Chapter 4

Camera traps in wildlife ecology: a review

Chapter overview

This chapter presents a review of camera trapping studies in wildlife ecology. The camera trapping technique shows particular promise for researching cryptic, low density animals, and so may assist with monitoring of responses in predator control programs. There is also the potential to use this technique with many other species, so I aimed to thoroughly investigate the existing literature. I compiled a total of 782 publications, including 479 peer-reviewed articles. Publications were added to a database that allows flexible searching, browsing and categorisation.

The use of camera traps has increased dramatically over recent years, with studies using camera traps to address a wide range of objectives. Some examples of the type of information that can be accessed using the database are presented, along with a review of key trends in the literature and some potential future directions. There are many advantages of using remotely deployed camera traps for observing animals, and they are rapidly becoming a dominant survey tool for many larger terrestrial animals and cryptic species such as mid-sized predators. I use the findings of the review subsequently to test and improve monitoring protocols in the Southern Ark program.

4.1 Introduction

In earlier chapters I drew attention to the importance of monitoring the effects of management interventions on animal populations, and noted in particular the difficulties of doing this effectively if the animals in question are rare or cryptic. In the Southern Ark program in Victoria, which seeks to reduce the predatory impacts of the red fox *Vulpes vulpes* on populations of native vertebrates, these problems are acute. Foxes are themselves cryptic and hard to find, especially when at low density (Vine et al., 2009), and prey species in the Southern Ark region such as bandicoots *Perameles nasuta* and *Isoodon obesulus* and potoroos *Potorous* spp. are generally very scarce. How should such species be monitored to determine whether an imposed management regime is having desired effects? Although many means are used to detect animals including direct (e.g. observation or live trapping), and indirect methods (e.g. signs such as spoor or nests), camera trapping has been used increasingly in recent work and has been recommended specifically for monitoring populations of the red fox (Vine et al., 2009).

In consequence, this technique is reviewed in detail here, and its potential application to programs such as Southern Ark is explored. In this review, I trace historical developments in camera trapping, describe current practice and discuss possibilities for the future.

Camera traps—remotely deployed animal-triggered imaging devices—provide a lasting and easily interpreted record of the presence of an animal at a particular place and time. Advances in technology have greatly increased their utility and their use is now widespread in animal surveys. A comprehensive review of the camera trapping literature in 1999 by Cutler and Swann located almost every article published between 1950 and March 1997. They presented a table of 107 studies, categorised by the class of equipment used and the study objective. This widely cited review has been of great benefit to the field. Advances in both the technology and in the analysis of photographs over the last decade have prompted my follow-up review here, which provides a comprehensive analysis of the literature, and makes available more broadly the complete catalogue of published works.

Thorough reviews of the existing literature are a recommended starting point for almost all research (Pan, 2007). However, the time and effort required to do a comprehensive search mean that field researchers are often unable to find all the appropriate material, or do not have easy access to it (Francis & Goodman, in press). This is especially difficult for practitioners in developing countries without major institutional support (Sunderland et al., 2009). In addition, many resources are difficult to identify, especially grey literature or that outside the mainstream of scientific publishing. For example, one study searched for camera trapping literature in the *Web of Science* database to show the increase in studies on the subject, and identified 151 articles, with none before 1993 (Rowcliffe & Carbone, 2008). A comprehensive search identifies more than three times that number of peer-reviewed publications. Tools which assist with identifying existing research are a valuable addition to any field, and this research aims to fill that gap.

Camera traps for photographing wild animals have been used for over 100 years. Initially, naturalists took pictures for aesthetic reasons, or recreationally as a replacement for hunting. Scientists soon saw the potential for camera traps to be incorporated into field methods, especially in the survey of animal diversity. More recently, techniques have been developed to estimate relative or absolute animal abundances from camera trap photographs, and the technique is in continuous development.

4.2 Methods

I aimed to review every article that used camera traps in wildlife ecology published before October 2009. I used a wide range of database search tools to identify articles, using combinations of relevant search terms, and also chaining (i.e. following references [*sensu* Talja & Maula, 2003]). I have aimed particularly to achieve complete coverage of the peer-reviewed literature, and have also compiled many non peer-reviewed articles, conference papers, theses, reports and other grey literature.

Details of all these publications were added to a Zotero bibliographic database, an open-source document and reference manager (www.zotero.org), and the 'full-text' of almost every article was indexed (752/ 770, 98%). In this chapter, I have comprehensively analysed a random sample of around half the articles in peer-reviewed publications for details of methods, equipment and results, and added the results to a customised relational database, programmed in Structured Query Language (SQL), the standard form for online delivery of information (IBM, 2006).

I included all studies reporting results from animal-triggered still cameras, and studies reviewing their use. I specifically excluded animal-mounted cameras (e.g. Rutz & Bluff, 2008), photo-point monitoring (e.g. O'Connor & Bond, 2007), remote thermal-imaging (e.g. Lavers et al., 2005), or time-lapse and continuous video monitoring (e.g. Reif & Tornberg, 2006), except those studies reviewed previously by Cutler and Swann (1999). I summarise some key trends in the literature and identify landmark studies and directions in research. I have not attempted to be comprehensive in the presentation of these analyses, as the database itself is such that any combination of factors may be searched and identified, and detailed exploration can be left to the database user. However, I have tried to identify key uses and biases of camera trapping that would guide my use of the technique in the Southern Ark monitoring program, and describe these aspects further in subsequent chapters.

4.3 Results

Compilation of studies into the database

782 articles were reviewed and added to the database (Table 4.1). A complete list of all the articles incorporated into the database is detailed separately in Appendix 4; tables in this chapter refer to numeric identifiers in this appended list. Of the 479 articles published in peer-reviewed journals, a random sample of 271 were analysed comprehensively for all details of methods and results.

The database will be made freely available online alongside the final published version of this review, and will form a key supplement to it. It allows flexible browsing, sorting, categorisation, and complex searches of all details of articles. Analysis of trends in methods, equipment or other key features is also easily accomplished. Studies previously reviewed by Cutler and Swann (1999) have been added to the database, both for completeness, and because their review and data presentation was constrained by the nature of print publishing.

The full-text of many articles had to be withheld from the online database due to copyright restrictions, but online sources are provided for 92% of articles, so that authorised users can access publications directly. While this is the most comprehensive literature review on the subject that has been attempted, it is still probable that a few articles were overlooked, especially if they appeared in publications not indexed by major databases or not referenced in other publications. There is also probably a bias towards articles in English, although the database holds 39 publications in other languages, 30 of which have English summaries.

Terminology

A wide variety of terms has been used for camera trapping studies. In the peer-reviewed literature, "camera trap" is the most popular term (261/479, 54%), ahead of "remote camera" (83/479, 17%), "remote photography" (68/479, 14%), "photo-trap"(29/479, 6%) and "automatic photography" (27/479, 6%). At least eight other terms have been used for the technique. Many articles use multiple terms; one article used five separate terms interchangeably.

