Howl I get to know you?

A Review of Behavioural Observation Methods: Implications for Monitoring Wild Wolves

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Abstract

Observation is a key method in the field of animal ecology and behavioural research. Field studies often add to information collected via experimental methods to inform of their ecological validity. The grey wolf (*Canis lupus*) is an important species for wildlife management and conservation as well as comparative and cognitive studies which often use observational methods for data collection.

Despite the interest in the species, wolf behaviour is challenging to observe visually in the nature. To discuss how methodology could be improved to better study wolves in the wild, I looked at which methods have been used to study the behaviour of both wild wolves, and other terrestrial mammals. For this I conducted a systematic literature review on visual observation methods for wolves and other terrestrial mammals between the years 2001-2020.

I found that while binoculars and spotting scopes have remained the main visual observation method for wolf research, other terrestrial mammals are increasingly behaviourally monitored with camera traps and unmanned aerial vehicles (UAVs). Adapting these modern methods for wild wolf research could further our knowledge of their behaviour.

Developing ways to better observe the behaviour of wild animals in their natural environment may help us further understand their role in the environments they often share with humans. It can offer valuable information to aid conservation and management efforts, help minimize human-wildlife conflicts and economical losses, add to our understanding of evolution of social behaviour and ecological interactions, and offer possible ways to add ecological validity to experimental studies on canines. As technological advances provide us with more possibilities for observation, we can learn more about ourselves, and the canines living among us.

Contents

1. Introduction

1.1 Wild for Wolves

Wildlife observation is a key method in the field of ecology for obtaining information about many topics, including animal distribution, or behaviour (Kays et al., 2015). Observational research has been valuable for testing hypotheses and existing models, in natural experiments, and making new discoveries (Sagarin & Pauchard, 2010). Field studies can provide important inductive information that have possibilities for further applications (Guthrey, 2007).

Changes at the population level in animals depend on the behaviour of the individuals (Tuomainen & Candolin, 2011). If not taken into consideration, individual differences can introduce bias in ecological studies and affect management decisions. To distinguish different behaviours, it is important to obtain information of individual animals. (Merrick & Koprowski, 2017). However, observing the behaviours of individual animals can be challenging, especially for more cryptic species, like large carnivores (Boitani & Powell, 2012).

The grey wolf (*Canis lupus*), like other top predators, affects the dynamics of other predators, herbivores and, indirectly, other parts of their environment. Like many predators, wolves are returning to their earlier habitats, including those now more intensely inhabited by people, so understanding behaviour and ecological roles of wolves is important (Shores et al., 2019). This research could benefit from the collaborative work of behavioural ecology and conservation (Tuomainen, & Candolin, 2011).

1.2 Tracks in the Snow

Grey wolves are a popular study species. They have been studied via satellite or VHF-telemetry (species abundances, movement, dispersal, den and resting sites, habitat use etc.; see for example Mech & Cluff, 2011; Shipp, 2016), photo-identification, audio recorders (playback studies for pack size, communication, identification), capture (measurements etc.) and non-invasive genetic sampling from hair, urine and faeces (genetic information, e.g. identification, family lineages and relationships, traits etc., see for example Groot et al., 2016). Combinations of methods include direct observation and GPS collars (Patzelt et al., 2014), and studies combining cameras and genetic sampling can be used to attempt to identify individuals from their vocalisations (Sadhukhan et al., 2021) or scats (Mattioli et al., 2018).

Advances in wildlife monitoring technology may open up further possibilities for observing

animals in different ways (Kays et al. 2015; Pimm et al, 2015), perhaps even the elusive wolves. Unmanned aerial vehicles (UAV), or drones, are increasingly being used in wildlife monitoring (Hodgson et al., 2016; Nowak et al., 2018), but to the best of my knowledge, these have not been used to study wild wolves.

1.3 New Paths in Canine research

Combining wildlife monitoring tools with the knowledge from studies with captive individuals and pets may help bring ecology, ethology and cognitive research to new paths. For example, the research into the emotions and cognition in intraspecific social interactions is a new area of research (Nawroth & Langbein, 2019).

Wolves have been studied in captivity and comparative studies with wolves and dogs (*C. l. familiaris*) can give important insights into the evolutionary aspects of emotions, cognition and domestication (see for example Range et al., 2019). However, relevant behavioural traits to understand the cognitive skills in wolves have yet to be studied in the natural setting. (Miklósi & Topál, 2012).

The traditionally used technology can pose challenges for the study of many interesting new topics. As Cassidy & McIntyre (2016) comment: “Some behavior classified as possibly altruistic can be difficult to quantify in non-habituated, wild animals (e.g., regurgitation, food sharing, and parental care) when viewing of natural behaviors necessarily takes place at great distance or with a spotting scope.” (p. 940). However, some observations have revealed, for example, how the individual characteristics affect wolf hunting success (MacNulty et al., 2009), and how social structure affects the intergroup agonistic interactions in wolves (Cassidy et al., 2015).

