

INTRODUCTION

Space plays a vital role in virtually all ecological processes (Tilman and Kareiva, 1997; Hanski, 1999; Clobert et al., 2001). The spatial arrangement of habitat can influence movement patterns during dispersal, habitat selection, and survival. The distance between an organism and its competitors and prey can influence activity patterns and foraging behavior. Further, understanding distribution and spatial variation in abundance is necessary in the conservation and management of populations. The inherent spatial aspect of *sampling* populations also plays an important role in ecology as it strongly affects, and biases, how we observe population structure (Seber, 1982; Buckland et al., 2001; Borchers et al., 2002; Williams et al., 2002). However, despite the central role of space and spatial processes to both understanding population dynamics and how we observe or sample populations, a coherent framework that integrates these two aspects of ecological systems has not been fully realized either conceptually or methodologically.

Capture-recapture methods represent perhaps the most common technique for studying animal populations, and their use is growing in popularity due to recent technological advances that provide mechanisms to study many taxa which before could not be studied efficiently, if at all. However, a major deficiency of classical capture-recapture methods is that they do not admit the spatial structure of either ecological processes that give rise to encounter history data, nor the spatial aspect of collecting these data. **While many technical limitations of this lack of spatial explicitness have been recognized for decades** (Dice, 1938; Hayne, 1950), it has only been very recent (Efford, 2004; Borchers, 2012) that spatially explicit capture-recapture methods – those which accommodate space – have been developed.

Spatial capture-recapture (SCR) methods resolve a host of technical problems that arise in applying capture-recapture methods to animal populations. However, SCR models are not merely an extension of technique. Rather, they represent a

much more profound development in that they make ecological processes explicit in the model – processes of density, spatial organization, movement and space-usage by individuals. The practical importance of SCR models is that they allow ecological scientists to study elements of ecological theory using individual encounter data that exhibit various biases relating to the observation mechanisms employed. At the same time, SCR models can be used, and may be the only option, for obtaining demographic data on some of the rarest and most elusive species – information which is required for effective conservation. It is this potential for advancing both applied and theoretical research that motivated us to write this book.

1.1 THE STUDY OF POPULATIONS BY CAPTURE-RECAPTURE

In the fields of conservation, management, and general applied ecology, information about abundance or density of populations and their vital rates is a basic requirement. To that end, a huge variety of statistical methods have been devised, and as we noted already, the most well-developed are collectively known as capture-recapture (or capture-mark-recapture) methods. For example, the volumes by Otis et al. (1978), White et al. (1982), Seber (1982), Pollock et al. (1990), Borchers et al. (2002), Williams et al. (2002), and Amstrup et al. (2005) are largely synthetic treatments of such methods, and contributions on modeling and estimation using capture-recapture are plentiful in the peer-reviewed ecology literature.

Capture-recapture techniques make use of individual *encounter history* data, by which we mean sequences of (usually) 0's and 1's denoting if an individual was encountered during sampling over a certain time period (occasion). For example, the encounter history “010” indicates that this individual was encountered only during the second of three trapping occasions. As we will see, these data contain information about encounter probability, and also abundance, and other parameters of interest in the study of populations.

Capture-recapture has been important in studies of animal populations for many decades, and its importance is growing dramatically in response to technological advances that improve our ability and efficiency to obtain encounter history data. Historically, such information was obtainable using methods requiring physical capture of individuals. However, new methods do not require physical capture or handling of individuals. A large number of passive detection devices produce individual encounter history data including camera traps (Karanth and Nichols, 1998; O'Connell et al., 2010), acoustic recording devices (Dawson and Efford, 2009), and methods that obtain DNA samples such as hair snares for bears, scent posts for many carnivores, and related methods which allow DNA to be extracted from scat, urine or animal tissue in order to identify individuals. This book is concerned with how such data can be used to carry out inference about animal abundance or density, and other parameters such as survival, recruitment, resource selection, and movement using new classes of capture-recapture models which utilize auxiliary spatial information related to the encounter process. We refer to such methods as

459 spatial capture-recapture (SCR) models¹.

460 As the name implies, the primary feature of SCR models that distinguishes
 461 them from traditional CR methods is that they make use of the spatial information
 462 inherent to capture-recapture studies. Encounter histories that are associated with
 463 auxiliary information on the location of capture, are *spatial encounter histories*.
 464 This auxiliary information is informative about spatial processes including the spa-
 465 tial organization of individuals, variation in density, resource selection and space
 466 usage, and movement. As we will see, SCR models allow us to overcome critical
 467 deficiencies of non-spatial methods, and integrate ecological theory with encounter
 468 history data. As a result, this greatly expands the practical utility and scientific
 469 relevance of capture-recapture methods, and studies that produce encounter history
 470 data.