In this thesis I use the terms camera trap and camera trapping, and recommend the general adoption of these terms. They are unambiguous and meaningful; this was also the first term used to refer to this technique in print:

> "A device which might be arranged on the principle of a trap … would doubtless capture some interesting pictures" (Chapman, 1900, p. 25).

Despite widespread use (70/261, 27%), "camera trap" should not be hyphenated (J. Sheidlower, Oxford English Dictionary, personal communication).

Table 4.1: Categories of articles included in the camera trapping database. Numbers in brackets after categories are totals, while numbers in square brackets refer to references listed in Appendix 4.

PEER-REVIEWED JOURNAL ARTICLES (479)

[1, 2, 4-7, 9, 10, 16, 17, 20-24, 28-30, 33-35, 37, 38, 40, 42, 43, 48, 49, 53-58, 60-64, 66, 71, 72, 74, 75, 78, 80-84, 87, 88, 90-97, 99, 101, 106, 110, 112, 113, 115, 116, 118, 119, 121, 122, 125, 126, 128-143, 148-159, 161-169, 172, 175, 177, 180, 181, 188-190, 192-196, 198-200, 202, 205, 207-209, 216-220, 224-226, 228-232, 236, 237, 239, 240, 243-249, 251-254, 257, 259-267, 269-272, 275-281, 283-287, 289, 291, 297, 298, 301-309, 316-320, 323, 324, 326, 327, 329, 332, 333, 337, 339, 341-343, 348, 349, 351, 352, 354-357, 362-365, 367, 368, 370-372, 376-383, 385-387, 389-395, 399-403, 405, 407-411, 413, 416, 417, 419, 420, 423-429, 432, 433, 437-445, 447-452, 455, 457, 458, 461-464, 466, 468-473, 475-479, 483, 484, 492, 495-498, 503, 506, 507, 509-511, 513, 514, 517-523, 525-534, 536, 541-551, 553-558, 561, 563, 564, 566-569, 573-577, 579, 586-599, 601-606, 610-613, 615, 617-620, 626, 629, 630, 645, 648, 649, 652-655, 658, 659, 662-672, 675, 676, 679, 681-684, 688, 691, 692, 694, 695, 697-700, 702, 703, 705, 708, 711-717, 719, 720, 724-728, 732-734, 739, 742, 745-750, 754-758, 760, 762, 764-769, 772, 774-776, 780, 781]

PROFESSIONAL NEWSLETTER ARTICLES (78)

[11, 12, 19, 26, 27, 36, 45, 46, 59, 85, 110, 111, 117, 123, 124, 146, 170, 171, 178, 182, 183, 186, 201, 204, 211, 212, 214, 221, 227, 234, 235, 241, 273, 282, 295, 299, 328, 331, 340, 346, 350, 359, 388, 398, 406, 421, 435, 453, 465, 480-482, 499, 504, 559, 560, 572, 584, 585, 623, 627, 632-634, 656, 660, 673, 685, 706, 709, 721, 722, 729, 730, 741, 751, 770]

CONFERENCE PAPERS AND ABSTRACTS (51)

[3, 41, 67, 68, 76, 79, 98, 145, 197, 206, 210, 290, 293, 296, 310, 313, 315, 325, 334, 335, 361, 369, 412, 418, 422, 430, 434, 454, 485, 500-502, 508, 537, 562, 570, 582, 583, 621, 628, 641, 650, 657, 687, 710, 723, 735, 736, 740, 761]

THESES (18)

[8, 25, 86, 114, 160, 288, 330, 358, 384, 493, 539, 636, 644, 690, 707, 744, 753, 773]

REPORTS (48)

[39, 69, 77, 108, 109, 120, 127, 144, 147, 173, 179, 187, 222, 233, 242, 274, 294, 300, 311, 321, 347, 360, 366, 374, 375, 396, 415, 431, 446, 459, 460, 467, 486, 489, 490, 540, 565, 580, 581, 625, 631, 647, 674, 693, 737, 777, 778, 782]

BOOK CHAPTERS (12)

[50, 65, 89, 176, 213, 322, 336, 373, 414, 535, 609, 616]

BOOKS (11)

[102, 103, 238, 250, 397, 456, 491, 512, 622, 624, 640]

MAGAZINE ARTICLES (41)

[31, 32, 44, 47, 73, 100, 104, 105, 174, 184, 203, 223, 255, 268, 292, 312, 404, 474, 515, 516, 524, 538, 552, 600, 608, 635, 637-639, 646, 661, 678, 680, 686, 689, 696, 718, 731, 743, 759]

NEWSPAPER ARTICLES (7)

[191, 215, 345, 571, 642, 738, 771]

WEB PAGE REPORTS (21)

[13-15, 18, 51, 52, 70, 107, 256, 258, 314, 344, 487, 488, 505, 578, 614, 651, 677, 752, 763]

OTHER (16)

[6, 29, 115, 172, 185, 194, 209, 353, 382, 436, 484, 494, 514, 685, 704, 779]

4.3.1 Historical background

1900–1950

The first animal-triggered photographs were produced during the famous studies of animal movement by Eadweard Muybridge, using a series of cameras activated by tripwires (Muybridge, 1882). The use of remotely operated cameras for photographing wild animals was pioneered by George Shiras in the late 1890s. His work was the feature of the first major photographic spread in the *National Geographic Magazine* (Shiras, 1906), and later a book compiled his photographs and records of “Sixty-five years’ visits to the Woods and Waters of North America” (1936). By 1926, a textbook entitled “How to Hunt with the Camera” had a whole chapter on “Flashlight Trap Photography” (Nesbit, 1926, p. 62), and this in turn inspired more amateurs and scientists to experiment with animal-triggered cameras (e.g. Champion, 1927). Articles regularly describe camera trapping as a ‘new’ technique (e.g. Griffiths & van Schaik, 1993a; Carbone et al., 2001); yet more than 80 years ago, Carey (1926) was moved to call camera trapping an “ancient and honourable sport” (p. 278).

1950–1993

More analytical use of camera traps began in the 1950s with the work of Pearson and others investigating the use of runways by small rodents (Pearson, 1959; 1960a; 1960b; Abbott & Dodge, 1961; Osterberg, 1962). Biologists started to share information about modifying camera equipment (Gysel & Davis, 1956; Dodge & Snyder, 1960; Green & Anderson, 1961), with hobbyists also experimenting with taking remote photographs of animals (Shepherd, 1953; Rozelle, 1954).

The years from 1955 to 1993 saw a steady number of published articles. Several pioneering studies developed infra-red triggers, infra-red illumination, population estimates and techniques for individual identification. The first commercially produced camera trap was sold in 1983 (Rappole et al., 1985), and the increased availability of equipment from around 1992 (Kucera & Barrett, 1993b) generated an increase in the number of published studies, and has greatly extended the range of uses to which camera traps are now put (Rowcliffe & Carbone, 2008).

4.3.2 Numbers of publications

An explosion in use

There has been a rapid increase in the use of camera traps in recent years, with a great rise in the number of peer-reviewed publications reporting on their use, especially since the turn of the 21st century (Figure 4.1). The total number of publications in ecology and conservation has also increased during this period, but articles on camera trapping have outstripped that increase over the last decade, with over 50 studies published in each of the past four years (Figure 4.2).

