litter; Otto and Roloff 2011a) or artificial (i.e. wooden boards, sheet metal) cover object surveys for herpetofauna (reviewed by Dodd 2010) and intensive monitoring at avian nest sites or territories (Bolduc and Guillemette 2003, Manning and Kaler 2011).

Occupancy studies are often conducted over time periods (e.g. weeks, months) where it may be inappropriate to assume closure for some species. For example, sampling often occurs during the breeding season for many species (e.g. pond-breeding amphibians, migratory birds, spawning fish). If the species synchronously arrives to all sites and sampling events correspond to this time period, then the closure assumption is likely met. However if organism arrival or departure is asynchronous, or if sampling events do not correspond to the time period when occupancy is static, the resulting non-random process of species movement may cause bias in occupancy estimates obtained via single-season occupancy models (MacKenzie et al. 2002, 2006, Kendall et al. 2013). Thus, identifying the appropriate time-scale for assuming closure requires investigators to incorporate knowledge of species phenology and movement ecology into the sampling design (MacKenzie et al. 2006). Unfortunately planning for field studies is often based on convenient calendar dates (e.g. single month, field season, or year) rather than the ecology of the target organism. For example, Rota et al.

(2009) found substantial bias in songbird occupancy estimates when failing to account for violations of closure over sampling periods that are typical of ornithological research (i.e. spring and summer within a single year).

We used a sampling design that allowed us to evaluate potential changes in site occupancy for a terrestrial salamander during a time period that would normally be considered a single sampling season (i.e. data analyzed using a single-season model; MacKenzie et al. 2002). Specifically, we determined if repeated sampling events caused a chronic decrease in red-backed salamander (*Plethodon cinereus*) occupancy during the sampling season, or if sampling only caused a temporary reduction in salamander detection that persisted for a short time following a sampling event. We also investigated whether species occurrence changed within the season due to natural processes, like seasonal movement, and its influence on occupancy estimates obtained from single-season models. We generalized our findings by conducting a simulation study to evaluate the sensitivity of occupancy estimates to general violations of closure when failing to account for local extinction occurring within a season. We use our results to develop design- and model-based recommendations for minimizing bias caused by animal movements or sampling disturbances.

Methods

Study area

We conducted our study in the Cadillac- Traverse City area in the northwestern Lower Peninsula of Michigan, USA, in 2009. This area is characterized as a glacial outwash plain with porous, sandy soils (Albert 1995). Temperate coniferous forests dominated this landscape prior to European settlement, but have since been replaced by hardwoods. Our study occurred on state-owned forest lands that are currently managed for aspen (*Populus* sp.) production and have a history of timber harvest. We sampled three forest stands that were 5–8 yr post-harvest and 15–28 ha in size. Dominant understory woody plants were aspen, red maple *Acer rubrum*, and blackberry (*Rubus* spp.).

Site selection

We used a two-step approach to select sample sites (i.e. transects). First, we used Hawth's Tools (ver. 3.27, <www.spatial ecology.com/htools/>, accessed 1 Feb. 2009) in a Geographic Information System (ArcGIS 9.1; Environmental Systems Research Inst., Redlands, CA) to overlay each aspen stand with a sampling lattice comprised of 60 × 60 m cells (Supplementary material Appendix 1). We minimized potential heterogeneity in salamander occupancy from local landscape factors by eliminating all lattice cells whose borders intersected or encompassed an unharvested forest edge, active logging road, off-road recreational vehicle trail, or wetland appearing on 2005 National Agricultural Imagery Program imagery (Michigan Dept of Information Technology 2007). We considered all remaining lattice cells as potential sampling locations and randomly selected seven

within three aspen stands (i.e. 21 total cells). All selected cells were spaced ≥ 60 m apart. We assumed that habitat conditions known to affect red-backed salamander occurrence were relatively constant within each 60×60 m cell (e.g. amount and type of forest, elevation) with the exception of the number of natural cover objects (NCO) along each transect. We felt this assumption was reasonable because each forest stand was clearcut 5–8 yr ago, possessed similar vegetation characteristics, and had little topographic relief.

Second, we systematically placed six, 20×2 m NCO transects within each 60×60 m cell (Supplementary material Appendix 1). Within each cell, two transects were assigned to each of three transect ‘groups’. The groupings dictated when salamander sampling would be initiated: early May (Group 1), mid-June (Group 2), or late July (Group 3). Terrestrial salamanders, almost exclusively red-backed salamanders, are usually active and available during this period (Petranka 1998, Otto and Roloff 2011b), and thus, investigators would normally assume closure. Group 1 transects were oriented east to west, at the north and south ends of each cell. Group 2 transects were oriented north to south, at the east and west ends of each 60×60 m cell. Within each cell, we randomly selected the location (i.e. north, south, east, or west) of each transect in Group 3 (Supplementary material Appendix 1). We positioned all transects in the third group 5 m from, and running parallel to, transects Groups 1 or 2 (Supplementary material Appendix 1). Available literature on red-backed salamander home range size suggest 5 m spacing is enough to ensure independence among transects (home range size ≈ 0.03 – 0.61 m²; Mathis 1991). This design provided three groups of 42 independent transects ($n = 126$ transects). Grouping transects in this fashion allowed us to determine if salamander occupancy was influenced by repeated sampling disturbances or if occupancy varied across time within a single sampling season due to organism non-random movements. Each transect represented an independent site in our analyses, consisting of cover objects along this two-dimensional surface.