1.2 LIONS AND TIGERS AND BEARS, OH MY: GENESIS OF SPATIAL CAPTURE-RECAPTURE DATA

471 A diverse number of methods and devices exist for producing individual encounter
 472 history data with auxiliary spatial information about individual locations. Histori-
 473 cally, physical “traps” have been widely used to sample animal populations. These
 474 include live traps, mist nets, pitfall traps and many other types of devices. Such
 475 devices physically retain animals until visited by a biologist, who removes the indi-
 476 vidual, marks it or otherwise molests it in some scientific fashion, and then releases
 477 it. Although these are still widely used, recent technological advances for obtain-
 478 ing encounter history data non-invasively have made it possible to study many
 479 species that were difficult if not impossible to study effectively just a few years ago.
 480 As a result, these methods have revolutionized the study of animal populations
 481 by capture-recapture methods, have inspired the development of spatially-explicit
 482 extensions of capture-recapture, and will lead to their increasing relevance in the
 483 future. We briefly review some of these here, which we consider more explicitly in
 484 later chapters of this book.

485 1.2.1 Camera trapping

486 Considerable recent work has gone into the development of camera-trapping method-
 487 ologies. For a historical overview of this method see Kays et al. (2008) and Kucera
 488 and Barrett (2011). Several recent synthetic works have been published includ-
 489 ing Nichols and Karanth (2002), and an edited volume by O’Connell et al. (2010)
 490 devoted solely to camera trapping concepts and methods. As a method for estimat-
 491 ing abundance, some of the earliest work that relates to the use of camera trapping
 492 data in capture-recapture models originates from Karanth and colleagues (Karanth,
 493 1995; Karanth and Nichols, 1998, 2000).

¹In the literature the term spatially explicit capture-recapture (SECR) is also used, but we prefer the more concise term.



Figure 1.1. Left: Wolverine being encounter by a camera trap (Photo credit: Audrey Magoun). Right: Tiger encountered by camera trap (Photo credit: Ullas Karanth).

In camera trapping studies, cameras are often situated along trails or at baited stations and individual animals are photographed and subsequently identified either manually by a person sitting behind a computer, or sometimes now using specific identification software. Camera trapping methods are widely used for species that have unique stripe or spot patterns such as tigers (Karanth, 1995; Karanth and Nichols, 1998), ocelots (*Leopardus pardalis*; (Trolle and Kéry, 2003, 2005)), leopards (*Panthera pardus*; (Balme et al., 2010)), and many other cat species. Camera traps are also used for other species such as wolverines (*Gulo gulo*; (Magoun et al., 2011; Royle et al., 2011b)), and even species that are less easy to identify uniquely such as mountain lions (*Puma concolor*, (Sollmann et al., in revision)) and coyotes (*Canis latrans*, (Kelly et al., 2008)). We note that even for species that are not readily identified by pelage patterns, it might be efficient to use camera traps in conjunction with spatial capture-recapture models to estimate density (see Chaps. 18 and 19).

1.2.2 DNA sampling

DNA obtained from hair, blood or scat is now routinely used to obtain individual identity and encounter history information about individuals (Taberlet and Bouvet, 1992; Kohn et al., 1999; Woods et al., 1999; Mills et al., 2000; Schwartz and Monfort, 2008). A common method is based on the use of “hair snares” (Fig. 1.2) which are widely used to study bear populations (Woods et al., 1999; Garshelis and Hristienko, 2006; Kendall et al., 2009; Gardner et al., 2010b). A sample of hair is obtained as individuals pass under or around barbed-wire (or other physical mechanism) to take bait. Hair snares and scent sticks have also been used to sample felid populations (García-Alaníz et al., 2010; Kéry et al., 2010) and other species. Research has even shown that DNA information can be extracted from urine deposited in the

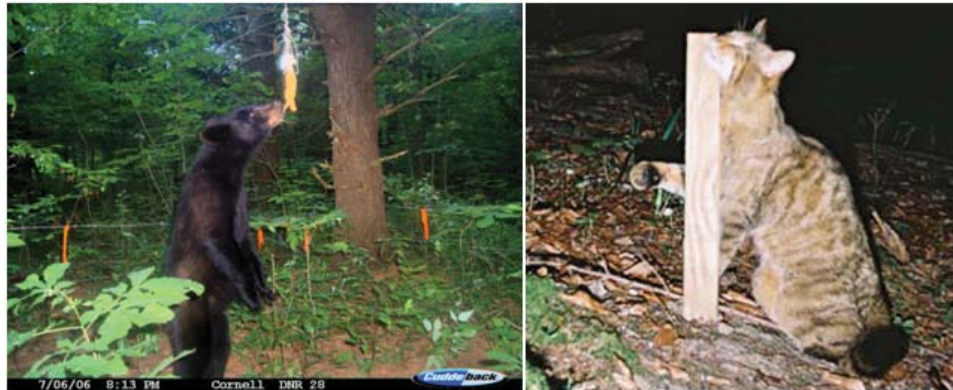


Figure 1.2. Left: Black bear in a hair snare (*Photo credit: M. Wegan*) Right: European wildcat loving on a scent stick (*Photo credit: Darius Weber*)

wild (e.g., in snow; see Valiere and Taberlet (2000)) and as a result this may prove another future data collection technique where SCR models are useful.