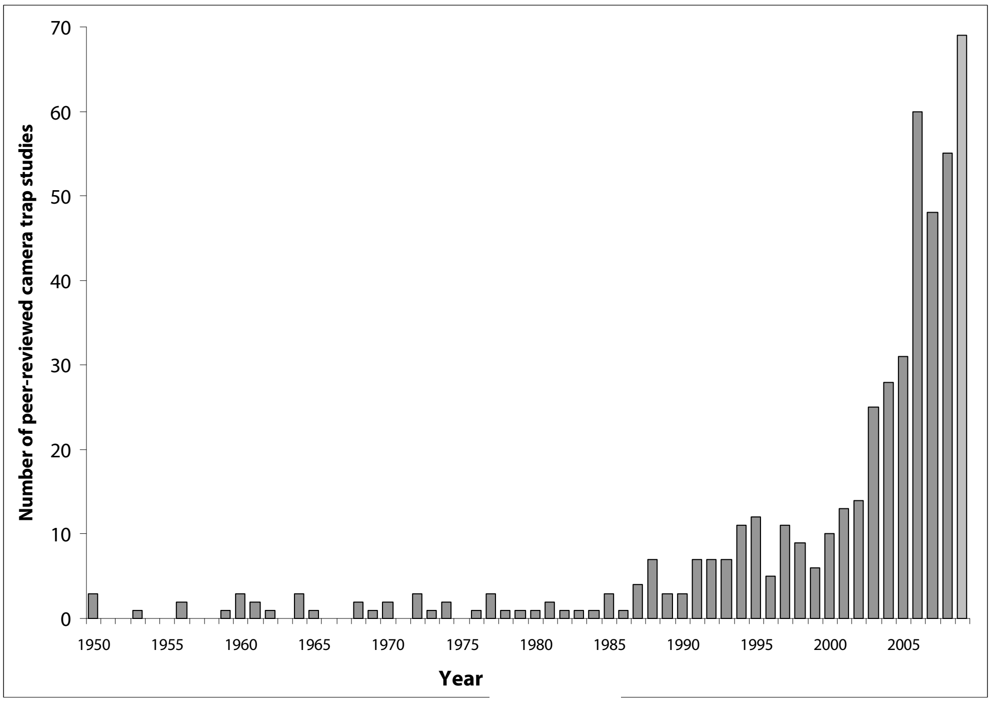

Figure 4.1: Number of camera trap studies published in the peer-reviewed literature from 1950–2009. 2009 data are extrapolated from numbers for the first ten months.

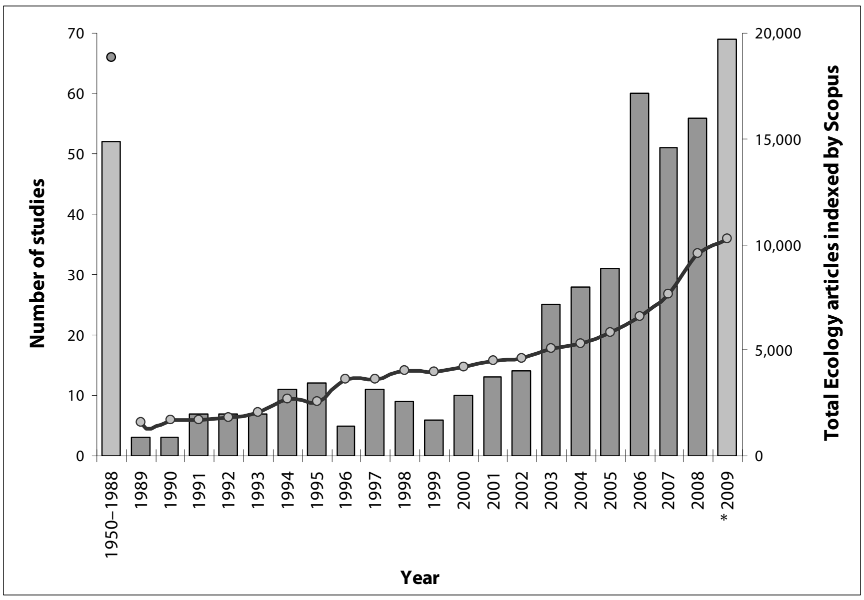

Figure 4.2: Bars show the number of camera trap studies published in the peer-reviewed literature from 1950–2009 (left axis), shown annually since 1989. The 2009 total is extrapolated from numbers of publications during the first ten months. Points and the line show the total number of studies in "Ecology" indexed by the Scopus database for each year (right axis).

The number of other types of publications, especially grey literature, has also risen, but it is more difficult to get a comprehensive picture as much of this material is less widely available. Nonetheless, the amount of grey literature included in the database has risen at a faster rate than that of peer-reviewed papers, although this may be biased by the increased public availability of biodiversity surveys, NGO reports and other information.

Peer-reviewed articles in the database come from 140 different publications. However, the 10 most prolific journals are responsible for 40% of these, and the top 20, 57%. While American journals are responsible for most papers, proportionally, British-based journals publish more articles on camera trapping (Figure 4.3).

