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Quo vadis camera trap research? A 50-year review of camera trap research goals and outcomes

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Summary

Recent explosion of camera trapping (CT) studies represents a great experiment and challenge in modern wildlife survey methodology. CT has successfully complemented and sometimes replaced various survey methods such as line transects, direct observations, identification of paths and feces, vocal identification, trapping and interviews with the local communities. The goal of this review is to evaluate different applications and outcomes of research that have used camera traps (CT) during the last few decades, at the global scale. Three historical periods are covered: 1956-1997 (with existing review), 1998-2008 and 2009-2016 (until July 2016). This review also documents the advantages and disadvantages of CT use over time, without focusing on data analysis, and some insights about the future of CT studies. The objectives of CT studies were classified into two categories (1) *science*, which included studies on population parameters (distribution, density, presence, occupancy and abundance), methodology, forest ecology, behavior and activity patterns, and (2) *conservation*, including subjects such as management, human conflicts and human disturbance, elusive and endangered species, habitat fragmentation, logging, hunting, inventory and methodology. Results revealed some gradual changes in CTs research goals and outcomes that vary geographically and includes different animal groups. Number of CT studies has increased abruptly in the last two decades and this trend persists. During the three periods examined CT studies with science application were more common than those with conservation focus: 1956-1997 – 108 publication in total (science/conservation=107/1); 1998-2008 – 156 total (science/conservation=124/34); 2009-2016 – 840 total (science/conservation=704/136). Leading scientific objectives in CT studies included population parameters, behavior and activity patterns, methodology and forest ecology, while conservation studies were focused on management, conflicts with human and human disturbance, fragmentation of habitat, logging and management. Currently the majority of CT studies are conducted in Asia and South and Central America, mostly in Brazil, Mexico, and India. Since the 90s mammals have dominated in 90% CT studies, with special attention paid to big carnivores as they are umbrella species and they attract public attention that is necessary for conservation action. Studies with multiple objectives and multiple taxa became more common in the last decades as complexity of research has increased to address current conservation problems.

Contents

Introduction

"Live and let live" was a motto of Barro Colorado Reserve, an artificially created island in Panama, where Frank M. Chapman (1927) for the first time in a purely scientific context, photographically documented the presence of species. The scientific need for "census of living, not a record of dead" and the simple question "how can we do it?" is standing at the base of camera trapping history.

Back in 1863, Professor G. Fritsch, a German explorer in South Africa, was the first to attempt to photograph wild animals with heavy, bulky equipment with slow film and lenses (O'Connell et al. 2010). Then, in the 1890s, George Shiras developed a method based on a trip wire and a flash system to induce wild animals to photograph themselves. His "flashlight" photographs won a gold medal at the 1900 Paris World Exhibition. Shiras recorded numerous wildlife species with trip wires and sometimes bait, including American mink (*Mustela vison)*, raccoons (*Procyon lotor)*, white-tailed deer (*Odocoileus virginianus)*, North American porcupines (*Erithizon dorsatum)*, and muskrats (*Ondatra zibethicus).* Between 1903 and 1904, in Equatorial East Africa*,* Schillings (1906) took spectacular photographs of many wildlife species including African lions (*Panthera leo*), leopards (*Panthera pardus)*, spotted hyenas (*Crocuta crocuta)*, and jackals (*Canis* sp.).

Decades later, cameras do not blind and deafen animals with an explosion of a magnesium powder camera flash, they are digital and autonomous, and have become a very powerful tool for ecologists. Camera trapping of wildlife in the last 30 years, has become easily available and much more affordable (Rowcliffe et al. 2008)Applications range from collecting species inventories to studying activity patterns (van Schaik and Griffiths 1996, Gomez et al. 2005), estimating animal density (Mace et al. 1994, Karanth and Nichols 1998, Silver et al. 2004a), relative abundance estimation (Carbone et al. 2001), estimating occupancy (MacKenzie 2006, Beaudrot et al. 2016), community ecology (Tobler et al. 2008), population dynamics (Karanth et al. 2006) and forest ecology (Kitamura et al. 2006), discovery of new species (Rovero et al. 2008) and conservation assessment (Kinnaird et al. 2003, Linkie et al. 2006).

Camera trap surveys have successfully complemented and sometimes replaced various survey methods such as line transects, direct observations, identification of paths and feces, vocal identification, trapping and interviews with the local community (Lyra-Jorge et al. 2008). Use of this equipment for big mammals' inventory in Emas National Park in Brazil was the most appropriate and precise when compared with line transects and track counts (Silveira et al. 2003a). Compared to counts obtained from helicopter surveys to estimate population of white-tailed deer in Texas, cameras performed equally or better (Koerth et al. 1997). The use of camera traps in ecological field studies offers a reliable, accurate and cost-effective strategy when compared with most traditional methods, and might have a major influence in future directions of research (Kays et al 2009).

The goal of this review is to evaluate different applications and outcomes of research that have used camera traps (CT) during the last decades at the global scale. Starting in the late 50's and throughout July 2016, I analyzed the application of CT in science and conservation, and evaluated future perspectives of its development and utility for research. This review also documents the advantages and disadvantages of CT use over time, without focusing on data analysis — which has been described elsewhere (Rowcliffe et al. 2008, Rowcliffe et al. 2013, Meek et al. 2014, Rowcliffe et al. 2014, Burton et al. 2015, Meek et al. 2015). It is important to point out that the ultimate objective of CT studies is aimed at science or conservation and management (Nichols et al., 2011). Therefore, individual animal photographs, detection history data and parameters generated from detection histories is only a step for a better understanding of how ecological system works (science) or how to inform conservation and management action. Following this point of view, I have classified the goals of CT research as either science or conservation, acknowledging some overlap. It is very important to distinguish between studies that are advancing science versus, informing management (O'Connell et al. 2010). Simplifying, the primary utility of data from CT studies for science will provide the observations that are used to discriminate among competing hypotheses (Nichols et al. 2011). While to implement appropriate management and conservation strategies it is critical to understand how animal populations respond to threats, and to document the functioning of ecosystems and degree of intra-community interactions in populations and communities (Trolliet et al. 2014). In this review, I paid special attention to studies focused on conservation and management that use CT to estimate parameters of populations (e.g. relative abundance, density, occupancy, distribution) or communities (e.g. inventory, richness, diversity) to address most urgent current ecological problem as biodiversity loss, habitat fragmentation, human impact or invasive species.

Methods

This work is based on an existing historical review and is complemented with new exhaustive reviews covering the last two decades. Thus, three historical periods are covered: late 50's until 90's based on review of Cutler and Swann (1999), 1998-2008 and 2009-2016 (until July 2016), both included in this study.

Cutler and Swan (1999) limited the scope of their review to primary, peer-reviewed literature that used remote photography in wildlife ecology. They conducted a formal literature search in computerized BIOSIS database using the keywords "photography" and "camera" with "wildlife", "animals", "birds", "mammals", "reptiles", and "amphibians" resulting in 107 papers which were reviewed and categorized by primary objective, equipment type and target taxa studied. Additionally, I have reviewed these studies to extract countries where fieldwork was carried out, which permitted a creation of CT studies map over the world.