1.4 Marking the Territory (This study and Research Questions)

As the previous examples show there might be a need for better understanding of individual wild wolf behaviour in better detail, as well as for consistent visual behavioural monitoring of wild wolves. It also seems that the modern technology is advancing to make all that more possible than ever. But to get to the future, we must look to the past. To understand on the one hand how wolves have been studied in the past 20 years, and in comparison, how prevalent modern observational methods are used in the study of the behaviour of other terrestrial mammals, I conducted a systematic review for studies on wolves, and on visual observation methods.

The preliminary literary search and personal communication with professionals with experience in wild wolf observation led me to focus on the emerging visual methods that were

not yet in much use with wild wolves, but which were being used to study other terrestrial mammals. So in addition to wolves, I was also interested in finding out how the behaviours of other terrestrial mammals were observed with visual methods. To answer this question I looked at the use of drones (also called UAVs, UASs, or remotely piloted aicrafts, see Hyun et al., 2020 for definitions) and camera traps.

I wanted to look at which visual methods are used to observe the behaviour of wild wolves, and how UAVs and camera traps are used to observe the behaviour of wild wolves and other terrestrial mammals?

I expected to find that wild wolf behaviour has been observed visually mainly using camera traps and direct observation, and that UAVs and camera traps have been more widely used in behavioural monitoring with other terrestrial mammals compared to wolves.

2. Methods

I did a three-part literature survey to answer my research questions. First I searched for all studies with grey wolves which used visual observation methods to observe behaviour. Then I searched for studies that used UAVs or camera traps to observe the behaviour of other terrestrial mammals. This was done to get an overview of the use of the more modern or recent observation methods.

To get a review of the more recent studies, I did the search for the years 2001-2020. I used the PRISMA 2009 guidelines for systematic reviews (Moher et al., 2009). I searched the Scopus database and only included articles and reviews in peer-reviewed journals. The protocol and full search criteria used are listed in Appendix 1.

2.1 What's in a Howl?! (Terminology & Definitions)

Scientists have not reached a consensus on what constitutes 'behaviour' (Levitis et al., 2009). For this study I have defined behaviour as visually observable movement of an animal. Therefore, location data or mentions of movement from A to B were omitted from inclusion. Also assumptions of behaviour, without any further definition, for example assumption of feeding from a single photograph were omitted (series of photographs were included) because the purpose of this review was to look at which behaviours could be seen with visual methods.

In this thesis I concentrate mainly on the grey wolf and its closest subspecies like the arctic wolf (*Canis lupus* arctos), or the Italian wolf (*C. l. italicus*). More distant species (Parker, 2012), like the domestic dog or the dingo (*C. l. dingo*) have been left out of first part of the search (search of articles studying wolves) for clarity and simplicity.

Visual observation methods in this this review are direct observation (by the naked eye, spotting scope, or binoculars, the observation notes with which are often recorded in a voice recorder or similar device); video camera; trail camera / camera trap; and UAVs. Videos are included, as well as photographs with certain criteria (single photographs are excluded but series of photographs are included).

2.2 Systematic review criteria

In accordance with PRISMA 2009 guidelines I used predefined inclusion and exclusion criteria to narrow the search. For the studies on wolf observations I only included articles dealing with wild, live wolves, studies using visual observation methods, and studies

describing visually observed behaviour. With the UAV and camera trap studies I only included articles dealing with terrestrial mammals describing visually observed behaviour. The full inclusion and exclusion criteria used are listed in Appendix 1.

3. Look What the Wolf Dragged In! (Results)

3.1 Visual methods to study wolf behaviour

Out of the 2482 articles in the initial search result, 54 articles were analysed in this review. The main method used was direct observation, in 48 articles. Camera traps were used in 2 articles, and video together with direct observation was used in 4 articles. The main behaviours observed in these studies were inter- or intraspecies interaction (18); hunting (18); feeding (8); marking (4); and other / many (6).

Of the articles included in the analysis 35 were research articles, and 19 were classified as a note or short communication. I have included both research articles and notes, on the one hand to highlight the low number of research articles using visual methods to study wild wolf behaviour, and on the other hand to showcase the potential options for future behavioural research if methods are improved.

3.2 UAVs and camera traps for wildlife research

To look at how UAVs and camera traps have been used to observe the behaviour of wild wolves and other terrestrial mammals I conducted separate searches for UAVs and camera traps. The details of the search are in Appendix 1.

