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You Must Estimate Before You Indicate: Design and Model-Based Methods for Evaluating Utility of a Candidate Forest Indicator Species

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**YOU MUST ESTIMATE BEFORE YOU INDICATE: DESIGN AND MODEL-BASED
METHODS FOR EVALUATING A CANDIDATE FOREST INDICATOR SPECIES**

A Thesis Presented

by

JILLIAN FLEMING

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University of Massachusetts Amherst in partial fulfillment
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DEDICATION

To my dog Marley, thanks for being the best pup.

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ABSTRACT

YOU MUST ESTIMATE BEFORE YOU INDICATE: DESIGN AND MODEL-BASED METHODS FOR EVALUATING A FOREST INDICATOR SPECIES

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The red-backed salamander (RBS; *Plethodon cinereus*) has a large geographic range and, though it is common throughout, abundance varies spatially. It has been studied extensively for at least a century and as a result; its distribution, habitat use, behavioral ecology, reproductive ecology, and ecological role are well understood in comparison to other cryptic wildlife. Multiple sampling methods have been developed to monitor RBS, and I discuss in detail one common method – artificial cover objects (ACOs). Spatial capture-recapture (SCR) is uniquely suited to estimate population parameters, including true density, and is paired well with spatially referenced sampling methods, such as ACOs, and animals capable of retaining unique marks, such as RBS. In the introduction of this thesis, I review RBS, ACOs, and SCR independently in detail, and go on to discuss their compatibility for monitoring terrestrial salamander populations.

Detailed, and often range-wide, monitoring of ecosystems is necessary to gather the information needed to achieve broad multiple-scale conservation objectives. Indicator species are recommended tools for filling in gaps of knowledge where these range-wide data do not exist. The use of indicator species is precluded by the lack of evaluation of candidate indicators and their relationship to indicated processes. In this thesis, I discuss in detail the practicality of indicator species as wildlife management tools, and challenges in their application – primarily their practicality when direct measurement of a variable of interest is possible. I advocate for integrative indicator species applications that make use of relationships to latent variables, review

two conceptual models involving latent variables, and propose a modification to these models that makes relationships between variables more explicit.

Inference of among-population variation to adaptive capacity, response to large-scale threats, and the condition of ecosystems is limited in part by unstandardized methods. Ecological relationships are made difficult to characterize by gaps in data - and this is especially true of links between indicator species their and related ecosystem processes. Using a candidate indicator species, I tested the congruence of population parameter estimates from study designs that varied. In Wendell State Forest, MA, I manipulated spatial arrangements of artificial cover objects (ACO) arrays and evaluated their use for monitoring terrestrial salamanders. ACOs mimic natural habitat - and attraction of RBS to traps may induce behavioral bias in parameter estimates if not accounted for. I sought to determine if variation in ACO design can be accommodated to make comparable estimates. I found that analyzing data from ACOs using spatial capture-recapture (SCR) modeling produces consistent within-population density estimates regardless of ACO configuration.

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CHAPTER 1

A PRIMER ON THE ECOLOGY AND MONITORING OF THE RED-BACKED SALAMANDER

1.1 The Red-backed Salamander

The red-backed salamander (RBS; *Plethodon cinereus*) is a woodland species belonging to the family *Plethodontidae*. *Plethodontidae* is the most speciose family of the Order Caudata, characterized by a shared quality of lunglessness. Lunglessness is believed to have evolved in fast moving Appalachian streams where it was selected for to reduce buoyancy and ultimately downstream displacement of larvae (Dunn 1926). This would have benefited ancestral species as they had long larval periods of several years (Beachy and Bruce 1992). However, this theory is controversial and is contradicted by evidence that the ancestral genus, *Desmognathus*, re-evolved an aquatic larval stage after being outcompeted by the terrestrial genus, *Plethodon* (Chippendale and Wiens 2005). The current RBS range expands northward to southeast Canada, southward to North Carolina, and westward to Michigan/Minnesota (Figure 1; Petranka 1998). Despite the stream-dwelling origin of the family *Plethodontidae*, this species has evolved to be exclusively terrestrial. The shift to terrestrial dwelling is not well understood, but may be derived from the avoidance of intense inter-male competition at aquatic breeding sites (Reagan and Verrell 1991).

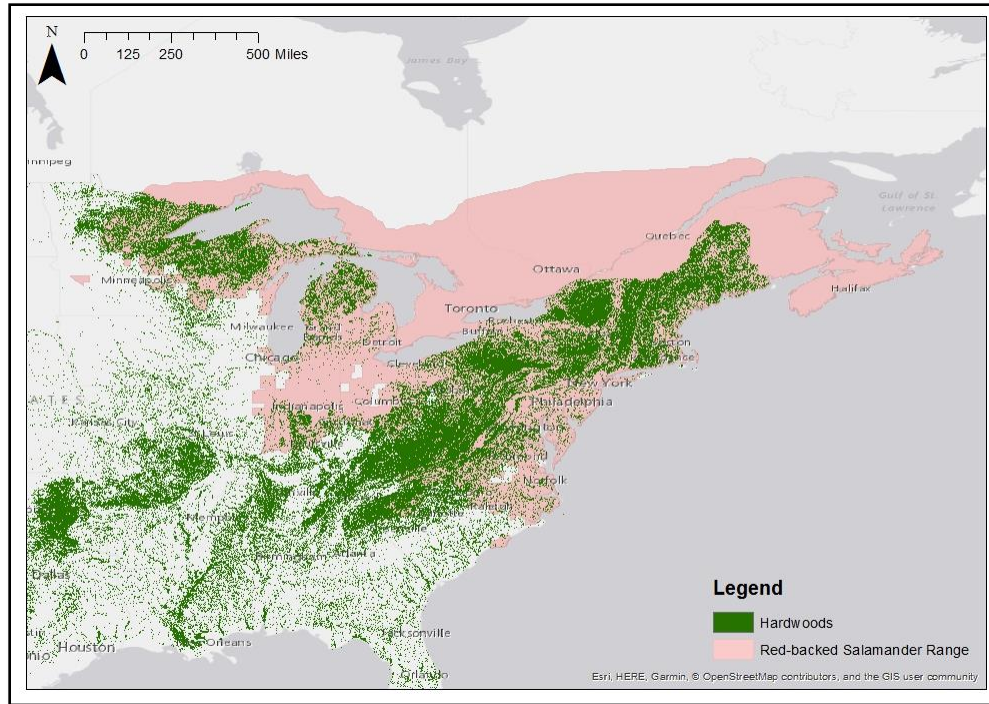


Figure 1: Geographic range of the red-backed salamander (*Plethodon cinereus*; IUCN 2015) as well as the US distribution of the hardwoods that are associated with northern hardwood forests (Ruefenacht et al. 2008).

RBS is common within its range, but abundance appears to be highly variable, even on local scales (Milanovich and Peterman 2016; Peterman and Semlitsch 2014). This likely results from its limited movement due to restrictive physiological tolerances (Heatwole 1962), particularly the dependence on moisture for cutaneous respiration (Feder 1983). Abundance is often highest in cool, moist habitat – conditions that favor RBS physiological tolerance (Heatwole and Lim 1961; Ellis et al. 2012). Populations within a landscape are genetically distinct, even when habitat is contiguous (Cabe et al. 2007). These genetic data support hypotheses of limited dispersal between adjacent habitat patches due to physiological restrictions (Ellis et al. 2012).

However, studies are often conducted on small spatial scales relative to the range of RBS. Physiological tolerances of RBS may vary throughout its range (Muñoz, unpublished data) and without representative subsampling, local population declines may be masked by apparent stability in range-wide status assessments (Miller and Grant 2015). As a result, it is difficult to extrapolate assessments for local populations to larger scales.

1.1.1 Habitat Use and Preference

RBS is most abundant in northern hardwood forests (NHF), but is also found in oak-hickory forest, pine barrens, and birch and mixed forests (Heatwole 1962). Despite being a habitat generalist, occurrence throughout RBS range is related to certain habitat characteristics (Table 1). First, natural cover objects (e.g., rocks and logs) are essential microhabitat used for foraging and maintaining moisture when individuals are active on the soil surface. The observed density of cover objects is correlated with both surface activity and individual mass (Grover 1998), implying RBS has greater access to prey on the soil surface than it does below, if the protection of cover is available. Cover objects provide necessary refugia for surface-active salamanders from predators like ring-necked snakes (*Diadophis punctatus*) – as a result, home ranges typically center on a cover object(s) (Kleeberger and Werner 1982; Sullivan et al. 2002). Given the small home ranges of RBS (~13-24m²; Kleeberger and Werner 1982; Muñoz et al. 2016), even subtle changes in the forest floor structure (i.e., area of cover) may lead to responses expressed in a heterogeneous distribution.

Table 1: Relationships between RBS traits, space use, and site characteristics

<i>Environmental Gradient</i>	<i>Implications for Space Use and Availability</i>	<i>Among Site Variation</i>
Moisture	Respiratory limitations	Microtopography, substrate moisture
Temperature	Metabolic limitations	Canopy cover, elevation
pH	Osmoregulatory limitations	Acidic precipitation, tree composition
Cover Density	Surface habitat	Stand age, topology
Conspecific Density	Territory boundaries	Sex ratio, age ratio

In addition to structural habitat features like cover, RBS distribution is sensitive to certain soil conditions, with higher abundances in shaded soil with low acidity (~4.0, peak of 7.0-7.5) and high moisture (16% soil moisture; Heatwole 1962; Sugalski and Claussen 1997). Soil acidity

disrupts sodium balance and thereby osmoregulation, and pH is perhaps more influential in soil preference than both moisture and light exposure (Frisbie and Wyman 1991). Acidic soils, which are more typical of softwood stands, therefore affect spatial distributions and exclude RBS from over a quarter of forested habitats in some parts of its range (Wyman and Hawksley-Lescault 1987). As a result, RBS populations are expected to be sensitive to altered soil qualities and/or structural features (e.g., forest patch creation, fire). Observed responses to management actions that mimic natural processes (e.g., selective timber harvest, prescribed burns) have been well documented, but there are challenges in classifying a response as either behavioral (i.e., surface activity) or population-based (i.e., abundance, demographics), particularly when sampling is almost always limited to surface-active individuals. This variability has resulted in multiple competing hypotheses for observed responses to changing forest conditions (e.g., Ash 1997; Kroll et al. 2009; Pough et al. 1987).

As is true of all amphibians, especially Plethodontids, RBS relies on moisture for cutaneous respiration, and has permeable skin that provides little barrier to evaporative water loss (Pough et al. 2015). Therefore, RBS is restricted in its distribution and activity by its ability to retain moisture and avoid desiccation. Heatwole and Lim (1961) defined the ‘absorption threshold’ as the level of substrate moisture above which there is net gain in body water by dehydrated salamanders and below which there is a net loss. They provide empirical evidence that RBS actively seeks soil moisture above the absorption threshold. Soil depressions retain moisture longer than level soils and are preferentially used by RBS in dry periods and avoided in wet periods (Heatwole 1962). The absorption threshold of RBS falls somewhere between 1.0-1.5 atm soil moisture tension, and it will adjust within the microtopography of its home range to remain above the threshold. This demonstrates how space use observed in RBS can be explained in part by physiological thresholds like absorption. Further, it provides evidence that RBS is indeed sensitive to some process(es) of the forest ecosystem – and the process(es) is/are related to ecosystem functions like decomposition, tree growth, seed set and germination, denitrification.

During conditions in which desiccation is unlikely (i.e., cool rainy nights), RBS will move from cover into the leaf litter for foraging and as conditions become less ideal, salamanders will retreat to cover objects and subsequently below soil surface (Connette et al. 2015; Jaeger 1980). Given this behavior, one hypothesis could be that during ideal surface microclimate conditions, distributions will be random, during moderate conditions distributions will be heterogeneous and higher around cover objects, and in conditions outside of RBS physiological tolerance populations distributions will change to some unobservable distribution underground (Vernberg 1953).

Such tolerance thresholds require that the species is largely subterranean with as little as 2%, and as much as 32%, of the population on the surface at any time (Taub 1961). RBS has been recorded as deep as 30 cm below the soil surface, but detecting salamanders at depths greater than this is difficult (e.g., pit tag frequencies are disrupted by soil), and true depth distributions of RBS are still unknown (Connette and Semlitsch 2015; Taub 1961; Sterrett, unpublished data).

Temporary subterranean emigration is conditional on various spatial, temporal, and environmental factors (e.g., season, elevation, etc.; Bailey et al. 2004a), and these conditional probabilities can be used to estimate ‘superpopulation’ abundance (Kendall 1999) – i.e., the total population present at a site above and below ground. Subterranean emigration often assumed random (Bailey et al. 2004b), though there is evidence that some individuals remain below-ground for long periods of time (Connette and Semlitsch 2015; Taub 1961).

Burrowing ability is limited to leaf litter and the organic layer, and RBS relies on burrows created by other forest floor dwelling species (Jaeger et al 2016). Since burrowing ability is poor, RBS employs alternative methods for avoiding environmental hazards that potentially result in desiccation (Heatwole 1960). RBS will first seek more favorable sites with tolerable temperature and moisture conditions. If it fails in its search, it will then attempt to burrow if substrate is loose enough, and if not, the salamander will ‘coil’ to decrease surface area for evaporation to occur.

Finally, RBS engages in a behavior called ‘wandering’, in which it wanders erratically until it desiccates and dies, presumably in a final effort to find more suitable conditions.

Timing of surface activity differs throughout its range due to variation in climate, but emergence is triggered by cues in water relationships and temperature (Heatwole 1962). RBS occupy shallow depths when the water table is high and temperatures are moderate (> 4 C), and deeper depths as the water table is lowered (Taub 1961). Temperature affects the metabolic rates of RBS, and extreme temperatures are energetically costly (Homyack et al. 2010) and avoided via subterranean refuge. While RBS can remain fossorial for extended periods of time, terrestrial breeding, rearing of young, and foraging require it to emerge regularly when conditions permit (biannually in the central part of range; Taub 1961).

In addition to heat and moisture, RBS responds to cold temperatures that are typical throughout its range as well. RBS hibernates in the soil column, apparently below depths of soil freeze (Petranka 1979). Unlike a co-occurring amphibian, the wood frog (*Lithobates sylvaticus*), RBS is not entirely freeze tolerant. In fact, freezing temperatures around -2 Celsius result in mortality before 24 hrs (Storey and Storey 1986). Vernberg (1953) estimated winter mortality in RBS at 57%, though that estimate has been widely discredited because salamanders were restricted in movement during his experiment. In his central Kentucky study sites, after a winter with extreme cold temperatures, Petranka (1979) was unable to detect salamanders in $>50\%$ of sites that were previously occupied. This sensitivity to extreme cold and soil freeze is concerning in light of climate change predictions, as snow pack is expected to decrease, and without snow pack insulation, soils freeze at greater depths (Groffman et al. 2001).

Dispersal in RBS is not well studied, but some evidence suggests that there are demographic differences. Females exhibit greater philopatry than males – indicating that dispersal is more related to male-male competition than resource competition (Liebgold et al. 2011). Juveniles are at greater risk of desiccation than adults because they have greater surface area when compared to body size – potentially making their dispersal dangerous. However, they are

not restricted to territories as are adults, and can move among cover objects (Jaeger 2016; Wicknick 2005). Dispersal appears to be limited by physiological tolerance as evidenced in genetically distinct subpopulations in contiguous forest (Cabe et al. 2007).

RBS diet consists of a large diversity of invertebrates (Burton 1976). Within the leaf litter, RBS diet will change according to weather conditions suggesting that, despite generalist qualities, it does practice some prey selection. On rainy nights, the red-backed salamander will seek out small soft bodied invertebrates that are easily digested (Jaeger 1978), and in dry conditions is more likely to consume hard-bodied invertebrates that are more energetically costly to consume (Jaeger 1990). Prey selection implies that RBS distribution is influenced by a number of environmental variables, and is not conditional on cover availability and soil qualities alone.

1.1.2 Behavioral Ecology

Communication and interactions between individuals must be in tactile or chemical form, because RBS, like most salamanders, is generally near-sighted and nocturnal, making visual communication less effective (Pough et al. 2015). In addition to the chemical-sensing organs found in all salamanders, plethodontids have unique structures, nasolabial grooves, that move chemicals from a surface to their nares (Pough et al. 2015). This anatomy enables salamanders in the genus *Plethodon* to discern odors deposited in fecal pellets of conspecific, and in some cases congeneric, individuals as well as their sex, age, and fitness (Jaeger et al. 2016). Species, sex, and fitness of neighbors determine perceptions of threat, reproductive opportunity, and ultimately how individuals use space in relation to one another (Jaeger et al. 2016; Walls et al. 1989).