1.2.3 Acoustic sampling

Many studies of birds (Dawson and Efford, 2009), bats, and whales (Marques et al., 2009) now collect data using devices that record vocalizations. When vocalizations can be identified by individual from multiple recording devices, spatial encounter histories are produced that are amenable to the application of SCR models (Dawson and Efford, 2009; Efford et al., 2009b). Recently, these ideas have been applied to data on direction or distance to vocalizations by multiple simultaneous observers and related problems (D. Borchers, ISEC 2012 presentation).

1.2.4 Search-encounter methods

There are other methods which don't fall into a nice clean taxonomy of "devices". Spatial encounter histories are commonly obtained by conducting manual searches of geographic sample units such as quadrats, transects or road or trail networks. For example, DNA-based encounter histories can be obtained from scat samples located along roads or trails or by specially trained dogs (MacKay et al., 2008) searching space (Fig. 1.3). This method has been used in studies of martens, fishers (Thompson et al., 2012), lynx, coyotes, birds (Kéry et al., 2010), and many other species. A similar data structure arises from the use of standard territory or spot mapping of birds Bibby et al. (1992) or area sampling in which space is searched by observers to physically capture individuals. This is common in surveys



Figure 1.3. Left: A wildlife research technician for the USDA Forest Service holding a male fisher captured as part of the Kings River Fisher Project in the Sierra National Forest, California. Right: A dog handler surveying for fisher scat in the Sierra National Forest. *Photo credit: Craig Thompson.*

539 that involve reptiles and amphibians, e.g., we might walk transects picking up box
 540 turtles (Hall et al., 1999), or desert tortoises (Zylstra et al., 2010), or search space
 541 for lizards (Royle and Young, 2008).

542 These methods don't seem like normal capture-recapture in the sense that the
 543 encounter of individuals is not associated with specific trap location, but SCR
 544 models are equally relevant for analysis of such data as we discuss in Chapt. 15.

1.3 CAPTURE-RECAPTURE FOR MODELING ENCOUNTER PROBABILITY

545 We briefly introduced techniques used for the study of animal populations. These
 546 methods produce individual encounter history data, a record of where and when
 547 each individual was captured. We refer to this as a *spatial encounter history*. Histor-
 548 ically, auxiliary spatial information has been ignored, and encounter history data
 549 have been *summarized* to simple “encounter or not” for the purpose of applying
 550 ordinary CR models. The basic problem with these ordinary (or “non-spatial”)
 551 capture-recapture models is they don't have any sense of space in them, the spatial
 552 information is summarized out of the data set, so we aren't able to use such mod-
 553 els for studying things such as movement, or resource selection, etc~~dots~~. Instead,
 554 ordinary capture-recapture models usually resort to models of “encounter prob-

555 ability,” which is a nuisance parameter, seldom of any ecological relevance. We
556 show an example here that is in keeping with the classical application of ordinary
557 capture-recapture models.

558 1.3.1 Example: Fort Drum bear study

559 Here we confront the simplest possible capture-recapture problem – but one of great
560 applied interest – estimating density from a standard capture-recapture study. We
561 use this as a way to introduce some concepts and motivate the need for spatial
562 capture-recapture models by confronting technical and conceptual problems that
563 we encounter. The data come from a study to estimate black bear abundance on
564 the Fort Drum Military Installation in upstate New York (-Wegan (2008), see also
565 Chapt. 4 for more details). The specific data used here are encounter histories on
566 47 individuals obtained from an array of 38 baited “hair snares” during June and
567 July 2006. The study area and locations of the 38 hair snares are shown in Fig.
568 1.4. Barbed wire traps (see Fig. 1.2) were baited and checked for hair samples
569 each week for eight weeks. Analysis of these data appears in Gardner et al. (2009)
570 and Gardner et al. (2010b), and we use the data in a number of analyses in later
571 chapters.

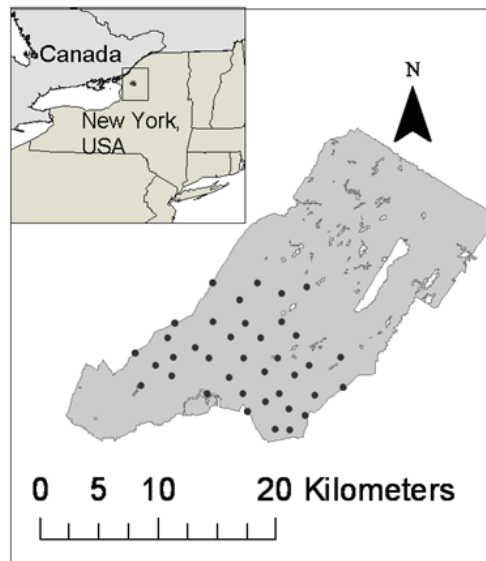


Figure 1.4. Locations of hair snares on Fort Drum, New York, operated during the summer of 2006 to sample black bears.