For the two following periods 1997-2008 and 2009-2016 a formal literature search of peer-reviewed literature was carried out in August 2016. I systematically searched within the Web of Science™ database for 'camera trap' within paper title, abstract and keywords. Search with the same set of keywords like Cutler and Swan (1999) used resulted in large number of publication (~60000) as "photography" is used in multiple studies and search of all keyword with connector "AND" and "OR" gave limited number of publication in comparison with single "camera trap". Also during the last 20 years "camera trap" appears as a consistent and well described term in itself, while in previous periods different longer and more descriptive terms were used, such as: "remote photography" or "videophotography of wild animals in the absence of the researcher". An unfiltered first search resulted in 466 (1998-2008) and 1434 (2009-2016) publications. In order to narrow down to studies on wildlife I applied a filter that excluded publication that are not biological in scope, and are instead placed in categories like biotechnology, telecommunication, microbiology, physics, and astronomy. I discarded studies pertaining to non-terrestrial animal classes, such as fish studies. I included technical or impact papers, which did not refer explicitly to a particular species but which did include findings of implicit relevance to wildlife research. Not all published journals are listed in the Web of Science™ and not all camera trap studies have been published; however, those identified were assumed to be representative of the most scientifically valid projects. Based on abstract I manually excluded studies that did not collect CT data to make inferences on an animal occurrence, abundance, behavior or inventory of species or conservation. In particular cases all content of paper was revised to confirm its utility for the review or when abstract did not provide sufficient information about the study. This process resulted in a sample of 156 (1998-2008) and 840 (2009-2016) studies. From each paper, the following variables were obtained: the objective of the research, ecological and conservation problem addressed, taxonomic group(s) sampled, and country where the research was carried out. During the revision process I decided to divide studies on those focused on explicit scientific objectives and those with an explicit conservation question. Undoubtedly, separation of science and conservation is not an easy task, as all conservation studies include scientific objectives, such as population parameters estimation, and base on these results to propose indicators to deal with particular conservation problem.

Thus, the objectives are organized into two categories with following range of objectives (1) science: population parameters (distribution, density, presence, occupancy and abundance), review and methodology, forest ecology, behavior and activity patterns (2) conservation: management, human conflicts and human disturbance, elusive and endangered species, fragmentation of habitat, logging, hunting, inventory and methodology. For studies with multiple objectives, each objective was extracted and assigned to the corresponding category, thus the total counts are higher than the number of publications per period itself. Nevertheless, the science and conservation categories were assigned for each individual paper. Considering the high importance of conservation research to cope with biodiversity threats, the description of CT studies in the last decade is dedicated to this category.

Results

From 1956 to 1997

Remote photography was used primarily to study avian nest predation, feeding ecology, and nesting behavior; additional applications included determining activity patterns, presence-absence monitoring, and estimating population parameters (Cutler and Swann, 1999). Authors define remote photography as the photography or videophotography of wild animals in the absence of the researcher, including time-lapse or animal-triggered system, both light triggered and mechanical. It appeared in the wildlife literature in the 1950s, 1960s and 1970s, with constantly changing equipment. Gysel and Davis (1956) described a simple system to photograph nest predation in Michigan. Then, Pearson (1960) designed a photographic system to monitor the activity patterns of small mammals in runways in California, identifying 26 species of mammals, birds, and lizards in his photographs. Osterberg (1962) adjusted this methodology for avian research. Then, Temple (1972) developed a time-lapse photographic system to study nesting behavior of peregrine falcons (*Falco peregrinus).*

The "modern" CT that we currently use, appeared on the market at the end of 80s, when Savidge and Seibert (1988) proposed a mechanism of an infrared transmitter that can trigger the automatic system of film cameras to take a picture as soon as the beam was disrupted by animal movement. They used this methodology to study nest predation. Seydack (1984) detected 14 species and recognized individuals of bushbuck (*Tragelaphus scriptus),* leopards and honey badgers (*Mellivora capensis*). Griffiths and Van Schaik (1993) used CT to evaluate the change of activity patterns and avoidance of areas used by humans by a variety of larger mammals in Sumatra. Mace et al. (1994) devised a remote photographic system for use in a systematic survey of grizzly bears in Montana.

Cutler and Swann (1999) noted that almost 68% of the studies focused on three main objectives with similar frequency: nest predation, feeding ecology and nesting behavior categorized as behavior and activity patterns (Figure 1.). The remaining studies were dedicated to methodology (19%) and two other minor population parameters topics (13%). Conservation CT studies were represented by only one publication (Foster and Humphrey, 1995). There were twice as many studies focused on birds than on mammals, while a minority of cases included multiple taxa or herpetofauna (Figure 2.). The CT methodology was predominantly applied in North America (USA and Canada accounted for 74%), with similar number of cases from Europe, Australia and the rest of the world (Figure 3 and 4) (see Cutler and Swann, 1999 for more details).

Advantage and disadvantage in CT usage: 1956 - 1997

Advantage

Following Cuter and Swann (1999), remote photography has advantages over traditional research methods for certain applications in wildlife research like:

1) Predator identification: such as anecdotal sightings, predator trapping, examining nest and eggshell remnants, identifying animal sign (e.g., track, scat, or hair analyses; identification of bill or tooth patterns on clay eggs), or analyzing stomach contents of predators.
2) Feeding ecology: direct observation, fecal analysis, pellet analysis, stomach analysis, ligatures, emetics, or using artificial nestlings.

3) Estimation of population parameters: observation or trapping (e.g., mark-recapture methods with physical recapture or recapture via radiotelemetry), drive counts, and track counts (e.g., natural tracks or track plates). Additionally, remote photography is ideal to identify different species that had similar tracks and could be used year-round versus the snow-track methods.

Firstly, remote photography can be less invasive, faster, and cheaper to perform than long-term direct observation of animals. Secondly, remote photography is ideal to record data at night and in inclement weather, in inaccessible locations such as dense forest and nest cavities, or in rugged terrain that is difficult to access (Capen 1978, Mace et al. 1994) Additionally, using remote photography may mitigate problems associated with observer bias because photographs can be reviewed by others and preserved for future analysis. A crucial advantage of using remote photography is the amount of time and money saved by forgoing labor-intensive direct observation.

Disadvantage

The most important disadvantage for that period seemed to be chronic mechanical problems. Equipment may be prone to mechanical and battery failures, programming errors by researchers, and various other problems. All camera systems require regular maintenance and some technical expertise. Many papers in the review of Cuter and Swan (1999) stated a concern that using remote photography equipment affects animal behavior. Human activity, scent, and a presence of remote photography equipment could attract or repel animals, disrupt nesting by potential nest abandonment, or influence activity patterns of predators. However, such effects, if they exist, are rarely evaluated and authors suggested a great need for studies which compare data obtain with remote photography to other technique.

Researchers should probably accept some equipment effect and attempt to minimize both the time spent at remote photography stations and modifications to the surrounding vegetation. A disadvantage was the use of bait to attract animals because individuals reacted differentially to bait. Finally, a very important disadvantage is the impracticality and expense of using a large number of CT typically needed for the study.

Importantly, authors of the review pointed out that, although photographs provide unmistakable evidence of an event of interest (e.g., an animal's presence at a given place and time), it is critical to recognize the limitations of such data. A number of photographs of a species is rarely an index of abundance, as it is usually not possible to determine whether multiple photographs represent repeated events from one individual or single events from multiple individuals. Animals must be marked or individuals easily distinguishable for information of abundance. Studies that compare number of photographs among species or locations make the implicit assumption that detectability is equal for all individuals, species, or locations, however small animals may not be detected at a photo station as freely as large animals.

Figure 1. Number of CT publication (A) and objective of CT studies (B and C) corresponding to "science" and "conservation" categories during three periods: 1956-1997 (adapted from Cutler and Swann, 1999), 1998-2008 and 2009-2016. Data was taken from a sample: (A) 1103 publication (B) 176 objectives (C) 1126 objectives.