We sampled all transects within an aspen stand twice in a 24-h period (i.e. two surveys), allowing us to use a dynamic occupancy model to formally test the closure assumption over a time period that closure would normally be assumed. We adopt nomenclature of MacKenzie et al. (2003) who use ‘primary period’ to denote a single, statistical season where sites are closed to changes in occupancy status and ‘survey’ to represent secondary sampling periods within each primary period. Under this approach, our two surveys within 24-h constituted a single-season (hereafter ‘primary period’: MacKenzie et al. 2003). For each survey, one observer searched for red-backed salamanders under cover objects > 4 cm diameter, > 15 cm long, and within 1 m of the transect centerline. All detected salamanders were measured and returned to the point of capture. We ensured that the same observer did not survey the same transect twice in a single primary period. Observers counted and then replaced all intact cover objects to their original point of origin and reconstructed fragmented cover objects to the best of their ability. After conducting two surveys within 24 h, observers revisited each transect 7–10 d later and continued sampling in this fashion until transect Groups 1 and 2 were surveyed

14 and 12 times, respectively (i.e. 7 and 6 primary periods). We surveyed Group 3 transects four times (i.e. 2 primary periods). Our sampling and handling protocols were approved by the Michigan State Univ. Animal Care and Use Committee (Animal Use Form no. 07/08-118-00).

Model development and analysis

We generated detection histories of red-backed salamanders for each transect. We coded detection histories so that each primary period represented the same calendar days for all transect groups. For example, detection histories for transects in each of the respective groups could include:

```

Group1-Transect1  10 11 10 00 00 00 00 -- -- ,
Group1-Transect2  11 10 00 11 10 01 00 -- -- ,
Group2-Transect3  -- -- -- 11 01 00 00 00 01,
Group2-Transect4  -- -- -- 00 01 11 00 00 00,
Group3-Transect5  -- -- -- -- -- -- -- 01 00,
Group3-Transect6  -- -- -- -- -- -- -- 11 10,

```

where ‘1’ represents a positive detection of at least one red-backed salamander during a single survey, ‘0’ represents non-detection, and ‘–’ represents a missing value, indicating that the transect was not surveyed. Focusing on the detection history for Group1-Transect1, an observer detected ≥ 1 red-backed salamander during the first survey of the first primary period, but failed to detect a salamander during the second survey. During the second primary period (i.e. 7–10 d later), ≥ 1 salamanders were detected during both surveys. During the third primary period the species was detected during the first survey, but not the second. Observers did not detect salamanders during the fourth, fifth, sixth, or seventh primary periods and the transect was not sampled during the final two primary periods (i.e. not surveyed in July). For Group1-Transect1, non-detections of salamanders during primary periods 4–7 could arise from 1) failure of the observer to detect red-backed salamanders when the transect (site) was occupied (i.e. false negative, false zero) or 2) localized extinction that resulted in the site becoming unoccupied, which would violate the closure assumption if it was applied to the entire sampling season.

We utilized dynamic occupancy models (MacKenzie et al. 2003) to estimate initial occupancy probabilities (Ψ_1) and time-specific extinction and colonization probabilities (ϵ_t, γ_t) and derive estimates of time-specific occupancy probabilities (Ψ_{t+1}). Our preliminary analysis revealed that salamander colonization probabilities were < 0.02 for all models we considered, thus, we fixed colonization probability at ‘0’ for all models in the final analysis to improve model convergence. We developed alternative occupancy models based on hypotheses common to any species that occurs seasonally or may be influenced by the sampling process. First, we considered a hypothesis where occupancy varied as a function of the total number of cover objects along each transect ($\Psi_1(Cover)$), but no site extinction ($\epsilon (= 0)$) or colonization ($\gamma (= 0)$) occurred throughout the duration of our study (see below for a description of Cover). Support for this hypothesis would suggest the closure assumption was not violated, thereby permitting use of a single-season model to fit data from the entire sampling season (MacKenzie et al. 2002).

We considered this our null hypothesis for comparison to dynamic occupancy hypotheses that included the processes causing changes in occupancy and extinction probabilities within the sampling season.

We hypothesized that occupancy would be higher, and extinction lower, for transects with a greater number of woody cover objects because of the increased availability of refugia (McKenny et al. 2006). We began our dynamic model development by fitting models where initial occupancy and extinction varied spatially as a function of woody cover (i.e. $\psi_1(\text{Cover})$, $\epsilon(\text{Cover})$, $\gamma(=0)$). We classified transects as having either high (>20 cover objects) or low (≤ 20 cover objects) levels of cover and included Cover as a categorical covariate. This model structure assumed occupancy decreased over the field season, and though extinction probability was constant across primary periods it varied spatially among transects with high and low Cover. This model represents the natural process of salamanders moving underground during warmer, drier months, especially for transects with few cover objects, resulting in decreased occupancy estimates for transects during later primary periods. Support for this hypothesis is based on observations of directional salamander movement from above ground refugia into the soil profile to escape desiccation as summer progresses (seasonal movement hypothesis; Taub 1961, Heatwole 1962).

We also developed a Trend model where salamander extinction probability varied linearly across each primary period (e.g. for a model with a $\epsilon(\text{Trend})$ structure, $\text{logit}(\epsilon_t) = \beta_0 + \beta_1(t)$). Support for this model would provide further evidence for the seasonal movement hypothesis and suggest that local extinction was not static over time. As an alternative, we hypothesized that changes in occupancy within our sampling season could result from the displacement of individuals caused by the cumulative effects of repeated sampling (cumulative sampling hypothesis). We represented our cumulative sampling hypothesis by including a Disturbance parameter on extinction probability that reflected the total number of times a transect was surveyed prior to primary period t (e.g. for a model with a $\epsilon(\text{Disturbance})$ structure,

extinction probability at time t was modeled as $\text{logit}(\epsilon_t) = \beta_0 + \beta_1(\text{number of surveys prior to } t)$).