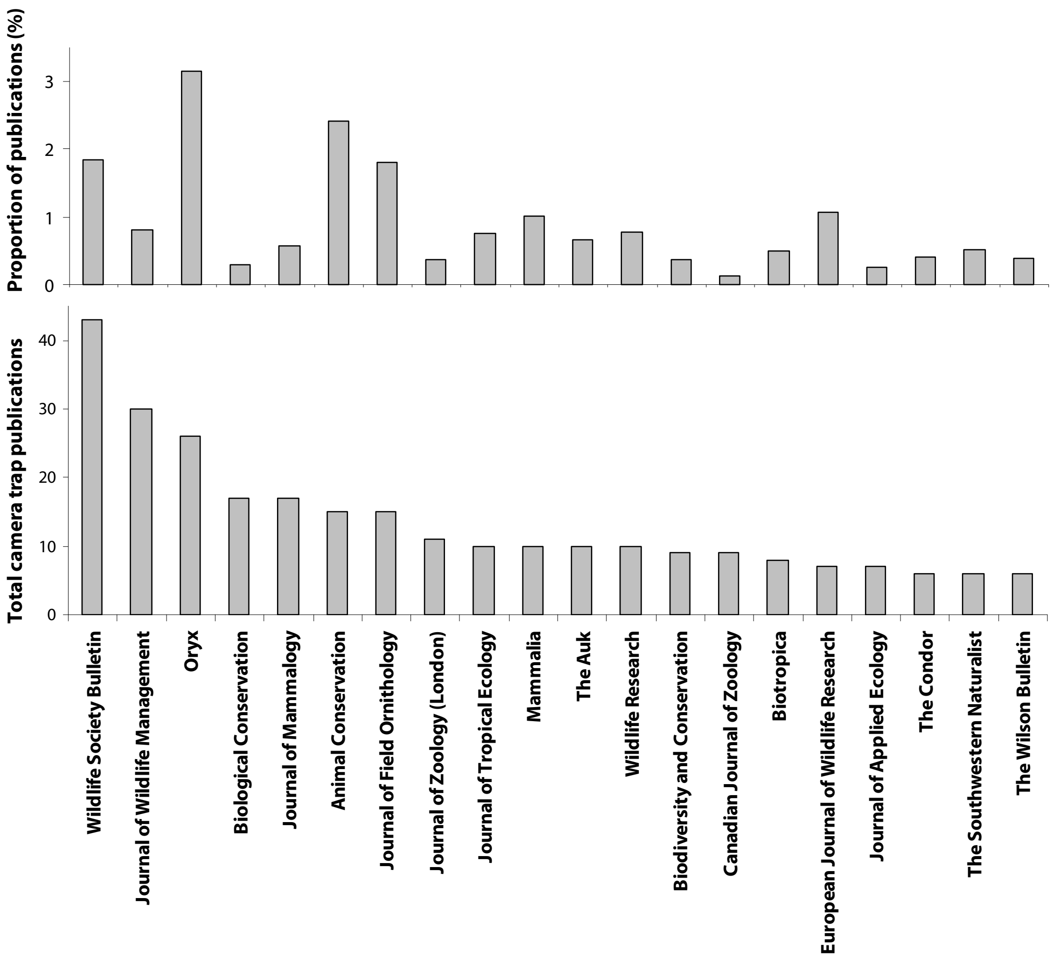

Figure 4.3: The top 20 most prolific journals publishing articles using camera-traps. The lower chart shows raw total numbers of articles. The upper chart shows camera trap studies as a percentage of the total number of articles indexed by the Scopus database for each journal. All other journals (not shown) account for 208 further peer-reviewed publications (43%).

Photographs provide a permanent record of the presence of an animal at a place and time. These photographs can also be of interest to the general public, and are regularly used in publicity material (e.g. ZSL, 2006). Detections of unusual animals, range extensions or other items of interest are sometimes reported in news articles (e.g. Walker, 2009).

4.3.3 Equipment

Camera trapping equipment has undergone rapid changes in recent years, and advanced equipment is now available widely at relatively low cost from any of at least 16 manufacturers, and many more semi-commercial 'home-brew' companies (Walker & Engdahl, 2002). As a sign of their growing popularity, counterfeit units can even be seen at online auction websites (personal observation).

In the peer-reviewed literature, the most widely cited commercial manufacturer is Trailmaster® (110/479, 23%), followed by CamTrakker® (64/479, 13%). However, many articles entirely omit the type or brand of camera trap used (62/271, 23%).

Commercialisation of the manufacture of camera traps has had major advantages to the biologist. Increasing availability has allowed camera trapping to become a standard method in some biological surveys, particularly for cryptic felids, and especially those with unique coat patterns. The reduced cost of equipment is such that larger deployments and more comprehensive coverage are becoming increasingly feasible.

Triggering mechanism

The mechanism by which an animal triggers the camera is the first element that has undergone improvement. All of the early camera traps relied on mechanical means to activate the camera shutter, a method still used in some studies (e.g. Moruzzi et al., 2002; Glen & Dickman, 2003b). Camera traps triggered by interruption of a light beam were first used in the 1950s (Pearson, 1959; Abbott & Coombs, 1964), with infra-red (IR) beams later found to be more reliable (Cooper & Afton, 1981). In more recent times, use of two types of trigger has been widespread. Active IR continues to be used: the camera is triggered when a beam of IR from a transmitter to a sensor is interrupted. Passive IR senses changes in the IR spectrum: animals are usually warmer than their surroundings, and so their movements cause fluctuations in near IR, which are detected by the sensor, and the camera is triggered. First mentioned in the literature in 1985 (Rappole et al.), these 'heat-in-motion' sensors are now by far the dominant type reported (116/121, 96%, of peer-reviewed studies in 2008–9).

Illumination

Early camera trappers used bright flashes of magnesium powder to illuminate animals (e.g. Schillings, 1905, p. 26), and later, electric flashbulbs (Rozelle, 1954). In the 1960s, IR illumination was first investigated using special IR-sensitive film (Knudsen, 1963). IR light had previously been used in direct observations of nocturnal animals, and was found to be less disturbing to animal behaviour (Southern et al., 1946). Recently, camera traps using digital IR sensors with illumination from IR light-emitting diodes (LEDs) have become commonplace. There is potential for confusion between these two types of infra-red, the *illumination* and the *triggering mechanism*, as some publications refer simply to "infra-red cameras".

Digital imaging

Digital cameras have revolutionised the photographic industry, and camera traps are no exception. Only one major company, Trailmaster® retains 35 mm film cameras as part of its system. Digital cameras have major implications for the speed of operation and the numbers of photographs that can be obtained. On the downside, digital cameras typically have a 'warm-up' period before the shutter opens. There can be a delay of several seconds between sensing movement and the exposure of the photograph. This leads to what I term a *slowfire*, where the animal triggers the camera, but has exited the field of view by the time the photograph is taken. This is compared to a *misfire*, when a photograph is triggered by something other than an animal, such as the movement of vegetation (e.g. Clark & Orland, 2008).

Increasing numbers of photographs

Large memory cards allow the storage of many thousands of digital images. This can facilitate acquisition of high quality data and permit different experimental approaches, but also leads to increasing challenges with managing very large numbers of photographs. This is not an entirely new problem; a number of researchers had previously used modified 8 mm or 16 mm movie cameras to take large numbers of photographs. For example, Weller and Derksen (1972) obtained 151,200 images of Adélie penguins *Pygoscelis adeliae*.

4.3.4 Survey costs

While costs have come down, camera trap equipment still forms a substantial part of the costs of many surveys, and camera traps remain more expensive than the equipment for competing methods (Barea-Azcón et al., 2007). The major cost in many surveys, however, is the manpower to run it, and transport to survey sites. As such, camera traps, especially digital camera traps able to remain in the field for long periods, might justify their higher initial costs (Lyra-Jorge et al., 2008), and the quality of results can often be higher than those obtained from comparable methods (e.g. Silveira et al., 2003; Roberts et al., 2006a; Vine et al., 2009). Camera traps are also relatively multipurpose units that can be used for a wide range of surveys for multiple taxa, and even tracking human activity (Griffiths & van Schaik, 1993b). When equipment is used for multiple purposes, costs can be shared.

For surveys that require repeat measures, such as site occupancy surveys, camera traps remove the requirement to visit repeatedly; time and date stamps that are often embedded into the photograph, and are always written into digital file metadata, allow the *post hoc* construction of detection histories (Thorn et al., 2009). Timestamps can also be used *post hoc* to examine activity patterns in animals, a technique that was previously possible only using radio-tracking or direct observations (e.g. van Schaik & Griffiths, 1996; Grassman et al., 2006; Chen et al., 2009).

Camera traps are prone to damage, either by animals or human vandalism (e.g. Mohd. Azlan & Lading, 2006). As an obviously hi-tech asset, usually deployed in remote areas, they are clear targets for casual theft (e.g. Numata et al., 2005). Many commercial cameras are designed to be secured with cable locks, and special security boxes have been developed to help reduce theft and damage (Fiehler et al., 2007). Bears and elephants are particularly liable to damage equipment, and cameras traps have also been armoured to protect them from these animals (Grassman et al., 2005).