Although each bear was captured, or not, in each of the 38 hair snares, we start by treating this data set as a standard capture-recapture data set and summarize to an encounter history matrix with 47 rows and 8 columns with entries y_{ik} , where $y_{ik} = 1$ if individual i was captured, at any trap, in sample occasion k and $y_{ik} = 0$ otherwise. There is a standard closed population model, colloquially referred to as “model M_0 ” (see Chapt. 4), which assumes that encounter probability p is constant for all individuals and sample periods. We fitted model M_0 to the Fort Drum data using traditional likelihood methods, yielding the maximum likelihood estimate (MLE) of $\hat{N} = 49.19$ with an asymptotic standard error (SE) of 1.9.

The key issue in using such a closed population model regards how we should interpret this estimate of $\hat{N} = 49.19$ bears. Does it represent the entire population of Fort Drum? Certainly not – the trapping array covers less than half of Fort Drum as we see in Fig. 1.4. So to get at the total bear population size of Fort Drum, we would have to convert our \hat{N} to an estimate of density and extrapolate. To get at density, then, should we assert that N applies to the southern half of Fort Drum below some arbitrary line? Surely bears move on and off of Fort Drum without regard to hypothetical boundaries. Without additional information there is simply no way of converting this estimate of N to density, and hence it is really not meaningful biologically. To resolve this problem, we will adopt the customary approach of converting N to D by buffering the convex hull around the trap array. The convex hull has area 157.135 km^2 . We follow Bales et al. (2005) in buffering the convex hull of the trap array by the radius of the mean female home range size.

The mean female home range radius was estimated (Wegan, 2008) for this study region to be 2.19 km, and the area of the convex hull buffered by 2.19 km is 277.01 km^2 . (**R** commands to compute the convex hull, buffer it, and compute the area are given in the **R** package **scrbook** which accompanies the book). Hence, the estimated density here is approximately 0.178 bears/ km^2 using the estimated population size obtained by model M_0 . We could assert that the problem has been solved, go home, and have a beer. But then, on the other hand, maybe we should question the use of the estimated home range radius – after all, this is only the female home range radius and the home ranges change for many reasons. Instead, we may decide to rely on a buffer width based on one-half mean maximum distance moved (MMDM) estimated from the actual hair snare data as is more customary (Dice, 1938). In that case the buffer width is 1.19 km, and the resulting estimated density is increased to 0.225 bears/ km^2 about 27 % larger. But wait – some studies actually found the full MMDM (Parmenter et al., 2003) to be a more appropriate measure of movement (e.g. Soisalo and Cavalcanti (2006)). So maybe we should use the full MMDM which is 2.37 km, pretty close to the telemetry-based estimate and therefore providing a similar estimate of density (0.171 bears/ km^2). So in trying to decide how to buffer our trap array we have already generated 3 density estimates. The crux of the matter is obvious: Although it is intuitive that N should scale with area – the number of bears should go up as area increases and go down as area decreases – in this ad hoc approach of accounting for animal movement N remains

the same, no matter what area we assert was sampled. The number of bears and the area they live in are not formally tied together within the model, because estimating N and estimating the area N relates to are two completely independent analytical steps which are unrelated to one another by a formal model.

Unfortunately, our problems don't end here. In thinking about the use of model M_0 , we might naturally question some of the basic assumptions that go into that model. The obvious one to question is ~~that which declares~~ that p is constant. One obvious source of variation in p is variation *among individuals*. We expect that individuals may have more or less exposure to trapping due to their location relative to traps, and so we try to model this "heterogeneous" encounter probability phenomenon. To illustrate this phenomenon, here are the number of traps that each individual was encountered in:

```
# traps:  1   2   3   4   5   6   9
# bears: 23  13   6   2   1   1   1
```

meaning, ~~for example~~, 23 bears were captured in only 1 trap, and 1 bear was captured in 9 distinct traps. The variation in trap-encounter frequencies suggests quite a range in traps exposed to bears in the sampled population. Historically, ~~researches~~ try to reduce spatial heterogeneity in capture probability by placing > 1 trap per home range (Otis et al., 1978; Williams et al., 2002). This seems like a sensible idea but it is difficult to do in practice since you don't know where all the home ranges are and so we try to impose a density of traps that averages something > 1 per home range. An alternative solution is to fit models that allow for individual heterogeneity in p (Karanth, 1995). Such models have the colloquial name of "model M_h " (Otis et al., 1978). We fitted this model (see Chapt. 4 for details) to the Fort Drum data using each of the 3 buffer widths previously described (telemetry, 1/2 MMDM and MMDM), producing the estimates reported in Table 1.1. While we can tell by the models' AIC that M_h is clearly favored by more than 30 units, we might still not be entirely happy with our results. Clearly there is information in our data that could tell us something about the exposure of individual bears to the trap array – where they were captured, and how many times – but since space has no representation in our model, we can't make use of this information. Model M_h thus merely accounts for what we observe in our data (some bears were more frequently captured than others) rather than explicitly accounting for the processes that generated the data.