We explored whether salamanders were temporarily affected by NCO disturbances or by prior capture by fitting models where: 1) detection probabilities were set equal between the first and second surveys within a primary period (i.e. within the same 24 h; $p(\dots)$), 2) detection probabilities varied for the second survey within each primary period for sites where the species was detected during the first survey ($p(\dots, \text{Trap-shy})$) and 3) detection probabilities varied between the two surveys, regardless of whether the species was detected during the first survey within a primary period ($p(\dots, \text{1st_2nd})$). The second detection structure represents a hypothesis where detection probability during the second survey may be temporarily lower for sites where the species was detected and handled by the observer (i.e. a capture effect; Zippin 1956, Otis et al. 1978). Conversely, the third detection structure represents a hypothesis where sampling for salamanders during the first survey within a primary period caused a temporary disturbance beneath cover objects and resulted in a decrease detection probability during the second survey. We considered this a site-effect that would occur regardless of whether red-backed salamanders were actually detected during the first survey, given they were present within the primary period. For $p(\dots)$, $p(\dots, \text{Trap-shy})$, and $p(\dots, \text{1st_2nd})$ we assumed that detection probability was constant among primary periods.

Incorporating the hypotheses described above we developed a candidate set of 14 models (Table 1). First, we fit five models consistent with the closure assumption for the entire sampling season (i.e. $\epsilon(=0)$, $\gamma(=0)$, Table 1). Within this initial set, we included $\psi(\text{Cover})$, $\epsilon(=0)$, $\gamma(=0)$, $p(\text{Survey})$ and $\psi(\text{Cover})$, $\epsilon(=0)$, $\gamma(=0)$, $p(\text{Trend})$ because time-dependent models has been proposed to reduce bias in single-season models caused by violations of closure (MacKenzie et al. 2006, p. 106). The $p(\text{Survey})$ model allowed detection to vary with each survey occasion (i.e. survey-specific detection probability), and the $p(\text{Trend})$ model forced a linear relationship on detection probability across all surveys.

Table 1. Selection results for models fit to detection of red-backed salamanders sampled using natural cover object (NCO) surveys in northern Michigan, 2009. ΔAIC_c represents the difference between AIC_c values for model i and the top-ranking model; w is the Akaike weight; K is the number of parameters; $-2l$ is twice the negative log-likelihood. We report baseline occupancy estimates for the initial sampling period for sites with low or high levels of natural cover (Cover covariate). 95% confidence intervals are in parentheses.

Model	ΔAIC_c	w	K	$-2l$	Initial occupancy probability	
					Low cover	High cover
$\psi_1(\text{Cover})$, $\epsilon(\text{Disturbance} + \text{Cover})$, $\gamma(=0)$, $p(\dots, \text{1st_2nd})$	0.00	0.67	7	830.5	0.65 (0.29–0.89)	0.87 (0.59–0.97)
$\psi_1(\text{Cover})$, $\epsilon(\text{Cover})$, $\gamma(=0)$, $p(\dots, \text{1st_2nd})$	3.11	0.14	6	835.7	0.73 (0.33–0.94)	0.91 (0.57–0.99)
$\psi_1(\text{Cover})$, $\epsilon(\text{Trend} + \text{Cover})$, $\gamma(=0)$, $p(\dots, \text{1st_2nd})$	5.13	0.05	7	835.7	0.73 (0.31–0.94)	0.92 (0.49–0.99)
$\psi_1(\text{Cover})$, $\epsilon(\text{Disturbance} + \text{Cover})$, $\gamma(=0)$, $p(\dots)$	5.41	0.05	6	838.0	0.65 (0.29–0.89)	0.87 (0.58–0.97)
$\psi_1(\text{Cover})$, $\epsilon(=0)$, $\gamma(=0)$, $p(\text{Trend})$	5.71	0.04	4	842.3	0.48 (0.30–0.66)	0.81 (0.66–0.90)
$\psi_1(\text{Cover})$, $\epsilon(\text{Disturbance} + \text{Cover})$, $\gamma(=0)$, $p(\dots, \text{Trap-shy})$	7.36	0.02	7	837.9	0.65 (0.29–0.89)	0.87 (0.59–0.97)
$\psi_1(\text{Cover})$, $\epsilon(=0)$, $\gamma(=0)$, $p(\text{Survey})$	7.61	0.01	20	810.9	0.45 (0.27–0.63)	0.80 (0.64–0.90)
$\psi_1(\text{Cover})$, $\epsilon(\text{Cover})$, $\gamma(=0)$, $p(\dots)$	8.48	0.01	5	843.1	0.73 (0.33–0.94)	0.92 (0.56–0.99)
$\psi_1(\text{Cover})$, $\epsilon(\text{Cover})$, $\gamma(=0)$, $p(\dots, \text{Trap-shy})$	10.5	0.00	6	843.1	0.73 (0.33–0.94)	0.91 (0.57–0.99)
$\psi_1(\text{Cover})$, $\epsilon(\text{Trend} + \text{Cover})$, $\gamma(=0)$, $p(\dots)$	10.5	0.00	6	843.1	0.74 (0.31–0.95)	0.92 (0.48–0.99)
$\psi_1(\text{Cover})$, $\epsilon(\text{Trend} + \text{Cover})$, $\gamma(=0)$, $p(\dots, \text{Trap-shy})$	12.5	0.00	7	843.0	0.74 (0.31–0.94)	0.92 (0.48–0.99)
$\psi_1(\text{Cover})$, $\epsilon(=0)$, $\gamma(=0)$, $p(\dots, \text{1st_2nd})$	21.29	0.00	4	857.9	0.42 (0.26–0.60)	0.77 (0.62–0.87)
$\psi_1(\text{Cover})$, $\epsilon(=0)$, $\gamma(=0)$, $p(\dots)$	26.26	0.00	3	864.9	0.42 (0.26–0.60)	0.77 (0.63–0.87)
$\psi_1(\text{Cover})$, $\epsilon(=0)$, $\gamma(=0)$, $p(\dots, \text{Trap-shy})$	27.30	0.00	3	863.9	0.43 (0.27–0.61)	0.78 (0.63–0.88)

Next, we fit nine models that relaxed the closure assumption and allowed occupancy and extinction probability to vary within our sampling season as a function of Trend or Disturbance (Table 1). For each dynamic occupancy and extinction structure we fit models where detection probability was constant ($p(\dots)$) or varied due to a trapping response ($p(\dots, \text{Trap-shy})$) or temporary habitat disturbance ($p(\dots, \text{1st_2nd})$) within a primary period.