4.3.5 Objectives and methods in camera trap studies

A range of approaches, studies, methods, aims, objectives and techniques can use camera traps as a survey tool. Some examples are provided below, along with several examples of the potential for using the database to search for studies on particular topics, species or time periods.

Species inventory

Species inventory is a common use of camera traps (171/479, 36%). They may confirm the presence of animals within an area that other techniques fail to find (e.g. Chiang, 2007). Even with camera traps, some surveys must continue for a very long time to inventory all species in an area (e.g. Beisiegel, 2009), but generally they can compile a species list more quickly and reliably than a human survey (e.g. Trolle et al., 2007). They can also survey for a range of species simultaneously; up to 91 species have been reported from a single camera trap study (Augeri, 2005a). The 271 articles intensively analysed name 383 species as having been photographed, of which 302 are mammals, 58 birds and 14 reptiles.

Cameras have also been used to identify new species (Rovero et al., 2008) or provide additional data to determine the existence of a new species (Kitchener et al., 2006). They are also used to identify extensions to the known range of animals (Table 4.2). While there is debate about the validity of some of these observations (Meijaard et al., 2006; McKelvey et al., 2008), it is clear that camera traps can in many cases provide unequivocal evidence of the presence of species.

Table 4.2: Peer-reviewed literature reporting new records for species or distributions. Numbers in brackets refer to the number of separate discoveries, as some discoveries elicited multiple publications. Numeric references refer to Appendix 4.

Study reports	Number	Reference
Discovery of new species	5 (3)	[355, 588, 589, 593, 757]
Rediscovery of species	6 (4)	[146-148, 221, 390, 444]
Debate over new species	2 (1)	[106, 452]
Major extension to species distribution	10 (8)	[19, 45, 146, 148, 390, 444, 453, 454, 507, 590]

Table 4.3: Peer-reviewed literature that has reported using camera traps for site occupancy studies, by year. Numeric references refer to Appendix 4.

Year of publication	Number	Reference
2009 (Jan–Oct)	9	[386, 407, 498, 536, 592, 697, 705, 732, 762]
2008	14	[137, 144, 342, 347, 348, 378, 392, 478, 497, 509, 510, 595, 625, 703]
2007	6	[253, 391, 400, 415, 442, 481]
2006	4	[142, 225, 389, 513]
2005	1	[26]
2004	2	[86, 333]

Site occupancy

Site occupancy models apply statistical techniques to simple presence-absence data, using repeat surveys to estimate the detection probability, and thus gain an understanding of the likelihood of a false negative result (MacKenzie et al., 2002). Camera traps are an ideal method for collecting presence-absence data for site occupancy modelling, especially for larger species, and an increasing number of studies use this method (Table 4.3). They provide unequivocal confirmation of the presence of a species at a given site, and detection histories can be constructed *post hoc*, allowing remotely operated camera traps to determine a detection probability, within the existing data. In addition, the technique works best when detection probabilities are >0.3 (MacKenzie & Royle, 2005), so data can be analysed *post hoc* to determine the appropriate pooling period for detections.

Population estimates

Absolute population numbers are often desirable in conservation monitoring, but reliable estimates can be challenging, especially for rare or cryptic species (Thompson, 2004). Capture-recapture methods are typically the most suitable for this, but have traditionally relied on live-capture of animals.

If individuals can be identified positively from camera trap photographs, then capture-recapture techniques for population estimation become possible. If animals are captured prior to the survey, they can be marked individually and recognised from future photographs (Buckner, 1964; Mace et al., 1994). Natural markings have the obvious advantage of allowing these methods to be used non-invasively, i.e. without physical capture (Garshelis, 2006). This method was first applied to photographs of tigers *Panthera tigris* by Griffiths (1993) to determine movements and estimate population size. It was extended to capture-recapture models by Karanth (1995), and this approach has been widely adopted for felids with distinctive coat patterns. Individual identification has been demonstrated in a wide range of species (Table 4.4). As the quality of camera trap images improves, it is becoming increasingly possible to use less obvious characteristics to identify individual animals, including minor differences in skin patterns or coat colour (e.g. Oliveira-Santos et al., 2009; Sarmento et al., 2009). Some observers have been able to identify animals from seemingly tiny differences in photographs, for example of swans (Bateson, 1977).

For especially sparse populations, estimates of detection probability have been ‘borrowed’ from larger populations elsewhere of the same species (e.g. Lynam et al., 2009). Such borrowed detection probabilities have also been used for surveys of related species, by assuming that sightability and behaviour are similar enough to warrant pooling of data (Bowkett et al., 2008).

The ranges and movements of animals can also be inferred through identifying individuals from time-stamped camera trap photographs (Griffiths, 1993). For those species with stable social groups, this may provide estimates of populations. For example, for strongly territorial animals populations might be estimated by determining the size of territories and assuming continuous occupation throughout the area of interest. A similar measure is being used to estimate tiger numbers through site occupancy studies in 17 × 17 km grid squares, and assuming that the population size is related to the number of squares occupied (Sunarto, 2008).

Table 4.4: Peer-reviewed literature, primary scientific reports and theses, reporting on camera traps studies that individually identified animals. Numeric references refer to Appendix 4.

Species		**Number**	**Reference**
Common name	**Scientific name**		
Tiger	*Panthera tigris*	42	[38, 91, 108, 241, 260, 261, 279, 288, 306-308, 317-320, 323, 324, 330, 332, 333, 352, 389, 392, 393, 407, 408, 415, 460, 463, 464, 471, 511, 564, 598, 599, 630, 649, 699, 742, 748, 749, 756]
Jaguar	*Panthera onca*	23	[145, 155, 201, 262, 263, 402, 416-418, 448, 449, 472, 500-502, 527, 584, 606, 647, 648, 655, 739, 747]
Leopard	*Panthera pardus*	20	[33, 34, 109, 113, 147, 186, 220, 259, 267, 274, 347-349, 366, 441, 496, 540, 662, 672, 748]
Lynx	*Lynx lynx*	19	[39, 50, 90, 187, 374, 375, 431, 454, 467-469, 498, 610, 710, 777, 778, 780-782]
Ocelot	*Leopardus pardalis*	15	[145, 155, 157, 160-162, 254, 289, 402, 417-419, 636, 714, 715]
Puma	*Puma concolor*	15	[19, 42, 49, 115, 137, 224, 262, 263, 343, 402, 417, 472, 501, 549, 631]
Bobcat	*Lynx rufus*	9	[62, 137, 188, 265, 271, 272, 342, 380, 400]
Snow leopard	*Uncia uncia*	7	[291, 293-295, 313, 411, 767]
Cheetah	*Acinonyx jubatus*	5	[111, 185, 340, 341, 435]
White-tailed deer	*Odocoileus virginianus*	5	[139, 297, 363, 740, 745]
Black bear	*Ursus americanus*	4	[71, 72, 358, 506]
Tapir	*Tapirus sp.*	4	[212, 499, 519, 709]
Domestic cat	*Felis cattus*	3	[580, 581, 612]
Coyote	*Canis latrans*	2	[379, 626]
Jaguarundi	*Puma yagouaroundi*	2	[19, 138]
Andean bear	*Tremarctos ornatus*	1	[576]
Domestic dog	*Canis familiaris*	1	[668]
Maned wolf	*Crysocyon brachyurus*	1	[717]
Red fox	*Vulpes vulpes*	1	[613]
Spot-tailed quoll	*Dasyurus maculatus*	1	[118]