So what are we left with? Our density estimates span a range from 0.17 to 0.43 bears/km² depending on which estimator of N we use and what buffer strip we apply. Should we feel strongly about one or the other? Which buffer should we prefer? AIC favors model M_h , but did it adequately account for the differences in exposure of individuals to the trap array? Are we happy with a purely phenomenological model for heterogeneity? It assumes that all individuals are independent and identically distributed (*iid*) draws from some distribution, but does not account for the explicit mechanism of induced heterogeneity. And, further, we

657 have information about that (trap of capture) which model M_h ignores. And if we
658 choose one type of buffer, how do we compare our density estimates to those from
659 other studies that may opt for a different kind of buffer? The fact that N does not
660 scale with A , as part of the model, renders this choice arbitrary.

Table 1.1. Table on estimates of density (D , bears/~~km~~²) for the Fort Drum data using models M_0 and M_h and different buffers. Model M_h here is a logit-normal mixture (Coull and Agresti, 1999).

Model	Buffer	\hat{D}	SE
M_0	telemetry	0.178	0.178
M_0	MMDM	0.171	0.171
M_0	1/2 MMDM	0.225	0.225
M_h	telemetry	0.341	0.144
M_h	MMDM	0.327	0.138
M_h	1/2 MMDM	0.432	0.183

661 **1.3.2 Inadequacy of non-spatial capture-recapture**

662 The parameter N (population size) in an ordinary capture-recapture model is func-
663 tionally unrelated to any notion of sample area, and so we are left taking arbitrary
664 guesses at area, and matching it up with estimates of N from different models that
665 do not have any explicit biological relevance. Clearly, there is not a compelling
666 solution to be derived from this “estimate N and conjure up a buffer” approach
667 and we are left not much wiser about bear density at Fort Drum than we were
668 before we conducted this analysis, and certainly not confident in our assessments.
669 Closed population models are not integrated with any ecological theory, so our N
670 is not connected to the specific landscape in any explicit way.

671 The capture-recapture models that we used apply to truly closed populations
672 – a population of goldfish in a fish bowl. Yet here we are applying them to a
673 population of bears that inhabit a rich two-dimensional landscape of varied habitats,
674 exposed to trapping by an irregular and sparse array of traps. It seems questionable
675 that the same model that is completely sensible for a population of goldfish in a
676 bowl, should also be the right model for this population of bears distributed over
677 a broad landscape. Ordinary capture-recapture methods are distinctly non-spatial.
678 They don’t admit spatial indexing of either sampling (the observation process) or
679 of individuals (the ecological process). This leads immediately to a number of
680 practical deficiencies: (1) Ordinary CR models do not provide a coherent basis
681 for estimating density, a problem we struggled with in the black bear study. (2)
682 Ordinary CR model and sampling methods induce a form of heterogeneity that
683 can only at best be approximated by classical models of latent heterogeneity. SCR
684 models formally accommodate heterogeneity due to the juxtaposition of individuals
685 with the encounter devices. (3) Ordinary CR models do not accommodate trap-

level covariates which exist in a large proportion of real studies; (4) Ordinary CR models do not accommodate formal consideration of any spatial process that gives rise to the observed data.

In subsequent chapters of this book, we resolve these specific technical problems related to density, model-based linkage of N and A , covariates, spatial variation, and related things all within a coherent unified framework for spatial capture-recapture.

1.4 HISTORICAL CONTEXT: A BRIEF SYNOPSIS

Spatial capture-recapture is a relatively new methodological development, at least with regard to formal estimation and inference. However, the basic problems that motivate the need for formal spatially-explicit models have been recognized for decades and quite a large number of ideas have been proposed to deal with these problems. We review some of these ideas here.

1.4.1 Buffering

The standard approach to estimating density even now is to estimate N using conventional closed population models (Otis et al., 1978) and then try to associate with this estimate some specific sampled area, say A , the area which is contributing individuals to the population for which N is being estimated. The strategy is to define A by placing a buffer of say W around the trap array or some polygon which encloses the trap array. The historical context is succinctly stated by (O'Brien, 2011) from which we draw this description:

“At its most simplistic, A may be described by a concave polygon defined by connecting the outermost trap locations (A_{tp} ; Mohr (1947)). This assumes that animals do not move from outside the bounded area to inside the area or vice versa. Unless the study is conducted on a small island or a physical barrier is erected in the study area to limit movement of animals, this assumption is unlikely to be true. More often, a boundary area of width W (A_w) is added to the area defined by the polygon A_{tp} to reflect the area beyond the limit of the traps that potentially is contributing animals to the abundance estimate (Otis et al., 1978). The sampled area, also known as the effective area, is then $A(W) = A_{tp} + A_w$. Calculation of the buffer strip width (W) is critical to the estimation of density and is problematic because there is no agreed upon method of estimating W . Solutions to this problem all involve ad hoc methods that date back to early attempts to estimate abundance and home ranges based on trapping grids (see Hayne, 1949). Dice (1938) first drew attention to this problem in small mammal studies and recommended using one-half the diameter of an average home range. Other solutions have included use of inter-trap distances (Blair, 1940; Burt, 1943), mean movements among traps, maximum movements among traps (Holdenried, 1940; Hayne, 1949), nested grids (Otis et al., 1978), and assessment lines (Smith et al., 1971).”

