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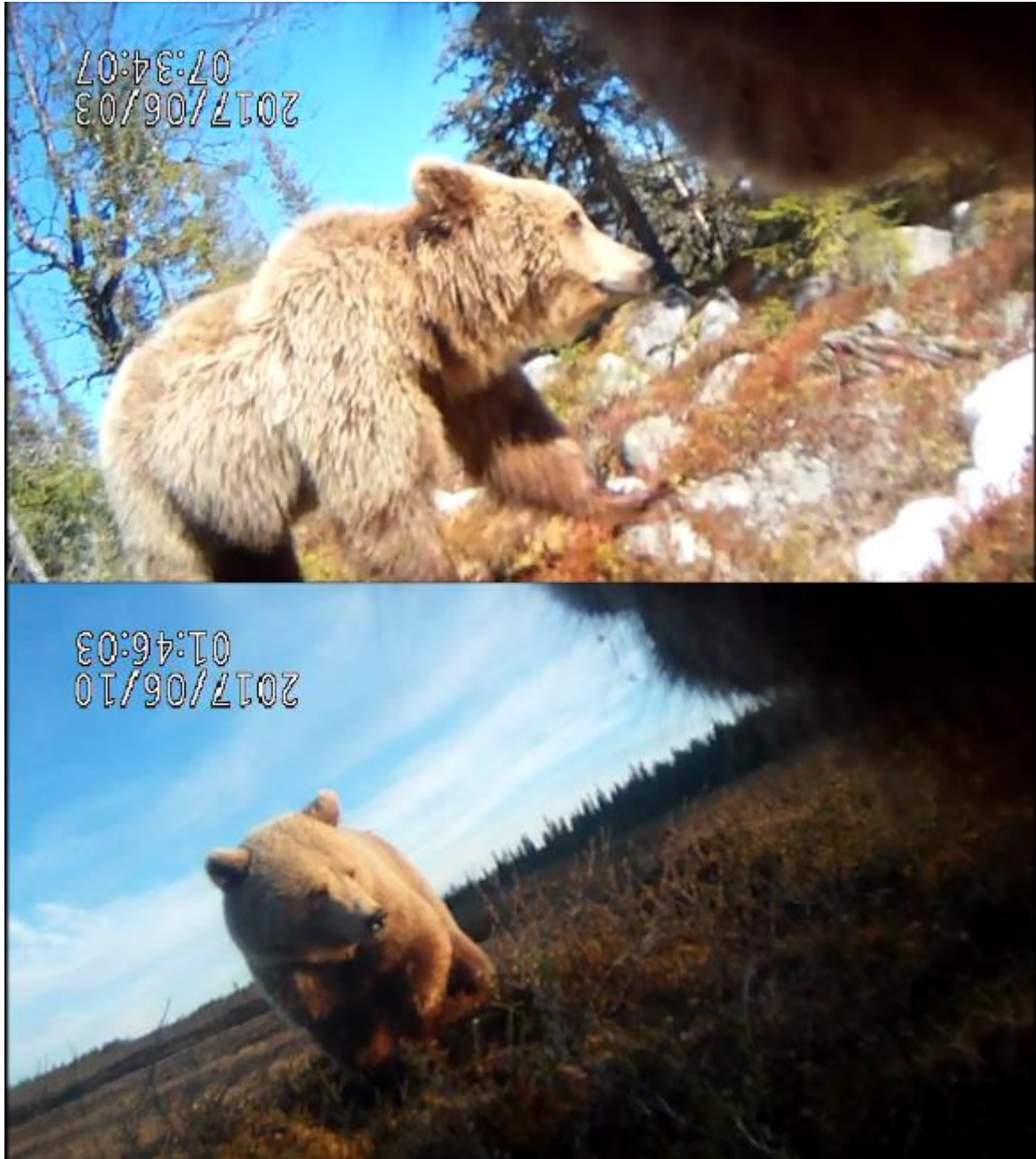
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The Use of Animal-Borne Video Systems to Study Foraging Ecology and Diel Behaviour: A Review and Case Study on the Scandinavian Brown Bear (*Ursus arctos*)

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Koskin's mating partner: Screenshots taken from video clips of the June 2017 male

Abstract

Animal-borne video systems, also known as Crittercams, were developed by Greg Marshall in the 1980s to capture video footage from the animal's perspective. Primarily deployed on marine species, such as attached to the carapace of green sea turtles (*Chelonia mydas*), animal-borne video systems have allowed researchers to gain novel insight into the behaviours and trophic interactions of elusive species. The objectives of this thesis are to review the published literature on animal-borne video systems in relation to foraging ecology and diel behaviour to provide a current synthesis of the capability of the technology and areas which require improvement. As well as present a case study on the use of video camera collars on Scandinavian brown bears (*Ursus arctos arctos*), with regard to their diel behaviour, food item consumption, and ungulate kill-rates. Literature was retrieved from online publication databases using keywords and sorted into six categories; reviews, methods, kill-rates, diet, activity patterns, and foraging behaviours which formed the basis of the review. The case-study was carried out in northern Sweden in 2017 and 2018. During this period, 4 brown bears (1 male, 3 female) were captured and fitted with video camera collars as well as a GPS tracking device. Video clips were recorded for 5 or 10 seconds every 3.5 or 5 minutes and all data were stored on board. Clips were then classified by behaviour (such as feeding or resting) and feeding behaviours were subcategorised into food items (reindeer calf *Rangifer tarandus f. domesticus*, moose *Alces alces*, vegetation etc.). For one bear, a reindeer calf kill-rate was estimated by the number of calves killed that were visible on video during deployment. To substantiate the video data kill-rate estimations, field observations were carried out at GPS cluster locations for one bear to look for carcasses. Animal-borne video systems enable further insight into cryptic species' diel activity, foraging behaviour, diet, and kill-rates. The use of this technology is still uncommon and it is limited by cost, weight and size, and battery life, however, there are a number of published studies which demonstrate its capabilities and the advantages it can have over other commonly used methods. The case study yielded 23 hours of useable video footage and showed that the bears in Spring spend the majority of time travelling whilst the Autumn bears were primarily resting or feeding on vegetation. Food item consumption was dependent on time of year and the results from the video data reflect those of previous research. It was estimated that 0.6 reindeer calves were killed per day from the video data, but field data revealed a higher estimate of 1.3 calves per day due to difficulties identifying foods consumed as a result of poor clarity. Animal-borne video systems are a suitable method to study foraging ecology and diel behaviour in many species. The technology is not without limitations, however, and in order for this method to be more widely applied these limitations must be reduced.