Indices

The number of photographs of a particular species, corrected for sampling effort, is typically reported in camera trap studies. This is often termed the *photographic rate*, *capture rate*, or *encounter rate*, and often reported as the number per 100 or per 1,000 trap-nights. These numbers are equivalent to uncorrected counts of animals (White, 2005). Presumably they are in some way related to the number of animals, but will be influenced by a whole range of factors such as weather, season, the placement, scent, sight and sound of cameras, and animal behaviour in relation to camera traps and flashes, amongst many other potential factors.

If an index is related in a known way to absolute abundance then in principle it can be corrected (Caughley, 1977, p. 49). The photographic rate for tigers was shown by Carbone et al. (2001) to correlate with capture-recapture abundance estimates, but Jenelle et al. (2002) argued that this was encouraging the use of uncorrected indices, long shown to be unwarranted and possibly misleading. The photographic rate was also shown by Augeri (2005b; 2006) to correlate with measures of abundance in tigers and therefore extended to estimate numbers of bears. Garshelis et al. (2006) argued that this was "tainting perfectly good estimates of occupancy" with unwarranted claims of real numbers. While Carbone et al. (2001; 2002) stated appropriate caveats, their paper is widely cited by those using photographic rate as a surrogate for density (e.g. Yasuda, 2004; Gómez et al., 2005; Pei et al., 2010).

Other estimation techniques

On the assumption that animals move randomly—like an *ideal gas*—through areas of habitat, in principle knowing the detection area of the camera, and the average movement speed of the animals, the number of photographs obtained can be scaled up to reflect the number of animals in the area sampled (Rowcliffe et al., 2008). The assumptions of the model may be partially upheld with, for example, grazing animals in relatively uniform habitat. The original authors showed good results on semi-captive ungulates (Rowcliffe et al., 2008) and a recent field test on forest ungulates has confirmed this as a reasonable technique (Rovero & Marshall, 2009). The method has also been tested with observational data on otters *Lutra lutra* (García et al., 2009), and a recent demonstration using camera trap video of 12 species to estimate movement rates (Kays et al., 2009). Further research on the validity of the assumptions, and tests with other species, may identify modifications or corrections that can be applied to a wider range of species.

An index of overdispersion has been used to help interpret camera trap photographs of jackals *Canis mesomelas* (Kauffman et al., 2007). While intuitively it is clear that animals will repeatedly visit the same camera trap, and also that one animal might trigger adjoining cameras, the overdispersion method provides a quantitative approach to estimate this bias. This method has promise for determining the appropriate spatial scale for analysis, and for assessing independence in site occupancy studies. It is also potentially useful for other sources of data such as sand-plots.

A modified distance sampling method could potentially be applied to camera trapping studies. This is analogous to the lure method of Buckland et al. (2006), using a camera trap to determine the detection. The average detection area of a lure is calibrated, using a representative sample of animals of known location, for example via radio-tracking. Once this detection area is known, then the number of detections divided by the area represents the simple density estimate.

Behaviour and ecology

A range of behavioural attributes has been investigated using camera traps (Table 4.5). Activity patterns are one of the most common behaviours identified, probably because data are automatically collected on the time that photographs are taken and analysis requires little additional effort. If several species are detected, temporal or spatial partitioning of the habitat can easily be analysed (e.g. Jácomo et al., 2004).

Table 4.5: Peer-reviewed literature, primary scientific reports and theses, with objectives to investigate animal behaviour using camera traps. Numeric references refer to Appendix 4.

Study reports on	Number	Reference
Daily activity patterns	79	[8, 20, 60, 71, 72, 94, 97, 101, 112-114, 137, 138, 142, 151, 153, 155, 156, 158-160, 166, 224, 230, 232, 234, 243, 263, 282, 283, 288, 298, 333, 348, 365, 377, 379, 384, 386, 387, 394, 402, 405, 416, 417, 420, 421, 437, 442, 450, 457, 461, 464, 472, 477, 485, 499, 503, 517, 518, 521, 532, 533, 539, 550, 575, 577, 603, 619, 620, 626, 644, 662, 690, 692, 705-707, 724]
Niche partitioning	18	[112, 114, 145, 156, 188, 263, 290, 298, 367, 384, 421, 450, 501, 575, 577, 586, 705, 748]
Predation of nests	43	[7, 16, 17, 57, 58, 78, 122, 143, 149, 175, 202, 207, 226, 278, 285, 287, 381, 385, 424, 425, 427, 429, 432, 510, 525, 543, 546-548, 556, 567, 568, 574, 596, 615, 617, 653, 654, 669, 679, 695, 725, 754]
Feeding young at nests	26	[16, 35, 55, 101, 131, 134, 151, 198, 244, 246-249, 257, 286, 303, 356, 357, 433, 475, 554, 555, 596, 665, 671, 695]
Fledging from nests	9	[246, 281, 286, 303, 553, 555, 596, 653, 665]
Denning behaviour	11	[4, 71, 72, 86, 88, 121, 253, 310, 550, 690, 692]
Seed consumption	15	[30, 43, 96, 116, 136, 205, 301, 354, 401, 457, 522, 523, 558, 684, 727]
Use of road crossings	11	[79, 120, 167, 196, 495, 520, 621, 628, 650, 723, 753]
Scavenging	7	[42, 60, 99, 127, 153, 154, 305]
Vaccine uptake	7	[64, 251, 270, 430, 670, 697, 765]
Disease transmission	5	[121, 305, 523, 643, 766]

Predation events, especially at nests of eggs or nestlings, have been widely observed using camera traps (Table 4.5). Scavenging by predators can easily be investigated (e.g. Cederholm et al., 1989; Boone et al., 2009), and artificial nests have been often used to monitor nest predation (e.g. Picman, 1987; Marchand et al., 2002; Posa et al., 2007). Nests are also often observed with video cameras or time-lapse photography; studies published since 1997 using these methods are not included in the database.

Foraging on fruit or seeds, especially by ground-dwelling mammals, has also been widely investigated with camera traps (Table 4.5). Studies on seed consumption have largely been species inventories (e.g. Miura et al., 1997), although several recent studies have investigated seed consumption in a more experimental and quantitative manner (e.g. Takeuchi & Nakashizuka, 2007; Prasad et al., 2010).

4.3.6 Assumptions and analyses

Almost every comparative study on camera trapping equipment has shown substantial differences in the detection and performance of different camera trap models (e.g. Lu et al., 2005; Clark & Orland, 2008; Kelly & Holub, 2008; Parker et al., 2008; Dixon et al., 2009). Many studies mix and match different camera trap models (49/271, 18%) and some 21% fail to report the type of camera trap used. While this is reasonable when the study is simply an inventory, it is important for some experimental designs that detection efficiency is comparable.