The idea of using $1/2$ mean maximum distance moved (“MMDM” Wilson and Anderson, 1985b) to create a buffer strip seems to be the standard approach even today, presumably justified by Dice’s suggestion to use $1/2$ the home range diameter, with the mean over individuals of the maximum distance moved being an

estimator of home range diameter. Alternatively, some studies have used the full MMDM (e.g. Parmenter et al. (2003)), because the trap array might not provide a full coverage of the home range (home ranges near the edge should be truncated) and so 1/2 MMDM should be biased smaller than the home range radius. And, sometimes home range size is estimated by telemetry (Karanth, 1995; Bales et al., 2005). Use of MMDM summaries to estimate home range radius is usually combined with an AIC-based selection from among the closed-population models in Otis et al. (1978) which most often suggests heterogeneity in detection (model M_h). Almost all of these early methods were motivated by studies of small mammals using classical “trapping grids” but, more recently, their popularity in the study of wildlife populations has increased with the advent of new technologies, especially related to non-invasive sampling methods such as camera trapping. In particular, the series of papers by Karanth and Nichols (Karanth, 1995; Karanth and Nichols, 1998, 2002) has led to fairly widespread adoption of these ideas.

1.4.2 Temporary emigration

Another intuitively appealing idea is that by White and Shenk (2000) who discuss “correcting bias of grid trapping estimates” by recognizing that the basic problem is like random temporary emigration (Kendall et al., 1997; Chandler et al., 2011; Ivan et al., 2013a,b) where individuals flip a coin with probability ϕ to determine if they are “available” to be sampled or not. White and Shenk’s idea was to estimate ϕ from radio telemetry, as the proportion of time an individual spends in the study area. They obtain the estimated “super-population” size by using standard closed population models and then obtain density by $\hat{D} = \hat{N}\hat{\phi}/A$ where A is the nominal area of the trapping array (e.g., minimum convex hull). A problem with this approach is that individuals that were radio collared represent a biased sample i.e., you fundamentally have to sample individuals randomly from the population *in proportion to their exposure to sampling* and that seems practically impossible to accomplish. In other words, “in the study area” has no precise meaning itself and is impossible to characterize in almost all capture-recapture studies. Deciding what is “in the study area” is effectively the same as choosing an arbitrary buffer which defines who is in the study area and who isn’t. That said, the temporary emigration analogy is a good heuristic for understanding SCR models and has a precise technical relevance to certain models.

Another interesting idea is that of using some summary of “average location” as an individual covariate in standard capture-recapture models. Boulanger and McLellan (2001) use distance-to-edge (DTE) as a covariate in the Huggins-Alho type of model. Ivan (2012) uses this approach in conjunction with an adjustment to the estimated N obtained by estimating the proportion of time individuals are “on the area formally covered by the grid” using radio telemetry. We do not dwell too much on these different variations but we do note that the use of DTE as an individual covariate amounts to ~~some kind of~~ intermediate model between simple

closed population models and fully spatial capture-recapture models, which we address directly in Chapt. 4.

While these procedures are all heuristically appealing, they are also essentially ad hoc in the sense that the underlying model remains unspecified or at least imprecisely characterized and so there is little or no basis for modifying, extending or generalizing the methods. These methods are distinctly *not* model-based procedures. Despite this, there seems to be an enormous amount of literature developing, evaluating and “validating” these literally dozens of heuristic ideas that solve specific problems, as well as various related tweaks and tunings of them and really it hasn’t led to any substantive breakthroughs that are sufficiently general or theoretically rigorous.

1.5 EXTENSION OF CLOSED POPULATION MODELS

The deficiency with classical closed population models is that they have no spatial context. N is just an integer parameter that applies equally well to estimating the number of unique words in a book, the size of some population that exists in a computer, or a bucket full of goldfish. The question of *where* the N items belong is central both to interpretation of data and estimates from all capture-recapture studies and, in fact, to the construction of spatial capture-recapture models considered in this book. Surely it must matter whether the N items exist as words in a book, or goldfish in a bowl, or tigers in a patch of forest! That classical closed population models have no spatial context leads to a number of conceptual and methodological problems or limitations as we have encountered previously. More important, ecologists seldom care only about N – space is often central to objectives of many population studies – movement, space usage, resource selection, how individuals are distributed in space and in response to explicit factors related to landuse or habitat. Because space is central to so many real problems, this is probably the number 1 reason that many ecologists don’t bother with capture-recapture. They haven’t seen capture-recapture methods as being able to solve their problems. Thus, the essential problem is that classical closed population models are too simple – they ignore the spatial attribution of traps and encounter events, movement and variability in exposure of individuals to trap proximity. These problems can be addressed formally by the development of more general capture-recapture models.