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1. Introduction

From attaching helium-filled balloons to turtles in the early 1960s (Carr, 1962) to outfitting penguins with video-recorder backpacks (Ponganis et al., 2000); wildlife researchers have continuously been able to discover novel insight into even the most elusive of species with the use of animal-borne devices. Bio-logging, the tracking of individual animals by attached tags, enables researchers to measure many aspects of species life such as their physiology, behaviour, interactions, and ecology (Wilmers et al., 2015). Time depth recorders (TDRs) and swim speed recorders allow for detailed dive profiles of marine species, whilst tri-axial accelerometers and global positioning system (GPS) tags enable precise location information and movement data for both marine and terrestrial species (Evans, Lea, and Patterson, 2013). Tags are also used for studies of the external environment, such as temperature and salinity, which aid further knowledge of species ecology and their adaptations to the ever-changing environment (Wilmers et al., 2015). Bio-loggers can be attached to almost any species large enough to carry the weight of the device, and methods of attachment include epoxy glue, harnesses, collars, and suction cups (Kooyman, 2007). The size and weight of the device was previously its main limiting factor, yet with increasing miniaturisation of such devices, researchers have been able to attach bio-loggers to individuals that weigh no more than 200g, such as the common diving petrel *Pelecanoides urinatrix* (Bocher, Labidoire, and Cherel, 2000).

With an ever-increasing overlapping human and wildlife niche, human-wildlife conflicts are inevitable as populations struggle to co-exist. To effectively manage such conflicts, it is vital to collect as much information about the species involved so that policies can be implemented efficiently and animal-borne video systems are one such method of data collection.

The objectives of this thesis are twofold: first, to present a thorough review of the literature regarding the use of animal-borne video systems to study foraging ecology and diel behaviour and evaluate its benefits and limitations. Secondly, present a case study on brown bears (*Ursus arctos*) in northern Sweden; and the capability of video data to provide an estimated ungulate kill-rate, document diel behaviour, and investigate food choices. The estimated kill-rate will be compared with field data collected from visited GPS cluster sites.

2. Literature review

2.1. Introduction

Although bio-loggers such as TDRs and GPS can give great insight into elusive species, humans tend to have a 'bias towards vision' (Ropert-Coudert and Wilson, 2005); which is perhaps why a bio-logger that can film events from the animal's perspective was revolutionary in the 1980's when Greg Marshall first created Crittercam and attached it to loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) turtles (Marshall, 1990). Since their conception, animal-borne video systems are most frequently used for public education and entertainment, and are still seldom used for ecological research (Moll et al., 2007). However, their use on marine species has revealed the first documented case of jellyfish consumption by a population of green sea turtles *Chelonia mydas* (Arthur et al., 2007) and more recently, researchers were able to uncover the mechanics of a 360 degree lunge roll used by blue whales (*Balaenoptera musculus*) to capture krill (Goldbogen et al., 2013). The use of animal-borne video systems in terrestrial species has documented intraspecific predation in brown and black bears (*Ursus americanus*) of North America, a behaviour once thought to be rare (Bowersock et al., 2015; Brockman et al., 2017), as well as the post-parturition behaviour of woodland caribou *Rangifer tarandus caribou* (Thompson et al., 2012). Furthermore, bird-borne video cameras demonstrated the potential to capture unknown foraging tactics in New Caledonian crows (*Corvus moneduloides*) with their use of hooked tools (Troschianko and Rutz, 2015).

Though the use of animal-borne video systems is somewhat extensive on marine animals, at least for marine reptiles, the technology has sparsely been applied on large carnivorous terrestrial mammals and published research is limited. This is likely due to differences in data collection methods between marine research and terrestrial research. In marine species fitted with cameras, data is often stored on-board and retrieved after re-capture. However, in terrestrial studies the majority of data was transmission-based, which required continuous proximity to the study subject, and this was problematic when studying potentially dangerous or shy species (Moll et al., 2009). Fortunately, with the transition to on-board storage systems for terrestrial studies, animal-borne video research on large carnivores is slowly gaining popularity (Moll et al., 2007). Devices are often also limited by weight and size (in spite of increased miniaturisation), battery duration, and cost; all of which can make animal-borne video systems the less-desirable method when other suitable methods exist. However, with recent advancements in these areas, their use is beginning to be recognised in the scientific field and they are enabling new insights into once enigmatic species, both in marine and terrestrial ecosystems.

More generalised reviews of animal-borne video systems and their applications in ecology have previously been published (Kooyman, 2007; Millsbaugh et al., 2008; Moll et al., 2007; Wilmers et al., 2015). However, the technology is advancing at such a rate that previous reviews are rapidly becoming outdated. What were once critical limitations are now less of an issue, such as device weight and data storage capacity. This review will provide researchers with up-to-date information on the applications of animal-borne video systems to study foraging ecology (kill-rates, diet, activity patterns, and foraging behaviour) and allow for a current assessment on whether this technology might now be as good as more traditional methods in foraging ecology research. The purpose is to document how far the technology has come, and how far it still has to go.

2.2. Methods

Google Scholar and Web of Science were used to search for all published literature. Key search terms used were 'animal borne video', 'animal borne sensors', 'animal video collar', 'camera collar on animals', and 'Critttercam'. The large scope of keywords was used as there is no official specific terminology for the use of animal-borne video systems, meaning much of the research could have been missed if the correct key word was not searched for. Furthermore, the search did not include terms related to foraging behaviour, kill-rates, diel behaviour, or diet as this was also found to exclude some research which utilised other terms. Therefore, after the initial search for the above keywords, all studies that included data about foraging behaviour, diel behaviour, kill-rates, and diet were included and the rest discarded due to irrelevance. In addition to these searches, reference lists from discovered studies were also used to find other relevant research. The literature includes all terrestrial and aquatic animals. Literature was then categorised thematically into 6 groups: studies of kill-rates, studies of diet, studies of activity patterns, studies of foraging behaviour, reviews, and methodological studies.