“Big cat” era: 1998-2008

Undoubtedly, the first period of CT research above showed multiple benefits of this technique, including a possibility to observe cryptic or elusive animals living in in-accessible habitats such as dense tropical forests (Trolliet et al. 2014). The use of camera traps has been revolutionary for studying the presence and the behavior of carnivores, due to their solitary nature which results in difficult direct observation. Karanth (1995) in the 1990s initiated a series of studies using CT for the purpose of large mammal conservation. His group focused on the tiger (*Panthera tigris*) with the initial aim of estimating its home range span and population size. This species was designated as endangered and furthermore since 1986 elected one of few “flagship” species listed on the IUCN red-list (Trolliet et al. 2014).

Big cats are considered umbrella species in their corresponding geographic region, therefore conservation effort paid to these species is expected to have a positive effect at community level (Garcia-Rangel and Pettorelli, 2012). Hence, more than one-third of camera trap research from late 90s and the beginning of 2000 were dedicated to big cats and felids, an evident change from the previous period. Estimation of density was the most common type of study (18, Table 1), followed by presence (13) and abundance (11), which are all population parameters. “Big cat era” was particularly marked in Asia with 24 published studies. Density estimation based on individual identification of tigers (*Panthera tigris*) and other big cats was initiated by Karanth (1995) under a formal capture–recapture (CR) modeling approach. His research group’s work was extended to several sites across India to estimate tiger densities (Karanth and Nichols 1998, Carbone et al. 2001, Karanth et al. 2004, Karanth et al. 2006). Similar analyses were applied to other felids in Asia, such as tigers in Malaysia and Indonesia (Azlan and Lading 2006, Azlan and Sharma 2006, Linkie et al. 2006, Linkie et al. 2008) and snow leopards (*Panthera unica*) in China (Jackson et al. 2006, McCarthy et al. 2008, Xu et al. 2008). Long-term monitoring of these populations allowed the authors to estimate survival, recruitment, temporary emigration, transience, and rates of population change in a tiger population in Nagarahole (Karanth et al. 2006).

In South and Central America, 18 studies were conducted, among them 9 on jaguar (*Panthera onca*) (Silver et al. 2004a, Soisalo and Cavalcanti 2006) and 9 on ocelot (*Leopardus pardialis*) (Trolle and Kéry 2003, Di Bitetti et al. 2006, Dillon and Kelly 2007) using also capture-recapture modeling. Puma (*Puma concolor*) and bobcat (*Lynx rufus*) captured researchers' attention in North America (Bauer et al. 2005, Heilbrun et al. 2006).

Table 1. Different study objectives related with felids across the world in 1998-2008. Data was taken from a sample of 54 objectives.

Principal objective	Africa	Asia	Europe	North America	South and Central America	sum
abundance		7			4	**11**
density		6		3	9	**18**
distribution		2	1		1	**4**
habitat use		1				**1**
inventory		1				**1**
predation risk				1		**1**
presence		5	1	3	4	**13**
review		1		1		**2**
richness		1				**1**
scavenging				1		**1**
scent-marking	1					**1**
	1	**24**	**2**	**9**	**18**	**54**

Throughout the 1990s, camera trapping was being used in an increasing variety of studies (Figure 1.). The 156 CT studies that were reviewed were published in 50 journals and at an increasing rate over the 10-year period (Figure 5.). Almost half of the studies (45%) were focused on population parameters, followed by behavior and activity patterns studies (e.g. nest predation, nest defense or habitat use - 20%) and forest ecology (seed dispersal - 6%). About 10% of the studies were dedicated to reviewing and comparing methodology or proposing new ones. Conservation topics like habitat fragmentation, hunting, occurrence of rare species, endangered or new species, monitoring, management or fire use, represent 21% of studies.

During this period mammals were the main target of camera trap research (90%), while birds studies represented only small fraction (3,3%) of all studies. There are only 1% of reptile studies with CT (Figure 2.). O'Brien and Kinnaird (2008) consider that camera trapping may be most appropriate for the study of large, ground-dwelling birds, such as cracids and pheasants, but they remain underrepresented in the reviewed studies. Research involving plant-animal interactions (i.e. seed dispersal studies), increased in frequency and provided useful information about the biology of different plant species as well (Main and Richardson 2002, Kitamura et al. 2004, Kitamura et al. 2006). One-third of the CT studies from this period were carried out in Asia, followed by South and Central America (28%) and North America (23%) (Figure 3 and 4), marking a significant change with the previous period, when the vast majority of studies were performed in North America.

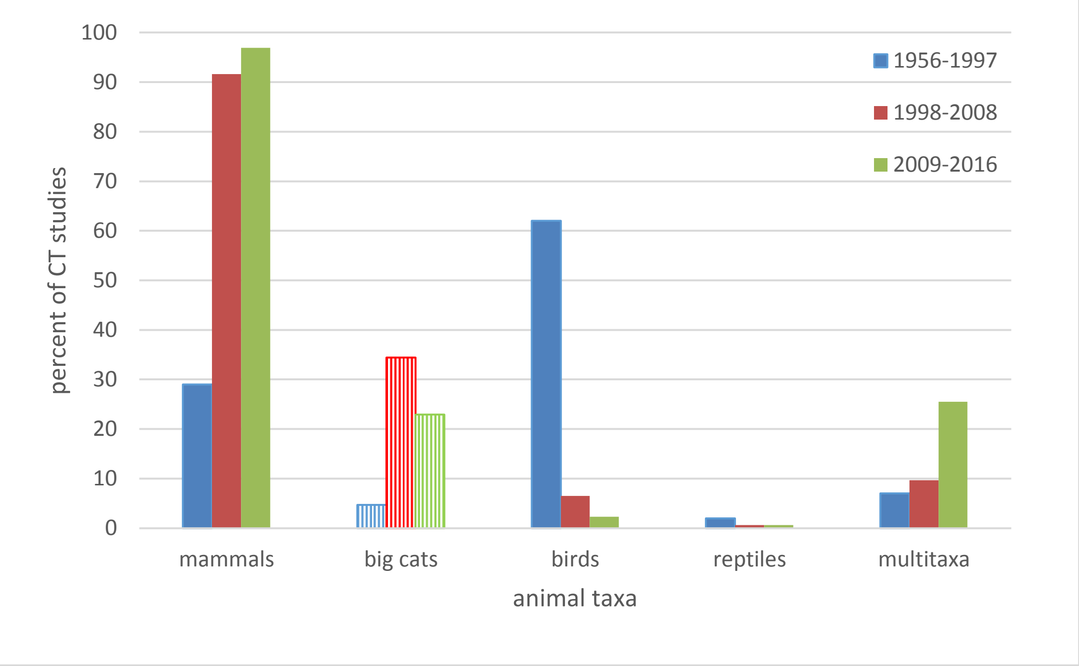

Figure 2.Variety of animal taxa present in CT studies during three periods: 1956-1997 (adapted from Cutler and Swann, 1999), 1998-2008 and 2009-2016. Data was taken from a sample of 940 publications.

Science approach

Practical and theoretical aspect of density and abundance estimation have been extensively covered in numerous studies (Karanth and Nichols 1998, Trolle and Kéry 2003, O'Brien et al. 2003, Silver et al. 2004b, Jackson et al. 2006, Soisalo and Cavalcanti 2006, Rowcliffe et al. 2008). Hence, this review focuses on different objectives of scientific research with CT.