1.5.1 Towards spatial explicitness: Efford’s formulation

The solution to the various issues that arise in the application of ordinary capture-recapture models is to extend the closed population model so that N becomes spatially explicit. Efford (2004) was the first to formalize an explicit model for spatial capture-recapture problems in the context of trapping arrays. He adopted a Poisson point process model to describe the distribution of individuals and essentially a distance sampling formulation of the observation model which describes the

probability of detection as a function of individual location, regarded as a latent variable governed by the point process model. While earlier (and contemporary) methods of estimating density from trap arrays have been ad hoc in the sense of lacking a formal description of the spatial model, Efford achieved a formalization of the model, describing explicit mechanisms governing the spatial distribution of individuals and how they are encountered by traps, but adopted a more or less ad hoc framework for inference under that spatial model using a simulation based method known as inverse prediction (Gopalaswamy, 2012).

Recently, there has been a flurry of effort devoted to formalizing inference under this model-based framework for the analysis of spatial capture-recapture data (Borchers and Efford, 2008; Royle and Gardner, 2011; Borchers, 2012; Gopalaswamy, 2012). There are two distinct lines of work which adopt the model-based formulation in terms of the underlying point process but differ primarily by the manner in which inference is achieved. One approach (Borchers and Efford, 2008) uses classical inference based on likelihood (see Chapt. 6), and the other (Royle and Young, 2008) adopts a Bayesian framework for inference (Chapts. 5 and 17).

1.5.2 Abundance as the aggregation of a point process

Spatial point process models represent a major methodological theme in spatial statistics (Cressie, 1991) and they are widely applied as models for many ecological phenomena (Stoyan and Penttinen, 2000; Illian et al., 2008). Point process models apply to situations in which the random variable in question represents the locations of events or objects: trees in a forest, weeds in a field, bird nests, etc. . . . As such, it seems natural to describe the organization of individuals in space using point process models. SCR models represent the extension of ordinary capture-recapture by augmenting the model with a point process to describe individual locations.

Specifically, let $\mathbf{s}_i; i = 1, 2, \dots, N$ be the locations of all individuals in the population. One of the key features of SCR models is that the point locations are latent, or unobserved, and we only obtain imperfect information about the point locations by observing individuals at trap or observation locations. Thus, the realized locations of individuals represent a type of “thinned” point process, where the thinning mechanism is not random but, rather, biased by the observation mechanism. It is also natural to think about the observed point process as some kind of a compound or aggregate point process with a set of “parent” nodes being the locations of individual home ranges or their centroids, and the observed locations as “offspring” - i.e., a Poisson cluster process (PCP). In that context, density estimation in SCR models is analogous to estimating the number of parents of a Poisson cluster process (Chandler and Royle, In press).

Most of the recent developments in modeling and inference from spatial encounter history data, including most methods discussed in this book, are predicated on the view that individuals are organized in space according to a relatively simple point process model. More specifically, we assume that the collection of individ-

ual activity centers are independent and identically distributed random variables distributed uniformly over some region. This is consistent with the assumption that the activity centers represent the realization of a Poisson point process or, if the total number of activity centers is fixed, then this is usually referred to as a binomial point process.

1.5.3 The activity center concept

In the context of SCR models, and because most animals we study by capture-recapture are not sessile, there is not a unique and precise mathematical definition of the point locations \mathbf{s} . Rather, we imagine these to be the centroid of individual's home ranges, or the centroid of an individual's activities during the time of sampling, or even it's average location measured with error (e.g., from a long series of telemetry measurements). In general, this point is unknown for any individual but if we could track an individual over time and take many observations then we could perhaps get a good idea of where that point is. We'll think of the collection of these points as defining the spatial distribution of individuals in the population.

We use the terms home range or activity center interchangeably. The term "home range center" suggests that models are only relevant to animals that exhibit behavior of establishing home ranges or territories, or central place foragers, and since not all species do that, perhaps the construction of SCR models based on this idea is flawed. However, the notion of a home range center is just a conceptual device and we don't view this concept as being strictly consistent with classical notions of animal territories. Rather our view is that a home range or territory is inherently dynamic, temporally, and thus it is a transient quantity - where the animal lived during the period of study, a concept that is completely analogous to the more conventional notion of utilization distributions. Therefore, whether or not individuals of a species establish home ranges is irrelevant because, once a precise time period is defined, this defines a distinct region of space that an individual must have occupied.

1.5.4 The state-space

Once we introduce the collection of activity centers, $\mathbf{s}_i; i = 1, 2, \dots, N$, then the question "what are the possible values of \mathbf{s} ?" needs to be addressed because the individual \mathbf{s}_i are *unknown*. As a technical matter, we will regard them as **random effects** and in order to apply standard methods of statistical inference we need to provide a distribution for these random effects. In the context of the point process model, the possible values of the point locations referred to as the "state-space" of the point process and this is some region or set of points which we will denote by \mathcal{S} . This is analogous to what is sometimes called the *observation window* for \mathbf{s} in the point process literature. The region \mathcal{S} serves as a prior distribution for \mathbf{s}_i (or, equivalently, the random effects distribution). In animal studies, as a description

of where individuals that could be captured are located, it includes our study area, and should accommodate all individuals that could have been captured in the study area. In the practical application of SCR models, in most cases estimates of density will be relatively insensitive to choice of state-space which we discuss further in Chapt. 5 and elsewhere.