We analyzed our data using program MARK (ver. 5.1, <<http://warnercnr.colostate.edu/~gwhite/mark/mark.htm>>, accessed 7 July 2010) and used Akaike's information criterion, adjusted for small sample size (AIC_c), to rank models (Burnham and Anderson 2002). We used cumulative AIC_c weights ($w+$) and evaluation of 95% confidence intervals to determine relative importance of covariates and model parameters. We report model averaged estimates and unconditional 95% confidence intervals for all real parameters unless otherwise noted. Relative bias in occupancy estimates was calculated as $(\hat{\psi}_{closed} - \hat{\psi}_1) / \hat{\psi}_1$ where $\hat{\psi}_{closed}$ is estimated occupancy probability for our AIC_c 'best' model that assumes closure and $\hat{\psi}_1$ is the estimated probability for our 'best' dynamic model during primary period 1 (Bailey et al. 2007).

Simulation study

To generalize our field study findings, we evaluated the sensitivity of single-season occupancy models to violations of the closure assumption by quantifying bias for scenarios where local extinction occurs within a primary period. Here, we envision a general sampling situation where occupancy of the species of interest declines throughout the sampling season, however, the investigator wrongfully assumes the system is closed and uses a single-season occupancy model for data analysis. We used a dynamic occupancy framework to generate expected values and then fit the data using a single-season occupancy model. This approach allowed us to assess bias when multi-season data, which violate the closure assumption, were fit to single-season occupancy models (see Bailey et al. 2007 for more details and associated software). We considered cases with either high or low initial occupancy probabilities ($\psi_1 = 0.7, 0.4$) and moderate or low detection probabilities ($p = 0.4, 0.2$). For each combination of ψ_1 and p we allowed extinction probability (ϵ) to vary between 0.0 and 1.0 between each primary period, which consisted of two independent surveys. Although the focus of our simulation was on extinction, we also considered two colonization probabilities that reflect our study system and may be realistic for biological systems experiencing a chronic decrease in occupancy over time ($\gamma = 0.0, 0.05$).

For all simulations we considered designs with two or four primary periods (T) and two surveys (j) within each primary period for $n = 150$ sites. Here, occupancy state is allowed to change via local extinction and colonization between primary periods only. These simulations mimic traditional sampling designs with a single observer for each site survey, similar to our salamander data, where the total number of independent surveys is equal to $T \times j$. We used a dynamic occupancy structure ($\psi_1(\dots), \gamma(\dots), \epsilon(\dots), p(\dots)$; MacKenzie et al. 2003), and known parameter values for

$\psi_1, \gamma, \epsilon, p, T$ and n , to generate expected values for all possible detection histories in program GENPRES (Bailey et al. 2007, ver. 3.0, <www.mbr-pwrc.usgs.gov/software/presence.html>, accessed 29 March 2011). We analyzed these expected values data to approximate bias and precision via an analytic-numeric approach (Burnham et al. 1987) using a closed occupancy model where the number of surveys was equal to $T \times j$. We fit three single-season models to each set of expected values, one model where detection probability was held constant ($\psi(\dots), p(\dots)$), a second model that allowed detection probability to vary across all surveys (i.e. survey specific model; $\psi(\dots), p(\text{Survey})$), and a third model where detection probability vary linearly across all surveys ($\psi(\dots), p(\text{Trend})$). Similar to our field study, we included the second and third models because time-dependent models have been proposed as a technique for reducing bias caused by violations of closure (MacKenzie et al. 2006, p. 106). We calculated relative bias as $((E(\hat{\psi}_{closed}) - \psi_1) / \psi_1)$ where $E(\hat{\psi}_{closed})$ is the estimated occupancy probability from our closed models fit to each expected value data set and ψ_1 is the 'true' initial (i.e. first primary period) occupancy value used to generate these data.

Results

Salamander field study

The closure assumption over our sampling season was not well supported by the field data; the five models with constant occupancy and no extinction probability (i.e. closed models) received < 0.05 weight and AIC_c values were ≥ 5 units greater than our best models. Occupancy bias for our 'best' static model ($\psi_1(\text{Cover}), \epsilon(=0), \gamma(=0), p(\text{Trend})$) was -0.26 and -0.07 for low and high quantities of Cover, respectively, when compared to initial occupancy estimates ($t = 1$) from our 'best' dynamic model ($\psi_1(\text{Cover}), \epsilon(\text{Disturbance} + \text{Cover}), \gamma(=0), p(\dots, \text{1st_2nd})$; Table 1). Initial occupancy estimates for our 'best' dynamic model had broadly overlapping confidence intervals for sites with high ($\hat{\psi}_{1\text{High}} = 0.87$, 95% CI; 0.59–0.97) and low (0.65, 0.29–0.89) levels of woody cover; however, confidence intervals for high (0.81, 0.66–0.90) and low (0.48, 0.30–0.66) sites did not overlap for our best static model (Table 1).

As we predicted, model-averaged derived estimates of salamander occupancy decreased across primary periods (Fig. 1). Transects with high Cover had higher occupancy and lower extinction probabilities than transects with low Cover (Fig. 1, 2). Model selection results revealed support for a cumulative sampling effect that resulted in increased extinction probabilities over a sampling season (i.e. Disturbance effect, $w+ = 0.74$; Table 1, 2). For example, among transects in the low Cover category, model averaged extinction estimates in early June (i.e. between primary period 4 and 5) were $\approx 45\%$ higher for transects in Group 1 (previous surveys = 8; Fig. 2b) when compared to transects in Group 2 (previous surveys = 2).