2.3. Literature overview

Of the searched literature, 62 published papers were relevant (see table 1). There were seven review articles which discussed the use of animal-borne video cameras in varying detail and focus and the remaining 47 papers were original research. Of the themes, the majority of published papers related to foraging behaviour and diet of species and very few focused on activity patterns or kill-rates. Not all research was carried out with clear hypotheses or objectives, for some of the terrestrial mammal research the motivation was rather to test the technology and demonstrate what it can be used for. There were also a number of papers which concentrated entirely on the methodology and the results from these were referred to in the limitations section of the review. Most of the relevant

research pertains to marine species; however, there is still considerable diversity among study species with all classes of vertebrates represented, excluding amphibians.

2.4. Results and discussion

Table 1: List of literature reviewed

Objective	Study species	Sample size	Key findings	Reference
Diet	Green turtle (<i>Chelonia mydas</i>)	17	Gelatinous prey more important than previously thought and seagrass not as important	Burkholder et al., 2011
Diet	Green turtle (<i>Chelonia mydas</i>) Loggerhead turtle (<i>Caretta caretta</i>)	25	Loggerhead fed on artificial debris 2 times. Green turtles ingested artificial debris 21 times	Fukuoka et al., 2016
Diet	Green turtle (<i>Chelonia mydas</i>) Loggerhead turtle (<i>Caretta caretta</i>)	25	Surprisingly large number of green turtles foraged on gelatinous prey. Approx. 40 jellyfish/day	Heithaus et al., 2002b
Diet	Woodland caribou (<i>Rangifer tarandus caribou</i>)	15	Video did not have same species resolution as DNA barcoding. Video can provide relative preference for diet	Newmaster et al., 2013
Diet	Hawaiian monk seal (<i>Neomonachus schauinslandi</i>)	9	All prey were cryptic benthic species, sand prey dominant species and not coral fish as previously thought	Parrish et al., 2005
Diet	Adélie penguin (<i>Pygoscelis adeliae</i>) Yellow-eyed penguin (<i>Megadyptes antipodes</i>) Magellanic penguin (<i>Spheniscus magellanicus</i>) Little penguin (<i>Eudyptula minor</i>)	106	Predation on jellyfish for all 4 penguins. 0.9 gelata/hour. Jellyfish were often consumed whole even when other prey was abundant	Thiebot et al., 2017
Diet & Foraging behaviours	Harbour seals (<i>Phoca vitulina</i>)	39	Cruising tactic for sand lance prey, digging not used often, seals regurgitate prey	Bowen et al., 2002
Diet & foraging behaviours	Green turtles (<i>Chelonia mydas</i>)	34	Consumption of brown macrolage and annelid worms which were novel findings	Seminoff, Jones, and Marshall, 2006
Diet & activity	North American brown bear	3	Black bears had greater variety in diet. Brown bear more carnivorous	Bowersock et al., 2015

patterns	<i>(Ursus arctos horribilis)</i> American black bear (<i>Ursus americanus</i>)			
Diet & methods	Green turtle (<i>Chelonia mydas</i>)	8	Gelatinous prey was more important than previously thought and diet is more diverse	Arthur et al., 2007
Diet & methods	Domestic dog (<i>Canis familiaris</i>)	6	69% of contact was direct physical, food items identified were soiled nappies, chicken, raw bones, carcasses, and grass	Bombara et al., 2017
Diet & methods	Australian fur seals (<i>Arctocephalus pusillus doriferus</i>)	16	Great variety of prey, great individual variation: some specialist others generalist	Kernaleguen et al., 2016
Diet & methods	Yellow-eyed penguin (<i>Megadyptes antipodes</i>)	1	Prey pursuits and captures all occurred in benthic zone. Opal fish and blue cod as important as first thought	Mattern et al., 2018
Diet, foraging behaviours & methods	Domestic cat (<i>Felis catus</i>)	60	30% capture success, reptiles dominant prey, only 28% of prey consumed, 49% left at capture site	Loyd et al., 2013
Diet, kill-rates & methods	Domestic cat (<i>Felis catus</i>)	31	6.15 kills/day, invertebrate kills: 4.95/day, vertebrate kills: 4.37/day, 44% efficacy, efficacy reduced for mammalia. Dusk and dawn key time	Hernandez et al., 2018
Diet, kill-rates, activity patterns & methods	Brown bear (<i>Ursus arctos</i>)	17	Majority of time resting. 1.2 calf kills/day. Intraspecific predation observed	Brockman et al., 2017
Diet, activity patterns, foraging behaviours & methods	Adélie penguin (<i>Pygoscelis adeliae</i>)	15	Krill dominant prey, remarkably fast prey capture of 2 krill/second	Watanabe and Takahashi, 2013
Activity patterns	Woodland caribou (<i>Rangifer tarandus caribou</i>)	5	Feeding occurred 30% of the time, fed entirely on ground and arboreal lichens	Thompson et al., 2012
Activity patterns & methods	white-tailed deer (<i>Odocoileus virginianus</i>)	1	120 food choices made, documented time spent feeding, resting, grooming, and breeding	Beringer et al., 2004
Activity patterns, kill-rates, foraging behaviours & methods	American alligator (<i>Alligator mississippiensis</i>)	15	0.49 attacks/hour and 0.52 captures/attack. Most attacks at night, greatest success in morning. Position in water column influenced success	Nifong et al., 2014
Foraging behaviours	Blue whale (<i>Balaenoptera musculus</i>)	17	Feeding by upwards lunges into prey and inversion on approach to prey	Calambokidis et al., 2002