3.2.1 UAVs for observing terrestrial mammal behaviour

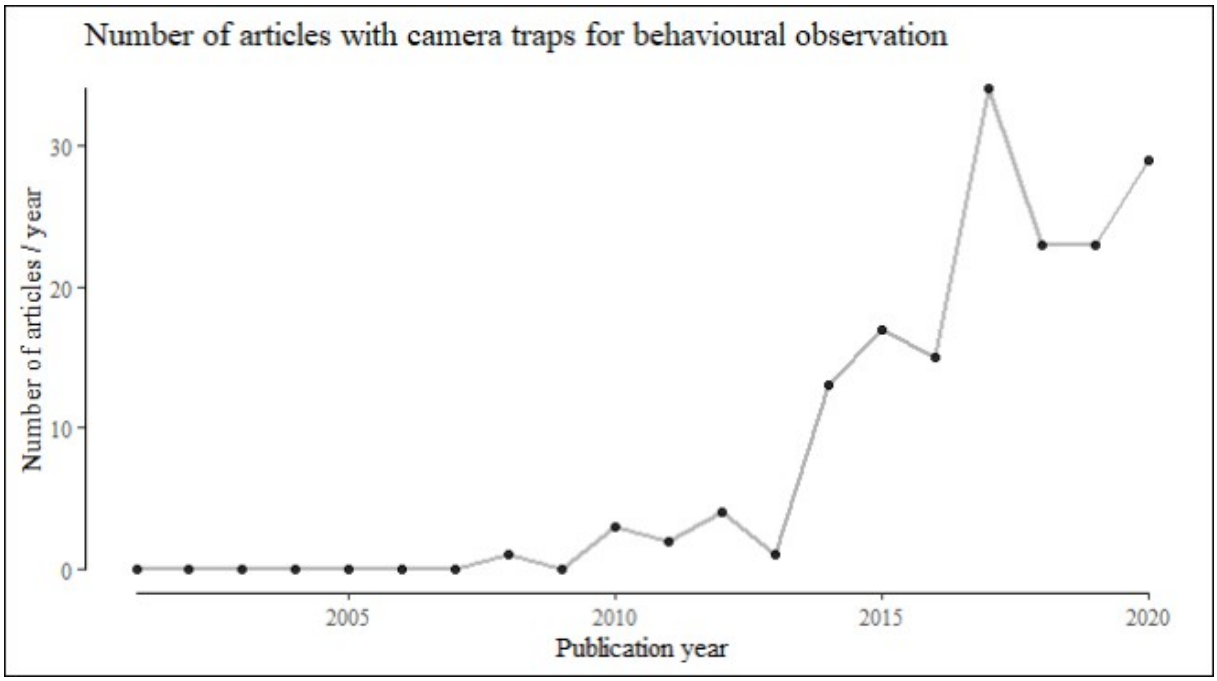
The initial search resulted in 154 articles, of which 4 research articles, 3 reviews, and 1 note were analysed. 6 articles were about responses of animals to drones and 2 were about herding. 2 of the articles dealt with multiple species, 5 with herbivores, and one with polar bears.

3.2.2 Camera traps for observing terrestrial mammal behaviour

The initial trail camera search resulted in 794 articles, of which 168 were analysed. The main taxa were primates (31), felids (19), rodents (13), bears (11), canids (10), and deer / moose (10). 30 articles dealt with several species. Other (44) included a large variety of species, from rhinos to armadillos.

The main behaviours observed with camera traps were feeding (43), marking (18), tool use (8), vigilance (10), intra- or interspecies interaction (9), and hunting (8). Other behaviours (28) included digging, climbing, and learning, and 41 articles described many behaviours.

The number of articles describing behaviours using camera traps has increased rapidly. The first decade, 2001-2010, saw only 5 articles that were included in this thesis. In the first half of the recent decade, 2011-2015 the number jumped to 39, and for the final five years, 2016-2020, the total had reached 124 articles.



4. Will The Old Dog Learn New Tricks?

In this literary review, I wanted to see what methods were being used to visually observe the behaviours of wolves, and for comparison, other terrestrial mammals. I found that wolves are mainly observed by direct human observation, whereas with other animals, new technologies like camera traps and UAVs are being increasingly used.

Although direct observation seems to remain as the main visual observation method for the behavioural research of wild wolves, in conjunction with the increase in the use of camera traps for behavioural studies with other terrestrial mammals, the use of camera traps is also becoming more common in the behavioural research of wild wolves. Additionally, although only a single UAV study with captive wolves (Chrétien et al., 2015) is among the recently published articles, it may not be unreasonable to predict that the use of UAVs will also make its way to wild wolf research, as it has with other species, seen in the results of this study.

4.1 Sniffing for the Next Catch (Future research topics)

For some reason the wolves don't seem as popular a subject for behavioural studies using camera traps or UAVs as many other species. This may be due to their elusive behaviour, crepuscular and mobile activity pattern or large home range (Mech & Boitani, 2003). As the advances in technology may make these studies easier to conduct in the future, I think the next step for the wolf research could be to ask what challenges and opportunities might be relevant to the use of modern visual technology, like camera traps and UAVs in observing wild wolf behaviour.