The study of distribution and niche separation is the basis of ecological knowledge of many species: From relatively well known species like the lynx (*Lynx lynx*) in Switzerland's Alps (Capt 2007), to the preliminary investigation of the presence and distribution of small carnivores in the Empty Quarter of Saudi Arabia (Wacher and Attum 2005). For example, the presence of large carnivores might be limited by the productivity of the environment and the availability of prey. Tilson et al. (2004) surveyed an area of southern China looking for the south China tiger (*P. t. amoyensis),* and found no evidence of the tiger's presence. Maffei et al. (2004) reported an effort to trap jaguars (*Panthera onca*) on CT in the dry forests of the Kaa-Iya del Gran Chaco National Park in Bolivia and estimated a population of over 1000 adult and juvenile jaguars, the largest single population of jaguar reported anywhere. In a forest reserve on Malaysian Borneo, Wong et al. (2005) used remote photography to monitor the physical condition, and document the starvation of radiocollared sun bears and bearded pigs (*Sus barbatus*) due to prolonged scarcity of fruit during an intermast interval in the study area. An example of niche separation was studied in central Brazil where the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) differ in diet, habitat and activity patterns (Jacomo et al. 2004). Also, differential habitat use of two sympatric brocket deer species (*Mazama americana* and *M. gouazoubira*) in a seasonal Chiquitano forest of Bolivia were evaluated by comparing use of habitat and activity patterns estimated from CT data (Rivero et al. 2005).

CT was also increasingly being used to study plant-animal interactions, including seed dispersal and predation (Kitamura et al. 2004), grouped under forest ecology (4%). Use of CT allows the identification of diurnal, nocturnal, and elusive species that would not be possible to detect with for example, direct observation (Trolliet et al. 2014). Work in Thailand indicated that one-to-one relationships between frugivores and plants were very unlikely, but large-seeded plants depended on few large frugivores, resulting in restricted disperser assemblages (Kitamura et al. 2004). In eastern Peru, Beck and Terborgh (2002) studied seed predation on palm *Astrocaryum murumuru* var. *macrocalyx* seeds comparing solitary trees and dense groves; with CT they recognized several unexpected seed predators. Using CT, Babweteera et al. (2007) examined the juvenile spatial distribution of *Balanites wilsoniana*, and confirmed that elephants were the only frugivores feeding on and thus dispersing these seeds.

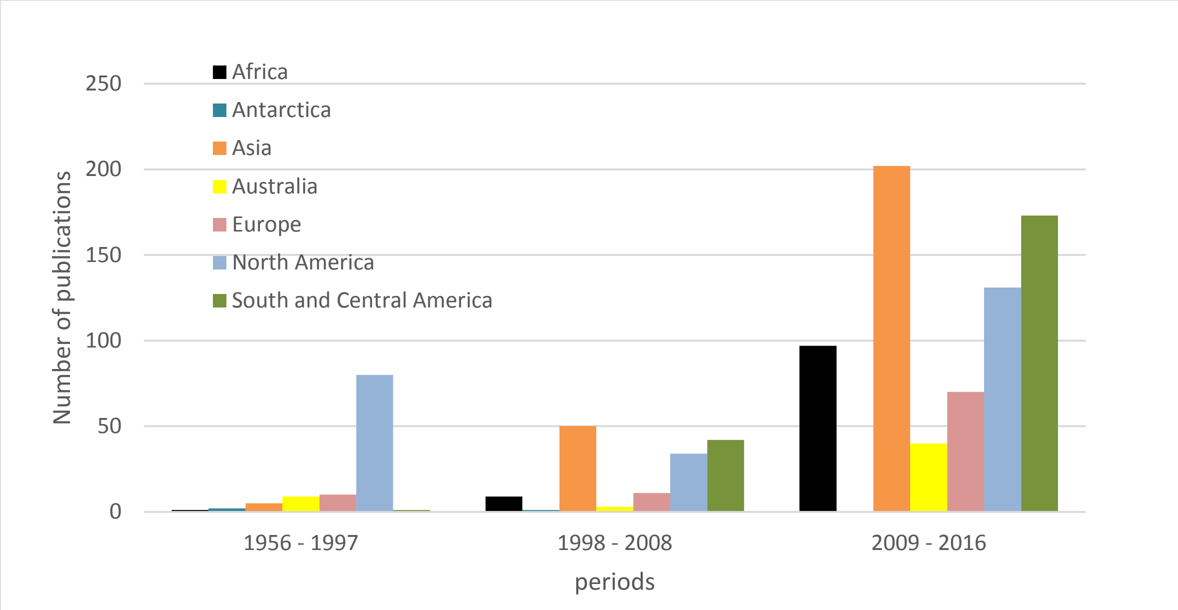

Figure 3. Number of CT studies among continents for three periods: 1956-1997, 1998-2008 and 2009-2016. Data was taken from a sample of 971 publications.

Conservation approach

Crucial topics of wildlife conservation have been researched with CT, and the current trend is to combine various objectives to answer bigger, ecological questions (Trolliet et al. 2014). Leading conservation application of CT studies include fragmentation of habitat, conservation management and monitoring of threatened and elusive species. Therefore, currently the large part of studies using CT struggle with the estimation of population density or basically with the presence of species in given areas. Management CT studies include topics like: recovery strategies for species, fire management, removal of pests and vaccine control.

The increasing problem of hunting was evaluated by Rao et al. (2005) in National Park in Myanmar, where they measured the effect of hunting on the distribution and relative abundance of wildlife. In Sumatra, O'Brien et al. (2003) studied the relationship between human density, habitat loss, abundance patterns and illegal hunting of prey and tigers.

Another current, hot topic is wildlife response to habitat fragmentation. In a highly fragmented, Amazonian forest landscape Michalski and Peres (2007) studied the correlation between forest-patch metrics and forest disturbance with estimated richness and abundance of medium- to large-bodied mammals. Results showed that 90% of the variation in species richness can by explain by changes in the forest fragment size. Lomolino and Perault (2001) expanded the island biogeography paradigm to test whether mammalian communities of the heavily, anthropogenically fragmented temperate rainforests of the Olympic Peninsula were influenced by local environmental conditions, biogeographic factors (fragment area and isolation) and characteristics of the surrounding landscape.

New species were also registered by camera traps, such as in the case of giant sengi or elephant-shrew (genus Rhynchocyon) in Udzungwa Mountains of Tanzania (Rovero et al. 2008). However, a particularly important, valuable and recent use of CT is the documentation of the presence of rare, elusive or presumed-extinct animals. A CT study recorded the presence of the endangered asian tapir (*T. indicus*) in a national park in Sumatra, where park rangers had never seen this animals before (Holden et al. 2003). With CT, Gonzalez-Esteban et al. (2004) evaluated the distribution of the European mink (*Mustela lutreola*) in northern Spain, and found them more effective than livetrapping. A range expansion of the elusive and endemic Sulawesi palm civet (*Macrogalidia musschenbroekii*) was documented by Lee et al. (2003). Effect of fire management and prescribed burning of forests on wildlife was also evaluated by CT. Results obtained by Main and Richardson (2002) in southwest Florida indicated that wildlife did not avoid pine flatwoods habitat at up to 30-month post-fire recovery.

Innovative uses of CT continued to be reported. Hegglin et al. (2004) monitored the uptake of bait mixed with a rabies vaccine by red foxes (*Vulpes vulpes*) in Zurich, Switzerland. These data were useful to design bait stations that increased vaccination efficiency and reduced loss of such bait to different species. Stoats (*Mustela erminea*) are an important predator of many forest bird species in New Zealand, and the most effective – although controversial – control method seems to be the delivery of poison in eggs (Dilks and Lawrence 2000).