Conspecific interactions in RBS reflect the “dear enemy effect” in which individuals are more likely to respond aggressively to an unfamiliar individual than to an individual with a neighboring territory (McGavin 1978). Invasions revolve around cover objects that are marked by inhabitants as territory, and unfamiliar individuals are perceived as more likely to challenge territory (Jaeger 1981). As a result, individuals dispersing to new habitat, perhaps due to

environmental changes (e.g., habitat destruction, resource depletion), may affect territorial behavior and ultimately distribution and space use (i.e., home range) of resident individuals. Further, territories and territorial behavior are made even more complicated by sex dynamics. For example, when males and females share a territory, the individual that is the same sex of the intruder is most aggressive (Lang and Jaeger 2000).

Both inter-specific and intra-specific competition has been studied extensively in RBS and other plethodontids in the Eastern US. For example, it has been speculated that the Shenandoah salamander (*Plethodon shenandoah*) evolved to persist in dry talus slopes having been outcompeted in the surrounding soil habitats by RBS (Jaeger 1970;1971), but more recent measures of cohabitation contradict a directly competitive relationship (Grant et al., unpublished data; Amburgey et al., unpublished data). Fraser (1976) studied a similar system - two plethodontids with overlapping resource use – and found that direct competition between RBS and the valley and ridge salamander (*Plethodon hoffmani*) was rare because high surface densities are restricted to seasonal weather events conducive to surface activity, and emergence for feeding is otherwise staggered. Bayer et al. (2012) studied potential competition with the big levels salamander (*Plethodon shenando*), concluding that the difference in distribution resulted from different habitat preferences, not biotic interaction. Many of these species have co-evolved for millions of years, so the dynamics of interspecific relationships and their geographic ranges are difficult to interpret from current states (Hairston 1987), especially as habitats are being altered for human use.

1.1.3 Reproductive Ecology

Surface activity and space use of RBS is partly motivated by activities associated with reproduction. Males are more aggressive in establishing territories and attracted females will establish within these territories, resulting in a kind of social monogamy. Further, gravid females are more likely to cohabitate with males than non-gravid. Breeding pairs maintain territories

throughout the year but vary in surface activity (Mathis 1989).

One potential hypothesis is that these female-male territories foster an even sex distribution of adult RBS throughout a population, but the distribution of individuals of a particular sex may be determined by individually-varying characteristics. A male in a territorial contest is benefited by length of residency, body size, and tail condition (Mathis 1990; Nunes and Jaeger 1989; Wise and Jaeger 1988). Sexual selection by females favors larger males and larger territories, and females can detect diet composition in male fecal pellets, preferring males with a high-quality diet (e.g., termite) than a lower quality diet (e.g., ants) (Mathis 1991; Walls et al. 1989). Individuals reach sexual maturity around 2 (for males) and 3 (for females) years of age (Gillette 2003). The longevity of RBS has not been well studied, but one article placed average lifespan at 8-9 years (Leclair et al. 2006). In the central part of its latitudinal range, Massachusetts, USA, RBS courtship occurs in the fall. Males are annual breeders and females breed biannually due to the reproductive cost of brooding (Yurewicz and Wilbur 2004; Wise 1995). This results in a mean generation time of approximately 3-4 years (Figure 2; Hairston 1987).

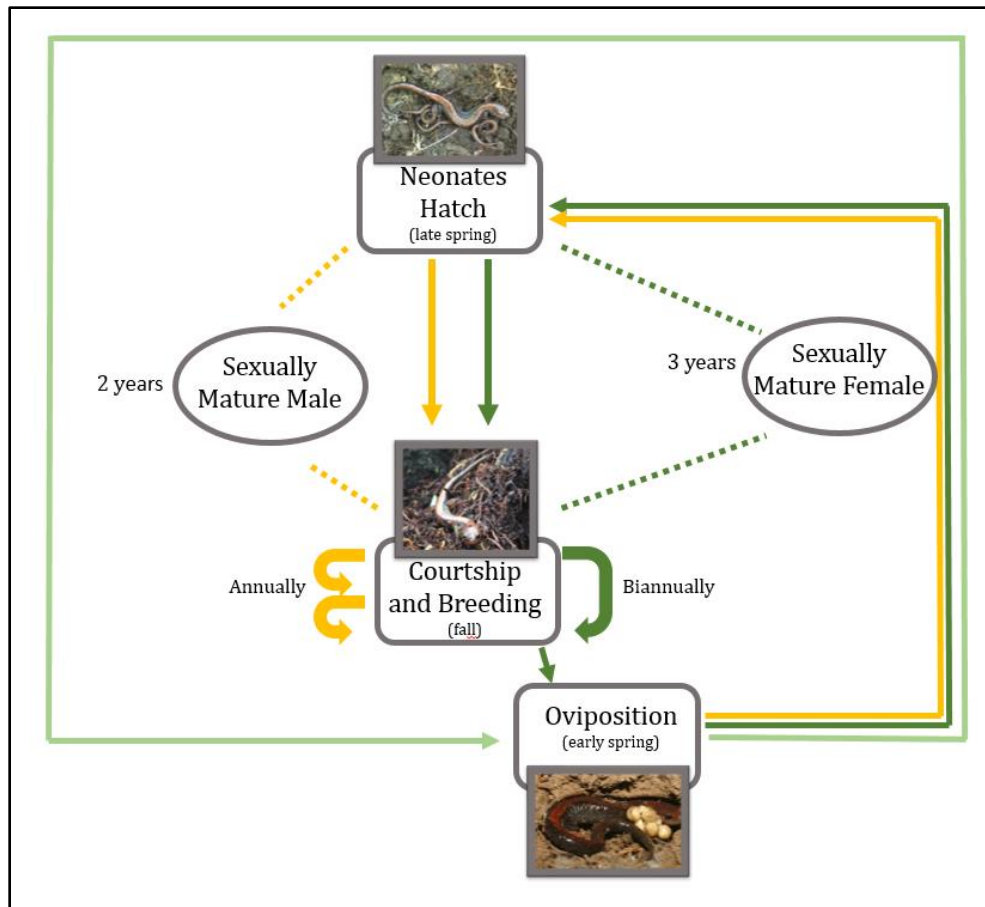


Figure 2: The life cycle and annual activity of the red-backed salamander (male activity in yellow; female activity in green; rectangle around text signifies surface activity). After hatching, RBS time to maturation (dashed lines) is sex-specific; males are sexually mature at 2 years and females at 3 years. Activity of juveniles before sexual maturity is not well understood, and not represented here. Males breed annually, and females breed biannually. Some females are believed to ‘skip a year’ and remain entirely fossorial for a non-breeding annual activity cycle (light green arrow; bottom photo credit: Michael Bernard).

Gestation occurs through the winter, followed by the selection of brooding sites where eggs are oviposited by females in spring. Oviposition takes place within decaying woody debris or in shallow burrows, and the larval stage of RBS occurs within the egg (Petranka 1998). Average clutch size is 8.4 eggs (Nagel 1977). Females attend to and care for eggs for 6-9 weeks to prevent desiccation and fungal infection, and aggressively defend eggs against predators and conspecific cannibalism (Figure 2; Gillette 2003). Brooding behavior of females is proven to be effective in promoting growth and survival of eggs (Highton and Savage 1961). Egg survival to hatching is nearly perfect when clutches are attended to, partly explaining the remarkably high

abundance of RBS in some forests within its range (Homyack and Haas 2009). Young are directly developed, and neonates emerge from eggs in the form of small adults with an average snout-vent length (SVL) of 14.9mm (Leclair et al. 2006). Female space use and access to resources during brooding is restricted by clutch attendance, so females rarely eat during this time.

Fecundity – which may be an effect of offspring survival and/or rate of ova production – in female RBS varies with body condition (i.e., amount of fat reserves). There are several possible explanations for individual-level variation in female depletion of fat reserves during brooding, some related to physiology and habitat quality. However, there may be a behavioral hypothesis as well – speculating that females exhibit behavioral plasticity and discriminate in investment of fat reserves each breeding season. If the mechanism behind fat investment is indeed behavioral, a female RBS may adopt one of two reproductive ‘strategies’.

(1) A female will invest more fat reserves during brooding to increase survival rate of neonates. This approach favors the female’s current clutch. However, the female’s exhausted fat reserves slow the development of ova for the following breeding season, and may therefore affect brooding success of the following clutch.

(2) A female will invest less fat reserves, and her current clutch will have low survival. However, the female will be in better condition post-brooding (i.e., higher fat reserves), and this increases the rate of new ova production. These females have a ‘head-start’ in ova development, and highly developed ova may increase survival of the following clutch.

Drivers of female choice in reproductive strategy in a given breeding season are otherwise unknown. Females may choose to bypass breeding seasons in poor conditions (e.g., drought), and instead invest in developing ova for future clutches. Alternatively, since neonates born to smaller females are less likely survive, and size is correlated with age (Sayler 1966), it is possible that some females will skip brooding until reaching a certain size. Tail intactness is also a measure of

individual condition – decreased rates in ova production are found in females regenerating tails (Yurewicz and Wilbur 2004).

Little is known about the ecology and behavior of juveniles. Observations of juveniles suggest they forage in the leaf litter in moist conditions with mild temperatures and seek cover, primarily within territories of adults, in exceptionally dry conditions (Jaeger 2016). Juveniles are tolerated by territory-holding adults, even when they are not necessarily related, possibly due to differences in prey items and/or lack of sexual competition (Jaeger et al. 2016, Wicknick 2005). An alternative hypothesis is that adults tolerate juveniles as a result of kin recognition. Females in a laboratory setting cannibalize offspring as often as they do unrelated neonates (Wise 1995). However, overlap in territories may be the primary mechanism of kin recognition – supported by an experiment that reported higher juvenile growth rates when housed with familiar adults compared to unfamiliar adults, but adults need not be related (Leibgold and Cabe 2008).

1.1.4 Ecological Role

The RBS is locally abundant in many parts of its range and researchers have made a number of efforts to estimate population density. Many conclude that densities are remarkably high – as first implied by the famous study by Burton and Likens (1975a) that estimated RBS densities in a New Hampshire forest at around 2,950 individuals/ha. (0.295 inds/m²), equating to a biomass of 1,770 g/ha (0.177 g/m²). Though Burton and Likens (1975a) estimates were extraordinary in relation to other co-occurring vertebrates, if accurate, they may in fact be quite low for RBS compared to other parts of its range. Recent studies have used more rigorous sampling and analytical methods and have estimated much greater densities in some forests; Semlitsch et al. 2014 (0.55-0.84 inds/m²), Sutherland et al. 2016 (1.3-2.2 inds/m²), Mathis 1991 (2.82 inds/m²). Still, other locations within RBS range using similar robust methods to Sutherland et al. (2016) are estimated to have densities more similar to or lower than those of Burton and Likens (1975a; Chapter 3; E.H.C. Grant, US Geological Survey, personal communication). When

compiled, these local estimates imply high variability in density throughout its range. Though wide-ranging, all of these estimates place RBS as one of the most abundant – and often the most abundant – vertebrate in NHF forests. Its abundance alone implies that it plays an important role in ecosystem functions (Davic and Welsh 2004), but this role is seemingly context-dependent and therefore difficult to understand.

The expectation that these large population sizes of a top detrital predator should influence nutrient cycling has prompted several research articles that report conflicting conclusions (Homyack et al. 2010). The original study performed by Burton and Likens (1975b), in which salamanders were dried and measured for nutrient content, concluded that RBS was not a reservoir for otherwise unavailable nutrients (i.e., a nutrient sink). Further, they concluded that its relatively small-scale movement does not facilitate the spread of nutrients, and its stable populations result in no significant change in ecosystem nutrient stock. A 2014 study also conducted in New Hampshire performed removal and enclosure experiments and similarly failed to find any evidence of a RBS effect on nutrient cycling or decomposition (Hocking and Babbitt 2014). However, these results have justly been challenged. Over 30 years later, it is now apparent that Burton and Likens (1975a) estimates of RBS density are not consistent over the entirety of RBS range. Therefore, the results regarding nutrient cycling reported in Burton and Likens (1975b) can also not be extrapolated directly to other locations within the species range. Neither method used by Hocking and Babbitt (2014) reflected natural conditions, and their attempt to manipulate density in the experimental enclosures was unsuccessful. This leaves open the question of the role of salamanders in nutrient cycling, and the response of salamanders to changes in biogeochemical processes, unresolved.

Studies that have found a positive relationship of salamanders on nutrient cycling have noted that standing crop nutrients vary spatially, and that without accounting for natural spatial variation in salamander density, variation in nutrient dynamics can be overlooked (Milanovich and Peterman 2016; Semlitsch et al. 2014). The role of plethodontid salamanders in forest

nutrient dynamics requires further investigation, and future research will benefit immensely from representative, within-range subsampling and spatial population estimates.

The role of RBS in NHF food webs is more transparent. When compared with other taxonomic groups, RBS consumes less energy, but contributes more biomass (i.e. it has a high conversion efficiency; Burton and Likens 1975b; Pough et al. 1987). Further, RBS tissue is higher in protein content than birds or mammals, and is therefore not only an abundant prey item, but also a high-quality one (Burton and Likens 1975b; Milanovich and Peterman 2016; Semlitsch et al. 2014). The ability of RBS to contribute such a disproportionate biomass is due to its ability to exploit detrital invertebrates (Figure 3), which are too small for larger members of the food web to consume directly. In doing so, RBS provides a critical link in trophic levels within forest food webs (i.e., a channel of detrital energy to terrestrial and avian consumers) (Hairston 1987). Top-down relationships of RBS on invertebrate communities include two expected effects; 1) predation-induced reduction in detrital invertebrate abundance, and/or 2) increased diversity in detrital invertebrate communities via RBS selective predation on dominant species (Best and Welsh 2014).

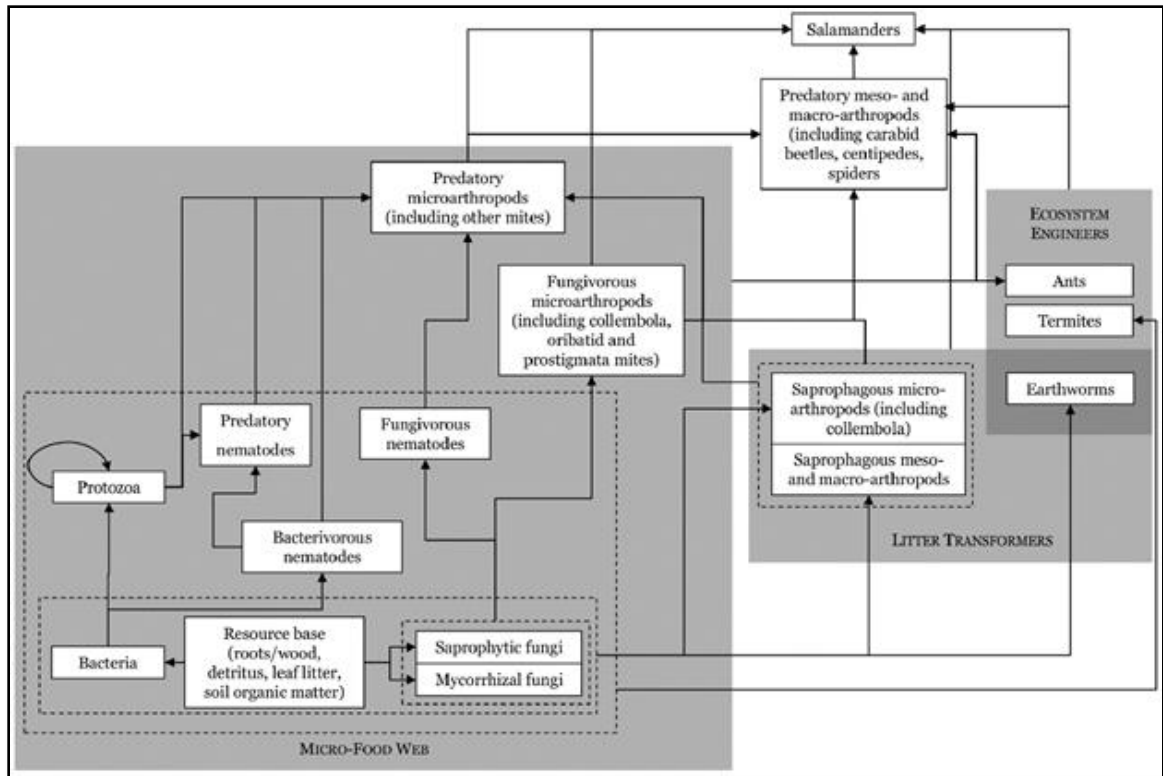


Figure 3: Role of RBS in forest food web (Source: Hocking and Babbitt 2014)

In their review of the ecological role of salamanders, Davic and Welsh (2004) propose that salamanders and their burrows are drivers of soil dynamics and may therefore be considered an “ecosystem engineer” – an animal that alters the physical or chemical structure of an ecosystem changing access or availability of resources (Jones et al. 1994). Given the limited burrowing ability of RBS, there is little evidence for this claim. However, with the abundance of RBS beneath the soil surface, Davic and Welsh (2004) present other compelling hypotheses including: 1) translocation of microorganisms from forest floor to subsurface plant roots, 2) deposition of excretory matter for use by bacteria and fungi, 3) dispersal of gasses through the soil matrix.