Opportunities can be seen for example in comparisons between video and photographic material. In monitoring animal behaviour, video image provides several advantages compared to photographic data, according to Ramsey et al. (2019). The video captures more individuals, where photographs may miss some of them. Videos are also better for recording a wider variety of behaviours, Videos are better than photographs for monitoring cryptic species, and video footage might be more useful than photos for management purposes (Ramsey et al, 2019).

UAVs, on the other hand, can be used to monitor or detect several species simultaneously, including wolves (Chrétien et al., 2015). Fields of ethology, behavioural ecology and others could benefit from improved methods for wild wolf monitoring, as discussed in the

introduction. However, as many studies with UAVs show, it is important to establish the level of disturbance to the animals caused by the used equipment, and to assess the behavioural reactions to the drones in detail. Studies to test reactions of wolves to the UAVs still have not been published, or even conducted to the best of my knowledge.

Continuing to combine methods might be useful to compare their benefits and disadvantages for obtaining behavioural information (Rahman & Rahman, 2021). Future studies could include a pilot using camera traps and drones for testing extended close-up wild wolf behavioural monitoring. The results from the pilot could then be used to improve on the methods and use them for future research. Reactions to UAVs could be conducted in captive conditions (see Ditmer et al.,2019, for bears) and then with collared wolves (comparing reactions from wolves trapped from (threat from) air (helicopters) and ground (snares). Animals living closer or further to human habited areas (urban, agricultural, minimal human influence) (see Turner et al., 2019, for hyenas), as well as ones living in different habitats (cluttered, open) may show differences in behaviour, and this might be the case with wolves too, possibly including reactions to drones.

In conclusion, modern technology can open many opportunities for obtaining new and unique information of individual wolves and their behaviours in their natural environment. Steps to move forward need to be taken cautiously (see for example Wilson et al., 2021) but the rewards could be reaped by many fields with stakeholders with interest in wild wolves, including cognitive science, conservation ecology, evolutionary biology, wildlife management and local human populations.

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6. APPENDIX 1

6.1 Protocol and Summary of Results for Thesis part 1

My first questions were: 1) Which visual methods are used to observe the behaviour of wild wolves? and
2) How are UAVs and trail cameras used to observe the behaviour of wild wolves?

Following the structure of the PRISMA 2009 guidelines for a systematic review, I processed the literature in four stages: 1) identification, 2) Screening, 3) Eligibility, and 4) Included.

In the 1) identification, articles were identified through the Scopus database search. I used the following query string: TITLE-ABS-KEY("canis lupus") AND (LIMIT-TO (DOCTYPE,"ar") OR LIMIT-TO (DOCTYPE,"re")) AND (LIMIT-TO (SRCTYPE,"j")) AND (LIMIT-TO (EXACTKEYWORD,"Canis Lupus") OR LIMIT-TO (EXACTKEYWORD,"Wolf") OR LIMIT-TO (EXACTKEYWORD,"Wolves") OR LIMIT-TO (EXACTKEYWORD,"Gray Wolf") OR LIMIT-TO (EXACTKEYWORD,"Grey Wolf"))
I included the full years 2001-2020.

The search result was 2482 articles, which I screened with predetermined inclusion and exclusion criteria.

In the 2) Screening phase, the abstracts of the 2482 articles were screened using the following inclusion and exclusion criteria:

Records excluded for the following reasons:

- Did not study wolves
  - Studied other canids, e.g. jackals, dingoes, dogs,
  - Studied other species, e.g. Deer
  - Did not study animals, e.g. Grey Wolf Optimizer algorithm
- Did not study wild wolves
  - Studied captive individuals
- Did not study live wolves
  - Studies used blood, bone, tissue, hair, feces, urine etc. samples
- Did not use visual observation methods
  - Studies used radiotelemetry (e.g. GPS, VHF), accelerometers, tags, scratch etc. marking, tracks, interviews, surveys, literature reviews, acoustic methods (e.g. howling surveys)

Records included for the following reasons:

- Studied wolves
- Studied wild wolves
- Studied live, wild wolves
- Used visual observation methods, e.g. UAV, UAS, drone, trail camera, game camera, camera trap, binoculars, spotting scope, direct observation, including observations from ground, aircraft etc.

At the Screening phase 2309 articles were excluded and 173 articles were moved on to the next phase (Eligibility).based on the above inclusion and exclusion criteria.

In the 3) Eligibility phase, the full texts of the 173 articles were screened using the following inclusion and exclusion criteria:

Records excluded for the following reasons:

- Did not study wolves
- Did not study wild wolves
- Did not use visual observation methods
- Did not study behaviour

Records included for the following reasons:

- Studied wolves
- Studied wild wolves
- Used visual observation methods
- Studied behaviour

In the Eligibility phase 119 articles were excluded and 54 articles moved on to the next phase (Included), based on the above inclusion and exclusion criteria.