Models that held extinction probability constant across primary periods ($\epsilon(\text{Cover})$) received 0.15 of the cumulative model weight (Table 1). Extinction probabilities for the top model that possessed this structure were 0.17

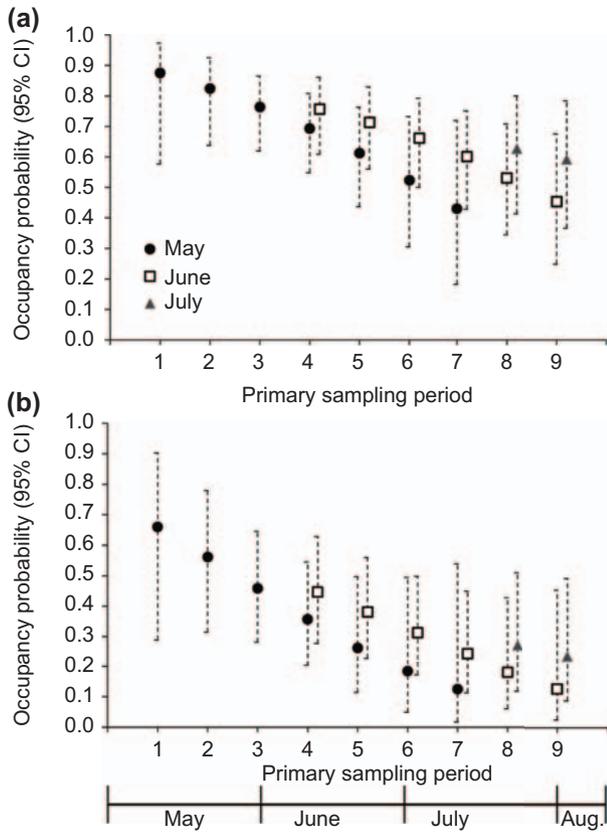


Figure 1. Model averaged derived occupancy probabilities for red-backed salamanders residing on transects with (a) high or (b) low levels of natural cover objects ($NCO \geq 20$ or $NCO < 20$, respectively). Black circles represent Group 1 transects initiated in early May and surveyed through early July; open squares are Group 2 transects initiated in mid-June and surveyed through late July; gray triangles are Group 3 transects initiated in late July and surveyed through early August. Each primary period was separated by 7–10 d.

(0.09–0.30) and 0.07 (0.01–0.31) for low and high Cover transects, respectively. We found little support for models containing the Trend covariate ($w+ = 0.05$; Table 1). The beta estimate for the top model that included Trend was -0.03 (-0.35 – 0.30 ; Table 2). Collectively, our results provide strong evidence of a systematic decrease in salamander occupancy caused by localized extinction within a field season. This decrease was likely due to a chronic disturbance effect associated with cumulative NCO surveys and natural movements of salamanders as the summer progressed.

Models that included $p(Trap-shy)$ structure on salamander detection probability had cumulative model weight $w+ = 0.02$ (Table 1) and confidence intervals for the Trap-shy parameter overlapped 0 for the top-ranking model that included a handling effect. However, model selection results revealed substantial support for a temporary habitat disturbance effect: models that allowed detection to vary between the 1st and 2nd survey within a 24 h period had cumulative weight $w+ = 0.86$ (Table 1). As we predicted, detection probability decreased during the second survey within a primary period ($\hat{p}_{1st} = 0.27$, 95% CI: 0.21–0.34; $\hat{p}_{2nd} = 0.18$, 0.14–0.24; Table 2).

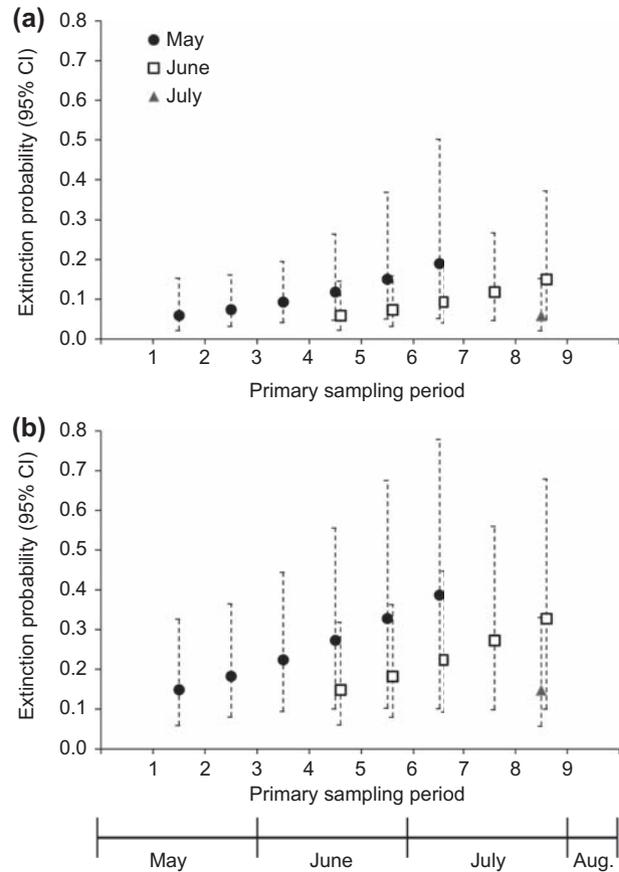


Figure 2. Model averaged extinction probabilities for red-backed salamander transects with (a) high or (b) low levels of natural cover objects ($NCO \geq 20$ or $NCO < 20$, respectively). Black circles represent Group 1 transects initiated in early May and surveyed through early July; open squares are Group 2 transects initiated in mid-June and surveyed through late July; gray triangles are Group 3 transects initiated in late July and surveyed through early August. Each primary period was separated by 7–10 d.