Many studies use either one or both of the major classes of triggering mechanism, but few have tested them side by side (but see Clark & Orland, 2008). Misfires and slowfires are especially related to the triggering mechanism: misfires are more common with active sensors, as debris or branches can interrupt the beam. Slowfires are more problematic with the passive sensors, due to delays in opening the camera shutter. Some studies have used both types of mechanism, but did not test the assumption that results would be constant (e.g. Tsukada et al., 2006; Soisalo & Cavalcanti, 2006).

Placement of cameras is often convenience sampling (Anderson, 2001), such as along or close to roads or tracks. They are also commonly placed at 'likely' locations, such as waterholes, mineral licks, game-trails or other locations where sign has been sighted (e.g. Balme et al., 2009). In some cases, such as species inventories, this is valid. But for other sampling designs, especially those seeking to determine indices or densities, these methods assume with little justification that camera trap placement is representative of the area of interest (Sanderson, 2007).

The challenges of low-density monitoring

Analytical methods for camera trap data are similar to those used in other survey methods. The quality of inference from camera trapping data has advanced greatly with increased use of statistical methods (Karanth et al., 2003). Quite often though, numbers are simply inadequate to draw any firm conclusions. Camera traps are commonly used to target rare, cryptic or wary animals; these animals are, by definition, present at low densities and hard to spot. A single photograph of such an animal over many thousands of trap-nights is not greatly informative, beyond simply confirming the species' presence (e.g. Aronsen, 2009). The species could be rare, wary, camera trap shy, or simply do not often use the habitat where cameras are placed. Site occupancy modelling is potentially a solution to help determine detection probabilities, but with few data, empirical methods will remain a challenge (Anderson, 2003).

4.3.7 The effects of flash

A recent study is potentially important in showing the effects of white-light flash on animals. Abelson (2009) estimated the effect of standard deployment of a Trailmaster® active IR camera trap with a white flash. He used a 'covert' Reconyx® camera, handled to leave minimal scent, and placed it in the field for eight weeks before deploying a Trailmaster® camera within the field of view of the Reconyx® camera. The encounter rate of deer and other species with the Reconyx® camera trap dropped by two-thirds, presumably indicating an aversive reaction to the white flash or the presence of the Trailmaster® equipment, and a subsequent avoidance of the area.

Specific aversive behaviour to white flashes has been reported in five studies, and speculated about in a further nine articles, but particularly commented upon in red foxes (Dixon et al., 2009) and especially kinkajous (Schipper, 2007). With the widespread concern about the intensity of spotlights on the eyes of nocturnal animals (Wilson, 1999; Wolf & Croft, 2008) it is strange that camera flashes, many times brighter, have not prompted the same concerns. It may be that these techniques are so much less invasive than many alternatives such as live trapping, that the small and presumably transitory impact of a flash is seen as necessary. Many camera traps now have IR flash, so these impacts may be reduced as technology improves.

It may be that behaviour or patterns of movement are affected by flash aversion, thus violating the assumptions of survey methods (Wegge et al., 2004). Earlier authors report animals becoming accustomed to cameras and flashes (Nesbit, 1926, p. 71), despite the "cannon-like report of the flash powder" (Chapman, 1927, p. 336) being audible over

3 miles (4.8 km) away (Shiras, 1936, p. 68). If a simple inventory is the objective, then aversion may not be a problem. However, for quantitative methods that rely on recapturing animals or seek unbiased understanding of movement patterns or other behaviour, this is a potential problem (Gibeau & McTavish, 2009).

Visibility of IR

At least one study has speculated on predators being able to see nests illuminated with IR light, potentially increasing the risks of predation (Brown et al., 1998). It is certainly the case that some animals can see light in the IR spectrum, and there may be individual differences (Newbold, 2007), but there is little empirical research on non-human animals (cf. Arrese et al., 2002; 2005). Nocturnal animals are possibly more suited to seeing higher (i.e. non-red) wavelengths, which are more prominent at lower light intensities (Autrum, 1968). Anecdotal observations are that animals are less affected by IR illumination than white light (Marks et al., 2003). It may be that some species can see the IR radiation, and have a greater aversion than others. Techniques that rely on comparisons between species might be biased by any such differences.

4.3.8 Data management

The large number of photographs produced by digital cameras has encouraged the development of specific methods and software for managing images. Even short studies can generate many tens of thousands of photographs. One PhD study, using 35 mm film cameras, analysed 10,804 photographs, only 107 of which were of the target animal (Augeri, 2005a). Chapters 5, 6 and 8 of the present thesis report on my analysis of 21,092 photographs taken over an 18 month period. A one month study of bait uptake in feral pigs *Sus scrofa* generated over 60,000 photographs (S. Lapidge, personal communication).

This volume of information poses a challenge to practitioners for viewing, managing and analysing the data. Existing computer software for photographic management will likely be widely used, as much of it is free or low cost. Flexible software that allows tagging and complex manipulation of photographs is preferable (e.g. Exifpro, Kowalski, 2009). Specialist software written for camera trap studies is also available (e.g. Camera Base, Tobler, 2007), and software is sometimes provided by camera trap manufacturers (e.g. MapView, Reconyx Inc., 2009).

Automated photographic analysis

Computer-aided matching can provide significant labour-saving for matching photographs of individual animals (Hiby & Lovell, 1990; Kelly, 2001). Techniques recently developed for pattern matching in whale sharks *Rhincodon typus* use algorithms based on star-pattern identification (Arzoumanian et al., 2005), a model that could be extended to other distinctive species (Speed et al., 2007). For example, recent research on tiger coat patterns has allowed automatic matching of photographs, and because the software places the photograph over a 3D framework, can also match tiger skins seized from the illegal trade with camera trap photographs of the wild animals (Hiby et al., 2009).

4.3.9 General guides for practical camera trapping

Several practical guides to camera traps now exist to pass on field experience. The review by Kays and Slauson (2008) is probably the most comprehensive, but the general documents of Nelson and Scroggie (2009), Brown and Gehrt (2009) and Jackson et al. (2005) are also of use. A recent book, aimed at hobbyists and hunters has some relevant advice (Scorzafava & Larsen, 2008), and a major scientific book is forthcoming (O'Connell et al., in press).

Some of the early ideas and expressions from the pioneers of camera trapping are still relevant and poignant:

> "If there be any sport in which the joys of anticipation are more prolonged, the pleasures of realization more enduring, than that of camera trapping in the Tropics, I have yet to find it! From the moment when, after consideration of all the possibilities, you select a place in which to set your trap until the developments of the dark room show you what you have, or have not, captured, imagination keeps pace with expectation. The result is often complete disappointment, but it may bring such elation that, so narrow is the boundary line between the manifestations of uncontrolled enthusiasm and dementia, it is safe to give full expression to your feelings only when you are alone!" (Chapman, 1927, p. 331).