1.2 Artificial Cover Objects (ACOs)

All methods for monitoring wildlife require careful consideration of the focal species’ ecology and behavior. Because RBS is naturally cryptic, it calls for sampling methods that makes

individuals easily observed (Grant et al. 1992). Artificial cover objects (ACOs) operate by mimicking natural cover (DeGraaf and Yamaski 1992) – essential microhabitat that facilitates surface activity by maintaining conditions (e.g., moisture, temperature; Grover 1998) affecting RBS physiology (O’Donnell et al. 2014). Conditions provided by cover objects allow RBS to have access to food resources and create opportunity for conspecific interaction (Fraser 1976; Jaeger 1980). ACOs vary in their spatial application but are often arranged in arrays (Figure 4; Willson and Gibbons 2010; Grant et al. 1992), and much like a natural cover objects, individuals can be found in their retreats between the cover object and the soil surface.



Figure 4: An array of ACOs used in a mark-recapture study of RBS. The non-uniform natural cover (i.e., rocks and logs) beyond the array illustrates the unique ability of ACOs to standardize sampling of surface active RBS.

ACOs have been used in the herpetological literature for at least 60 years (Stebbins 1954). By facilitating observations of individuals, captures require little effort and minimize between-observer bias (Fellers and Drost 1994). For questions that require minimal disturbance of focal populations, ACOs are superior to other sampling methods used for amphibians, such as

removal sampling (Grant et al. 1992). ACOs can be standardized in their size, material, and spatial arrangement, and they are an inexpensive sampling tool given their longevity (Hesed 2012). Techniques such as visible implant elastomer (VIE) can be used in combination with ACOs and are effective at assigning unique marks to salamanders and are retained over time (Grant 2008). Because ACOs can be sampled repeatedly, they are conducive to mark-recapture techniques (Muñoz et al. 2016; Sutherland et al. 2016). and can generate robust data sets with their high capture rates (Monti et al. 2000).

Nearly all methods used to monitor animals, especially those used for amphibians, may interrupt an individual's normal activity. For example, pit fall trapping and drift fencing disturb populations because they restrain animals and impede space use (Corn 1994). Of concern for the sampling of free-ranging amphibian populations (i.e., individuals can enter and exit traps freely) are the sampling-related changes in behavior, as these can bias population estimates if not accommodated in models (Marsh and Goicochea 2003; Siddig et al. 2015). The primary criticism of ACOs is that captures may not reflect the natural surface activity of a population due to the introduction of suitable habitat – which may act as an attractant. As a result, ACOs have the potential to artificially inflate surface activity (Willson and Gibbons 2010) and therefore estimates of population abundance or density.

1.2.1 Current and Previous Use

Since being introduced to herpetological literature, ACOs have remained a popular sampling method for the monitoring of many amphibians and reptile species – particularly terrestrial salamanders. ACOs are justified in their wide-spread application as evidenced by their productive capture rates and feasibility of intensive sampling. ACOs generate more captures with less sampling bias than leaf litter quadrant surveys, natural cover transects, pit fall trapping, among others (Monti et al. 2000; Hyde and Simons 2001). Teams of two or more people can sample 200 ACOs in under an hour (Grant et al. 1992), making the accumulation of rich data sets

possible with little effort. Furthermore, with relatively low disturbance, ACO sampling may offer the greatest potential to understand terrestrial salamander population dynamics.

Despite their appeal, ACOs, like most sampling methods, are not infallible and may be susceptible to biases resulting from; material, size, age, placement, and sampling frequency (Hesed 2012; see Taub 1961, Monti et al. 2000; Grant et al. 1992). Additionally, there is potential for disproportionate use of ACOs by certain size (Mathis 1990; Hyde and Simons 2001) or age classes (Marsh and Goicochea 2003), and individuals detected may not be representative of the whole population. If sampling is staggered appropriately (≥ 7 days; Otto et al. 2013), ACOs maintain stable microclimates– but, when sampled more frequently, detections may be biased low (Marsh and Goicochea 2003). Still, ACOs should be preferred over natural cover for studying populations as sources of bias can be standardized in systematic study designs, strengthening inference by limiting sampling variability and making observations comparable (Hyde and Simons 2001; Fellers and Drost 1994).

ACO number and spacing is a potential source of bias that was briefly addressed by Fellers and Drost (1994) who hypothesized that heterogeneity of habitat, site fidelity of organism, size of sampling area, and type of data (i.e., count or unique individuals) are factors that should be considered to determine the number of boards necessary for robust analysis – and noted that if detections are rare or highly variable, more ACOs should be added. It was also recommended that ACOs should be arranged in gridded arrays rather than transects if the objective is to understand space use, because movement can be observed in multiple directions (not restricted along a transect), and a large array (≥ 100 ACOs) would be necessary to make reliable conclusions about movement.

The long history and wide-spread use of ACO sampling, suggests that an abundance of data exists in the herpetological community, which may be exploited for range-wide and historical analyses (e.g., Gibbons and Willson 2010). While ACOs are widely-accepted as efficient capture methods for terrestrial salamanders, the ability to compare these data across time

and among locations is in part limited by the lack of standardization among monitoring efforts (Hesed 2012). To date, consistencies in study design between researchers (i.e., materials, spatial design, visit protocol, etc.) are few, and this lack of coordination limits large-scale inference. As they currently exist, data acquired by ACOs provide potentially biased snapshots of population dynamics throughout their range, and estimating parameters and identifying trends range-wide is therefore challenging (Gula and Theuerkauf 2013; Miller and Grant 2015).

1.3 Spatial Capture-Recapture (SCR)

Effective wildlife science relies on the ability to estimate the number of individuals per unit area, i.e., population density (Bart et al. 2004). Population density can reflect ecological processes related to habitat quality, reproductive success, partitioning behavior and others – all of which are relevant to estimating trends in species biogeography and adaptive capacity, among others (Lomolino 2001).

Spatial capture-recapture (SCR) methods are uniquely capable of estimating the true density of wildlife populations and providing real insight into these important ecological processes. The consideration of space is crucial for understanding population dynamics, and was historically underdeveloped in wildlife science (Efford 2004). SCR is a relatively recent advancement in traditional capture-recapture (CR) methods that explicitly accounts for the space of a sampling area as well as the number and distribution of individuals within that space, ultimately enabling the estimation of true population density (Efford et al 2009; Royle et al. 2014).

1.3.1 SCR₀: The Basic Model

The most basic CR model, referred to as M_0 , considers processes related to detection probability (p) to be constant between individuals (i) and traps (j) sampled (Otis et al. 1978). This means that encounters are completely random, and at no point are individuals within the population more or less detectable among traps or throughout sampling occasions. This is an

important distinction because estimates of density and abundance are reliant on p for the inclusion of n_0 (individuals not encountered). Model M_0 can be refined by adding covariates to the p parameter. In those models, estimates of abundance allow for variation in p to be explained by behavioral, environmental, and/or individual covariates (i.e., territoriality, habitat, or sex, respectively) (Otis et al. 1978).

An important factor that is overlooked by traditional CR methods is the heterogeneity in detection probability due to the individual's location in relation to a trap (Borchers and Efford 2008; Royle et al. 2017). To estimate density or abundance at a capture-recapture site, space around the trapping area needs to be considered in the effective sampling area to account for individuals on the periphery of the trapping area that are captured (Efford 2004). When using traditional (non-spatial) CR methods, this is done by adding a buffer defined by the researcher, most often the mean maximum distance moved (MMDM), or half mean maximum distance moved ($1/2$ MMDM), and can result in vastly different estimates of N based on the buffer chosen (Sutherland et al. 2016). Furthermore, while adjustments are made to account for individuals outside the trapping area, CR methods do not consider heterogeneity of p resulting from individuals' proximity to traps within the trapping area.

The introduction of SCR methods means heterogeneity in capture rates based on the individual's proximity to traps can be accounted for in an area of known size. The most basic SCR model (SCR_0) can be thought of as a CR model with an individual level covariate in which the covariate is the individual's location (Royle et al. 2017). But, instead of defining the covariate to be the distance between the individual and the center of the trapping array (Boulanger and McLellan 2001), SCR_0 defines J covariates as the distance to each trap. SCR_0 considers the probability of detecting an individual at a trap (p_{ij}) to be a decreasing function of the distance between that individual's activity center (s_i) and the trap. SCR models are unique in that they make use of this spatial encounter information that is not fully applied in traditional CR models,

and are thereby capable of not only estimating population size, but also true population density as the sum of distributed activity centers ($\mathbf{s}_1, \dots, \mathbf{s}_N$) within an area (Royle et al. 2014).

To determine an individual's activity center, a state space (S) needs to be established that encompasses the distribution of all individuals available for capture (Patterson et al. 2007). This S is an assemblage of all the possible activity centers that are to be considered by the SCR models. Points within S include trap locations (\mathbf{x}_j) in addition to a grid of points between and outside of traps that is fine enough to capture the distribution of activity centers throughout the effective sampling area (i.e., to approximate continuous space), but coarse enough to allow for reasonably efficient and timely computation. If S is large enough to include all animals with a non-negligible p (evaluated by testing the assumption that p_{ij} is a decreasing function of the distance from j to \mathbf{s}_i) density estimates are not susceptible to bias via size of S (Sollmann et al. 2012).

For compiling spatially and temporally indexed encounter histories, SCR₀ uses a 3-d Bernoulli encounter model that summarizes individual (i), occasion (k), and trap (j) level encounters. This process creates a 3-d matrix of binary encounters with values describing each observed individual's location on each occasion it was captured or not captured (y_{ijk}):

$$y_{ijk} \sim \text{Bernoulli}(p_{ijk})$$

Resulting binary encounters are considered random variables by SCR₀. These encounter histories differ from model M₀ which only considers a 2-d matrix describing occasions an individual was captured because p is assumed constant over the k occasions.

Each trap has a location \mathbf{x}_j , and for individuals with whom spatial recaptures (captures at multiple trap locations) are made, \mathbf{s}_i is determined to be the average location of all captures, which is also where p_{ij} is greatest (Efford 2004; Bourchers and Efford 2008; Royle and Young 2008). Spatial recaptures provide data that are essential for the employment of SCR methods as they determine the spatial scale of detection, i.e., the distance from \mathbf{s} in which p_0 is non-negligible (σ).

$$\text{logit}(p_{ijk}) = p_0 * \exp(-d(\mathbf{x}_j, \mathbf{s}_i)^2 / \sigma^2)$$

In estimating detection probability and σ from encounter history data, the location and number of unobserved individuals (n_0) are estimated as well, and combined are an estimate of total abundance ($N = n_{obs} + n_0$). Simultaneously, a Poisson spatial point process estimates the distribution of N activity centers. SCR₀ models s as a random effect, and reflects complete spatial randomness from which estimates of true density are made (Efford 2004).

Ultimately, SCR models have 3 basic components, all of which are of potential interest for wildlife scientists studying populations. These components are baseline detection probability p_0 , spatial scale of movement σ , and population density D – and under the basic model SCR₀, these parameters are not modeled for any environmental, behavioral, and/or individual effect (Royle et al. 2017).

1.3.2 Adding Effects to SCR Models

It is often the case that detection probability, scale of movement, and population density cannot be assumed to be independent of the effects mentioned above (i.e., environment, behavior, and individual). Consequently, these effects need to be incorporated into these parameters as covariates for accurate estimates of population parameters (Royle et al. 2013; Sollmann et al. 2011). This can be done with categorical variables (e.g., sex), as well as continuous variables (e.g., temperature).

Detection covariates can be trap-specific, occasion-specific, individual-specific, or a combination of any of the three. Covariate effects are often included in the baseline detection parameter, p_0 , and space use parameter, σ , using a linear regression, specifically a binomial GLM. This is done by relating baseline detection or space use to specific covariates, C , that relate to some hypothesized relationship where α are the regression coefficients (Royle et al. 2014).

$$\text{logit}(p_{0,i,j,k}) = \alpha_0 + \alpha_2 C_{i,j,k}$$

Effects that act on the density parameter, D , differ from the SCR₀ model in that s is heterogeneous and does not reflect complete spatial randomness. Effects on the distribution of s

are modeled in a linear regression that incorporates the covariate in the D component in a log linear GLM (Efford 2008).

$$\log(D(\mathbf{s})) = \beta_0 + \beta_1 C(\mathbf{s})$$

When evaluating multiple models with different covariates, maximum likelihood estimation (MLE) can be used to evaluate the models that best explain the spatially referenced capture-recapture data. Akaike Information Criterion (AIC) provides Δ AIC scores and model weights to describe the best fit models and is useful for interpreting results (Borchers and Efford 2008; Efford et al. 2009).

1.4 Summary and Synthesis

To make accurate and logical inference in wildlife research, all three of the previous subjects – species ecology, sampling protocols, and analytical method – need to be considered carefully and in congruence with one another. The grouping of RBS, ACOs, and SCR is a framework for estimating population parameters that is supported by complementary relationships in both the sampling and analysis stages of a study (Sutherland et al. 2016).

First, surface activity of RBS is facilitated by cover, a habitat requirement that when using ACOs allows for high capture rates and acquisition of large data sets (Monti et al. 2000). Environmental conditions relating to RBS physiology (i.e., soil moisture, pH) affect use and preference of cover objects (Joppa et al. 2009). Natural cover objects vary in their ability to maintain ideal and stable conditions (MacNeil and Williams 2013), but standardized ACOs should have a more uniform response – and are favored when estimating population parameters.

Additionally, sampling RBS with ACO arrays results in data that are efficiently applied to SCR analysis. ACOs are spatially referenced – ideally in gridded arrays, such as those recommended by Fellers and Drost (2004) – and fit neatly into the gridded state spaces used by SCR models. State spaces assigned to SCR models should be large enough to encompass the distribution of all individuals sampled (Sollmann et al. 2012). If state spaces are so small that

there is no heterogeneity in detectability of individuals, then the SCR detection function (detection probability decreases with distance from activity center) would not be applicable for estimating movement and density, but ACO arrays are easily made large enough to allow for heterogeneity in detectability.

Thus, the issue of sampling scale is problematic for research focused on animals with large home ranges because their movement (i.e., spatial scale of detection) is difficult to capture in a sampling area (Sun et al. 2014). The area around the activity center for which detection probability is > 0.05 is sometimes used as a measure of home range. In a simulation of a black bear population, home range was estimated at 100 km^2 in females, and 260 km^2 for males (Sollmann et al. 2013)- which, for reference, is 5,917-15,385 times a home range estimate for RBS (16.9 m^2 ; Sutherland et al. 2016). Area-demanding sampling designs, which are typical of megafauna like bears, may limit data collection due to their demanding amount of effort (Sollmann 2012). Data are made even less inclusive of individuals in a population when detections are limited by restrictions such as property boundaries – which are irrelevant to a species ecology but preclude total observation of an individual’s movement – or natural obstructions that prevent captures and whose ecological role in population is not observed. Since large sampling areas are not always feasible, analytical methods must accommodate smaller sampling areas. The black bear simulation experiment performed by Sollmann et al. (2012) artificially manipulated sampling area and distance between traps – and the resulting SCR models performed well at trap spacings double the size of individuals’ range of movements – where CR models would require sampling areas many times the size of an individual’s home range.

As discussed above, spatial recaptures are essential for the application of SCR methods, and optimal designs are those that maximize number of individuals detected and spatial recaptures (Royle et al. 2014). RBS movement is captured sufficiently within trapping arrays of $5 \times 10 \text{ m}$ and when buffered by 5 m , result in a state space that is 245.25 m^2 in area (Sutherland et al. 2016; Muñoz et al. 2016). Furthermore, ACOs are compact and lightweight, making it easy to

test for optimal sampling design by manipulating their spatial arrangement. Conversely, state spaces used in the analysis of wide-ranging megafauna such as black bears (2,525 km²; Sollmann et al. 2012) and ocelots (15,832 km²; Sollmann et al. 2011) require greater effort in testing for optimal trap arrangement, and have instead relied on simulation.

Enabling spatial recaptures requires consideration of the species' movement. Given what is known about RBS ecology, environmental conditions are likely to affect the detection and space use parameters (e.g., weather and availability of cover, territorial behavior and forest structure, respectively; Bailey et al. 2004c; Sun et al. 2014). Using SCR, these environmental conditions can be modeled as covariates for the p and σ parameters (e.g., weather and availability of cover, territorial behavior and forest structure, respectively).

RBS, ACO, and SCR have been evaluated as an analytical framework in applied monitoring and were found to be compatible for the analysis of terrestrial salamander populations (Sutherland et al. 2016). However, in nearly any ecological model there are assumptions made, and if ACOs are to be useful for monitoring and research at range and landscape scales, those involving ACOs should be recognized. For instance, most capture-recapture efforts focus on animals that move on the surface (i.e., 2-d movements), but interpretations of RBS captures are more complicated as it moves on both a terrestrial plane and through the soil column (i.e., 3-d movements). As a result, temporary emigration from a study area is difficult to understand (Bailey et al. 2004a; b; c), and encounters are limited to the soil surface – a part of its habitat that represents some unknown proportion of its total space use (Test and Bingham 1948).