Simulation study

Single-season occupancy models generally showed sensitivity to violations of the closure assumption, with the strength and direction of bias varying between simulations (Fig. 3). For example, when ϵ was high (e.g. 0.75), ψ was typically positively biased for all closed models regardless of colonization levels. The only exception was when $\gamma = 0.0$ and data were modeled with time-varying detection probabilities $\psi(\cdot)$, $p(Survey)$ and $\psi(\cdot)$, $p(Trend)$: here, bias was slightly negative (Fig. 3e–h). For lower values of ϵ , bias was generally smaller but the direction of the bias was positive when some colonization also occurred, $\gamma = 0.05$, and was negative when $\gamma = 0.0$. As expected, $\hat{\psi}$ from simulations with four primary periods had greater bias, but smaller standard errors, than those with only two primary periods (Fig. 3; Supplementary material Appendix 1). For most simulations the $\psi(\cdot)$, $p(Survey)$ and $\psi(\cdot)$, $p(Trend)$ models yielded occupancy estimates that were less biased than the $\psi(\cdot)$, $p(\cdot)$ model; however, there were several situations where the opposite was true. For example, when there were four primary periods, bias for $\hat{\psi}$ was generally greater for $\psi(\cdot)$, $p(Survey)$ and $\psi(\cdot)$, $p(Trend)$ than $\psi(\cdot)$, $p(\cdot)$ (Fig. 3d, g, h). Bias was generally lower for moderate

Table 2. Parameter estimates and 95% confidence intervals for red-backed salamanders sampled using natural cover object (NCO) surveys in northern Michigan, 2009. Disturbance, Trend, and Cover are the beta estimates representing logit-linear effects of DISTURBANCE, TREND, and COVER on occupancy and extinction probabilities, respectively. 1st_2nd surveys are the beta estimates for salamander detection probability parameters. We report estimates for the top three models ($w > 0.05$).

Parameter	Model		
	$\psi_1(\text{Cover}), \epsilon(\text{Disturbance} + \text{Cover}), \gamma(=0), p(.,1st_2nd)$	$\psi_1(\text{Cover}), \epsilon(\text{Cover}), \gamma(=0), p(.,1st_2nd)$	$\psi_1(\text{Cover}), \epsilon(\text{Trend} + \text{Cover}), \gamma(=0), p(.,1st_2nd)$
Initial occupancy			
Intercept	0.61 (−0.89–2.11)	0.99 (−0.69–2.69)	1.03 (−0.77–2.83)
Cover	1.26 (−0.69–3.21)	1.38 (−1.31–4.08)	1.43 (−1.50–4.37)
Extinction			
Intercept	−2.07 (−3.13 to −1.01)	−1.56 (−2.28 to −0.85)	−1.49 (−2.61 to −0.38)
Disturbance	0.16 (0.01–0.31)		
Trend			−0.03 (−0.35–0.30)
Cover	−1.07 (−2.13 to −0.01)	−0.95 (−1.92–0.03)	−0.94 (−1.92–0.05)
Detection			
1st survey	−0.97 (−1.27 to −0.68)	−1.00 (−1.30 to −0.71)	−1.00 (−1.30 to −0.71)
2nd survey	−0.51 (−0.89 to −0.14)	−0.51 (−0.89 to −0.14)	−0.51 (−0.89 to −0.14)

versus low values of p ; a pattern that was consistent for all but one simulation (Fig. 3c). The pattern of bias was nearly identical for both high and moderate levels of ψ_1 when $\gamma=0$, but bias was often higher for moderate levels of ψ_1 when $\gamma=0.05$.

Discussion

Obtaining unbiased estimates of occupancy is important for long-term monitoring of species distribution patterns and when making inferences regarding the effects of ecological covariates on species presence (Yoccoz et al. 2001, Mazerolle et al. 2005, MacKenzie 2006, Kéry and Schmidt 2008). We explored the potential for bias caused by two processes commonly linked to violation of the closure assumption in occupancy studies: 1) destructive sampling techniques or 2) sampling occurring over a time period during which organism movements result in variable occupancy status. Bias associated with the later of these two processes has been previously considered (Kendall and White 2009, Rota et al. 2009, Kendall et al. 2013); however, our treatment of destructive sampling is unique. Consistent with these concerns, we found evidence of a chronic decrease in occupancy, an increase in local extinction, and a temporary decrease in detection probability, associated with repeated sampling disturbances in our salamander system. We also found evidence for changes in seasonal occurrence of salamanders that was independent of the sampling process. Our analysis revealed that the magnitude of the estimation bias was not equivalent among site types: sites with low levels of natural cover had greater, negative bias than sites with high levels of cover. Furthermore, the relative effect of our Cover covariate was dependent on whether we used static or dynamic models to estimate occurrence. Collectively, these findings suggest that violations of closure can influence estimated properties of ecological covariates, and result in biased estimates of occupancy over time.

Although destructive sampling techniques have been acknowledged as a potential source of sampling bias in

occupancy studies (Smith and Petranka 2000, Bailey et al. 2004, Otto and Roloff 2011b), our research is the first to explicitly test for and quantify sampling disturbance effects. We emphasize this concept by acknowledging that the effects of sampling disturbances can be both short-term and temporary, or long-term and persistent or permanent. Our analysis provides evidence that destructive sampling causes short- and long-term effects on salamander detection and occupancy probabilities, respectively. We observed a 31% decrease in detection probability during the second survey within a primary period, suggesting that salamanders temporarily migrated either horizontally (i.e. outside the transect width) or vertically (i.e. into the leaf-litter or soil) following the first NCO survey. Limited support for $p(\text{Trap-shy})$ suggest that decreases in detection probabilities during the second survey were independent of whether the species was detected and handled during the first survey within a primary period. Rather, temporary disturbances to woody refugia likely caused salamanders to leave the site, but then return, and be available for capture, during subsequent primary periods.