Foraging behaviours	Blue whale (<i>Balaenoptera musculus</i>)	35	Feeding depth was shallower at night in response to migration of prey, rapid acceleration towards prey and sudden deceleration just before patch	Calambokidis et al., 2007
Foraging behaviours	Weddell seal (<i>Leptonychotes weddellii</i>)	10	Found contradictory results to foraging dive types than previously reported	Davis et al., 2003
Foraging behaviours	Weddell seal (<i>Leptonychotes weddellii</i>)	22	Found supporting results to their previous study, foraging primarily in type I dives	Davis et al., 2013
Foraging behaviours	Weddell seal (<i>Leptonychotes weddellii</i>)	10	Less time in meandering descent led to more successful dives	Fuiman et al., 2007
Foraging behaviours	Blue whale (<i>Balaenoptera musculus</i>)	22	The roll enables whales to reach the krill patch, without it they would likely miss	Goldbogen et al., 2013
Foraging behaviours	Gyrfalcon (<i>Falco rusticolus</i>) Gyrfalcon/Saker falcon hybrid (<i>Falco rusticolus</i> X <i>F. cherrug</i>) Peregrine falcon (<i>F. peregrinus</i>)	8	No evidence of classical pursuit, use of shallow fovea, motion cues to track prey	Kane and Zamani, 2014
Foraging behaviours	Northern Goshawk (<i>Accipiter gentilis</i>)	1	Success of 6%/prey and 8%/pursuit, used classical pursuit for stationary prey and constant absolute target direction for moving targets	Kane, Fulton, and Rosenthal, 2015
Foraging behaviours	leopard seal (<i>Hydrurga leptonyx</i>)	7	Flush and stalk was more successful than chase pursuits, evidence of kleptoparasitism and scavenging	Krause, 2015
Foraging behaviours	Weddell seal (<i>Leptonychotes weddellii</i>)	13	3 distinct foraging groups identified, dive type dependent on preferred depth of prey, silverfish primary prey	Madden et al., 2008
Foraging behaviours	Polar bear (<i>Ursus maritimus</i>)	9	Scavenging muscle from subsistence hunted seals was common, locomotion was main energy expenditure not hunting	Pagano et al., 2018
Foraging behaviours	Hawaiian monk seal (<i>Neomonachus schauinslandi</i>)	44	Different feeding tactics depending on habitat, moving of heavy rocks with neck and shoulders, sharks used seals to flush out prey	Parrish and Littnan, 2007
Foraging behaviours	Hawaiian monk seal (<i>Neomonachus schauinslandi</i>)	24	All feeding was on demersal benthic fish. Seals fed in commercial fishery areas	Parrish et al., 2000
Foraging behaviours	Hawaiian monk seal (<i>Neomonachus schauinslandi</i>)	42	Escort behaviour was most common, greater feeding success for seals in presence on predatory fish	Parrish et al., 2008
Foraging behaviours	Thick-billed murre (<i>Uria lomvia</i>)	8	2.4 prey/ascent All subjects fed from prey between jellyfish tentacles, jellyfish blooms thought to create new feeding	Sato et al., 2015

		opportunities		
Foraging behaviours	Green turtle (<i>Chelonia mydas</i>) Loggerhead turtle (<i>Caretta caretta</i>)	26	Feeding in all dive types for green turtles, feeding in 4/6 for loggerhead. Gradual ascent important for green turtles for gelatinous prey consumption. All feeding for loggerhead on sea floor	Thomson, Heithaus, and Dill, 2011
Foraging behaviours	Cape gannet (<i>Morus capensis</i>)	36	Over 90% were associated with other predators when foraging, transfer of information between returning gannets and foraging gannets	Tremblay et al., 2014
Foraging behaviours	Woodland caribou (<i>Rangifer tarandus caribou</i>)	9	All females selected habitat for food abundance, calving mothers select habitat more to reduce predation risk than for food abundance	Viejou et al., 2018
Foraging behaviours	Humpback whale (<i>Megaptera novaeangliae</i>)	1	Bottom sea floor is contacted during the feeding roll, the roll begins at slow speed so is not a lunge	Ware et al., 2013
Foraging behaviours	brown booby (<i>Sula leucogaster</i>)	3	Young boobies fly and dive with conspecifics or other seabirds to gain foraging information	Yoda et al., 2011
Foraging behaviours & methods	Gentoo penguin (<i>Pygoscelis papua</i>)	38	No active pursuit for smaller prey but did for larger prey. Lobsters used grouping as predator avoidance strategy which led to lower capture rate	Handley et al., 2018
Foraging behaviours & methods	Emperor penguins (<i>Aptenodytes forsteri</i>)	3	Mean dive duration: 4.2 mins., 80% capture rate, hunting ascents were successful 77%	Ponganis et al., 2000
Foraging behaviours & methods	New Caledonian crows (<i>Corvus moneduloides</i>)	18	Highlighted importance of ground foraging, demonstrates extensive tool use and favouritism of tools	Rutz et al., 2007
Foraging behaviours & methods	New Caledonian crows (<i>Corvus moneduloides</i>)	19	¼ of activity involved foraging, 19% of foraging involved tools, 2 instances of hooked tool use	Troscianko and Rutz, 2015
Foraging behaviours, kill-rates & methods	Tiger shark (<i>Galeocerdo cuvier</i>)	22	5 successfully captured prey. Few encounters resulted in predation	Heithaus et al., 2002a
Foraging behaviours, kill-rates & methods	Feral cat (<i>Felis catus</i>)	13	7.2 kills/day, majority at night. 44% were frog species. Prey not consumed in 28% of kills. Success more likely in open habitats	McGregor et al., 2015
Kill-rates	Leatherback turtle (<i>Dermochelys coriacea</i>)	24	16 jellyfish consumed/hour	Wallace, Zolkewitz and James, 2018
Methods	Whitetailed deer (<i>Odocoileus virginianus</i>)	26	Deer-borne cameras are valuable in studying contact rates. Memory capacity is limited and capture of deer can lead to stress fatalities	Lavelle et al., 2012
Methods	Whitetailed deer (<i>Odocoileus virginianus</i>)	15	Camera collars can provide increased detail on food habits than other methods. Expense can be limiting	Lavelle et al., 2015