A 'super-population' N^* is an entire population at a given area and includes surface-active and subterranean individuals (Kendall 1999), the true population density of a given area is composed of both. Closed-population models, such as the ones used in the RBS-ACO-SCR framework, assume that no animal is undetectable – but, if there are indeed totally fossorial individuals, as some have suggested (Taub 1961), then ACOs would not detect them, thereby violating that critical assumption (and underestimating N^*). Bailey et al. (2004b) found that

despite attempts at prohibiting RBS surface dispersal from both natural cover and ACO transects, assumptions of closure were violated. Still, they identified that if completely random, temporary emigration in terrestrial salamanders would yield unbiased estimates of abundance. In their analysis, they concluded that though open-population models could estimate abundances of surface populations, only closed populations could estimate super-population abundance. In mark-recapture studies of terrestrial salamanders, it is important to note that if super-populations are to be estimated using surface sampling tools (i.e., ACOs, natural cover), it must be assumed that temporary subterranean emigration is random – though there is little empirical evidence to support or reject this assumption.

CHAPTER 2

INDICATOR SPECIES THEORY AND APPLICATION

2.1 The Call for Indicator Species

The complexity and ever-changing nature of ecological systems, and the costs associated with measuring each component of a target ecosystem, limit the feasibility of gaining a comprehensive understanding of the interactions among biotic and abiotic processes (Lindenmayer et al. 2015). Moreover, ecosystem interactions and drivers of ecosystem change may be scale-dependent (Manley et al. 2006; Parmesan and Yohe 2003). While populations function and conservation actions occur at local scales, understanding range-wide and large-scale drivers of ecosystem change necessitates making landscape-scale inference from local-scale studies (Miller and Grant 2015).

Populations are sensitive to multiple ecosystem components that are affected by management actions – and as a result, there are often tradeoffs to be considered in management decisions. For informing these decisions, a great deal of attention has been given to precise estimation of ecosystem change drivers and population status (e.g. Williams et al. 2002). However, because it is often difficult to identify when and how change occurs (particularly for complex ecosystems), ecologists have developed various approaches for measuring ecosystem states and processes. Surrogate species – broadly defined as species used to represent other species or aspects of the environment to attain a conservation objective (USFWS) – have been proposed for both measuring and managing ecosystem declines, but their application is complicated (Caro 2010).

2.1.1 Surrogate Species

Because of the challenges associated with comprehensive ecosystem inventory and monitoring at appropriately large spatial scales, the surrogate species concept is highly attractive (Lindenmayer and Likens 2011, USFWS 2015). Consequently, surrogate species and related concepts are used as buzzwords to attract attention to research, and the liberal use of surrogate terminology in the ecology community often suffers from lack of development and practical application when examined closely. Caro (2010) candidly describes reckless use of surrogate species terminology in his book, “Conservation by Proxy”:

“Mention ‘umbrella species’ or ‘flagship species’ and people will nod their heads sagely, but ask them to tell you what these phrases mean and they will mumble something incoherent. Talk to nature reserve managers about ‘keystone species’ and they will expostulate about important species in the ecosystem. Go to a conservation conference and you will hear ‘focal’ and ‘indicator species’ as catchwords thrown about with panache but little substance. Everyone is using these species-terms as shortcuts to achieving conservation goals, but few really know what they signify or whether they are of any real use as conservation tools.” (Page XV)

Despite this, where time, funding, and/or abundance of data are limiting factors, carefully selected surrogate species may offer insights to components of greatest concern in an ecosystem, or of greatest relevance to the most working parts of an ecosystem (i.e., species presence, ecosystem processes; Favreau et al. 2006).

Appropriately, the legitimacy of surrogate species as a management tool has been challenged for decades (Wiens et al. 2008, Favreau et al. 2006), and multiple versions of surrogate species have been proposed to overcome identified deficiencies in their application (Table 2; USFWS 2015). However, along with the ambiguous definition of surrogate species in general, the overlap in definitions of surrogate types has allowed for conflicting interpretations.

Table 2: Definitions and examples of surrogate species types

Surrogate Type	Definition	Traits	Example
<i>Umbrella Species</i>	Species whose conservation benefits other species	Large home range, diverse use of resources	Northern spotted owl (<i>Strix occidentalis caurina</i>)
<i>Keystone Species</i>	Performs essential function for maintaining an ecosystem state; disproportionate effect relative to biomass	Transformative of habitat and/or trophic cascade	North American beaver (<i>Castor canadensis</i>)
<i>Flagship Species</i>	Encourages public support of conservation efforts	Charismatic, vulnerable to extinction	Giant panda (<i>Ailuropoda melanoleuca</i>)
<i>Indicator Species</i>	Signifies change in environmental gradient and/or some aspect of ecosystem health	Sensitive to change in environmental gradient(s)	Red-backed salamander (<i>Plethodon cinereus</i>)
<i>Focal Species</i>	Suite of species, each of which used to define spatial and compositional attributes of an ecosystem	Dependent on and limited by unique ecosystem features	Timber rattlesnake (<i>Crotalus horridus</i>)

For example, each focal species may also be an umbrella species (Lambeck 1992); likewise, a keystone species may also be an umbrella species. Flagship species garner public support, and can therefore be referenced as umbrella species because the protection of their habitats benefits co-occurring species. Further; umbrella, focal, and keystone species can be referred to as indicator species – if the author considers the species to indicate biodiversity or certain community dynamics (Ryti 1992). Thus, indicator species are arguably the most confusing in terms of their ambiguous interpretation because their definition can incorporate objectives associated with all other surrogate types – perhaps apart from flagship species (Table 2; Caro 2010). Therefore, indicator species are arguably the most interesting of the surrogate types, because if methods for their practical application are developed, they have the potential to aid in the most numerous and diverse – in terms of objective and scale – management decisions and ecosystem inventories.

2.1.2 Indicator Species

Indicator species and their applications are particularly vague when they are referred to – as they often are – as indicators of ‘ecosystem health’ because the term and its variations (e.g.,

forest health) are ambiguous measures that presumably refer to some aspect of ecosystem functionality. Common interpretations include:

- 1) Health as homeostasis
- 2) Health as absence of disease
- 3) Health as diversity or complexity
- 4) Health as stability and resilience
- 5) Health as vigor for scope or growth
- 6) Health as balance among system components

Entire books are dedicated to the concept of ecosystem health, and best efforts conclude that it is a normative concept related to desired outcomes (Costanza et al. 1992). To facilitate the appropriate and useful application of indicators of ecosystem health, ecosystem health must be defined a priori, with strict criteria of how it is measured and its significance to the ecosystem at large (Landres et al. 1988).

Indicator species need to meet certain criteria related to their responsiveness for ecologists to accurately detect processes (Dale and Beyeler 2001; Landres et al. 1988).

Conceptually, a species that meets a greater number of criteria has greater utility as an indicator, and some that are frequently found in indicator species literature are:

- 1) Easily measured
- 2) Sensitive to environmental stress
- 3) Respond in a predictable manner
- 4) Have low variability in response
- 5) Are anticipatory (i.e., signify impending change)
- 6) Predict changes easily averted with management practices
- 7) Are integrative (i.e., incorporate important and numerous variables)

However, selecting an indicator species is not as simple as checking off criteria, and there are trade-offs to consider. As an example, some indicator species roles may call for a stable

population, while others call for a sensitive population. The former benefits long term monitoring but may not respond to small changes, the latter is able to identify incremental changes but is susceptible to effects of conditions that are not of direct interest (Lindenmeyer et al. 2015). Decisions such as these require that ecologists have clearly defined questions and objectives before selecting indicator species (Landres et al. 1988).

Landres et al. (1988), in a review critiquing and making recommendations for the use of indicator species, was one of the first to define indicators which they described as:

“an organism whose characteristics (e.g., presence or absence, population density, dispersion reproductive success) are used as an index of attributes too difficult, inconvenient, expensive to measure for other species or environmental conditions of interest.”

The important distinction in this definition is that the indicator must have attributes which are linked to variation in ecosystem attributes, and that indirect measurement via indicator species attributes must be more practical than direct measurement of the attributes of the ecosystem (Lindenmayer and Likens 2011; Lindenmayer et al. 2015). This typically requires that indicators satisfy the criteria of being integrative (i.e., incorporate multiple relevant ecosystem gradients in their response) – a difficult quality to prove due to the challenges of conducting comprehensive monitoring of all ecosystem attributes. Scenarios in which a property cannot be measured but its relationships can are not common - but it is these relationships that call for the use of indicator species.

2.1.3 Amphibians as Indicator Species

In general, amphibians have characteristics that may qualify them as an indicator taxon, namely their high local abundances relative ease of sampling, complex life cycles that occur over a range of habitats, and permeable skin that is sensitive to environmental stressors (e.g., changes in weather, contaminants; Collins and Crump 2009). The global distribution of amphibians allows cross-continental comparison of amphibian-habitat relationships and population dynamics. These

relationships were examined in great detail following the recognition of enigmatic global amphibian declines, and resulted in extensive reporting on amphibians and their ecological tolerances (Alford and Richards 1990; Wake 1991). By the 1990s, amphibians were widely referred to as indicator species because of their sensitivity to habitat alteration, acidification, and pathogen spread, among others (Collins and Crump 2009).

Because of this purported sensitivity to environmental conditions, there has been focused interest in relating environmental contaminants to amphibian decline. Notably, Kerby et al. (2010) conducted a review and found greater response to chemical toxins in other taxa compared to amphibians, concluding that amphibians are ‘miners in a coal mine’ rather than ‘canaries in a coal mine’ – at least with respect to some chemical toxins. A similar criticism was levied by Collins and Crump (2009) – that amphibians, in general, may not be good indicators because not all declines can be linked directly to environmental stresses, but individual species or populations that are sensitive to particular contaminants affecting their ecosystem may be. The effect of mercury concentrations on stream salamander abundance varies with environmental gradients such as elevation and fire history (Bank et al. 2005). This less sensitive relationship – as opposed to complete intolerance – to environmental contaminants may be even more informative than a ‘canary in a coal mine’ when the contaminant is known to be present because it can identify important interactions with the environment. Beyond the mercury example, there are few studies that link amphibians to integrative processes in ecosystems that can be related to management decisions. One example is provided by Schurbon and Fauth (2003) who found that prescribed fire did not have direct effects on amphibian, likely because of their ability to retreat underground, but indirect effects (i.e., vegetative structure, leaf litter depth, nutrient availability) result in declines over time. Kerby et al. (2010) considered only a few species of amphibian, leaving open the possibility that other species have a combination of traits that better qualify them as indicators according to the criteria above (Schurbon and Fauth 2003; Townsend and Driscoll 2013).

Plethodontid salamanders are advocated as model organisms for indicating properties of ecosystem health generally, principally because of their sensitivity to environmental gradients, and their low variability in their response compared to other candidate indicators (e.g., birds, small mammals, and even other amphibians; Welsh and Droege 2001), meaning that changes in population size should be more easily related to driving variables. Other previously stated criteria are satisfied by plethodontid salamanders as well, such as their ease of sampling which produces sufficient observations for linking species to ecosystem attributes and processes (Fellers and Drost 1994). Due to their size and limited home ranges, plethodontids are expected to be sensitive to gradients on a fine scale (Heatwole and Lim 1961). However, it is presently unclear how well they can represent integrative processes relevant to management decisions.

2.2 Indicating Immeasurable Variables: Latent Models for Indicator Species

While part of the challenge in identifying and applying appropriate indicator species has been attributed to a lack of consensus on how an indicator species is defined (Caro 2010), there also lacks practical recommendations for using indicators to aid resource management and conservation (Hunter et al. 2016, Caro and O’Doherty 1999, Lindenmayer et al. 2015). Identifying ecosystem change only as it occurs precludes proactive management (Bahamondez and Thompson 2016), and indicator species can be valuable management tools when they can signal environmental variables that are impossible or difficult to observe (Dale and Beyeler 2001). Identifying reliable indicators of important ecosystem processes is challenging, as they rarely extend to appropriate spatial and/or temporal scales for practical use (Caro 2010; Gaston 1996). Finally, an indicator species’ primary obstacle for application is that direct measurement, when possible, is always preferred over indirect measurement (Landres et al. 1988). Given all these qualifications, the indicator must be accurate, scalable, and resourceful – a combination of qualities that is both difficult to identify and to justify in a species.

I find the most compelling conceptual models for the selection and use of indicator species to be those that indicate a latent variable. The first of this type of model was introduced by Landres et al. (1988; Figure 5), which expressed that an indicator species should have direct relationships with the same environmental factors as the species of interest, and that the species of interest is too difficult, inconvenient, or expensive to measure directly – therefore considered a latent variable requiring indirect measurement. Though not depicted in the conceptual model, the ‘species of interest’ may reasonably be replaced with an abiotic variable or ecosystem process. Landres et al. (1988) is highly cited in indicator species literature written since the time of its publication (952 times, according to Google Scholar), however, most refer to this paper for its critiques on the use of indicator species, and this idea of the latent variable has rarely been discussed since.

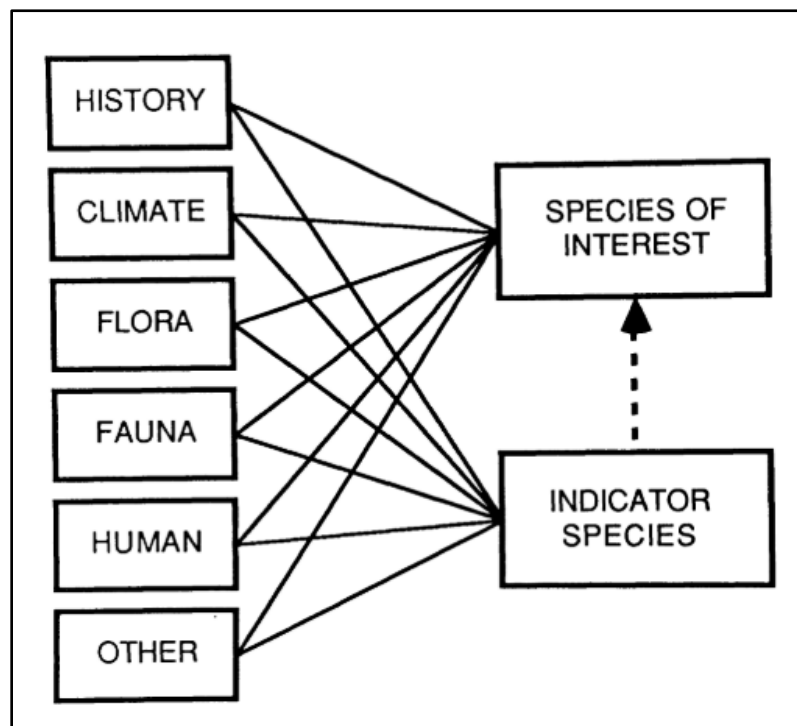


Figure 5: The first latent process conceptual model for indicator species that was proposed by Landres et al. (1988). In this model, the indicator species has similar relationships to environmental factors as the species of interest, which can be considered a latent variable because it is too difficult, inconvenient, or expensive to measure directly. Solid lines depict direct relationships and the dashed line depicts an extrapolation from indicator species to species of interest.

To my knowledge, it was not until 2015 that another conceptual model for indicators of latent variables was presented by Lindenmayer et al. (Figure 6). In this model, a latent variable (U) drives the ecological process of interest (T). U is unmeasurable, and the best indicator (S_i) of T is not necessarily one that is directly causal to the process of interest, but one that is most related to U . This introduction of a latent process to the conceptual model of indicator species emphasizes that direct measurement is not possible and/or practical. The trade-off in this model is that the farther S_i is removed from T , the more error is possible in the estimation of T .