We also found evidence of a long-term, persistent sampling effect resulting in a chronic decrease in salamander occupancy and an increase in local extinction probabilities among primary periods. Our sampling efforts caused unavoidable fragmentation of woody cover objects and reduced their overall contact with the soil and leaf litter, an outcome which is typical for NCO surveys (Dodd 2010, Otto and Roloff 2011b). Our salamander analysis showed that simply modeling variation in detection probability over time, such as $\psi_1(\text{Cover}), \gamma(=0), \epsilon(=0), p(\text{Survey})$ or $\psi_1(\text{Cover}), \gamma(=0), \epsilon(=0), p(\text{Trend})$ was not sufficient for reducing occupancy bias caused by violations of closure due to sampling disturbances. Our simulations provide additional scenarios that refute the assertion of MacKenzie et al. (2006) that use of time-dependent, single-season models should reduce occupancy bias when closure is violated. For example, occupancy estimates from $\psi(.,) p(\text{Survey})$ and $\psi(.,) p(\text{Trend})$ models showed higher (and negative) bias relative to the $\psi(.,) p(.,)$ model, for scenarios with moderate levels of extinction

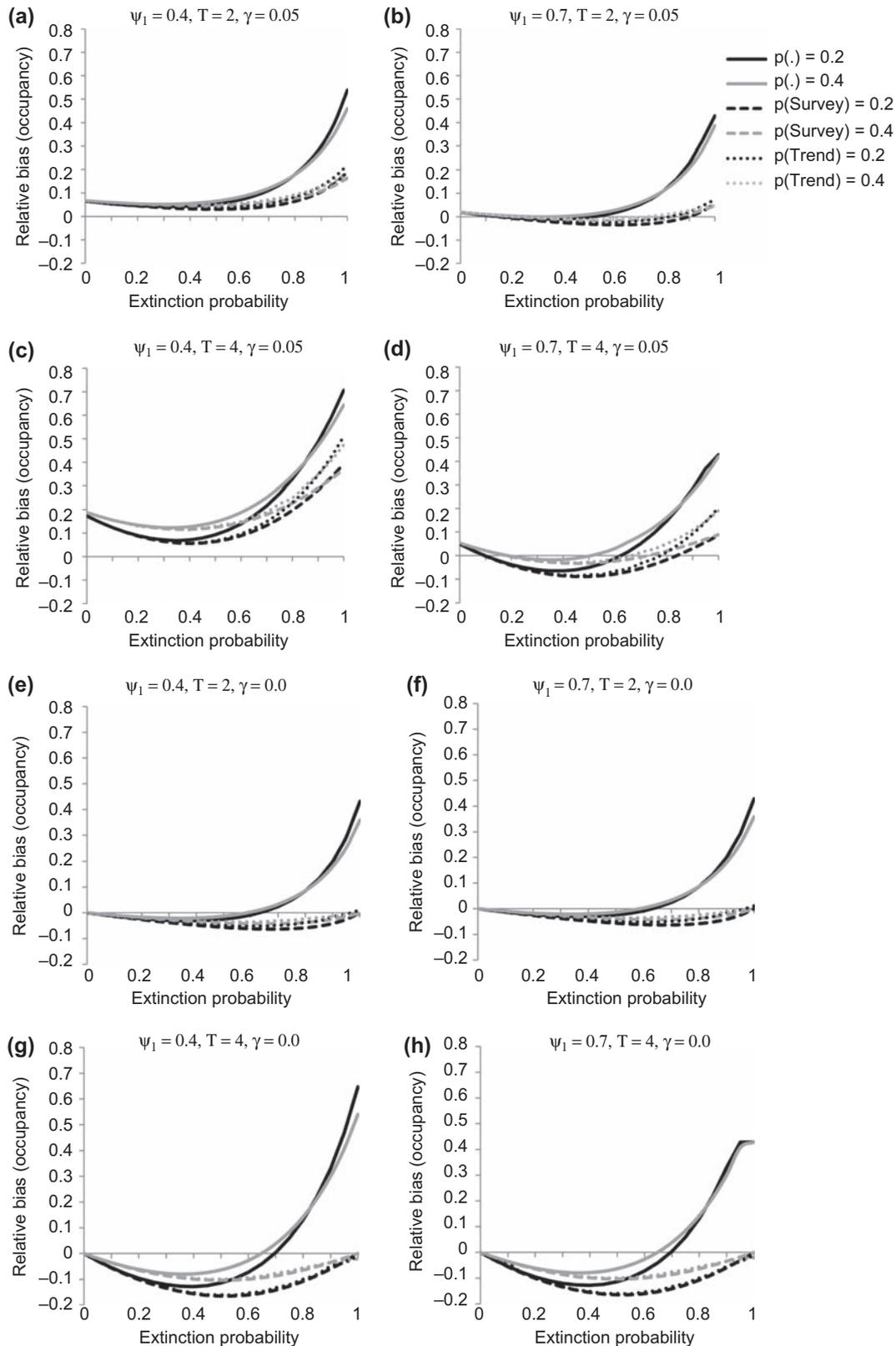


Figure 3. Estimates of relative bias in closed, single-season occupancy models when sites are open to local extinction events between primary periods. ψ_1 = initial occupancy probability, T = the number of primary sampling periods, γ = probability an unoccupied site during primary period t , becomes occupied at before primary period $t + 1$, ε = probability an occupied site during primary period t , becomes unoccupied before primary period $t + 1$, p = probability of detecting the species during a single survey, given its presence at a site. Expected values were analyzed using time-independent ($\psi(\cdot)$, $p(\cdot)$; solid line), time-specific ($\psi(\cdot)$, $p(\text{Survey})$; dashed line) and linear trend ($\psi(\cdot)$, $p(\text{Trend})$) closed occupancy models. Relative bias was calculated as $\text{bias} = ((E(\hat{\psi}_{\text{closed}}) - \psi_1) / \psi_1)$ where $E(\hat{\psi}_{\text{closed}})$ is the estimated occupancy for the closed model and ψ_1 is the initial (i.e. first primary period) occupancy values used to generate the data.

probability and no recolonization, especially in longer duration studies (4 primary periods). Our results suggest investigators should exercise caution when using a time dependent models to reduce bias caused by violations of closure and use simulations to investigate nuances unique to their study systems.