Current research: 2009-2016

The 840 CT reviewed studies were published in 158 journals and at an increasing rate over the 8-year period (Figure 5.). Almost half of all CT studies from this period were dedicated to population parameters (44%), followed by behavior and activity patterns studies (28%, e.g. diet, mineral licks use, nest predation, scavenging, foraging, niche and habitat use). Conservation (e.g. hunting, green passages, habitat fragmentation, elusive and endangered species, logging and management) and methodology topics, both represented for 14% of CT studies each (Figure 1 C.). Roughly half of the studies (43%) used CT data to address multiple analytical objectives (e.g. presence–absence and behavior) (Figure 5.). The vast majority of studies reviewed are focused on mammal species (95%), but birds were also represented (3%) and a few studies included reptiles (0.9%) and amphibians (0.3%) (Figure 2.). Mammalian carnivores were the most frequently targeted group (77%) – particularly large felids (18%) – followed by ungulates (19%) and primates (4%). Nearly one-quarter of studies focused on more than one species (24%), with species traits often varying considerably within multispecies studies (Figure 2.). Geographically, CT studies were reported from 60 countries and were most common in the USA (11.9%), Brazil (10%), Mexico (6%), India (6%) and Australia (5%) (Figure 3 and 4). Continental distribution of CT studies in this period became more uniform and the majority of studies took place in Asia (28%) and the Americas (South and Central 24%, North 18%), with fewer from Africa (14%), Europe (10%) and Australia (6%).

Conservation approach

CT studies that were dedicated to conservation and management became more numerous than in previous periods (Figure 1 C.). Thus, for this period, conservation application are discussed in more detail. Studies including management application were dominant (25% of all conservation studies) and dealt with issues like: biological control, oil palm plantation, disease transmission, invasive species, pest removal, reintroduction of species, fire management, hybridization of species, urban zone or tourism. Following application of CT studies for conservation were human conflict and human disturbance (16%), fragmentation of habitat and logging (13%), green passages and ecological corridors (10%) and monitoring (10%). Equally represented among conservation studies were those related to hunting (6%), elusive or endangered species (6%) inventory of species in protected areas (6%) and general taxonomic inventories (6%).

Conflict with humans and human disturbance

Overpopulation is one of the leading causes of extinction, as we are living in the Anthropocene. As a consequence, particularly large carnivores and ungulates, are not able to coexist with people at fine spatial scales (Carter et al. 2012). Different researchers investigated carnivores density and behavior in human-dominated landscapes with camera traps: tiger in India (Athreya et al. 2013), jaguar in Colombia (Boron et al. 2016), puma in Argentina (Quiroga et al. 2016), puma and jaguar in Belize (Foster et al. 2010), leopard cat in Singapore (Chua et al. 2016), leopard in Zambia (Rosenblatt et al. 2016), red fox in Europe (Diaz-Ruiz et al. 2016), grey wolf in Turkey (Albayrak 2011) and mammals in general (Di Bitetti et al. 2013, Goswami and Ganesh 2014, Khorozyan et al. 2014, Tsujino and Yumoto 2014). In overpopulated countries such as India protected areas are enormously important for the long term viability of biodiversity. Carter et al. (2012) found out that tiger home ranges spatially overlapped with those occupied by people, however the peaks of activity are different, as tigers are nocturnal and people are mostly active during a day. Tiger-human coexistence is likely to be enhanced by abundant tiger prey and low levels of tiger poaching. Athreya et al. (2013) observed that human attacks by leopards were sporadic although leopards were involved in some human-deaths cases in different regions of the Ahmednagar district. Different conservation programs have been developed, including radical measures likes resettling human communities outside protected areas. They conclude emphasizing the urgent need to shift from a protected area centric to a landscape level conservation approach, and general reconsideration of conservation policy, law and practice that are limited to wildlife inside protected areas.

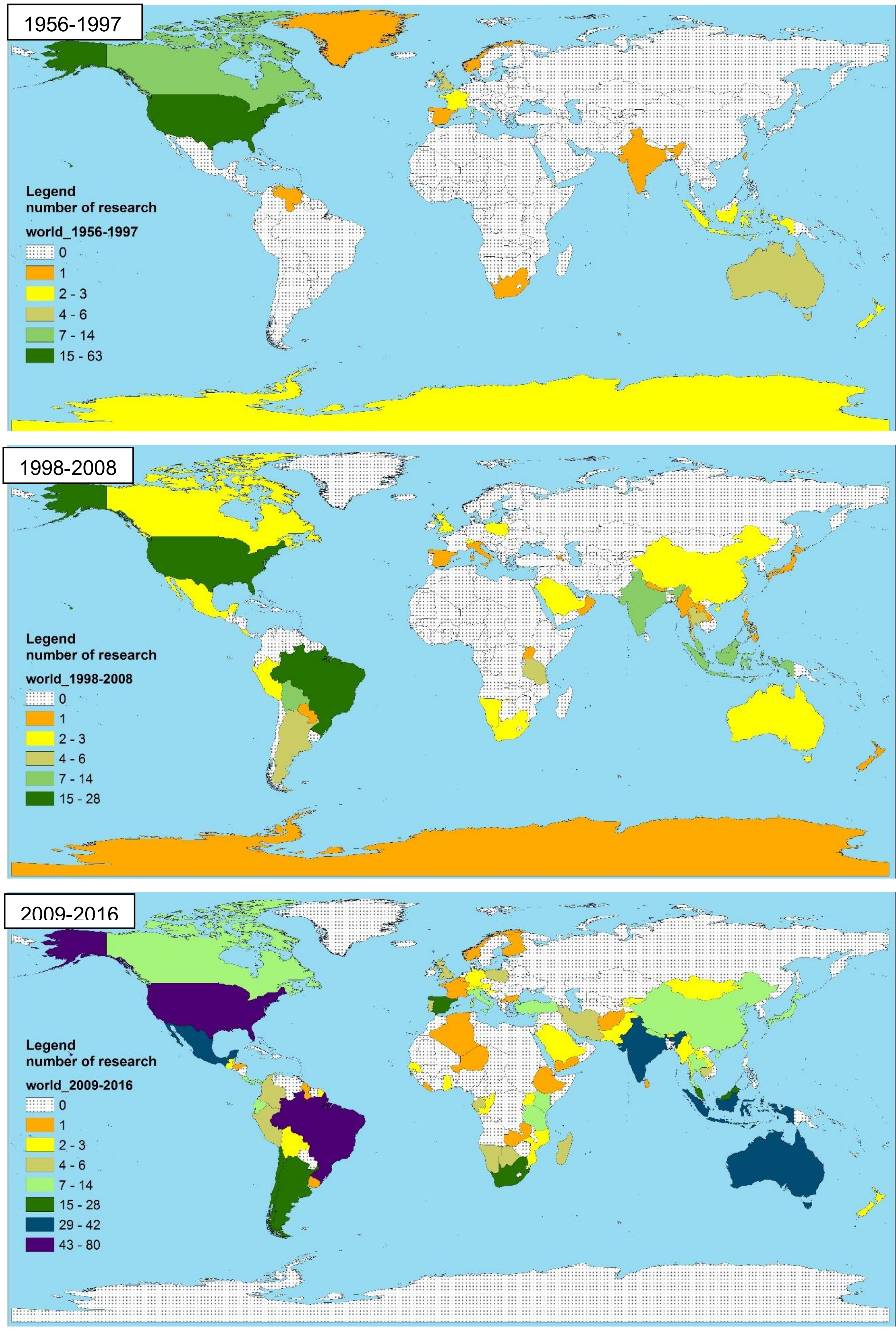

Figure 4. Worldwide distribution of CT studies during three, reviewed periods.