1.5.5 Abundance and density

When the underlying point process is well-defined, including a precise definition of the state-space, this in turn induces a precise definition of the parameter N , “population size”, as the number of individual activity centers located within the prescribed state-space, and its direct linkage to density, D . That is, if $A(\mathcal{S})$ is the area of the state-space then

$$D = \frac{N}{A(\mathcal{S})}.$$

A deficiency with some classical methods of “adjustment” is they attempted to prescribe something like a state-space - a “sampled area” - except absent any precise linkage of individuals with the state-space. SCR models formalize the linkage between individuals and space and, in doing so, provide an explicit definition of N associated with a well-defined spatial region, and hence density. That is, they provide a model in which N scales, as part of the model, with the size of the prescribed state-space. In a sense, the whole idea of SCR models is that by defining a point process and its state-space \mathcal{S} , this gives context and meaning to N which can be estimated directly for that specific state-space. Thus, it is fixing \mathcal{S} that resolves the problem of “unknown area” that we have previously discussed.

1.6 CHARACTERIZATION OF SCR MODELS

Formulation of capture-recapture models conditional on the latent point process is the critical and unifying element of *all* SCR models. However, SCR models differ in how the underlying process model is formulated, and its complexity. Most of the development and application of SCR models has focused on their use to estimate density and touting the fact that they resolve certain specific technical problems related to the use of ordinary capture-recapture models. This is achieved with a simple process model being a basic point process of independently distributed points. At the same time, there are models of CR data that focus exclusively on *movement* modeling, or models with explicit dynamics (Ovaskainen, 2004; Ovaskainen et al., 2008). Conceptually, these are akin to spatial versions of so-called Cormack-Jolly-Seber (CJS) models in the traditional capture-recapture literature, except they involve explicit mathematical models of movement based on diffusion or Brownian motion. Finally, there are now a very small number of papers that focus on *both* movement and density simultaneously (Royle and Young, 2008; Royle et al., 2011a;

921 Royle and Chandler, 2012) or population dynamics and density (Gardner et al.,
922 2010b).

923 A key thing is that these models, whether focused just on density, or just on
924 movement, or both, are similar models in terms of the underlying concepts, the
925 latent structure, and the observation model. They differ primarily in terms of the
926 ecological focus. Understanding movement is an important topic in ecology, but
927 models that strictly focus on movement will be limited by two practical consid-
928 erations: (1) most capture-recapture data e.g., by camera trapping ~~or whatever~~,
929 produces only a few observations of each individual (between 1-5 would be typi-
930 cal). So there is not too much information about complex movement models. (2)
931 Typically people have an interest in density of individuals and therefore we need
932 models that can be extrapolated from the sample to the unobserved part of the
933 population. That said, there are clearly some cases where more elaborate move-
934 ment models should come into play. If one has some telemetry data in addition to
935 SCR then there is additional information on fine-scale movements that should be
936 useful.

1.7 SUMMARY AND OUTLOOK

937 Spatial capture-recapture models are an extension of traditional capture-recapture
938 models to accommodate the spatial organization of both individuals in a population
939 and the observation mechanism (e.g., locations of traps). They resolve problems
940 which have been recognized historically and for which various ad hoc solutions
941 have been suggested: heterogeneity in encounter probability due to the spatial
942 organization of individuals relative to traps, the need to model trap-level effects
943 on encounter, and that a well-defined sample area does not exist in most studies,
944 and thus estimates of N using ordinary capture-recapture models cannot be related
945 directly to density.

946 As we have shown already, SCR models are not simply an extension of a tech-
947 nique to resolve certain technical problems. Rather, they provide a coherent, flex-
948 ible framework for making ecological processes explicit in models of individual en-
949 counter history data, and for studying animal populations processes such as individ-
950 ual movement, resource selection, space usage, population dynamics, and density.
951 Historically, researchers studied these questions independently, using ostensibly un-
952 related study designs and statistical procedures. For example, resource selection
953 function (RSF) models for resource selection, state-space models for movement,
954 density using closed capture-recapture methods, and population dynamics with
955 various “open” capture-recapture models. SCR can bring all of these problems
956 together into a single unified framework for modeling and inference. Most impor-
957 tantly, spatial capture-recapture models promise the ability to integrate explicit
958 ecological theories directly into the models so that we can directly test hypothe-
959 ses about either space usage (e.g., Chapt. 13), landscape connectivity (Chapt.
960 12), movement, or spatial distribution (Chapt. 11). We imagine that, in the near

961 future, SCR models will include point process models that allow for interactions
962 among individuals such as inhibition or clustering (Reich et al., 2012). In the
963 following chapters we develop a comprehensive synthesis and extension of spatial
964 capture-recapture models as they presently exist, and we suggest areas of future
965 development and needed research.