A sampling disturbance can be viewed as any act that is initiated by an investigator during the sampling process that results in increased variation, or reduced precision, of a parameter of interest (e.g. occupancy or detection probability). For example, detection probabilities may increase following first detection in cases where baits or lures are used (e.g. carnivore studies, Thorn et al. 2009). A similar effect can occur in volunteer-based monitoring programs when observers anticipate species that they have previously seen or heard at sample sites (Riddle et al. 2010). Alternatively, intensive monitoring at sites could decrease occupancy over time if the repeated presence of an investigator alters organism behavior or increases predation risk (Bolduc and Guillemette 2003, Manning and Kaler 2011). All these processes create variation in occupancy or detection probabilities, that if not modeled appropriately, lead to biased estimates of occupancy parameters and potentially influence inferences regarding the effect of habitat covariates, as shown here.

We also observed evidence of decreased occupancy across primary sampling periods in our salamander example that was independent of the sampling process. Our analysis provided some support for models that assumed extinction probability was constant over time, but varied spatially across transects with different quantities of natural cover. In this study we estimated the occurrence of salamanders on the two dimensional surface of the forest floor: our design does not allow us to infer patterns in below-ground salamander occurrence. A decrease in salamander surface occupancy across time is supported by past research showing that use of above-ground cover objects by red-backed salamanders decreases with drying soil conditions during summer months (Taub 1961, Heatwole 1962). As summer progresses, a portion of red-backed salamander populations may move underground, resulting in local and temporary extinction of the upper surface of the forest floor (Bailey et al. 2004, Dodd and Dorazio 2004).

An alternative explanation for decreasing occupancy over time is mortality of all individuals at occupied sites. However, we did not detect any dead or dying salamanders during our surveys, which suggests that mortality was not the mechanism for local extinction. While few survival estimates exist for red-backed salamanders, other plethodontids have relatively high survival probabilities in forested landscapes (Hairston 1983). Collectively, this suggests that non-random movement of salamanders is the only plausible explanation for decreasing occupancy over time. Although it was not our primary objective, our results demonstrate that dynamic occupancy models can be used to model species phenology (Kendall et al. 2013).

Movement of wildlife in response to environmental conditions or seasonal changes in behavior is expected, yet we are aware of only two studies that investigated sensitivity of occupancy models to violation of closure when species make non-random movements over the duration of a field study (Rota et al. 2009, Kendall et al. 2013). This is

problematic considering a vast majority of occupancy studies take place over multiple months (i.e. a field season); a timescale where investigators may wrongfully assume closure and use a single-season model to analyze occupancy data. In their study of migratory songbirds, Rota et al. (2009) determined that their study sites were likely open to changes in occupancy over timescales typical of other ornithological research. Kendall et al. (2013) showed that staggered arrival and departure of species at study sites can cause bias in occupancy estimates if closure is assumed over an entire sampling season. Similarly, our results highlight the importance of addressing closure in occupancy studies, even when sampling relatively sedentary organisms such as terrestrial salamanders. Still, our simulation also revealed situations where occupancy models are relatively robust to closure violations. This was particularly true when extinction probabilities and the number of primary periods were relatively low, a finding supported by Kendall and White (2009). In many field studies local extinction probability may be relatively low within a single sampling season for non-migratory species in fairly stable habitats, where sampling methods are relatively non-invasive. The closure assumption in these situations may be appropriate.

We suggest that investigators use phenological knowledge of the target species to develop sampling designs that minimize estimation bias associated with sampling disturbances and seasonal changes in occupancy. By addressing closure a priori in the design phase, investigators will reduce their dependency on sophisticated modeling to reduce bias attributable to a suboptimal study design. For example, when surveying red-backed salamanders, investigators should sample within a single month to minimize bias associated with non-random movements into the subterranean environment (Heatwole 1962, Otto and Roloff 2011b), but allow sites > 24 h to recover from sampling disturbances. Our field and simulation analyses suggest that limiting the number of repeated surveys to ≤ 4 within a 3–4 week primary period should minimize bias caused by sampling disturbances in our salamander system. However, if surveys must be conducted over a long time span, or if > 4 destructive sampling events must be used, then potential changes in occupancy over time should be accounted for within a dynamic occupancy framework (MacKenzie et al. 2003, Rota et al. 2009). Investigators may also consider pooling detection histories from $j \geq 2$ surveys into one pre- and one post-disturbance event to reduce bias caused by chronic emigration (Kendall 1999, Kendall and White 2009). Alternatively, researchers could substitute spatial subunits for temporal replicates when using destructive sampling (MacKenzie et al. 2006, Otto and Roloff 2011a). In this case the closure assumption applies to the spatial subunits and still must be addressed to reduce estimation bias (Kendall and White 2009). Ultimately, investigators should consider a combination of design- and model-based strategies for minimizing estimation bias and achieving strong inference in occupancy studies.

Acknowledgements – We thank Andrew Coleman and Rachelle Sterling for their assistance in the collection of field data. Mike Donovan and Kerry Fitzpatrick helped develop project objectives. A. J. Kroll, William Kendall, Elise Zipkin, and one anonymous reviewer provided insightful comments on an earlier version. Gary

White and Ken Burnham provided analysis suggestions. Support for this project was provided by the Michigan Dept of Natural Resources-Wildlife Division.

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Supplementary material (Appendix ECOG-00137 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.