Habitat fragmentation and logging

Habitat loss and fragmentation are one the most important drivers of biodiversity loss, raising the question: to which extent are species able to survive in human-modified landscapes (Fleschutz et al. 2016)? This question is especially relevant to carnivores. A study of bush dog (*Speothos venaticus)* and the short-eared dog (*Atelocynus microtis* detected by CT in fragmented landscape in southern Amazonia proved that these species are strongly vulnerable to fragmentation (Michalski 2010). Hydropower projects (dams) in many cases have forced forest vertebrate populations to inhabit islands, therefore most of the terrestrial and arboreal species have been driven to local extinction within the majority of the islands created by dams (Benchimol and Peres 2015). Nevertheless, some species are able to benefit from edge effects and the diversity of new habitats in fragmented landscape and adapt to these new conditions, such as the forest-dwelling guiña (*Leopardus guigna*) in Chile (Fleschutz et al. 2016). Lopez-Parra et al. (2012) proved that management can improve the continuity of geographical distribution of lynx in Spain and its population is currently less vulnerable to extinction than 10 years ago.

Worldwide, selective logging is one of the most common disturbances to tropical forests, however its impacts on large mammals is poorly known (Brodie et al., 2015). Mammals were target groups in logged forests in Malaysia: clouded leopard (Mohamad et al. 2015), Asian tapir (Rayan et al. 2012), Bornean orangutan pongo (Loken et al. 2015) among other mammals (Jennings et al. 2015, Granados et al. 2016, Wearn et al. 2016). Brodie et al. (2015) suggested that, if authorities maintain reasonable thresholds in logging intensity, they can avoid declines in habitat use by some taxa that are intolerant to intensive logging, such as carnivores.

The rapid spread of plantations is among the main reasons of deforestation in tropical regions (Yue et al. 2015). Plantations tend to support considerably lower biodiversity than native forest. Recently emerging conservation problems with oil palm plantations, especially in Indonesia, have been captured by CT observing loss in diversity of mammals community in Borneo (Bernard et al. 2014, Yue et al. 2015) and among small carnivores in Sumatra (Jennings et al. 2015).

Hunting

For the management of large carnivore populations, reliable data are fundamental, especially when those populations are subjected to trophy hunting. Thus CT methodology can provide solid population estimation for many carnivores like leopards (*Panthera pardus*) (Braczkowski et al. 2015). Unfortunately, in many cases governmental resources to implement such surveys over large spatial scales are lacking. Recently fragmented landscape can be more susceptible to increasing hunting pressure as easier access to previously remote habitats has been created (Kosydar et al. 2014). Hunting is seldom included in the design of fragmentation experiments, and only a small fraction of fragmentation studies consider the hunting impact on mammals. South-East Asia suffers the world's highest rate of wildlife declines, mainly due to poaching (Steinmetz et al., 2014). Thus, there is an urgent need for organized, well designed community projects that monitors biological and social outcomes, and include social-psychology approaches, such as the case study of Steinmetz et al. (2014) in Thailand. Initial results were promising and demonstrated that scientifically designed and well implemented activities might mitigate poaching and initiate wildlife recovery in South-East Asia.

Green passages and ecological corridors

Lack of habitat connectivity caused by construction of highways, large-scale agriculture, power lines, cattle ranching, and a growing human presence in already fragmented landscape, is another conservation problem, where CT research can be useful (Teixeira et al. 2013). The effect of the aforementioned barriers to wildlife movement can be mitigate by construction of wildlife passages that have lately become a popular conservation tool (Cove et al. 2013, LaPoint et al. 2013). However, this process must be followed by systematic monitoring (e.g. with CT) to evaluate their use and effectiveness to convince stakeholders of their value. Cove et al. (2013) integrated occupancy modeling and camera-trap data to estimate medium and large mammal detection and richness in a Central American biological corridor. Sver et al. (2016) used wildlife crossing structures as a tool to monitor of wolf (*Canis lupus*) abundance trends in Croatia. In the same country, Gužvica et al. (2014) evaluated effectiveness of green bridges methods on wildlife populations. In Australia arboreal mammals' road-crossing is considered too and rope-bridges have the potential to restore habitat connectivity disrupted by roads (Goldingay et al. 2013, Taylor and Goldingay 2013).

Elusive and endangered species

Camera traps proved to be a great tool for observation of elusive species like felids in Africa (Brassine and Parker 2015), remote and small populations of carnivores (Gerber et al. 2014), population of jaguar in critical status in Argentina (Quiroga et al. 2014), critically endangered Aders' duike in Kenya (Gerber et al. 2014) or West African lion (Kane et al. 2015). Newly described species are continuously detected with camera trap like white-cheeked macaque (*Macaca leucogenys*) from Medog, southeastern Tibet (Li et al. 2015).

Invasive species

Invasive species is another topic of CT research. Introduced mammals are believed to negatively influence native ecosystems in Patagonia (Gantchoff et al. 2013, Lantschner et al. 2013, Gantchoff and Belant 2016) where three invasive mammals were detected: european hare (*Lepus europaeus*), wild boar (*Sus scrofa*), and red deer (*Cervus elaphus*); while no native herbivorous or omnivorous mammals were found. The presence of cane toads (*Rhinella marina*: Bufonidae) is associated with lower faunal abundance and species richness, of native fauna in Australia (Jolly et al. 2015). Frigeri et al. (2014) pointed out that management of one of the most widely distributed invasive species – domestic dogs in agroforestry mosaics – should focus on the habits and behavior of humans.

Urban areas

Urbanization developments may disturb mammal communities due to factors related to human activities, like habitat loss or food subsidies (e.g. from trash), and CT can be used as a tool to study these systems. Ordenana et al. (2010) measured effects of urbanization on carnivore species distribution and richness in California, while Recio et al. (2015) investigated changes in Mediterranean mesocarnivore communities along urban and formerurban gradients. Widdows et al. (2015) evaluated factors affecting the distribution of large spotted genets (*Genetta tigrina*) in an urban environment in South Africa. In the urban zone in Tokyo metropolis Saito and Koike (2013) evaluated the effects of the urban-rural-forest gradient and spatial scale on the distributions of large and mid-sized mammals. Francis et al. (2015) made one step toward estimating the influence of road density, light and noise pollution on squirrel gliders distribution and habitat use inside the city (*Petaurus norfolcensis*).