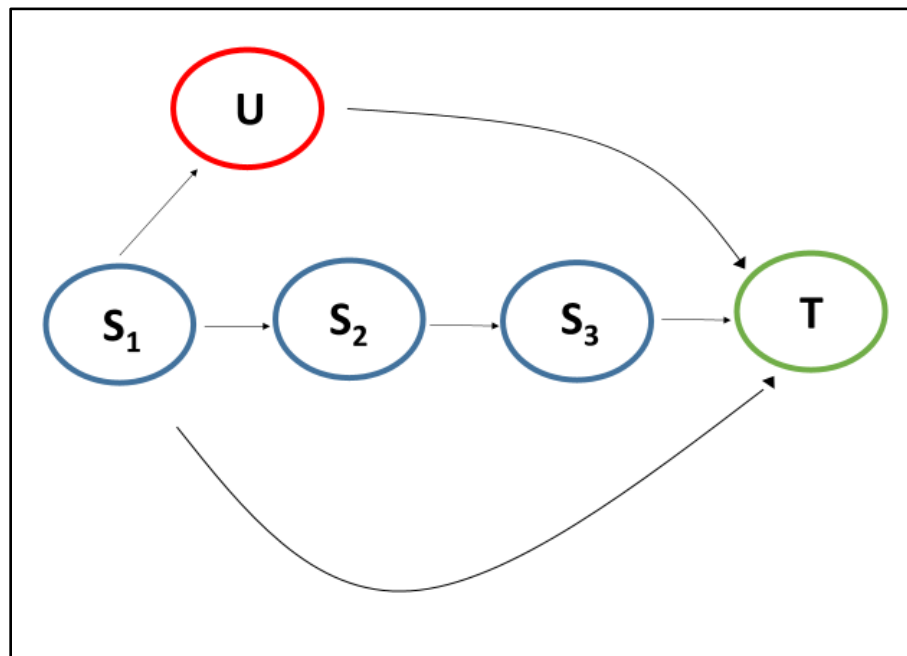


Figure 6: Surrogate model described by Lindenmayer et al. (2015) where S_1 , S_2 , and S_3 are candidate surrogates. S_3 is the most removed from the target (T), and also the most connected to an unmeasured latent variable (U); Figure source: Lindenmayer et al. 2015)

While this is conceptually attractive, it has yet to be applied empirically and the potential utility remains untested. The example provided in the original article outlines two suitable indicators $\{S_2 = \text{predator abundance}; S_1 = \text{herbivore abundance}\}$ and a target process $\{T = \text{grassland productivity}\}$, but does not identify a latent process $\{U\}$. It is explained that herbivores are better indicators of grassland productivity, as they are direct consumers of the vegetation. Perhaps a result of the latent variable not being identified, their example does not fit the conceptual model, where the more removed indicator (i.e., the predator) is the best representative

of the latent variable. Landres et al. (1988) was clear in suggesting that indicator relationships should be defined explicitly in order to be practical. It is difficult to identify clear relationships using the framework in Figure 6, including the example presented in the paper. Therefore, this conceptual model is too ambiguous to satisfy the criteria of Landres et al (1988) and requires more specificity if it is to be practical.

2.2.1 Modified Latent Model

An interest in indicator species in part derives from an interest in assessing the achievement of management objectives (e.g., ‘ecosystem health’) which are driven by latent and only partially observable ecological processes. While amphibians in general, and RBS in particular, have been identified as meeting many of the commonly accepted criteria (Dale and Beyeler 2001; Landres et al. 1988) for suitable indicator species (Welsh and Droege 2001; Townsend and Driscoll 2013; Wyman and Hawksley-Lescault 1987), the most important criterion – integrative of ecosystem processes – is perhaps the most difficult to support, especially when using single measurements (e.g., population density). Populations are affected by multiple ecosystem drivers, and sensitivity to a driver depends on intrinsic (e.g., life stage, individual condition) and extrinsic (e.g., covarying environmental conditions) factors. While Lindenmayer et al. (2015) provide a useful conceptual model, it does not include an explicit effect of latent ecosystem process(es) on multiple indicators, which may be expressed traits of an individual (e.g., fecundity) or a population (e.g., age structure).

To capture this, the model is revised so that U (i.e., latent ecosystem process) directly influences both the target T (i.e., integrative population metric), as well as multiple measured surrogates (S_{1-n}). The relationship of S and U is reversed so that the effect of U is possible to observe on each measured surrogate, and thus one may use multiple surrogates or traits as evidence of a relationship with the target variable (Figure 7). This requires specifying an ecological process model that states relationships among each surrogate S , and reduces ambiguity

enabling the relationships to be observed on each measured variable – an improvement on the Lindenmayer et al. (2015) conceptual model where effects of relationships are on an unobservable variable.

In addition, and in contrast to the Lindenmayer et al. (2015) model, each observed variable S_i can be related directly back to U , providing partial information about the range of values U may take. The outcome is that a greater number of S_i , measured with precision, can better inform the estimation of U . The rationale for this model is that either U or S_{1-n} can be used to estimate (or predict) T , but where U cannot be measured – or where U represents multiple axes of ecosystem function (i.e., ecosystem ‘health’) – S_{1-n} is the most suitable indicator measure.

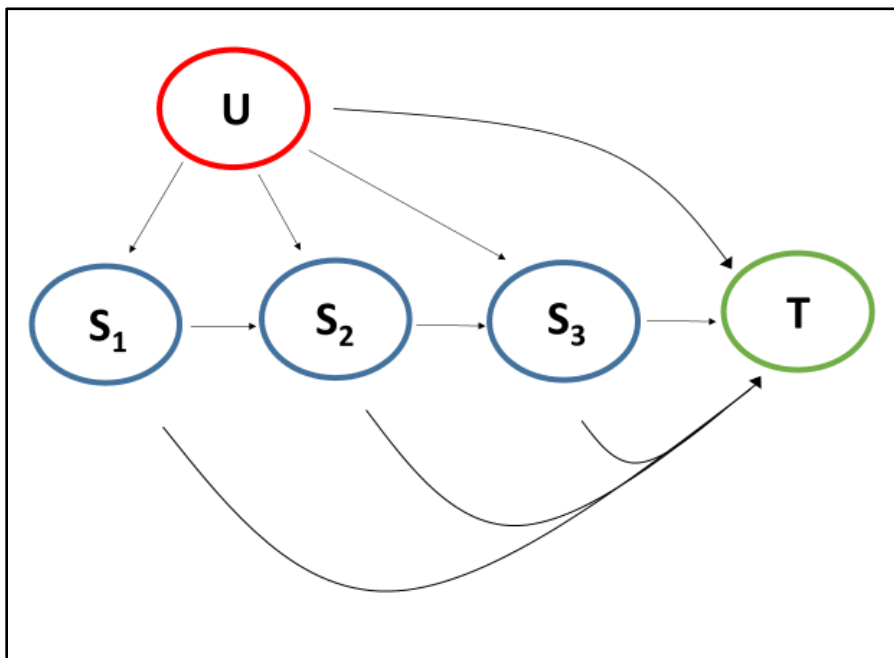


Figure 7: Proposed model for the incorporation of a latent variable for indicator species application. A latent model is described in Lindenmayer et al. (2015), and I have modified it here to make explicit the relationships of each part (i.e., S_1 , S_2 , S_3 , U , and T)

2.2.2 Modified Latent Model Applied to the Red-backed Salamander

I am interested in applying this modified latent conceptual model to a real system, and given the known sensitivities of RBS to environmental variables, I have identified an ecological process model that may, albeit hypothetically, fit these relationships. RBS is attractive as an

indicator species because of its ease of sampling and its occurrence in habitat that is both vulnerable and valuable. Survey methods for monitoring terrestrial salamanders are easy to use and inexpensive (Monti et al. 2000). Importantly, the NHF ecosystem of the RBS is threatened by changes in climate (Campbell et al. 2010) and the development of management tools like indicator species may help to develop and select among mitigation measures (Pastor and Post 1988).

In the thesis introduction, I describe in detail the physiological requirements and sensitivities of RBS to its environment – many of which are relevant to climate variables. Here, I connect those sensitivities in an ecological process conceptual model that relates RBS to climate – an integrative and difficult to measure, or in other terms, ‘latent’ variable (Figure 8).

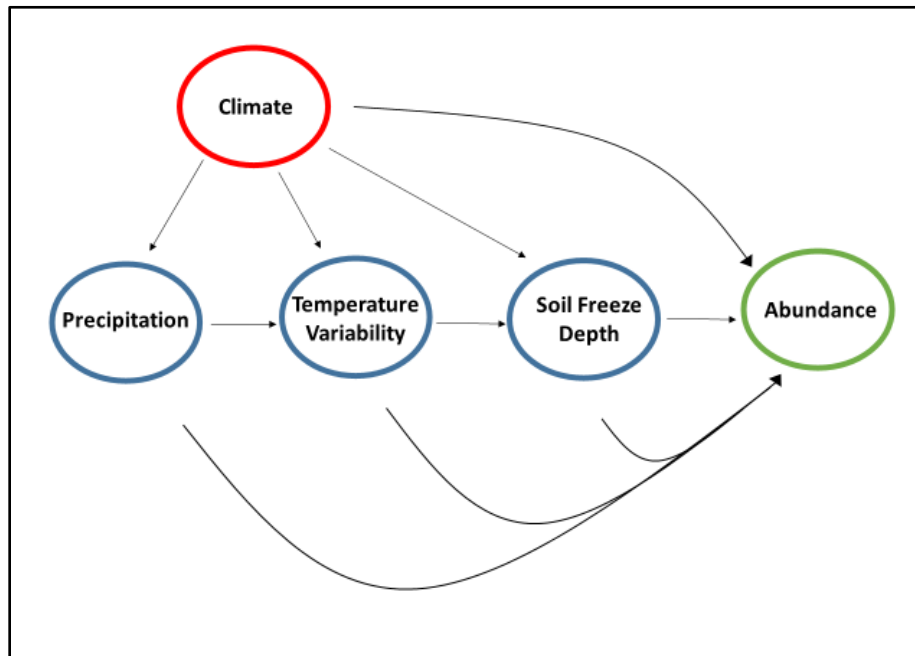


Figure 8: A proposed latent variable model – modified from Lindenmayer et al. 2015) – applied to the red-backed salamander and its multifaceted relationship to climate.

U: Qualities of local and global climates are of interest due to their effects on natural resources, human health, and economy (Stern 2008). Still, climate is notoriously difficult to quantify in a comprehensive and meaningful measure (Thuiller 2004; Pearson and Dawson 2003). When species ranges are large enough, climate change can be observed in changes in distribution

and biogeography (Davis and Shaw 2001). However, effects of climate change are difficult to observe on a local level because they are masked by non-climatic influences specific to location and time (Parmesan and Yohe 2003). As a result, reliable measures of climate on multiple scales are of exceptional value for strengthening understanding of environmental impacts.

*S*₃: Climate change projections include reduced snow-pack in the northeast, which is expected to result in soil freeze at greater depths (Groffman et al. 2001). RBS cannot tolerate freeze and relies on subterranean hibernation below the freeze level. In a winter with extreme freezing conditions, Petranka (1979) found that survival of plethodontid salamanders was confined to habitat in which there was access to deep burrows. Therefore, one can speculate that with greater soil freeze depths, RBS over-winter survival rates may decrease. Soil freeze depth is a concern in NHF in general, as it affects nutrient availability, increases deposition of N to water (Groffman et al. 2009), and ultimately alters wildlife habitat, timber production, and water resources. Furthermore, long-term increases in N deposition may not be detected until several decades after they have begun (Aber and Driscoll 1997), and an early indicator of these processes may allow appropriately timed management response. Finally, increased soil freeze increases the flux of nitrous oxide, an important greenhouse gas, from NHF to the atmosphere (Groffman et al. 2006b). Direct response of RBS to soil freeze is significant because of the wide-ranging ecological implications of soil freeze, and as Petranka (1979) demonstrated, extreme seasonal conditions affecting soil freeze may be evidenced in salamander abundance.

*S*₂: Increased variability in temperatures has important consequences for phenology globally, and this is especially well-documented in NHF. Warm temperatures in spring trigger bud break in woody plants – and frost events after warming, which have become more common in the past century, will damage buds thereby inhibiting or preventing plant growth and reproduction (Augspurger 2013). A concern for NHF composition is that increasing mismatch between seasonal temperatures and photoperiod has larger impacts on long-lived, late-successional species than early-successional species (Körner and Basler 2010). Interestingly,

temperature-photoperiod dynamics also determine the rate of spermatogenesis in male RBS (Werner 1969).

However, effect of temperature is most prominent on RBS surface activity, and as discussed in the thesis introduction, RBS behavior is often motivated by its avoidance of desiccation. Heat increases metabolic rates of RBS (Homyack et al. 2010), allowing RBS to become active for feeding and reproductive purposes as soil thaws. However, exposure to heat may also lead RBS to engage in energetically costly behaviors for avoiding desiccation (Heatwole 1960). RBS physiological tolerances require that it restrict activity to specific environmental conditions, and phenological changes make surfacing risky.

S_7 : Precipitation is in the position of S_1 because of its influence on temperature variability and soil freeze, its relevance to climate concerns (i.e., drought, atmospheric pollution), and its effects on salamander abundance. RBS relies on precipitation to provide moist environments necessary for its cutaneous respiration, as evaporative water loss from dry conditions threatens plethodontids (Pough et al. 2015). RBS has a strict ‘absorption threshold’ (discussed in Chapter 1) above which there is a net gain in body mass and below which there is a net loss (Heatwole and Lim 1961). Finally, RBS dispersal and climbing on plants – which allows access to high quality food items – is limited to rain events (Jaeger 1978).

As precipitation events become more irregular due to climate change, RBS phenology, and perhaps abundance will be impacted. Irregular precipitation is expected with warmer weather, because water capacity of air will increase (Trenberth 2011). Additionally, RBS is extremely sensitive to soil pH, as it disrupts sodium balance and ultimately osmoregulation (Frisbie and Wyman 1991). Acidic rains affecting the northeast US are a result of atmospheric pollution (Likens and Bormann 1974; Likens et al. 1996) and its introduction to the soil via precipitation (Krug and Frink 1983) is harmful to RBS. Acidic rain is also a concern for watersheds and freshwater ecosystems because of its effects on water chemistry and its observed impact on invertebrates and plants (Schindler 1988).

T: In studying plethodontid salamanders, myself and others are interested in measuring its abundance. As I explain above, it has important relationships with variables S_{1-3} , which are easily measured and are associated with climate. This comprehensive measurement of climate can be tested for its impacts on RBS abundance – with each S . providing partial information of climate. Importantly, RBS may serve as an indicator of climate as well, because certain effects of S_{1-3} are not easily measured. For example, effects of acid rain on soil chemistry, and ultimately detrital ecosystems are difficult to measure due to microsite variation (Boerner and Koslowsky 1989), and these difficulties have been validated in NHF. Further, lifespans of RBS, which are unknown but assumed to be >7 years (Leclair et al. 2006), may act as cumulative measures of climate and indicate lasting effects of climate change. These relationships can be observed on a local level, and because of the large range of RBS, it is possible that with cooperative range-wide monitoring, effects of climate change can be observed on a regional level (Midwest-Northeast US) using standardized measures as well.

RBS-Climate Summary: Without this key link – specification of a latent variable – evaluations of indicator species rarely identify the practicality of indirect measurement over direct measurement. The application of indicator terminology to species with explicitly identified relationships to ecological processes is common but often misguided because relationships alone do not constitute a viable indicator. The employment of indicator species should therefore be reserved for latent processes that demand indirect measurement because their direct measurement is not practical.

2.3 Summary

Indicator species have a long history in ecological literature, though their application is rare. Moreover, terminology is not consistent among articles, impeding communication on the topic. Amphibians are repeatedly referred to as indicators because of their biphasic life cycles and movement between aquatic and terrestrial habitats, but their practical use is unclear. Perhaps the

primary obstacle for applying indicator species in ecosystem research and management is that direct measurement is preferred over indirect measurement.

Because indirect measurement of measurable variables is not practical, indicators should be informative of latent, unmeasurable processes. These latent variables should be integrative, so that they can be evidenced and measured in multiple variables, and related to a target indicator species. The practicality of this latent process conceptual model is that the effect of the latent variable can be observed on the indicator species, but since the latent variable cannot be measured, S_{1-3} are measured, each providing partial information on both the latent variable and the indicator species. It should be noted that, as of now, this latent conceptual model is purely speculative, but it is more explicit in the relationships that constitute an indicator than other propositions, and may therefore create stronger indicator species application.

CHAPTER 3

SPATIAL CAPTURE-RECAPTURE ANALYSIS ALLOWS COMPARABLE ESTIMATES OF POPULATION DENSITY – INDEPENDENT OF STUDY DESIGN – AMONG RED-BACKED SALAMANDERS

3.1 Introduction

Due to rapid changes in species' abundances and distributions globally, there is an urgent need to develop tools for making strong inference about populations and their conservation statuses. Methods for estimating population state variables (e.g., abundance, range boundaries) are imperative for effective conservation and management of vulnerable species (Bahamondez and Thompson 2016; Marcot et al. 2001). Only with reliable estimates of these state variables can ecologists begin to predict change on multiple scales (i.e., population, landscape, range) and manage populations and entire species proactively (Grant et al. 2016). Currently, many tools for identifying species' needs, current conditions, and future conditions – the framework for species status assessments (USFWS 2018) – are limited in their ability to make certain crucial inferences. For example, habitat suitability indices and tools built through expert opinion are subject to bias by lack of empirical data (Johnson and Gillingham 2004; Williams 2001). Occupancy modeling is capable of estimating population vital rates (i.e., extinction, colonization), and is primarily useful in populations where intensive mark-recapture cannot be done, which is often the case (MacKenzie et al. 2006). However, it cannot be used as a tool for understanding distributions within populations; often necessary for the application of effective management actions. The identification of heterogeneity in species distributions allows ecologists to determine core habitats and enables managers to more precisely focus management actions on essential habitats and sustainable populations within their purview (Royle et al. 2013). For these reasons there is an

increasing need for the estimation of true population density, as it is the most appropriate state variable – due to it being spatially explicit – for understanding drivers in population dynamics, and for detecting changes across space and time (Royle et al. 2014; Bart et al. 2004).