Methods	Whitetailed deer (<i>Odocoileus virginianus</i>)	4	Camera collars allowed revealed data that no other method could collect but had limitations	Moll et al., 2009
Methods	Ocean sunfish (<i>Mola mola</i>)	4	Video cameras attached did not receive sufficient light at great depths to distinguish food items	Nakamura, Goto, and Sato, 2015
Methods	Loggerhead Turtles (<i>Caretta caretta</i>)	7	Video data provided data for turtle foraging locations but was limited by light	Narazaki et al., 2013
Methods	Dusky dolphins (<i>Lagenorhynchus obscurus</i>)	8	Dolphins did not exhibit any unusual or modified behaviour whilst cameras were attached	Pearson et al., 2017
Methods	Cape Gannets (<i>Morus capensis</i>)	36	Video cameras were able to observe the social interactions of gannets in flight. Cameras did not affect behaviour	Thiebault et al., 2014
Methods	Adélie penguins (<i>Pygoscelis adeliae</i>)	28	Devices have been miniaturised and are able to be applied to small species	Thiebot et al., 2016
Methods	Woodland caribou (<i>Rangifer tarandus tarandus</i>)	23	Videos were suitable to assess diet in caribou but technical issues prevented remote release for all individuals which led to re-capture	Thompson et al., 2015
Methods & review	-	-	Upgrades to the original Crittercam allow for deployment on smaller species and have higher storage capacity	Marshall et al., 2007
Methods & review	-	-	Chapter gives an overview of the technology and its applications as well as limitations	Millspaugh et al., 2012
Review	-	-	Animal-borne video cameras can provide precise data for species but are currently limited by cost and thus sample size	Evans, Lea, and Patterson, 2013
Review	-	-	Animal-borne video cameras can be attached in many different methods to suit all species of any shape or size	Kooyman, 2007
Review	-	-	Animal-borne video systems are an becoming more popular and the technology is rapidly improving, thus reducing limitations	Moll et al., 2007
Review	-	-	Video data is very beneficial as humans are often biased towards vision	Ropert-Coudert and Wilsson, 2005

Review	-	-	Bio-loggers are essential tools as they enable data collection on all aspects of an individual as well as the environment	Wilmers
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2.4.1. Animal-borne video systems and kill-rates

Determining the kill-rate informs researchers on the number of prey killed per individual predator over a given time and provides information on the predator’s consumption habits and energy budgets (Vucetich et al., 2011). Estimation of kill-rates not only provides information on prey-predator dynamics but can also aid management decisions for human-wildlife conflict in instances of livestock predation and protection of prey species and habitats to maintain equilibrium. Many methods for estimating kill-rates are practiced and none are without their limitations. However, the use of animal-borne video systems is allowing researchers to observe predation events as they happen and not infer them from movement sensors or observe them from short durations in aerial studies (Brockman et al., 2017).

Crocodylian species are an understudied predator and previous estimates of kill-rates were only possible by observing above-water events and stomach content analyses. With the use of animal-borne video systems, Nifong et al. (2014) conducted the first study on submerged and nocturnal feeding events in American alligators (*Alligator mississippiensis*). Though this estimate was higher than previous estimates for other crocodylian species from daytime observations, it was supported by stomach content analysis from other studies (Nifong et al., 2014). The observations obtained from the alligator-borne video cameras also provided temporal dimensions which linked high predation rates to specific times of day and this precision had not been achieved with any other method (Nifong et al., 2014). Other studies on reptilian species were able to attach video cameras to the carapace of leatherback turtles and identified an average kill-rate of 16 jellyfish per hour, which equates to roughly 50% of their body mass, and was in line with previous studies of energetic acquisition requirements for population viability (Wallace, Zolkewitz, and James, 2018).

For cryptic species, researchers were often reliant on inference data to estimate kill-rates, such as mortality in collared prey, and these methods are susceptible to under- or over-estimation and overlook individual differences (Rauset, Kindberg, and Swenson, 2012). Estimates of ungulate calf kill-rates by video collared American brown bears were found to be substantially higher than earlier estimates (Brockman et al., 2017) and this was also apparent in a study of tiger sharks (*Galeocerdo cuvier*) whereby 10 feeding events were observed via video data in only 49 hours (Heithaus et al., 2002a).

The importance of kill data is not limited to wild species, predation from domestic owned and feral cats (*Felis catus*) is of growing concern and in the United States alone, domestic cats are thought to kill 1.3-4.0 billion birds and 6.3-22.3 billion mammals annually (Loss, Will, and Marra, 2013). Very recent applications of animal-borne video systems on domestic cats show that there is little difference between the kill-rates of domestic cats and those of feral cats, with both averaging kill-rates of 6.15 and 7.2 kills per day respectively (Hernandez et al., 2018; McGregor et al., 2015).

The ability to utilise this technology to study individual predation events has allowed researchers to understand the extensive variation among individuals; one alligator demonstrated a feeding frenzy during the video camera deployment and attacked 18 prey in just one hour, 3 domestic cats consumed more than 12 prey in 24 hours, and calf kills varied from 0-30 during the brown bear video collar deployment (Nifong et al., 2014; Hernandez et al., 2018; Brockman et al., 2017). This individual variability in predation has important consequences for management strategies of species populations, whereby selective removal of high-predating individuals could prove more effective than random culling (Brockman et al., 2017).

2.4.2. Animal-borne video systems and diet

Much of the animal-borne video systems research has focused on marine species; none more so than the green sea turtle and this work has been remarkable for providing novel insight into their diet. Prior to the use of animal-borne video systems, the diet of green sea turtles was considered to be primarily of seagrass. However, multiple video studies have since discovered that the consumption of jellyfish and other ctenophores is not incidental but rather a primary food source and relatively little seagrass is consumed in comparison (Arthur et al., 2007; Burkholder et al., 2011; Heithaus et al., 2002b). Furthermore, another study revealed that green sea turtles also fed on brown macroalgae (*Phaeophyceae spp.*) and annelid worms (*Annelida spp.*), providing evidence for more varied diet than formerly known (Seminoff, Jones, and Marshall, 2006). The importance of gelata (gelatinous zooplankton) in marine species diets was also underestimated for some penguin species, Thiebot et al. (2017) recently discovered that yellow-eyed (*Megadyptes antipodes*) and Adélie penguins (*Pygoscelis adeliae*) not only consume gelatinous prey often, they also choose to consume it when other prey is abundant. Though not yet as common, animal-borne video systems on terrestrial species have also demonstrated the ability to reveal novel insight into enigmatic species. In two separate studies, video collars were able to capture intraspecific predation (cannibalism) events in brown and black bears which, though not unheard of, was thought to be an infrequent behaviour but perhaps it is more common given its occurrence in both video studies on bear species in North America (Bowersock et al., 2015; Brockman et al., 2017).