In the 4) Included phase, the 54 articles were analysed using the following categories:

4a) By (main) observational method:
Camera trap: 2
Direct observation: 48
Video together with direct observation: 4

4b) (Main) behaviours:
Hunting 18
Interaction 18
Feeding: 8
Marking: 4
Other (incl. many): 6

4c) Article type:
Research article: 35
Note / Short communication: 19

Full list of articles included in the analysis (in alphabetical order):

	Authors	Article title	Publication	Year	Method of observation	(Main) observed behaviour(s)	Source type
1	Almberg, E.S., Cross, P.C., Dobson, A.P., Smith, D.W. & Hudson, P.J.	Parasite invasion following host reintroduction: A case study of Yellowstone's wolves	The Royal Society Philosophical Transactions. Biological sciences	2012	Direct observation	Other	R
2	Almberg, E.S., Cross, P.C., Dobson, A.P., Smith, D.W., Metz, M.C., Stahler, D.R., Hudson, P.J.& Festa-Bianchet, M.	Social living mitigates the costs of a chronic illness in a cooperative carnivore	Ecology Letters	2015	Direct observation	Other	R
3	Atwood, T.C.	Behavioural interactions between coyotes, Canis latrans, and wolves, Canis lupus, at ungulate carcasses in southwestern montana	Western North American naturalist	2006	Direct observation	Interaction	N
4	Atwood, T.C. & Gese, E.M.	Coyotes and recolonizing wolves: social rank mediates risk-conditional behaviour at ungulate carcasses	Animal behaviour	2008	Direct observation	Other	R
5	Atwood, T.C. & Gese, E.M.	Importance of resource selection and social behavior to partitioning of hostile space by sympatric canids	Journal of mammalogy	2010	Direct observation	Interaction	R
6	Baan, C., Bergmüller, R., Smith, D.W. & Molnar, B.	Conflict management in free-ranging wolves, Canis lupus	Animal behaviour	2014	Direct observation, video	Interaction	R
7	Baruzzi, C., Lovari, S. & Fattorini, N.	Catch me if you can: antipredatory behaviour of chamois to the wolf	Ethology Ecology and Evolution	2017	Direct observation	Interaction	R
8	Blanco, J.C., Cortés, Y. & Virgós, E.	Wolf response to two kinds of barriers in an agricultural habitat in Spain	Canadian Journal of Zoology	2005	Direct observation	Other	R
9	Cassidy, K.A. & McIntyre,	Do gray wolves support pack mates during aggressive	Animal Cognition	2016	Direct observation,	Interaction	R

	R.T.	inter-pack interactions			video		
10	Cassidy, K.A., Mech, L.D., MacNulty, D.R., Stahler, D.R. & Smith, D.W.	Sexually dimorphic aggression indicates male grey wolves specialize in pack defence against conspecific groups	Behavioural Processes	2017	Direct observation	Interaction	R
11	Darimont, C.T., Reimchen, T.E. & Paquet, P.C.	Foraging behaviour by gray wolves on salmon streams in coastal British Columbia	Canadian Journal of Zoology	2003	Direct observation	Feeding	N
12	Frame, P.F., Cliff, H.D. & Hik, D.S.	Response of wolves to experimental disturbance at homesites	The Journal of wildlife management	2007	Direct observation, video	Other	R
13	Fremmerlid, M.A. & Latham, D.M.	Lone wolf, canis lupus, displaced from a kill by an adult black bear, ursus americanus, in northeastern Alberta	Canadian Field-Naturalist	2009	Direct observation	Hunting	N
14	Gunther, K.A. & Smith, D.W.	Interactions between wolves and female grizzly bears with cubs in Yellowstone National Park	Ursus	2004	Direct observation	Interaction	N
15	Heilhecker, E., Thiel, R.P. & Wayne, Jr.,H.	Wolf, Canis lupus, behavior in areas of frequent human activity	Canadian Field-Naturalist	2007	Direct observation	Many	R
16	Hendrickson, C.J., Samelius, G., Alisauskas, R.T. & Larivière, S.	Simultaneous den use by arctic foxes and wolves at a den site in Nunavut, canada	Arctic	2005	Direct observation	interaction	R
17	Homkes, A.T., Gable, T.D., Windels, S.K. &Bump, J.K.	Berry important? Wolf provisions pups with berries in northern minnesota	Wildlife Society bulletin	2020	Direct observation	Feeding	N
18	Jordan, P.A., Peterson, R.O. & Ledoux, K.A.	Swimming wolves Canis lupus, attack a swiming Moose, Alces alces	Canadian Field-Naturalist	2010	Video, Direct observation	Hunting	N
19	Kiss, B.W., Johnstone, S.K. & Berger, R.P.	Predation of a barren-ground caribou, Rangifer tarandus groenlandicus, by a single graywolf, canis lupus, in northern Manitoba, Canada	Canadian Field-Naturalist	2010	Direct observation	Hunting	N