Capture mark-recapture (CMR) techniques have revolutionized the study of demographic processes and the ability to monitor wild populations (Williams et al. 2002). This ability to infer population-level demographic rates is made possible by tracking marked individuals through space and time. Proper inference is reliant on individual encounter histories in which individuals can be ‘missed’, which allows for explicit accounting for imperfect detection (Link 2003). A key assumption of CMR is that detection probability is homogeneous throughout the trapping area, even when some individuals are exposed more frequently, because of where they live, to trapping (Efford 2004). In using these estimation methods, ecologists do not take advantage of the inherent spatial information built into CMR sampling designs.

Spatial capture-recapture methods (SCR: Efford 2004, Royle and Young 2008) extend classical CMR models to exploit spatially explicit individual encounter histories (individual-by-trap-by-occasion detections) and are now widely accepted as the preferred approach for estimating true population density. Fundamental to this development is that SCR explicitly integrates the spatial sampling design of a study and the spatial ecology of the focal species, offering a statistical framework for investigating a wide range of spatially-structured ecological processes (Royle et al. 2018). Furthermore, because SCR models estimate true population density – without the need for arbitrary ad hoc adjustments such as the maximum mean distance moved (MMDM or derivations of this method such as $\frac{1}{2}$ MMDM) – it offers an inferential framework that naturally facilitates comparisons of estimated state variables obtained from across a species’ geographic range (Borchers and Efford 2008). This is a critical advancement because, to date, range-wide monitoring of populations and evaluations of conservation status oftentimes lack the standardization necessary to produce consistent and comparable data across space and time.

The sampling design used to assess the status of wildlife populations can have important implications for the behavior of the focal species, introducing possible bias into estimates of population density (Rowcliffe et al. 2013; Sun et al. 2014). Further, separate populations within a species range may be exposed to inconsistent factors affecting behavior that are unrelated to sampling design (Grant et al. 2016), which makes it difficult to sparse sampling bias from natural variation in ecosystem processes (Gula and Theuerkauf 2013). If nonrandom and/or unidentified, these sampling-provoked behaviors have enormous implications on population estimates. Non-invasive methods such as remote camera traps, hair snares or scat surveys have become widely adopted in ecological monitoring studies, as they passively detect individuals and avoid disturbance-related behavioral responses that result in biased inference (Royle et al. 2009). However, not all organisms are detectable with noninvasive techniques, and physical capture, often with the use of attractants, is required to detect individuals where they are present. Attraction of the focal species with the use of, for example; bait, essential habitat features, or reproductive opportunities, for detection is concerning as it may disturb natural distributions (Rowcliffe et al. 2013). Behavior as a source of bias is a concern when an objective is to make inference about species status range-wide, especially if sampling method or behavior related to sampling vary locally – and thus has enormous implications for the ability to integrate local data for predicting population changes range-wide (Royle 2013).

For imperiled species, the focus is on making inference about ecological state variables at the scale of the landscape, region and even the entire range – which requires making inference to larger scales of phenomenon from sampling discrete populations. Integrating results across scales to identify trends and relate populations requires estimates to be comparable, which do not always come from standardized designs (Nichols et al. 2008). This ‘equivalency’ of inference depends on both the spatiotemporal aspects of sampling design, and the analytical methods applied to the resulting data (Gula and Theuerkauf 2013).

Incorporation of multiscale data is particularly important for amphibians, a taxon that has experienced global and enigmatic declines in recent decades (Stuart et al. 2004). The need for informed and effective amphibian conservation is urgent, and the establishment of long-term standardized monitoring in the present may not be sufficient. Integration of existing historic amphibian data sets and prior research results is made challenging by disparities in both sampling and analytical methods among them (Genet and Sargent 2003; Nelson and Graves 2004). In response, there have been repeated calls for development of rigorous methods that are ‘data inclusive’ and able to estimate key population parameters with data derived from historic and inconsistent spatial sampling designs (Beebee and Griffiths 2005). Because of the grave status of amphibian populations, biases of sampling designs may have important consequences, and therefore require urgent and thorough assessment.

RBS is an example of a species that has been studied extensively, but whose range-wide comparison in population parameters is limited by lack of standardization (Hesed 2012). While the species is considered common throughout its range, abundance varies spatially (see Muñoz et al. 2016, Sutherland et al. 2016; Peterman and Semlitsch 2014). It has well-defined tolerance thresholds (e.g., moisture, pH; see Chapter 1) and certain stressors such as climate change and urbanization are expected to induce changes in population state variables (Moore et al. 2018). Artificial cover objects (ACO) are a common RBS monitoring method that increases the likelihood of encountering individuals by imitating an essential habitat feature, natural cover (Grant et al. 1992; Grover 1998). If the method influences behavior by serving as an attractant, then I would expect these interactions to be revealed when the spatial configurations of traps are manipulated and compared. In this study, I use a model organism for which behavioral biases are expected, and a relatively small-scale sampling design which can be manipulated to evaluate the sensitivity of SCR-derived density estimates under experimental configurations of sampling arrays. In doing so, I test the potential for SCR models to accommodate among-site and among-design variation in capture rates for cross-study comparisons of density estimates.

3.2 Methods

The ecology of the RBS is reported in detail in Chapter 1 of this thesis. Here, I discuss the relevance of RBS ecology and its relationship to sampling methods. I go on to describe how this relationship can be used to exploit behavioral interactions with sampling design, and relate these interactions to spatially explicit population parameter estimates. Finally, I give a detailed summary of an experimental manipulation of sampling design, as well as an analytical approach for evaluating the impacts of spatial study design on species behavior and the derived parameter estimates.

3.2.1 RBS as a model system

RBS is a terrestrial forest-dwelling species, and is estimated to be the most abundant vertebrate species in northeastern (US) forests (Milanovich and Peterman 2016; Semlitsch et al. 2014). Because of its abundance and its ecological role in energy transfer and nutrient cycling, it is an important component of forest floor ecosystems within its range (Figure 1; Davic and Welsh 2004; Petranka 1998; Wyman 1998). RBS is most abundant in NHF, but is found in oak-hickory forest, pine barrens, and birch and mixed forests as well (Petranka 1998). RBS is a habitat generalist but has well-documented sensitivities to environmental thresholds, many of which are relevant to more general conservation issues such as climate change and urbanization (e.g., moisture, soil pH; Heatwole 1962; Heatwole and Lim 1961). Its measurable relationships to important environmental variables makes RBS a valuable candidate indicator species (Table 1). Data-rich monitoring catalogs can more precisely estimate those relationships, and potentially be used to refine the indicator species theory and application discussed in Chapter 2.

Cover objects are highly influential on the activity of RBS, as they provide the necessary moisture needed for cutaneous respiration. Surface activity (i.e., hunting, courtship, dispersal by juveniles) is facilitated by natural cover (Jaegar 2016). Therefore, RBS exhibits behaviors in

response to variation in cover object availability (e.g., refuge, territoriality, station-keeping; Jaeger et al. 2016), which has implications for surface activity and therefore the ability to detect it. As such, cover distribution can be expected to regulate changes in probability of detection throughout the forest floor – which, if not accounted for, may lead to biased estimates of population abundance or density. Given its small home ranges (~13-24m²; Kleeberger and Werner 1982; Muñoz et al. 2016), habitat restrictions, and limited dispersals, even the most subtle changes in forest floor structure (e.g., cover area and type) may lead to responses expressed in a heterogeneous distribution of RBS populations.

Compared to other organisms studied with mark-recapture techniques, RBS has exceptionally small home ranges that require little effort to observe in their entirety. For most animals, the issue of scale is problematic because their movement (i.e., spatial scale of detection) is difficult to capture in a sampling area. Other studies have attempted to experiment with trapping design and its effect on population estimates, but have required the use of simulations because of the impracticality of manipulating configurations on such large scales. For example, Sollmann et al. (2014) required simulation to test effects of trap configurations on a black bear population with an estimated home range of 100km² in females, and 260km² for males (Sollmann et al. 2013) – which, for reference, is 5,917-15,385 times a home range estimate for RBS (16.9m²; Sutherland et al. 2016). The small home ranges of RBS provide a unique opportunity to test the robustness of SCR to sampling design – potentially informing the design of studies where real manipulations are not practical.

3.2.2 ACOs as Standardized Methods for Physical Capture

Artificial cover objects (ACOs) are a sampling method used for capturing species reliant on natural cover, and are regularly employed in herpetological research (Fellers and Drost 1994). ACOs provide focal animals with high quality refugia (i.e., cover; essential habitat; Grover 1998), and their sampling designs, which are typically arranged in gridded arrays, are inherently spatial

with the demonstrated ability to produce spatially explicit density estimates (Muñoz et al. 2016; Sutherland et al. 2016; Schmidt et al. 2017). Artificial cover object (ACO) surveys have existed in herpetological literature for at least 64 years (Stebbins 1954), and are particularly useful for detecting terrestrial salamanders like RBS (Houze and Chandler 2002; Monti et al. 2000).

To detect RBS, ACOs take advantage of behaviors adapted to maintain physiological tolerances and avoid environmental threats. Environmental conditions outside RBS tolerance such as strong winds, acidic soils, and predator presence are related to physiological responses that may result in desiccation, osmoregulatory dysfunction, and energy depletion, respectively. Cover, either natural or artificial, provides a barrier between RBS and environmental hazards and is an essential habitat feature (Grover 1998). By operating as an essential habitat feature, ACOs make RBS available for physical capture. Sampling requires relatively little effort and minimal training, and the simplicity of the method reduces between-observer bias (Monti et al. 2000). Repeat visits and identifications of unique individuals produce versatile data that are suitable for a diverse range of analytical applications including occupancy, CMR, and SCR modelling.

However, spatially explicit analyses with the use of a method that mimics essential habitat may be inaccurate if their introduction causes individuals within a population to redistribute. Assumptions of SCR methods include that activity centers are independent of sampling design and that detection is a function of distance between the individual and its activity center (Royle et al. 2014; see also section “Statistical Analysis”). Therefore, if individual activity centers are biased around traps due to an attraction, then the incorporation of spatial design into population models may not be sufficient for eliminating spatial sampling bias in density estimates. If it is the case that features of the study design influence estimates by biasing activity center around traps, it is important to understand that relationship for calibration purposes (Siddig et al. 2015), and for establishing standards to replicate local surveys across a species’ ranges. If sampling decisions are made with broad research objectives in mind, ACO study designs are easily standardized to facilitate collaboration of partners with similar objectives – as long as any

biases associated with sampling design can be accommodated statistically. Researchers have direct control over ACO sampling design, and in applying ACO methods, make inherent choices about material, size, configuration, etc.

The advantages of ACO methods are evident and have resulted in an unknown, but presumably substantial, wealth of ACO derived data collected over spatially distributed monitoring efforts (Moore et al 2018). Further, data of these kind have been collected throughout RBS range, forming a distribution of representative sub-sampling conducive to multiscale inference (Miller and Grant 2015). However, strong inferences (i.e., population state variables on multiple scales) that are made possible with large data sets and range-wide sampling rely on careful data integration. Despite the ease of standardization, study designs related to existing ACO data sets are immensely variable, and are not currently suitable for integration. However, due to their easy design manipulation, these design biases may be realistically evaluated with experimental evaluations.

3.2.3 Study Area

This study took place in Wendell State Forest (Wendell, MA; USA) managed by Department of Conservation and Recreation (DCR), a Massachusetts state agency. Wendell State Forest is in the north-central part of Massachusetts, which lies approximately in the center of the RBS longitudinal range (Petranka 1998). The property spans 7,566 acres and is abutted by Erving State Forest adding another 2,422 acres of contiguous DCR-managed land (9,988 acres combined; DCR 2017a; b). Trails and ponds within Wendell State Forest are used for recreational purposes (e.g., hiking, biking, skiing, wading, and sporting). Previous surveys have been performed here to confirm the presence of RBS (USGS, unpublished data), and three experimental study sites were established within the forest (Figure 9).

Stand composition of the three sites is mixed hardwood with hemlock and pines, a forest type that is a dominant habitat in the Northeast US and is vulnerable to the effects of climate

change (Groffman et al. 2001). Overstory of the three sites were similar, made up of oaks (*Quercus alba*; *Q. rubra*; *Q. velutina*), American beech (*Fagus grandifolia*), Eastern hemlock (*Tsuga canadensis*), red and white pine (*Pinus resinosa*; *P. strobus*), and birches (*Betula alleghaniensis*; *B. lenta*) (K. DiNardo, MA Department of Conservation and Recreation, personal communication). According to a DCR database dating back to 1962, no timber harvests have taken place at any of the three sites in at least 56 years (K. DiNardo, MA Department of Conservation and Recreation, personal communication). Sites ranged in elevation from 273-317m.

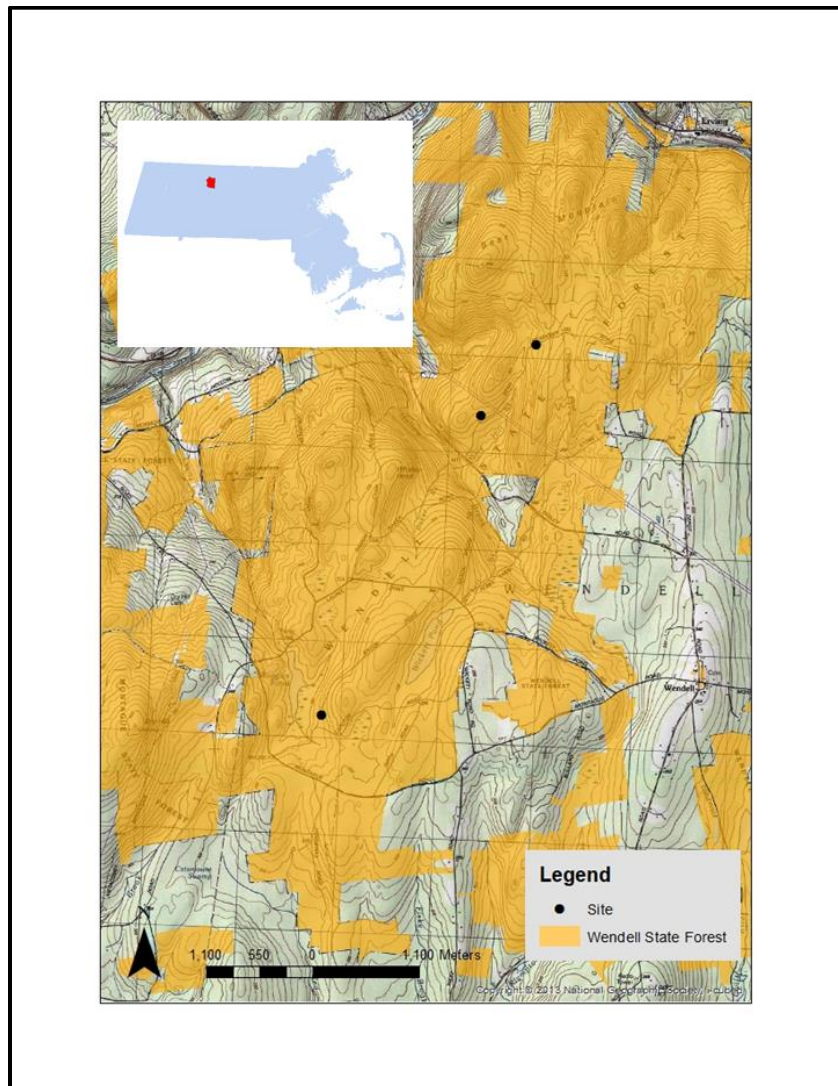


Figure 9: Three sites within Wendell State Forest (Wendell, MA; USA) in which five experimental configurations of artificial cover object arrays were installed to monitor three

separate populations of red-backed salamanders. The Massachusetts Town of Wendell is represented in red.