Moreover, the use of animal-borne video systems to study diet has enabled researchers to substantiate or contradict earlier findings using other methods such as stomach content or faecal analyses. Studies on penguins and domestic cats have demonstrated that video data are just as effective at studying diet composition as traditional methods (Mattern et al., 2018; Watanabe and Takahashi, 2013; Hernandez et al., 2018). Furthermore, some research indicates that video data is more accurate than stomach content analysis. In the case of harbour seals (*Phoca vitulina*), video footage shows seals regurgitating their prey at varying levels of digestion (Bowen et al., 2002). This makes it difficult for stomach content analysis to accurately know what has been consumed as some prey will not be left in the stomach. Similarly, the consumption of gelatinous prey is often misrepresented during analysis as it digests faster than other prey types (Heithaus et al., 2002b). Additionally, Hawaiian monk seal (*Neomonachus schauinslandi*) diets were presumed to consist of primarily coral fishes but video analysis found sand fishes to be more prevalent; likely due to the biases of faecal analysis in which specific classification of lower taxonomic ranks are usually unidentifiable below the family taxon (Parrish et al., 2005). However, more recent technology has enabled more in-depth analysis of faecal matter, for example DNA barcoding of faecal matter in woodland caribou was able to accurately identify diet items with high taxonomic specificity and the use of animal-borne video data was able to corroborate these findings (Newmaster et al., 2013). Isotope analysis has also been used to identify diets of species (Newmaster et al., 2013; Kernaleguen et al., 2016). This method is able to recognise long-term dietary preferences but cannot account for short-term changes or preferences. When compared with animal-borne video data, isotope analysis of Australian fur seal (*Arctocephalus pusillus*) whiskers did not concur with the diet assumptions (Kernaleguen et al., 2016). Animal-borne video systems are not designed for long-term deployments, which reduces their capability to study long-term behaviours but their design allows researchers to study fine-scale details at an individual level in the short-term which may have long-term impacts on populations.

Novel findings regarding the diets of species can have implications in terms of species and prey management, mitigating human-wildlife conflicts, and even understanding disease transmission. With the recent knowledge that Hawaiian monk seals predate more on sand fishes than coral species, it is in the interest of management groups to ensure that prey recruitment to the sand fields is not negatively impacted by oceanographic regimes (Parrish et al., 2005). Likewise, the effect on native reptilian and amphibious species from domestic cat predation warrants further investigation after it was found by multiple animal-borne video studies that they were the highly predated (Lloyd et al., 2013; Hernandez et al., 2018). This could have implications for both native reptile and amphibian species conservation but also for pest control of unwanted species in urban areas.

Bowersock et al. (2015) documented the feeding behaviour of both brown (grizzly) and black bears foraging in an apple orchard. Using the video data of these events could allow researchers to further accurately understand the impact and dynamics of large carnivores on crop raiding or livestock predation behaviours. For example, it was found that black bears pick individual fruits off the trees whereas grizzly bears were more likely to damage entire branches to get to the fruit (Bowersock et al., 2015). Though it was not the aim of the study, Bombara et al. (2017) observed a video-collared free-ranging domestic dog (*Canis lupus familiaris*) consuming a soiled nappy (diaper) and earlier studies showed that human faecal matter regularly appeared in the diet of such dogs. Coprophagy from domestic dogs is likely then to enable the transmission of zoonotic diseases to other dogs and to humans who have contact with them. Finally, with recent media attention of plastic waste, particularly in the oceans, the findings from video studies that turtles regularly consume gelatinous species has major implications for the impact of floating plastic in the ocean being consumed by marine species. In fact, green sea turtles were found to ingest artificial debris 21 times and loggerhead turtles on 2 occasions over the course of 52-60 hours of animal-borne video deployments (Fukuoka et al., 2016). This highlights the importance of reducing the plastic waste in the oceans as it bears a striking resemblance to sought-after prey for some species.

2.4.3. Animal-borne video systems and activity patterns

One of the primary benefits of employing animal-borne video systems to study behaviour is the minimal disruption to the individual and surrounding environment compared with other methods such as aerial observations or ground observations, whilst still allowing for visual data to be collected. Animal-borne video systems have the ability to capture behaviours unadulterated in natural habitats. For species in which direct observations are difficult, this is a valuable tool to understand the 'normal' habits and diel behaviour of species. During the video collar deployments on brown and black bears in North America, researchers were able to gain precious insight into the heterogeneity of diel activity patterns (Bowersock et al., 2015; Brockman et al., 2017) and for two deer species, knowing the time spent on specific behaviours has facilitated precise modelling of ecological energetics (Beringer et al., 2004; Thompson et al., 2012).

Research into the behaviour patterns of estuarine Floridian alligators is scarce, yet Nifong et al. (2014) using video data substantiated the postulation, from the sole previous study, that daytime activity was likely correlated to thermoregulatory behaviours such as basking and cooling, and their nocturnal activity was associated with foraging behaviours (Watanabe et al., 2013). Moreover, animal-borne video systems were able to document unique parturition behaviours in a woodland caribou cow and calf whereby predators were avoided by travelling to an island away from the

'nursery' area (Thompson et al., 2012). The capacity to link activity patterns to other factors, such as thermoregulation or parturition, allows researchers to gain intricate fine-scale knowledge of ecological processes, life-history, and general biology of species in their natural environments.