20	Landry, J-M., Borelli, J-L. & Drouilly, M.	Interactions between livestock guarding dogs and wolves in the southern French Alps	Journal of Vertebrate Biology	2020	Direct observation	interactions	R
21	Lewis, T.M. & Lafferty, D.J.R.	Brown bears and wolves scavenge humpback whale carcass in Alaska	Ursus	2014	Camera trap, Direct observation	Interaction	N
22	MacNulty, D.R., Varley, N. & Smith, D.W.	Grizzly bear, Ursus arctos, usurps bison calf, Bison bison, captured by wolves, canis lupus, in Yellowstone national park, Wyoming	Canadian Field-Naturalist	2001	Direct observation	Hunting	R
23	MacNulty, D.R., Mech, L.D. & Smith, D.W.	A proposed ethogram of large-carnivore predatory behavior, exemplified by wolf	Journal of Mammalogy	2007	Direct observation	Hunting	R
24	MacNulty, D.R., Smith, D.W., Vucetich, J.A.,(...), Stahler, D.R. & Packer, C.	Predatory senescence in ageing wolves	Ecology Letters	2009	Direct observation	Hunting	R
25	MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J.A. & Packer, C.	Nonlinear effects of group size on the success of wolves hunting elk	Behavioral Ecology	2012	Direct observation	Hunting	R
26	MacNulty, D.R., Tallian, A., Stahler, D.R. & Smith, D.W.	Influence of group size on the success of wolves hunting bison	PloS ONE	2014	Direct observation	Hunting	R
27	Martin, H.W., Mech, L.D., Fieberg, J., Metz, M.C., macNulty, D.R., Stahler, D.R. & Smith, D.W.	Factors affecting gray wolf (Canis lupus) encounter rate with elk (Cervus elaphus) in Yellowstone National Park	Canadian Journal of Zoology	2018	Direct observation	Hunting	R
28	Mattioli, L., Canu, A., Passilongo, D., Scandura, M. & Apollonio, M.	Estimation of pack density in grey wolf (Canis lupus) by applying spatially explicit capture-recapture models to camera trap data supported by genetic monitoring	Frontiers in zoology	2018	Camera trap	Other	R
29	Mech, L.D., Smith, D.W.,	Winter severity and wolf predation on a	The Journal of Wildlife	2001	Direct observation	Hunting	R

	Murphy, K.M. & MacNulty, D.R.	formerly wolf-free elk herd	Management				
30	Mech, L.D.	"standing over" and "hugging" in wild wolves, Canis lupus	Canadian Field-Naturalist	2001	Direct observation	Interaction	N
31	Mech, L.D., McIntyre, R.T. & Smith, D.W.	Unusual behavior by bison, Bison bison, toward elk, Cervus elaphus, and wolves, Canis lupus	Canadian Field-Naturalist	2004	Direct observation	Interaction	R
32	Mech, L.D.	Decline and recovery of a high arctic wolf-prey system	Arctic	2005	Direct observation	Urine marking	N
33	Mech, L.D.	Urine-marking and ground-scratching by free-ranging Arctic wolves, Canis lupus arctos, in summer	Canadian Field-Naturalist	2006	Direct observation	Urine marking	R
34	Mech, L.D.	Possible use of foresight, understanding, and planning by wolves hunting muskoxen	Arctic	2007	Direct observation	Hunting	R
35	Mech, L.D.	Proportion of calves and adult muskoxen, Ovibos moschatus killed by gray wolves, Canis lupus, in July on Ellesmere Island	Canadian Field-Naturalist	2010	Direct observation	Hunting	N
36	Mech, L.D.	Prolonged intensive dominance behavior between gray wolves, Canis lupus	Canadian Field-Naturalist	2010	Direct observation, video	Interaction	R
37	Mech, L.D.	Gray wolf (Canis lupus) movements and behavior around a kill site and implications for GPS collar studies	Canadian Field-Naturalist	2011	Direct observation	Hunting	N
38	Mech, L.D.	A gray wolf (Canis lupus) delivers live prey to a pup	Canadian Field-Naturalist	2014	Direct observation	Hunting	N
39	Mech, L.D.	Extinguishing a learned response in a free-ranging gray wolf (Canis lupus)	Canadian Field-Naturalist	2017	Direct observation	Other	N
40	Merkle, J.A.,	Interference	Canadian Journal of	2009	Direct	Interactio	R