3.2.4 Experimental Design

Sites were selected to represent three independent populations and were spaced $\geq 1\text{km}$ apart (Figure 9). Within each site, five ACO arrays were established close enough to assume limited variation in density (i.e., sampling of a single population), but far enough ($\leq 25\text{m}$) to avoid capture of individuals in multiple arrays within a sampling season (i.e., maintain independence). The five experimental ACO array designs were (Figure 10):

1. a *control* array as a rectangle with ACOs spaced 1m apart (7m x 5m with 35 ACOs)
2. a *control-size sparse* array with the same area as the control, but with ACOs spaced 2m apart (7m x 5m with 12 ACOs)
3. a *large sparse* array has the same number of ACOs as the control, but with ACOs spaced 2m apart (dimensions 10m x 14m with 35 ACOs).
4. a *control-size dense* array is the same area as the control with ACOs spaced 0.5 m apart (7m x 5m with 117 ACOs)
5. a *small dense* array has the same number of ACOs as the control, but is spaced 0.5 meters apart (dimensions of 2.5m x 3.5m with 35 ACOs)

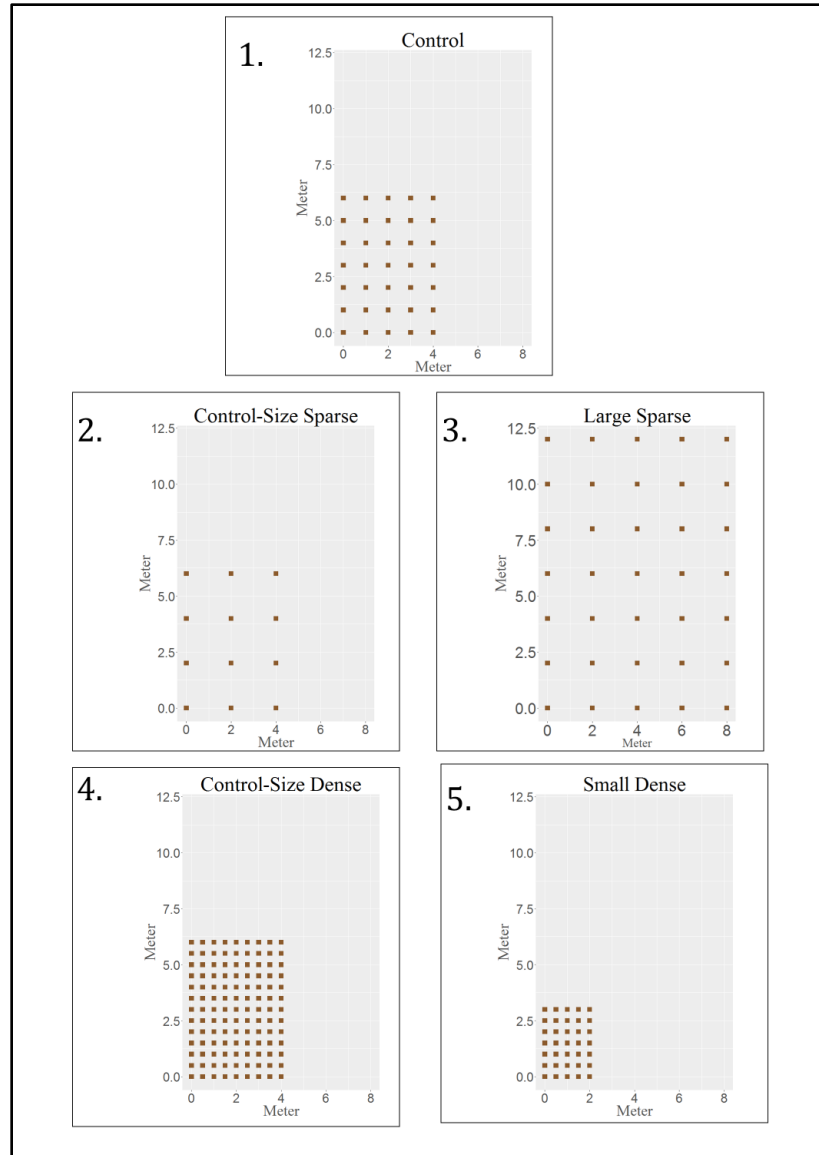


Figure 10: Five experimental ACO arrays used to survey three separate red-backed salamander populations in Wendell State Forest (Wendell, MA) in; Fall 2016, Fall 2017, and Spring 2017. From left to right; control, control-size sparse, control-size dense; small dense, large sparse.

The control design was chosen to mimic the standardized ACO array design of a long-term RBS monitoring network, the Salamander Population and Research Collaboration Network (SPARCnet), so that I could evaluate the integrity of its density estimates against the behavioral response of RBS to ACOs. Optimal study design for SCR is one that maximizes number of individuals encountered as well as number of spatial recaptures (Royle 2013), and space between traps should be no more than double the individuals' movement radius (Sollmann et al. 2013; Sun

et al. 2014). Movement radius of RBS has been estimated in the range of 1-3m (Muñoz et al. 2016; Sutherland et al. 2016), and therefore space between traps should not exceed 2m. I was interested in testing if expanding and/or decreasing the trapping area or the number of traps would allow us to encounter more individuals and/or spatial recaptures, and if these differences could be linked to behavioral bias.

ACOs were deployed 14 July 2016 and were left for 67 days which exceeds the minimum establishment period of one month for ACOs to settle and provide secure refuge and foraging habitat (Otto et al. 2013). Each site was sampled every 10-14 days within RBS activity windows in Fall 2016 (6 occasions), Spring 2017 (6 occasions), and Fall 2017 (5 occasions). On each sampling occasion, every ACO was checked for the presence of RBS, and individuals occupying ACOs were collected and given unique marks using visual implant elastomer (VIE, Grant 2008), and exact capture location (i.e., ACO ID) was recorded. Any environmental data expected to influence RBS detectability was recorded at the time of survey including air temperature and Julian day, the latter of which was supported as an effect on detection in previous studies (Muñoz et al. 2016, Sutherland et al. 2016).

3.2.5 Statistical Analysis

SCR models are unique in that they make use of spatial encounter information that is not fully applied in traditional CR models, and are thereby capable of not only estimating population size, but also true population density as the sum of distributed activity centers (s_1, \dots, s_N) within an explicitly defined area (Royle et al. 2014). The framework of SCR models consists of a biological process model and an observation model linked by a unique detection function.

In the context of SCR, point process models describe distributions of organisms in a predetermined state space (S) - which provides all possible activity centers considered by the models, and should encompass the home ranges of all observed individuals. The observation

model describes the detection data (y_{ijk}) of each observed individual (i) in each trap (j) on each occasion (k) as Bernoulli random variables ($y=1$ if captured and 0 otherwise:

$$y_{ijk} \sim \text{Bernoulli}(p_{ijk})$$

The process and observation models are linked by a detection function in which the probability of detecting an individual at a trap (p_{ij}) decreases with distance between that individual's activity center (\mathbf{s}_i) and the trap location (\mathbf{x}_j).

$$\text{logit}(p_{ijk}) = p_0 * \exp(-\text{dist}(\mathbf{x}_j, \mathbf{s}_i)^2 / \sigma^2)$$

Spatial captures provide data that are essential for fitting SCR models, as they determine the spatial scale of detection (σ), i.e., the Euclidean distance from \mathbf{s} over which p_0 declines to 0.

The relationship between σ and p_0 is at the center of the investigation into the effects of trap spacing on behavior, and on independence of parameter estimates. If N is biased around \mathbf{x} , then the spatial scale of detection is truncated, and, if not modelled, p_0 may be biased high, consequently biasing estimates of N . Inaccurate estimates of N have the potential to mislead conservation efforts, and should be avoided using careful consideration of sampling biases.

Here, the state space of each ACO array was defined as its area with a 3.6m buffer that is over 2x the pooled MMDM (1.66m). State spaces were made of a 0.25m resolution of \mathbf{s} within S , which was found to be capable of approximating continuous space while also allowing for reasonable computation.

It was assumed that populations in the arrays were 'closed' to demographic changes within seasons, but birth, death, and dispersal (i.e., immigration or emigration) could occur between seasons, resulting in 45 'sessions' (15 total arrays in 3 sampling seasons). Given the large number of covariate effects that could be considered for p , σ , and density (D) related to study design (Table 3), site, and survey conditions, a two-step approach was adopted in which effects on p and σ were first considered, and a session-specific density (D) model (i.e., the global model) was held constant.

All relevant models were fit with different combinations of covariates, these included study design covariates; site, array, and session, as well as environmental covariates; temperature (temp), quadratic effect of temperature (tempQ), Julian day (jday), and quadratic effect of Julian day (jdayQ; Table 3; Appendix A).

Table 3: Glossary of covariates used to model each of the three model components (ρ , σ , D) for evaluating effect of artificial cover object array design on red-backed salamander population parameter estimates.

Covariate	Component	Definition
1	σ , D	null model
b	ρ	a trap-specific behavioral response
site	ρ , σ , D	independent forest study sites
array	ρ , σ , D	spatial configurations of ACOs
session	ρ , D	period of demographic closure (i.e., within site, array, and season)
jday	ρ	Julian date of survey
jdayQ	ρ	quadratic effect of Julian date of survey
temp	ρ	air temperature at survey
tempQ	ρ	quadratic effect of air temperature at survey

In the first round of modeling, the null model of the p component was fit without environmental covariates, as well as the effects of; site, array, site+array, and session. Temperature and Julian day, as well as their quadratic effects, were fit to the p component on their own and as an additive effect with site and design covariates. Survey condition and additive models included; Julian day, temperature, site+Julian day, array+Julian day, site+array+Julian day, session+Julian day, temperature+site, temperature+array, temperature+array+site, temperature+session, as well as models in which these raw effects of Julian day and temperature were fit with their quadratic effects, which would allow for detection to peak between their highest and lowest values. Preliminary analysis showed a consistent and positive behavioral response (trap happiness), therefore a behavioral response was specified in all detection models which accounted for the tendency of individuals to be detected on consecutive sampling occasions (Royle et al. 2014).

Also in the first round of modeling, relevant models were fit for the σ component, and included the null model and effects of; array, site, array+site. I observed no spatial recaptures, which are essential for fitting SCR models, in 11 of the 45 sessions, precluding session-specific estimates of σ . All combinations of p and σ model components were fit resulting in a total of 100 models (Appendix B). The most-supported (by AIC) detection model structure (p and σ) was then used to investigate variation in density D – the primary interest - as a function of covariates (C) including site, treatment, site + treatment, and session.

All data preparation, processing and analysis were performed in R (R Core Team 2017), and the oSCR package (Sutherland et al. 2017) was used to fit SCR models.

3.3 Results

1579 captures of 910 individuals were recorded across the three sites from 19 September 2016 to 7 November 2017. Of 45 sessions, 34 had spatial-recaptures. MMDM session values ranged from 0.86-10.77m, and further emphasize the need to account for heterogeneity in distribution.

The first stage of modeling revealed that p was best described, based on AIC, by an additive effect of session (i.e., a site and treatment interaction; Table 4; Table 5), quadratic effect of Julian day, and a local behavioral response. As expected, other reasonable structures on p parameters included quadratic effects of temperature, which Julian day can reasonably be considered a coarser measurement of, but Julian day always outperformed temperature. The quadratic effect of Julian day supports, as expected, that surface activity peaks within seasons. An additive effect of site and treatment was the best supported effect on σ , with wide overlap in estimates when including 95% confidence intervals (Table 5; Table 6; Figure 11).

Table 4: MLE estimates with the most AIC support of the effect of session, Julian date, and behavior on the detection model.

Model	Covariate	Coefficient	Standard Error	Covariate	Coefficient	Standard Error
<i>Detection</i>	Intercept	-4.174	0.304	Session 25	1.862	0.559
	Session 2	-0.029	0.371	Session 26	1.577	0.415
	Session 3	-0.480	0.316	Session 27	1.832	0.492
	Session 4	0.085	0.330	Session 28	1.081	0.441
	Session 5	-0.062	0.433	Session 29	1.315	0.441
	Session 6	0.495	0.372	Session 30	1.762	0.529
	Session 7	0.642	0.409	Session 31	-0.580	0.334
	Session 8	-0.443	0.367	Session 32	-1.449	0.649
	Session 9	-0.068	0.340	Session 33	-1.112	0.361
	Session 10	0.143	0.510	Session 34	-0.425	0.343
	Session 11	0.313	0.347	Session 35	-0.645	0.521
	Session 12	0.206	0.434	Session 36	0.820	0.381
	Session 13	-0.222	0.372	Session 37	0.046	0.461
	Session 14	-0.024	0.351	Session 38	-0.233	0.369
	Session 15	0.170	0.429	Session 39	-0.157	0.382
	Session 16	1.388	0.344	Session 40	0.490	0.516
	Session 17	0.487	0.514	Session 41	0.093	0.364
	Session 18	0.288	0.412	Session 42	-0.186	0.476
	Session 19	0.573	0.413	Session 43	-0.418	0.390
	Session 20	0.729	0.520	Session 44	-0.263	0.368
	Session 21	1.619	0.457	Session 45	0.798	0.490
	Session 22	1.887	0.480	Julian Date	0.579	0.116
	Session 23	0.808	0.439	Julian Date ²	-0.476	0.059
	Session 24	1.328	0.432	Behavioral Effect	1.978	0.132

Table 5: 100 models with variations of p and σ components and with a session-specific (i.e., ‘global’) density component were evaluated. Models in this table were the most likely (ranked by AIC score) to explain the data derived from experimental artificial cover object array configurations.

Model	D	p	σ	logL	K
1	~session	~session+jdayQ+b	~site + array	6182	102
2	~session	~session+jdayQ+b	~array	6188	98
3	~session	~array+tempQ+b	~site + array	6227	62
4	~session	~session+jdayQ+b	~site	6191	98
5	~session	~site+array+tempQ+b	~site + array	6226	64

Table 6: MLE estimates of σ with 95% confidence intervals

	Site 1	Site 2	Site 3
	<i>Estimate (m)</i>	<i>Estimate (m)</i>	<i>Estimate (m)</i>
Array 1	0.8284 (0.6690-1.0258)	0.9693 (0.7934-1.1842)	1.1128 (0.8976-1.3797)
Array 2	0.7602 (0.5847-0.9884)	0.8895 (0.6974-1.1347)	1.0212 (0.8235-1.2666)
Array 3	1.0454 (0.8300-1.3167)	1.2232 (1.0142-1.4754)	1.4043 (1.2460-1.5828)
Array 4	0.8037 (0.6317-1.0226)	0.9404 (0.8251-1.0718)	1.07966 (0.9473-1.2305)
Array 5	0.6170 (0.4567-0.8393)	0.7220 (0.5623-0.9270)	0.8289 (0.6387-1.0757)

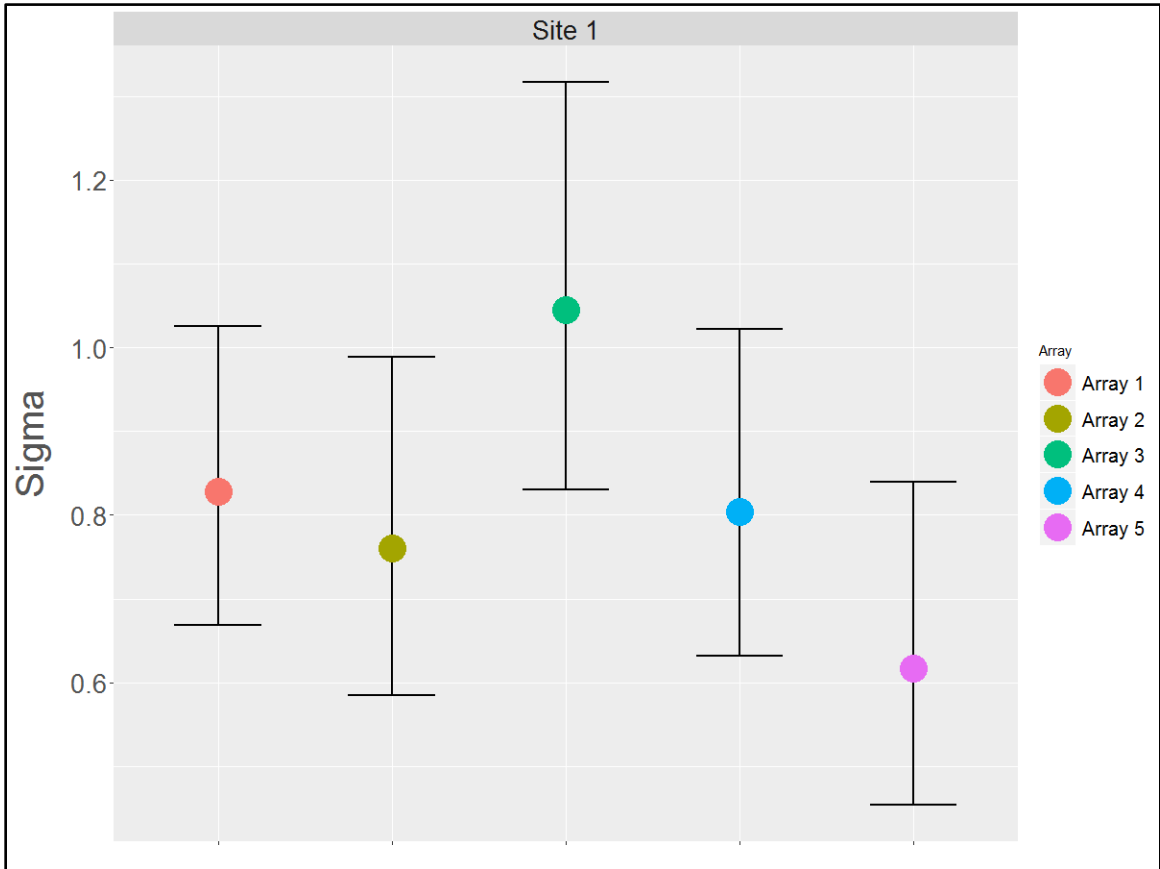


Figure 11: An effect of treatment was supported on σ (in m) in the top model structure. Here, array design is represented in color, each with an error bar representing a 95% confidence interval.