2.4.4. Animal-borne video systems and foraging behaviours

Capturing foraging events on video enables the observation of specific behaviours in relation to specific prey. Though many species are diet generalists, this does not necessarily mean that they have the same predation strategy for all prey or habitat types. Through animal-borne video cameras, seals have been observed performing multiple predation strategies such as cruising, stalking, and flushing. Each of these behaviours has been found to be prey and habitat specific and increases the chance of prey capture (Bowen et al., 2002; Parrish and Littnan, 2007). Similarly, video data revealed that green sea turtles, tiger sharks, and Weddell seals (*Leptonychotes weddellii*) also adapt their foraging strategy to prey types based on where in the water column they are located to ensure optimal foraging (Seminoff, Jones, and Marshall, 2006; Heithaus et al., 2002a; Madden et al., 2008). Furthermore, analysis of video data paired with movement data enables the classification of particular predation movements; such as dives in marine species and flight pursuits in avian species. For marine species such as penguins, seals, and turtles, the classification of dive types from video data shows the detailed sequence of events from prey encounter to prey capture and has provided fresh insight into when, how fast, and where foraging occurs (Davis et al., 2003; Davis et al., 2013; Fuiman et al., 2007; Ponganis et al., 2000; Watanabe and Takahashi., 2013; Thomson, Heithaus, and Dill, 2011). Finally, animal-borne cameras fixed to the head and backs of hunting birds revealed differing pursuit strategies in different birds and provided robust data that was used to understand the visual field of movement when prey was located and pursued in flight (Kane and Zamani, 2014; Kane, Fulton, and Rosenthal, 2015).

Animal-borne video data has also been used to describe trophic interactions in scarcely studied species. In leopard seals (*Hydrurga leptonyx*) for example, kleptoparasitism and scavenging were found to be frequent behaviours which demonstrates their ability to affect trophic levels in more ways than just direct predation (Krause et al., 2015). In addition, woodland caribou selected habitat with high dietary biomass but, upon calving, habitat was then chosen based on predator avoidance not on forage availability; suggesting that both top-down and bottom-up processes can influence their fitness (Viejou et al., 2018). Video data from foraging seabirds documented the unique direct impact of jellyfish blooms on marine predators and concluded that the blooms attracted aggregations of fish among the tentacles, which provided high prey density for marine predators thus providing a positive direct trophic impact (Sato et al., 2015). Exploitative competition, both

inter and intra-specific, can often negatively affect species fitness due to limitation of food resources. In monk seals, animal-borne video found that inter-specific competition between juvenile seals and sharks was high and prey was often 'stolen' after it was flushed by the seal (Parrish and Littnan, 2007; Parrish et al., 2008). Nevertheless, competition can sometimes benefit species and improve foraging efficiency if prey is abundant. Such as the case for Cape gannets (*Morus capensis*) and brown boobies (*Sula leucogaster*) carrying video devices; whereby the presence of conspecific and heterospecific predators led to an increase in forage patch detection and suggests that predator abundance could be more influential than prey abundance (Tremblay et al., 2014; Yoda et al., 2011). Furthermore, prey abundance must not be assumed to equal prey availability. Although abundant, it was observed via animal-borne video data that lobster-krill (*Munida spp.*) employed behaviourally mediated predator avoidance, in the form of communal defence, to reduce predation from Gentoo penguins *Pygoscelis papua* (Handley et al., 2018). This finding demonstrates the importance of multiple methods to study predator-prey interactions to avoid over-simplifying a complex marine dynamic.

Studying the effect of human presence on wild animals is vital for creating effective and beneficial management and legislation and animal-borne video cameras can add further knowledge to the role of humans in non-human animal ecology. This can be illustrated by the animal-borne video footage of polar bears (*Ursus maritimus*) consuming the remains of seals from subsistence hunting humans (Pagano et al., 2018). Though human populations may have a negative impact on polar bears through a variety of channels such as climate and habitat change, this data has also shown that polar bears' diets can be subsidised by human hunting behaviours; consequently having a positive impact. Conversely, the overlap of human communities and other species can also be detrimental to both parties. Animal-borne video data revealed that monk seals also forage in commercial fishing waters, which will likely increase the conflict between livelihoods of fishermen and the already endangered monk seal (Parrish et al., 2000). Yet some perceived conflicts are born from false information, such as the high injury rate of commercial fish from cormorant (*Phalacrocorax spp.*) predation. Video analyses from bird-borne cameras were used to refute the claim after it was discovered that only 0.4% of prey was injured without ingestion (Grémillet et al., 2006). Other findings from video collars on domestic and feral cats exposed the need for altered management and research strategies. Half the captured prey by video-collared domestic cats was left at the capture site and not ingested, which calls into question the validity of stomach content analysis and prey brought home as a means of determining the effect of these skilled predators on wildlife (Lloyd et al., 2013). Furthermore, McGregor et al. (2015) found that video-collared feral cats were more successful hunters when prey was in open areas. Therefore, in order to reduce the impact of predation on native species, it is

proposed that restoration of dense grassy areas, management of feral herbivore populations, and prevention of wildfires would offer more refuge to prey.

The application of animal-borne video systems' greatest benefit is perhaps its use to detect novel behaviours. Researchers deploying suction-cup attached video cameras to the backs of blue and humpback whales (*Megaptera novaeangliae*) have been able to document for the first time the exact movement, both spatially and temporally, involved in 360 degree rolls used when foraging krill patches (Calambokidis et al., 2002; Calambokidis et al., 2007; Goldbogen et al., 2013; Ware et al., 2013). Lastly, bird-borne video cameras have added further knowledge into the tool-use phenomena by New Caledonian crows. On 2 separate deployments, New Caledonian crows were seen foraging on the ground using crafted sticks to dig up substrate and creating hooked tools to more effectively forage in tree bark, both of which have not been documented before (Rutz et al., 2007; Troscianko and Rutz, 2015). In addition, one crow utilised the same tool for more than 18 minutes and flew with it to different foraging locations, indicating that not only do crows commonly create their own tools but they have preferred tools (Rutz et al., 2007).