4.4 Future trends and potential

The use of camera traps is likely to continue to increase, and it may become the dominant survey method within just a few years, especially for terrestrial mammals that are 'medium-sized' and larger. Reductions in price, advances in technology, new analytical methods, and a wider appreciation of the benefits, are all likely to see the camera trap supplant many types of standard methods, especially similar indexing methods such as footprint or scent stations. In addition, international collaboration in data availability might lead to a revolution in ecological survey data, as has been seen, for example, with genetic database projects (Benson et al., 2008).

4.4.1 Technology

Camera traps themselves are likely to continue to become smaller, easier to run, cheaper to purchase and more widely available. Technological innovations, such as remote access to photographs through telecommunications networks (e.g. Yasuda & Kawakami, 2002), and the enhancement of those networks will likely have substantial implications to real-time accessibility of data (for a related example, see real-time remote acoustic monitoring of koalas by Planitz et al., 2009).

The specificity of IR LEDs should improve to reduce leakage of light into the visible wavelengths, while conserving power. Current technology reduces dramatically, but cannot completely eliminate, all light emission in the human-visible spectrum (Anon., 2009). Further development may allow even less invasive, and potentially entirely covert, monitoring of animal presence, movements and behaviours.

Existing camera traps suffer from high rates of failure (many studies report on this, e.g. Rice, 1995; Vine et al., 2009), and inter and intra-unit variability (Swann et al., 2004). They also lack compensation mechanisms for environmental factors which, along with variation in camera trap placement, will violate assumptions of equal detection in any controlled index or capture-recapture study (e.g. Larrucea et al., 2007; Waldstein et al., 2009). Such factors may be improved as manufacturers respond to increasing demand from field biologists. Battery life is likely to continue to increase, in line with advances in general battery technology. Cameras using current technology can last up to three months between battery changes, and solar panels can extend battery life indefinitely.

Laboratory tests of equipment are rare (but see Swann et al., 2004), and most evaluation of equipment by scientists is in the field (e.g. Kelly & Holub, 2008; Parker et al., 2008; Dixon et al., 2009). At least one amateur group provides detailed testing of camera traps (www.chasingame.com), and this controlled approach deserves increasing scientific attention.

Reliably taking identifiable photographs of smaller animals is a recurring weakness of the current technology (Torre et al., 2005), although cameras are being used increasingly to study 'small carnivores' and other smaller mammals (Hayes et al., 2006; Chen et al., 2009). Camera traps have been modified to focus and trigger on much closer and smaller objects such as invertebrates (Carthew, 1993). This could be of use, for example, in studies of pollination or insect ecology (e.g. Law & Lean, 1999).

4.4.2 Novel camera trap placement

Innovative placement of camera traps seems likely to be more widely explored to provide information about a greater number of species. Placement of camera traps in trees is one clear possibility (Schipper, 2007; Oliveira-Santos et al., 2008), and with very many species that are arboreal and difficult to study, this is likely to provide new insights. Other unusual placements, such as in subterranean environments (Griffiths, 2008), or floating at sea (Fjalling et al., 2007), should also provide information on animals in environments where conventional methods are difficult or impossible to implement.

4.4.3 Standardisation in methodology

Standard methodologies are likely to be implemented increasingly by national and local government agencies charged with managing wildlife (e.g. Nelson, 2007), especially in developed countries where equipment is relatively more affordable and labour costs for traditional field surveys are higher (Matthews et al., 2007). Standardised methods are also likely to be adopted within NGOs and encouraged for use in developing countries where NGOs provide financial support and technical advice (Martins et al., 2007). For example the Conservation International 'TEAM' project has produced clear guidelines for standard methods for mammal survey, predominantly using camera traps (TEAM Network, 2008). Further standards will be welcome, and should enable comparisons of results from different areas and periods.

4.4.4 Standardisation of data storage

The standardisation of image metadata, storage and distribution is surely the key area that would allow camera trapping to become a dominant survey method worldwide.

Museum-like historical data

At present, museum specimens provide historical data about the presence of species at a particular location and time, and fill an important role in ecology and conservation (Pyke & Ehrlich, 2010). Camera trapping information could equally fill this role, as camera trap photographs are, in principle, the same type of data: a lasting record of the presence of species. Camera trap data also have the clear advantages of representing non-destructive sampling, and in recent times, the straightforward distribution of digital photographs through the internet.

Two articles discuss standardisation in storing metadata on photographs, but only at a local or national level (Kawanishi, 2001; Botello et al., 2007). If these data were based on international museum standards (e.g. Graham et al., 2004) then the potential for camera trap data to contribute to the body of existing knowledge is enormous.

An online repository of images

A central online repository of images and metadata is another clear opportunity. Images could be uploaded by practitioners, and this data-bank would become a virtual museum storehouse of data from camera traps, including all 'non-target' data, which are currently wasted. Data sharing is of obvious importance to current and future biologists (Arzberger et al., 2004), and should conform to existing Biodiversity Information Standards (TDWG) (Edwards, 2004). In addition, this would likely be of interest to the public, and would be a positive way for scientists to transparently share data, raise awareness and showcase their craft. Issues of confidentiality or putting animals at hunting risk could be dealt with in accordance with existing Global Biodiversity Information Facility (GBIF) guidelines (Chapman, 2007).

4.5 Conclusions

The use of camera traps has increased dramatically in recent years, and will continue to expand. Analytical methodologies are developing rapidly, and while study objectives and situations vary, there is very wide agreement on the major advantages of using remotely deployed camera traps for observing animals.

Standardisation of field protocols across programs will allow more valid comparisons to be drawn between different areas and times. Improvements in the understanding and testing of camera technology should also help to standardise equipment for more comparable results. Photographic rate will no doubt continue to be widely used by practitioners and managers, despite potential theoretical concerns. Such indices are likely to continue to be used as surrogate measures by routine monitoring programs worldwide. Calibration of indices may be used more widely to improve their validity. One way to account for imperfect detection is via site occupancy studies, and these are slowly becoming more widespread in the literature. Camera traps are an obvious way to determine the presence of an animal, with the added benefit of determining the pattern of detections *post hoc*.

The public availability of the database compiled here will ensure easy access to the complete catalogue of all camera trapping papers published up to the end of 2009. It will make literature reviews substantially easier and should assist time-poor practitioners to survey relevant information in the field before starting their study. It allows straightforward systematic review relating to specific questions on equipment, methodology, locations or any number of other possibilities. It should also allow meta-analysis of relevant results and will hopefully lead to advances in techniques and inferences. It aims to ensure a solid foundation of knowledge for the future of camera trapping.

This review shows clearly that camera traps have great potential for monitoring species populations, including the effects of invasive predator control programs on both predators and their prey. In Chapter 5 I build on some of the findings presented above and provide an example that confirms the validity of existing monitoring methods in Southern Ark using cameras as an adjunct tool. Chapter 6 shows an example of estimating relative population size with camera traps using an index of activity, and also the application of site occupancy models to account for variation in detectability. In Chapter 8, I directly compare two models of camera trap with three conventional survey techniques for monitoring medium-sized mammals.