The second step in modeling revealed that the model with the most support specified site-specific differences in density (D ; Figure 12; Table 7) among sites 1, 2, and 3 - and produced MLEs of 0.41ind/m²(0.33-0.52), 0.17ind/m² (0.14-0.21), and 0.23ind/m² (0.19-0.28), respectively. Density was constant across arrays within sites, which supports the expectation that for a single population for which density is assumed to be uniform, configuration does not influence density estimates.

Table 7: Five density models were evaluated and ranked by AICc score based on the data derived from experimental artificial cover object configurations. All density models have the p and σ component structure with highest AIC support from the first round of modeling, in which all possible detection parameters were evaluated with a global (i.e., session) density model; $p(\sim\text{session} + \text{Julian day} + \text{Julian day}^2)$ and $\sigma(\sim\text{site}+\text{treatment})$.

Model	D	p	σ	logL	K	dAICc	Cumulative Weight
1	$\sim\text{site}$	$\sim\text{session}+\text{jday}Q+b$	$\sim\text{site}+\text{array}$	6221	60	0.00	0.57
2	$\sim\text{site}+\text{array}$	$\sim\text{session}+\text{jday}Q+b$	$\sim\text{site}+\text{array}$	6217	64	0.56	1
3	$\sim\text{session}$	$\sim\text{session}+\text{jday}Q+b$	$\sim\text{site}+\text{array}$	6182	102	19.00	1
4	$\sim\text{array}$	$\sim\text{session}+\text{jday}Q+b$	$\sim\text{site}+\text{array}$	6235	62	31.20	1
5	~ 1	$\sim\text{session}+\text{jday}Q+b$	$\sim\text{site}+\text{array}$	6240	58	33.44	1

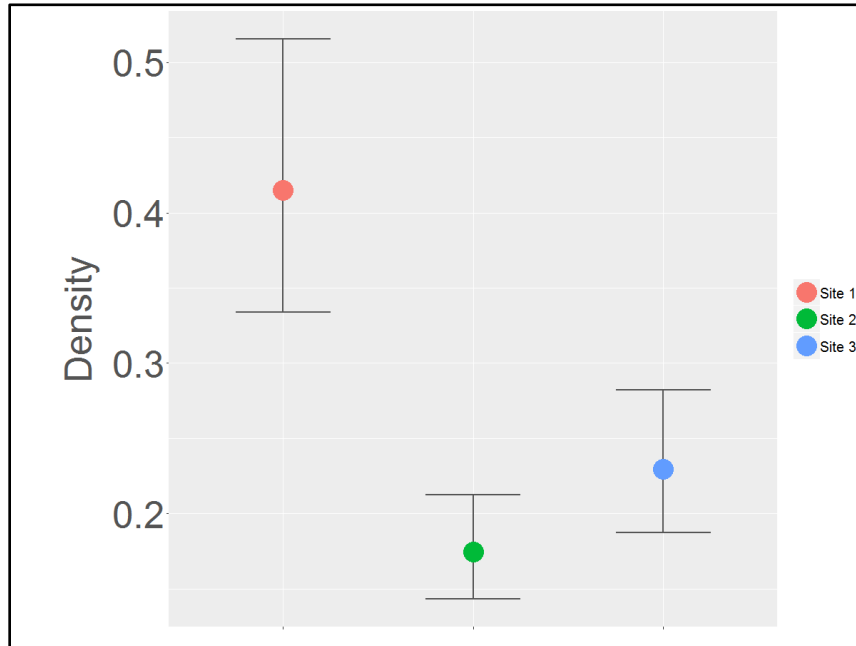


Figure 12: Site-specific estimates of density (individuals/m²) of RBS from three populations in Wendell State Forest. Densities estimated using the model structure with the most AICc support – ($D\sim\text{site}$), ($p\sim\text{session}+\text{jday}+\text{jday}^2$), ($\sigma\sim\text{site}+\text{treatment}$).

The additive effect of Treatment does appear in the second model (Table 7). When models are within 2 AIC scores of one another, both are often interpreted as having similar empirical support. However, this interpretation can be problematic when the model structures are only separated by one parameter. The added parameter in the more complex model may not have any true explanatory power, but the increase in K is not a strong enough penalty to separate the models by greater than 2 AIC scores (Arnold 2010). This is true in the case presented here where the added parameter, array, is redundant – because log-likelihood value is only decreased by 4, the number of variables added. Uninformative parameters can appear in AIC tables when attached to otherwise high-performing models, and should not be considered to have empirical support. Because of this, I chose to interpret the results using only the most supported model.

These results speak to the robustness of ACOs as a sampling method, and are an example of successful data integration. However, it is important to note that the estimates were not totally free of study design conflict. Variation in ACO spacing made the inclusion of array design in the spatial scale parameter, σ , necessary - and density estimates would be biased without it. Further, a positive local (i.e., ACO-specific) behavioral response was observed on the detection parameter, and though unrelated to array design, supports the hypothesis that ACOs are attractive to focal species

3.4 Discussion and Summary

Analyses of population density require knowledge of both distribution and abundance - but, without empirical data available to be used in rigorous spatial population models (i.e., SCR), these assessments are limited by biased or imprecise population estimates (Engeman 2003). The ability to incorporate data from various study designs may help resolve data deficiencies, but must be done carefully so that accuracy of estimates is not in jeopardy (Link and Sauer 1996). Accommodating common analytical obstacles, such as behavioral responses to sampling design, makes incorporated data sets increasingly powerful as their scope of inference is widened. SCR

methods are renowned for their ability to exclude bias in their parameter estimates, most notably with accommodation of heterogeneity in detection probability (Royle et al. 2014). Exclusion of biases is made possible by the flexibility of SCR models, and this experiment demonstrated that flexibility by finding comparable density estimates - even where spatial sampling design varied.

The effect found of array design on σ is reflective of RBS ecology – because of its reliance on moisture, movement is dependent on precipitation and/or moisture-retentive cover objects (Jaeger 1980; 2016) – and therefore, it is unsurprising that the highest estimates of σ , the movement parameter, are found in Array 3 where cover is most spread out. The inclusion of covariates in detection parameters (p or σ) can accommodate sources of variation that decrease precision in estimates of population parameters (Bailey et al. 2004a; c; Efford and Fewster 2013). Variation in capture probability can be reduced by either 1) standardizing protocols or assuming similar responses across all monitored populations, or 2) by using models and covariates to generate unbiased parameter estimates and standard errors of data derived from non-standardized methods (Nichols et al. 2008). These results demonstrate that the inclusion of study design in detection parameters (i.e., the effect of array on σ) removes the potential bias of spatial study design in density estimates. Since density is the parameter of interest, and not σ , allowing space use to be an effect of sampling design removes a source of variation and ensures the integrity of density estimates (Borchers and Efford 2008).

A benefit of non-standardization is that potential study design biases are known. However, while this experiment proved comparison of estimates between study designs is possible, standardization should still be the preferred approach. The inclusion of array design in the top model - albeit, not on density - is evidence that not only does variation in study design need to be accounted for in model input (i.e., separate state spaces, or state spaces large enough accommodate all configurations), but it also complicates model output and computation time. Added parameters are penalized in AIC model evaluation, and therefore the true density model can be masked by models with fewer parameters in the corresponding detection components

(Arnold 2010). Standardization can avoid added parameters associated with study design and allow for more parsimonious inference (Gula and Theuerkauf 2013).

Correct inference requires that potential biases be identified, evaluated and accommodated in the design and analysis phases of research (Williams et al. 2002). One untested criticism of ACOs is that they induce a behavioral response and therefore bias capture rates and violate model assumptions. These results suggest that certain sampling biases can be embraced when the method is otherwise robust. ACOs can generate high capture rates and are easily sampled, but have been subjected to criticism as a sampling method (Marsh and Goicochea 2003; Hyde and Simmons 2001) because of their potential attractive qualities. In this analysis, I could both estimate biases and accommodate those biases for the estimation of the state variable of greatest interest – true density.

Because of the small spatial scales of RBS movement and ACO study designs, as well as the attraction of RBS to cover, I could test the effects of behavior on SCR estimation. Though these results were found in a unique system, I believe they are relevant to others as well – because many SCR studies take place on larger scales and cannot feasibly manipulate trap design as was done here. Most studies, particularly those affecting time-sensitive management decisions, are interested in the densities of populations, but many do not have access to large standardized data sets. I demonstrated that even when there is behavioral bias to study design, SCR methods can still make robust estimates of density. I therefore recommend that researchers interested in density, but concerned with behavioral responses to trapping, carefully consider these behaviors and how they may affect detection and movement (i.e., cover availability and RBS movement) – because, in doing so, aspects of study design may be included in detection parameters, removing bias in density estimates.

SCR methods can broaden the scope (either temporally or spatially) of inference for difficult conservation problems by enabling to incorporation of data from diverse methods for the compilation of robust data sets. In the case of amphibians, there is a lack of historical data that

can inform ecologists of the drivers behind current rates of decline; even robust, large-scale, contemporary data cannot precisely determine global or regional drivers of population change (Grant et al. 2016). Furthermore, declines occurring at the local scale are not always detected at the regional scale; underlining the value of representative sub-sampling throughout species ranges (Miller and Grant 2015). This is evidenced in the relatively low RBS densities (0.41, 0.17, 0.21 ind/m²) found in this study in Wendell State Forest, which appears to be quality habitat (i.e., NHF). Other studies using similar methods have found higher densities, for example 0.423-0.473 (Muñoz et al. 2016) and 1.33-2.16 (Sutherland et al. 2016). The abundance and biomass of RBS and its effects on forest ecosystems have been examined for decades, and despite their relevance to questions related to forest productivity and food dynamics, are still unclear (Davic and Welsh 2004) – partially due to the unpredictable variation in population density. The wide range of density estimates in different parts of RBS range supports conclusions (Peterman and Semlitsch 2013; Milanovich and Peterman 2016) that densities, and therefore biomass and nutrient standing stock, vary spatially – though the drivers behind variation are not always evident and require further investigation.

Analysis of among-population adaptive capacity and response to threat is difficult without rich data sets – which are frequently precluded by non-standardization. The integration of data derived from different spatial study designs will allow for more robust data sets with stronger conclusions. I stress the importance of systematically distributed range-wide data collection in compensating for the lack of historical data, as drivers of population demographics and processes can be compared across unique populations within species range (Miller and Grant 2015). While standardization strengthens the inference of monitoring programs, this experiment demonstrates that where standardized range-wide data are not available, population parameters and state changes may still be estimated where study design varies.

3.5 Acknowledgement of Assumptions

Variation in density estimates is difficult to explain, especially with a lack of site-specific biotic and abiotic data. It is important to note that these results were found in three sites in one state forest, which is very small in relation to the entire species range. Further, I collected data during two fall sampling seasons and one spring sampling season, but activity during these seasons is known to be different (e.g., courtship vs. brooding; Petranka 1998). This study took place near the center of RBS range, and timing of surface activity is different on range edges. Though RBS occurs in urban areas, I chose to study a relatively undisturbed area, which is only reflective of parts of its range. Effects of temporary emigration between terrestrial and fossorial environments in RBS is unclear, and if emigration is not random between individuals, the SCR density estimates would be compromised (Bailey et al. 2004b).

APPENDICES

APPENDIX A

R CODE USED FOR STATISTICAL ANALYSIS

(R Core Team 2017; Sutherland et al. 2017)

```
#Libraries

library(oSCR)
library(lubridate)
library(formula)

#Load data object

load("C:\\ACOConfiguration.RData")

#load data frame
sf
#load state space
ss

#Fit any combinations of the below

Dmods <- c( ~1,
            ~session,
            ~site,
            ~treatment,
            ~site+treatment)

Smods <- c( ~1,
            ~site
            ~site+treatment)

Pmods <- c( ~b,
            ~session+b,
            ~site+b,
            ~treatment+b,
            ~site+treatment+b,
            ~temp+b,
            ~temp+temp2+b
            ~jday+b
            ~jday+jday2+b
            ~session+temp+b
            ~session+temp+temp2+b
            ~session+jday+b
            ~session+jday+jday2+b
            ~site+temp+b
```

APPENDIX A CONT'D

R CODE USED FOR STATISTICAL ANALYSIS

```
~site+temp+temp2+b
~site+jday+b
~site+jday+jday2+b
~treatment+temp+b
~treatment+temp+temp2+b
~treatment+jday+b
~treatment+jday+jday2+b
~site+treatment+temp+b
~site+treatment+temp+temp2+b
~site+treatment+jday+b
~site+treatment+jday+jday2+b)

#select model to fit

mod <- list(Dmods[[1]], Pmods[[1]], Smods[[1]])

fm <- oSCR.fit(model = mod,
               scrFrame = sf,
               ssDF = ss,
               multicatch = T,
               trimS = 3.6,)
```

APPENDIX B

TOTAL DETECTION PARAMETERS MODEL SET

Model	D	p	σ	Model	D	p	σ
1	~session	~b	~1	31	~session	~temp+b	~array
2	~session	~b	~site	32	~session	~temp+b	~site+array
3	~session	~b	~array	33	~session	~tempQ+b	~1
4	~session	~b	~site+array	34	~session	~tempQ+b	~site
5	~session	~site+b	~1	35	~session	~tempQ+b	~array
6	~session	~site+b	~site	36	~session	~tempQ+b	~site+array
7	~session	~site+b	~array	37	~session	~site+jday+b	~1
8	~session	~site+b	~site+array	38	~session	~site+jday+b	~site
9	~session	~array+b	~1	39	~session	~site+jday+b	~array
10	~session	~array+b	~site	40	~session	~site+jday+b	~site+array
11	~session	~array+b	~array	41	~session	~site+jdayQ+b	~1
12	~session	~array+b	~site+array	42	~session	~site+jdayQ+b	~site
13	~session	~site+array+b	~1	43	~session	~site+jdayQ+b	~array
14	~session	~site+array+b	~site	44	~session	~site+jdayQ+b	~site+array
15	~session	~site+array+b	~array	45	~session	~array+jday+b	~1
16	~session	~site+array+b	~site+array	46	~session	~array+jday+b	~site
17	~session	~session+b	~1	47	~session	~array+jday+b	~array
18	~session	~session+b	~site	48	~session	~array+jday+b	~site+array
19	~session	~session+b	~array	49	~session	~array+jdayQ+b	~1
20	~session	~session+b	~site+array	50	~session	~array+jdayQ+b	~site
21	~session	~jday+b	~1	51	~session	~array+jdayQ+b	~array
22	~session	~jday+b	~site	52	~session	~array+jdayQ+b	~site+array
23	~session	~jday+b	~array	53	~session	~session+jday+b	~1
24	~session	~jday+b	~site+array	54	~session	~session+jday+b	~site
25	~session	~jdayQ+b	~1	55	~session	~session+jday+b	~array
26	~session	~jdayQ+b	~site	56	~session	~session+jday+b	~site+array
27	~session	~jdayQ+b	~array	57	~session	~session+jdayQ+b	~1
28	~session	~jdayQ+b	~site+array	58	~session	~session+jdayQ+b	~site
29	~session	~temp+b	~1	59	~session	~session+jdayQ+b	~array
30	~session	~temp+b	~site	60	~session	~session+jdayQ+b	~site+array

APPENDIX B CONT'D

TOTAL DETECTION PARAMETER MODEL SET

Model	<i>D</i>	<i>p</i>	σ	Model	<i>D</i>	<i>p</i>	σ
61	~session	~site+temp+b	~1	91	~session	~site+array+jday+b	~site
62	~session	~site+temp+b	~site	92	~session	~site+array+jdayQ+b	~site
63	~session	~site+temp+b	~array	93	~session	~site+array+temp+b	~array
64	~session	~site+temp+b	~site+array	94	~session	~site+array+tempQ+b	~array
65	~session	~site+tempQ+b	~1	95	~session	~site+array+jday+b	~array
66	~session	~site+tempQ+b	~site	96	~session	~site+array+jdayQ+b	~array
67	~session	~site+tempQ+b	~array	97	~session	~site+array+temp+b	~1
68	~session	~site+tempQ+b	~site+array	98	~session	~site+array+tempQ+b	~1
69	~session	~array+temp+b	~1	99	~session	~site+array+jday+b	~1
70	~session	~array+temp+b	~site	100	~session	~site+array+jdayQ+b	~1
71	~session	~array+temp+b	~array				
72	~session	~array+temp+b	~site+array				
73	~session	~array+tempQ+b	~1				
74	~session	~array+tempQ+b	~site				
75	~session	~array+tempQ+b	~array				
76	~session	~array+tempQ+b	~site+array				
77	~session	~session+temp+b	~1				
78	~session	~session+temp+b	~site				
79	~session	~session+temp+b	~array				
80	~session	~session+temp+b	~site+array				
81	~session	~session+tempQ+b	~1				
82	~session	~session+tempQ+b	~site				
83	~session	~session+tempQ+b	~array				
84	~session	~session+tempQ+b	~site+array				
85	~session	~site+array+temp+b	~site+array				
86	~session	~site+array+tempQ+b	~site+array				
87	~session	~site+array+jday+b	~site+array				
88	~session	~site+array+jdayQ+b	~site+array				
89	~session	~site+array+temp+b	~site				
90	~session	~site+array+tempQ+b	~site				

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