	Stahler, D.R. & Smith, D.W.	competition between gray wolves and coyotes in Yellowstone national park	Zoology		observation	n	
41	Nathan, W., Gustaf, S., Alisaukas, R.T., Bantle, J.L., Christopher, J., Alain, L., Phipps, K.J. & Justin, P.	Foraging behaviours and diets of wolves in the queen maud gulf bird sanctuary, Nunavut, Canada	Arctic	2009	Direct observation	Feeding	R
42	Nichols, T.C.	Cooperative hunting of Canada Geese (Branta canadensis) by gray wolves (Canis lupus) in Northern Quebec	Canadian Field-Naturalist	2015	Direct observation	Hunting	N
43	Potvin, M.J., Peterson, R.O. & Vicetich, J.A.	Wolf homesite attendance patterns	Canadian Journal of Zoology	2004	Direct observation	Other	R
44	Sands, J. & Creel, S.	Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, Canis lupus	Animal behaviour	2004	Direct observation	Interactio n	R
45	Sewerniak, P.	Wolves (Canis lupus) in the Torun basin (N Poland): Actual status and problems concerning the population	Ecological Questions	2015	Direct observation	Urine marking	R
46	Smith, D.W., Murphy, K.M. & Moger, S.	Killing of a bison, Bison bison, calf by a wolf Canis lupus, and four coyotes, Canis latrans, in Yellowstone National Park	Canadian Field-Naturalist	2001	Direct observation	Hunting	N
47	Smith,T.S., Partridge, S.T. & Schoen, J.W.	Interactions of brown bears, Ursus arctos, and gray wolves, Canis lupus, at Katmai National park and reserve, Alaska	Canadian Field-Naturalist	2004	Direct observation	Interactio n	N
48	Smith, D.W.,	Infanticide in	Journal of	2015	Direct	interactio	R

	Metz, M.C., Cassidy, K.A., Stahler, E.E., MacIntyre, R.T., Imberg, E.S.A. & Stahler, D.R.	wolves: seasonality of mortalities and attacks at dens support evolution of territoriality	Mammalogy		observation	n	
49	Stahler, D.R., Smith, D.W. & Landis, R.	The acceptance of a new breeding male into a wild wolf pack	Canadian Journal of Zoology	2002	Direct observation	Interaction	N
50	Tallian, A., Smith, D.W., Stahler, D.R., Metz, M.C., Wallen, R.L., Geremia, C., Ruprecht, J. Wyman, C.T., macNulty, D.R. & Costa, D.	Predator foraging response to a resurgent dangerous prey	Functional Ecology	2017	Direct observation	Hunting	R
51	Thiel. R.P.	Condition for sexual interactions between wild grey wolves, Canis lupus, and coyotes, Canis latrans	Canadian Field-Naturalist	2006	Direct observation	Interaction	R
52	Watts, D.E., Butler, L.G., Dale, B.W. & Cox, R.D.	The Ilnik wolf Canis lupus pack: use of marine mammals and offshore sea ice	Wildlife biology	2010	Direct observation	Feeding	R
53	White, K.S., Golden, H.N., Hurdertmark, K.J. & Lee, G.R.	Predation by wolves, Canis lupus, on wolverines, Gulo gulo, and an american marten, Martes americana, in Alaska	Canadian Field-Naturalist	2002	Direct observation	Hunting	N
54	Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M. & Getz, W.M.	Trophic facilitation by introduced top predators: Grey wolf subsidies to scavengers in Yellowstone National park	The Journal of animal ecology	2003	Direct observation	Feeding	R

6.2 Protocol and Summary of Results for Thesis part 2 (drones)

My second question was: How are 1) UAVs and 2) camera traps used to observe the behaviour of wild terrestrial mammals?

Following the structure of the PRISMA 2009 guidelines for systematic reviews I processed the literature in four stages: 1) identification, 2) Screening, 3) Eligibility, and 4) Included.

In the 1) identification, articles were identified through a Scopus database search. I used the following query string: (TITLE-ABS-KEY (*behavio** AND (*wildlife* OR *animal*) AND (*drone* OR *uav* OR *uas* OR *rpas*)) AND NOT TITLE-ABS-KEY (*insect* OR *bee* OR *drosophila* OR *apis*)) AND (LIMIT-TO (SRCTYPE , *"j"*)) AND (LIMIT-TO (DOCTYPE , *"ar"*) OR LIMIT-TO (DOCTYPE , *"re"*))

The search result was 154 articles, which I screened with predetermined inclusion and exclusion criteria.

In the 2) Screening phase, the abstracts of the 154 articles were screened using the following inclusion and exclusion criteria:

Records excluded for the following reasons:

- Did not study behaviour
- Did not use visual observation methods
- Did not study terrestrial mammals

Records included for the following reasons:

- Studied behaviour
- Used visual observation methods
- Studied terrestrial mammals

139 articles were excluded in the 2) Screening phase based on the above inclusion and exclusion criteria. 15 articles were included and moved on to the 3) Eligibility phase.

In the 3) Eligibility phase the full texts of 15 articles were read using the following inclusion and exclusion criteria:

Records excluded for the following reasons:

- Did not study behaviour
- Did not use UAVs
- Did not study terrestrial mammals
- Did not study wild animals

Records included for the following reasons:

- Did study behaviour
- Used visual observation methods

- Did use UAVs
- Did study wild animals

7 articles were excluded in the 3) Eligibility phase based on the above inclusion and exclusion criteria. 8 articles were included and moved on to the 4) Included phase.

In the 4) Included phase, the 8 articles were analysed.