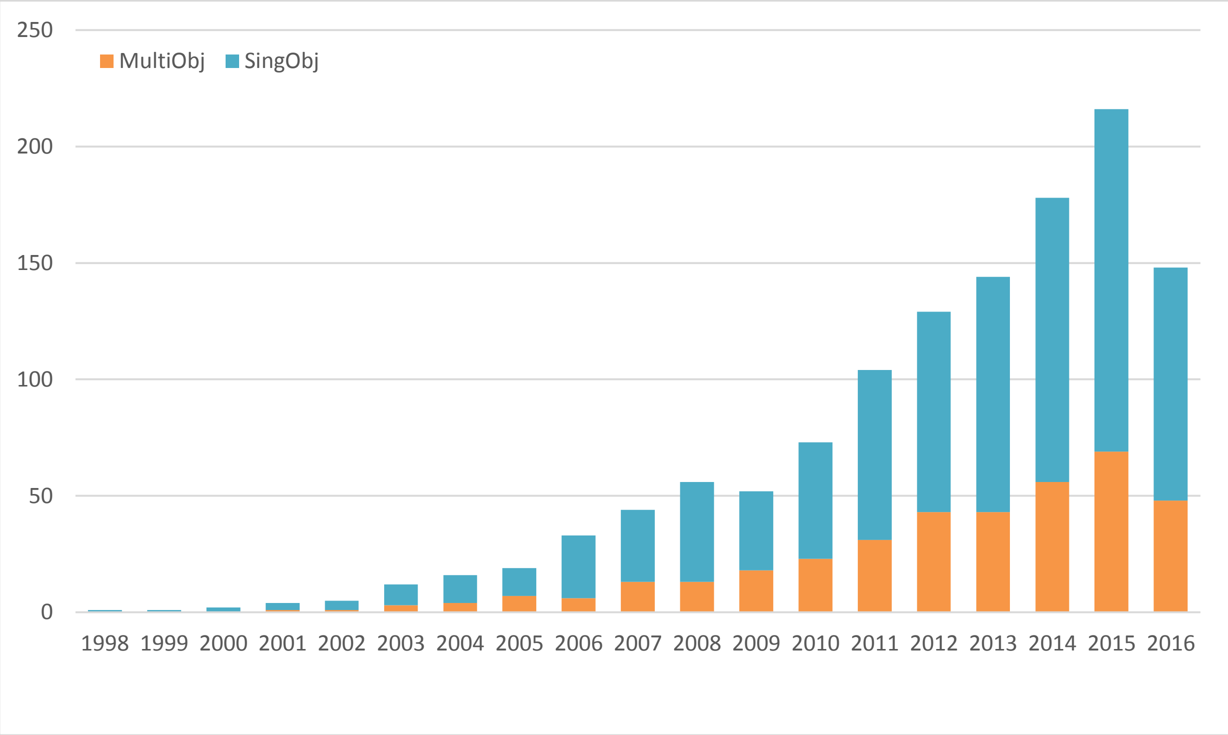

Figure 5. Number of CT single- and multiple objective studies in 1998-2016 (until July 2016). Data was taken from a sample of 996 publications.

Tourism

Interestingly, tourism and sport have also been the objectives of camera CT research as the pressure of outdoor activities on natural landscapes has increased dramatically. Rupf et al. (2011) assessed the spatio-temporal pattern of winter sport activities to minimize disturbance of capercaillie (*Tetrao urogallus*) habitats in the Alps. Main winter skiing routes crossed capercaillie large habitat dividing it in smaller parches, suggesting that this conflict of interest could be resolved by proper management. In Malaysia, Aihara et al. (2016) evaluated the feasibility of mammalian wildlife tourism in tropical rainforests of Endau Rompin National Park by measuring the density of species.

Advantages and disadvantages of CT usage: 90's-2016

Cutler and Swann (1999) exhaustively described advantages of CT as they are cost-effective, flexible, enabling a number of different surveying options, non-invasive and permit register cryptic and elusive species. CT methodology offers robust data: photographs are analogous to museum specimens as they are a permanent record of date, location, and species (Kays et al. 2009). Silveira et al. (2003b) concluded also that, despite relatively high initial costs, camera trapping was preferred over track surveys and direct counts in conducting rapid faunal assessments of mammals.

Disadvantages of CT studies have changed and mechanical problems do not cause major problems as in the 60s-90s period. However, use of CT for behavioral research seems to be questionable as the emission of light and sound from camera traps can be intrusive (Meek et al. 2016). Meek et al. (2014), however, found no consistent response to CT within species; both attraction and repulsion were observed. Additionally, behavioral responses to CT could affect detection probabilities that result in unmeasured biases in abundance estimation (Meek et al. 2014). Frequently, a complex sampling design is required to estimate population density and minimize numerous biases (Trolliet et al. 2014). Another issue reported by Burton et al. (2015) is missing documentation of basic information regarding technical details, such as type of camera used, how and when they were installed at a site, number of sites sampled and how those sites were defined and chosen. Considering that CT protocols and sampling design are crucial for estimating the detectability of individuals and species, and the interpretation of broader ecological processes, rigorous reporting is needed to assess the reliability of CT inferences. CT methodology has become more accessible (lower prices of equipment, available protocols for data analysis), resulting in constant increase of CT research. Nevertheless, CT practitioners must learn the lesson from decades of quantitative assessment of animal populations (Burton et al. 2015) and strictly follow protocols, without shortcuts.

Looking into the future

From the early work of Shiras and Chapman, CT methodology has evolved into an effective, revolutionary, high-tech discipline, and has the capacity to address an immense variety of scientific and conservation questions (O'Connell et al. 2010). When the first fascination for this new powerful methodology disappeared, several concerns have emerged. Burton et al. (2015) suggest that, more important than technical details, is that methodological specifications are explicitly related to survey objectives. Special attention should be paid to experimental design that would increase the potential for comparison and synthesis of results across studies (Linkie et al. 2013).

Technical aspects of CT seem to be already properly tested, and basic approaches to the estimation of different population parameters have now been provisionally accomplished. It is time for scientists and managers to shift primary focus from the methods themselves to their application in science and conservation at the global scale (O'Connell et al. 2010). Estimation and monitoring are no longer considered primary research activities, but parts of a larger process, leading to development of new schemes of data management such as the Tropical Ecology Assessment and Monitoring (TEAM) (Ahumada et al. 2011, Ahumada et al., 2013), the Wildlife Picture Index (www.wildlifepictureindex.org) and Tigers Forever (www.tigersforever.org) (Rowcliffe and Carbone 2008). TEAM presented data of minor widespread biodiversity declines in comparison with reports based on secondary data and expert opinion (Beaudrot et al., 2016). On the other hand, they indicated that there is urgent need of robust indicators created from standardized monitoring practice to precisely access population parameters and form the most appropriate conservation strategies. A major priority is the implementation of a global data facility for camera trapping studies, similar to existing initiatives in other areas of ecological research, such as Movebank (www.movebank.org), which would aim to bring together wildlife movement-tracking data (Rowcliffe and Carbone 2008).

Recent and rapid advances in technology such as the electronic flash, smaller batteries, and batteries continuously recharged with solar panels (O'Connell et al. 2010) make CT methodology more efficient, but the possibility of new technological combination remains open. In comparison with helicopter counts to estimate population of white-tailed deer in Texas, CT has performed equally or better (Koerth et al., 1997), however use of drones or Unmanned Aerial Vehicle (UAV) has not been explored sufficiently. Current developments in unmanned aerial vehicles (UAV), artificial intelligence and miniaturized thermal imaging systems signify new challenges and opportunities for wildlife experts to inexpensively survey relatively large areas (Gonzalez et al. 2016). Authors suggest that existing ground-based monitoring like CT is considered logistically complicated and time consuming, therefore thermal video data from ground based and test flight footage may detect, and more efficiently target wildlife. Nevertheless, a probable combination of camera trap and UAV methodology should be considered. The possibility of combining CT methodology with other methods remains open, like in the case of integration of bioacoustics and CT for better detection of golden jackals (*Canis aureus*) (Comazzi et al, 2016).

Conclusion

Recent explosion of CT studies represents a great experiment and challenge in modern wildlife survey methodology (Burton et al. 2015). There is a huge potential for CTs to generate important new data, catalyze analytical improvement and capture public attention so important for any conservation action (O'Connell et al. 2010).