4a) (Main) behaviours:
Response to drones: 6
Heding: 2

4b) (main) species/taxa:
Herbivores: 5
Polar bears: 1
Many: 2

4c) Article type:
Research article: 4
Review: 3
Note: 1

Drone articles all authors

	First author	Article title	Journal	Year	Main behaviour	Main taxa / species	Article type
1	Go, C.K., Ringhofer, M., Lao, B., (…), Yamamoto, S. & Ikeda, K.	A mathematical model of herding in horse-harem group	Journal of Etholog y	2020	Herding	Horse	R
2	Schroeder, N.M., Panebianco, A., Musso, R.G. & Carmanchahi, P.	An experimental approach to evaluate the potential of drones in terrestrial mammal research: A gregarious ungulate as a study model	Royal Society Open Science	2020	Response to drone	Guanaco (Lama guanicoe)	R
3	Ringhofer, M., Go, C.K., Inoue, S., (…),	Herding mechanisms to maintain the	Journal of Etholog	2020	Herding	Horse	R

	Ikeda, K. & Yamamoto, S.	cohesion of a harem group: two interaction phases during herding	y				
4	Bennitt, E., Bartlam-Brooks, H.L.A., Hubel, T.Y. & Wilson, A.M.	Terrestrial mammalian wildlife responses to unmanned aerial systems approaches	Scientific Reports	2019	Response to drone	7 herbivore species	R
5	Rebolo-Ifran, N., Grilli, M.G. & Lambertucci, S.A.	Drones as a threat to wildlife: YouTube complements science in providing evidence about their effect	Environmental Conservation	2019	Response to drone	many	Review
6	Barnas, A.F., Felege, C.J., Rockwell, R.F. & Ellis-Felege, S.N.	A pilot(less) study on the use of an unmanned aircraft system for studying polar bears	Polar Biology	2018	Response to drone	Polar bear	N
7	Mulero-Pázmány, M., Jenni-Eiermann, S., Strebel, N., (...), Negro, J.J. & Tablado, Z.	Unmanned aircraft systems as a new source of disturbance for wildlife: a systematic review	PLoS ONE	2017	Response to drone	many	Review
8	Christie, K.S., Gilbert, S.L., Brown, C.L., Hatfield, M. & Hanson, L.	Unmanned aircraft systems in wildlife research: Current and future applications of a transformative technology	Frontiers in Ecology and the Environment	2016	Response to drone	caribou	Review

6.3 Protocol and Summary of Results for Thesis part 2 (camera traps)

My third question was how camera traps are used to observe the behaviour of wild wolves and other terrestrial mammals.

Following the structure of the PRISMA 2009 guidelines for a systematic review, I processed the literature in four stages: 1) identification, 2) Screening, 3) Eligibility, and 4) Included.

In the 1) identification articles were identified through a Scopus database search. I used the query string: (TITLE-ABS-KEY (*behavio**) AND TITLE-ABS-KEY (*camera* W/3 *trap* OR *game* OR *trail*)) AND (LIMIT-TO (DOCTYPE , *"ar"*) OR LIMIT-TO (DOCTYPE , *"re"*)) AND (LIMIT-TO (SRCTYPE , *"j"*))
The search resulted in 794 articles, which I screened with predetermined inclusion and exclusion criteria.

In the 2) Screening phase, the abstracts of the 794 articles were screened using the following inclusion and exclusion criteria:

Records excluded for the following reasons:
- Did not study behaviour
- Did not study wild terrestrial mammals
- Did not use visual observation methods

Records included for the following reasons:
- Did study behaviour
- Did study wild terrestrial mammals
- Did use visual observation methods, e.g. trail camera

622 articles were excluded in the 2) Screening phase based on the above inclusion and exclusion criteria. 190 articles were included and moved on to the 3) Eligibility phase.

In the 3) Eligibility phase the full texts of 190 articles was read using the following inclusion and exclusion criteria:

Records excluded for the following reasons:
- Did not study behaviour
- Did not use visual observation methods
- Did not study terrestrial mammals
- Did not study wild animals

Records included for the following reasons:
- Did study behaviour
- Did use visual observation methods
- Did study terrestrial mammals
- Did study wild animals

22 articles were excluded in the 3) Eligibility phase based on the above inclusion and

exclusion criteria. 168 articles were included and moved on to the 4) Included phase.

In the 4) Included phase, the 168 articles were analysed.

4a) (Main) behaviours:
Feeding (incl. foraging, drinking, geophagy): 43
Hunting (incl. predation): 8
Vigilance: 10
Inter-/intraspecies interactions: 9
Tool use: 8
Marking (urinary, rubbing etc.): 18
Response to camera traps: 3
Many: 41
Other (e.g. burrowing, digging, climbing, parental care, learning): 28

4b) (main) species:
Primates: 31
Rodents: 13
Felids: 19
Canids: 10
Bears: 11
Deer, moose: 10
Many: 30
Other (e.g.rhino, mongoose, peccary) :44