This literature review shows gradual changes in CTs research goals and outcomes that vary geographically and includes different target animal groups. Number of CT studies has increased abruptly in the last two decades, and this trend persists (Figure 5.). During three reviewed periods, CT studies with science application were dominating over those with conservation focus: 1956-1997 – 108 publication in total (science/conservation =107/1) (Cutler and Swann 1999); 1998-2008 – 156 publication in total (science/conservation =124/34); 2009-2016 (until July) – 840 publication in total (science/conservation =704/136; Figure 1.). Currently, the majority of CT studies are conducted in Asia and South and Central America, with I Brazil (10,1%), Mexico (5,8%) and India (5,6%) as leading countries (Figure 3 and 4.). Since the 90’s mammals have dominated in 90% CT studies, with special attention paid to big carnivores, while multi taxa studies are increasing in frequency (Figure 2.).

The gradual increase of multi-objective studies is noticed and possibly occurs due to standardized methods of CT studies (Figure 5.). In the 60s and 70s researchers had to design and build their own specific equipment adequate to solving specific study problems ("custom made"), while currently trademarks with optimized and standardized mechanisms are used, allowing more complex study approaches. Pioneer researchers had few cameras per study, and therefore focused on the behavior of individuals (a camera to monitor nest predation and nesting behavior studies from the first period 1956-1997), whereas today it is possible to place 30 or 60 cameras in one location to estimate population density or occupancy of species. Thus, the objective of studies has been changing though time; in the 60s-90s behavior and activity patterns dominated, followed by evaluation of equipment, while population parameter studies were not that common (Figure 1 A and B.). It has changed in recent periods, when these topics were leading. There is an urgent need to estimate densities, relative abundance, occurrence and distribution of population as they are basic parameters to be estimated before any conservation or management action starts. Behavior and activity patterns in CT studies are the second most common category during last two decades and they represent one-third of all studies. This category includes a wide variety of topics like behavior, activity patterns, diet, feeding ecology, nest predation, scavenging, foraging, niche and habitat use.

Another objectives are methodology, analysis and equipment consideration that during last decade have been widely described (Meek et al. 2014, Burton et al. 2015, Meek et al. 2015) and forms an important part of this literature review (14%), with increasing frequency. However, this review did not consider some critical but commonly reviewed aspects of CT research, like equipment, protocol, sampling design and analytical approaches. It is a positive sign for CT studies in general that there is room for criticism and discussion about current methods and development of new statistics and methodological approaches.

Technological advance allows increasing complexity of studies, both in equipment and analysis methods, and results in an opportunity to address conservation and management brain teasers. Studies that combine population parameters (relative abundance, density, distribution, occupancy) and community characteristics (inventory, richness, diversity of species) with conservation and management issues are taking more attention during last 20 years (Figure 1.) and respectively take 21% and 14% of CT studies. Human impact and human conflict are leading conservation problems represented in CT studies, especially conflicts with felids. Studies related with management in conservation, especially in last decade has increased. It is worth mentioning that during 1998-2008 period eight studies were conducted in national parks and two in natural reserves, while during the last period (2009-2016) these number of research conducted in protected area has increased significantly giving respectively 32 and 29 studies. The wide variety of management topics: biological control, oil palm plantation, disease transmission, invasive species, pest removal, reintroduction of species, fire management, hybridization of species, urban zone or tourism is an positive sign of effective management in conservation. Habitat fragmentation and consequences of logging are another topics that are gaining researcher's attention lately, as habitat loss is one of the biggest threat for biodiversity. Especially in last decade number of monitoring studies with CT has increased, a good sign that local conservation managers recognized CT as a useful tool. On the other hand, many studies claimed results of "conservation application", but do not give details on the expected application, nor do they provide quantitative data for this claim. Nichols et al. (2011) shared they concern about a lack of adaptive resource management program, where sequential decision-making processes are made periodically through time, which could be developed with monitoring program based on CT studies. Certainly, a number of CT studies have considered scientific hypotheses that should be relevant to conservation management. Conservation funds should be directed at animals that are charismatic or umbrella species (e.g., large cats and carnivores in general) (O'Connell et al. 2010) (Figure 2.) that easily sampled by camera traps. Increased funds dedicated to this kind of CT research is expected, and should be followed by focused conservation management efforts, guided by structured decision processes.

The geographic and animal taxa focus has shifted from a first review period dedicated mostly to birds in North America, to a period dedicated to big cat research in the tropics (1998-2009), and a recent trend toward multi-species or community approach in conservation applications in recent years (Figure 2, 3 and 4).

Interestingly, change in geographic location can be explained by increasing need of ecological and conservation studies in the tropics. The loss of biodiversity and the most pressing conservation problems, like habitat fragmentation, deforestation, hunting, conflicts with human, are concentrated in tropical regions. More than half of CT studies dedicated to conservation during last two decades took place in tropical countries in Asia, Africa and South and Central America. Surprisingly, no studies from Venezuela were obtained during the search from the last two decades, although a couple of studies are known: one about spotted paca (*Cuniculus paca*) and red-rumped agouti (*Dysaprocta leporina*) (Jax et al., 2015) and two publications about jaguars (Jędrzejewski et al. 2016).

South and Central America, as well as Asia, are relatively well covered with CT studies, but results from Africa are missing in the review. Especially in Congo River Basin there is a lack of baseline data on animal species occurrence and density across the basin (Gessner et al., 2013), not mentioning CT studies. Conservation CT studies effort should be proportionally distributed in tropics that is the home to half the world's species and currently suffer extinction of higher magnitude that rest of the world.

Recommendation

Worldwide geographic patterns of CT research can be biased by type of database used to perform the search, in case of Science Web™ - include some high impact scientific journals basically published in English. In different part of the world the gross of studies is published in different languages - Spanish (South and Central America) or French (Africa), especially in case of studies related to conservation – also, local reports for stakeholders, national parks' reports, local studies carried out by NGOs, database of national environmental offices and ministries constitute a large amount of grey literature that is not included in the search engine used. It is recommended to extend research methodology to other databases like Google scholar or Scopus and focus on continents, where, besides research conducted in English, other languages can be used. Following this revision, use of CT in conservation has increased, especially during last two decades, which brings benefits but also raised concerns. Based on examples such as community projects to monitor poaching in Thailand (Steinmetz et al., 2014) or establishment and monitoring of Ecological Corridors and green passages in Central America and Europe (Cove et al. 2013, LaPoint et al. 2013, Sver et al. 2016, Gužvica et al. 2014) CT methodology seems to be effective. The possibility to use photos and videos acquired from CT for education and divulgative purposes is a new and innovative in comparison with tradition methods of survey wildlife that are not transparent for the broad public. CT could perform well as a relatively cheap and easy to apply methodology to resolve conservation problems, a solution that stakeholders are constantly looking for. However, more detailed revision of CT studies for conservation is required to evaluate efficient, successful and unsuccessful application of this equipment depending on taxa, habitat and study objective. Rapid development of CT technology needs to go hand-in-hand with progress in methodology. Many obstacles that appear at study design and analysis level and include multi objective and multi species inference remains unsolved. As these data is used to established new conservation robust indicators, hence well estimation of population parameters is crucial. An important drawback is also the risk of CT robbery, when unique data and expensive equipment is lost, thus other non-invasive techniques such as genetic tagging, track stations and natural sign surveys should always be considered as they may complement sampling effort and help maintain continuity of data collection when CT is stolen.

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