2.5. Limitations

2.5.1. Weight and size

There are no specific guidelines or protocol regarding the application and deployment of animal-borne video systems, yet it is often considered most ethical to limit the device weight to 3-5% of the animals body weight (Millspaugh et al., 2012). This has long proved a challenge for researchers as reducing the weight means smaller batteries and therefore shorter deployment durations. However, as the technology advances, batteries have been minimised without drastically compromising their power capacity. This has facilitated the development of miniaturised animal-borne video devices which weigh no more than 15g (Thiebot et al., 2016). These devices are beneficial as they not only reduce the weight but also the size of the unit. Earlier studies using devices of the recommended weight stated that drag effects and excessive weight seemed to interfere with normal movement such as dive duration and depth in marine species (Ponganis et al., 2000; Handley et al., 2018) and jumping and climbing to catch avian prey in domestic cats (Hernandez et al., 2018). Nonetheless, there is also evidence to suggest that if there are effects, they are negligible and do not contribute to any long-lasting changes in behaviour or fitness as devices are not deployed for long periods (Pearson et al., 2017; Rutz et al., 2007; Thiebault et al., 2014). Regardless of long term effects, it is in the interest of researchers to ensure the devices used do not cause harm or alterations in behaviour so that the data collected is valid.

2.5.2. Battery performance

Restricted by weight and size, most devices cannot incorporate the battery capacity needed for long term-deployments and so the primary limitation of animal-borne video systems is the battery-life (Bombara et al., 2017; Kernaleguen et al., 2016). For some studies, this led to insufficient data collection for entire foraging trips of marine species; Thiebot et al. (2017) were only able to gather data for less than 25% of the duration for penguin foraging dives. Furthermore, battery-life was found to be significantly affected by extraneous factors such as temperature and insufficient housing, which likely reduced the battery life in one study by 30-40% when the temperatures dropped below freezing (Beringer et al., 2004; Moll et al., 2009). There are, however, a number of improvements that can be made to extend battery life. Duty cycling can be programmed so that video is only recorded during certain times of day that researchers feel would be the most important times to have footage for. Though ultimately there is a trade-off between capturing continuous footage for shorter durations or only capturing shorts clips throughout the deployment and risk missing vital information. Additionally, devices can be programmed to automatically switch off when no motion is detected or when light levels drop too low (Beringer et al., 2004; Lloyd et al., 2013). This enables researchers to preserve battery life without the risk of missing crucial behaviours or wasting storage and battery on unclear footage. Other solutions have involved fitting extra batteries to devices when the animals are large enough to carry more and using re-chargeable batteries (McGregor et al., 2015). Owing to their domesticity, the animal-borne studies on cats were able to increase deployment duration by charging batteries every 24 hours (Hernandez et al., 2018). Unsurprisingly, this is not feasible in most wild animal research but with the rate of technological progression battery limitations might soon be diminished.

2.5.3. Data collection

Original animal-borne video devices were severely limited in their capacity to store the video data. Marshall's first generation of CritterCam™ devices stored their data on-board 8mm video tapes which could only store up to 6 hours of footage and were extremely heavy and large (Marshall et al., 2007). For terrestrial species, many devices were transmission based and so did not suffer the capacity issues of on-board storage. However, transmission interference often caused poor quality footage, reduced battery life, and if transmission was lost (either out of range or no power) then all the data would be lost (Marshall et al., 2007). Beringer et al. (2004) cited transmission limitations in their study on white-tailed deer due to the short 500m range of the transmission and poor quality data from local interference. Most recently, memory cards such as Secure Digital (SD) are being used on animal-borne video devices and these have lowered the weight and size of units as well as

improved the capability and capacity to collect uninterrupted video data (Troscianko and Rutz, 2015). Yet, researchers have still found that memory cards become full sooner than they predicted (Lavelle et al., 2012), indicating that there are still improvements to be made. Be that as it may, the rate at which storage capacity is increasing for memory cards is phenomenal. Currently, commercial memory cards can store just over 500GB of data but it is expected that memory cards will soon be able to hold over 2TB of data to keep up with data-heavy formats such as 4K. After which, the limitation will shift from capacity to cost.

2.5.4. Cost

At present, the cost of the device comprises 4 components; the battery, the memory card, the video equipment, and the production. Though one might assume the cost of devices would decrease as technology becomes more readily available, devices are still fairly cost prohibitive. Prices of devices have been reported to be from anywhere between 300-900 US Dollars (Lavelle et al., 2015; Beringer et al., 2004) and as the battery, storage, and video technology improves the price also increases. Yet, the benefits of using animal-borne devices to acquire novel data are a potential justification to use such expensive equipment over traditional methods (Newmaster et al., 2013). Although for this data to be representative of populations it must contain a large sample, something of which is currently restricted due to the cost.

2.5.5. Sampling

From the present data collected via animal-borne video systems, sample sizes from each study varied from 1 individual to 106 (Ware et al., 2013; Thiebot et al., 2017), and the average sample size of 20 individuals. Small sample sizes are frequently due to either the cost involved or the time and effort required to capture the individuals and implement the devices. Without large sample sizes, data should not be generalised on a population level as the sample is not likely representative of the population as a whole (Croft, James, and Krause, 2008). Even with small samples, animal-borne video studies have documented the large variation in individual behaviours which could lead to false assumptions about populations (Brockman et al., 2017). As a result of the cost and difficulty in capturing study species, many samples are also not selected at random. Selection of individuals who are known to have high kill-rates has been favoured to ensure that there is data and the video footage is worthwhile (Brockman et al., 2017). Additionally, selection biases when capturing prey are also worth noting. Baiting of sharks for capture and subsequent video camera deployment introduces a sampling bias as famished sharks are more likely to go for the bait (Heithaus et al., 2002a). Yet, the data obtained from small, non-random sampled animal-borne video studies still has

tremendous value as curiosity-driven research which could warrant further study with larger random samples.

2.5.6. Technical faults

Methods with high failure rates are not likely to be favoured. Unfortunately, as with any technical device, malfunctions do occur in animal-borne video systems. For devices fitted with remote release, VHF transmitters are often built in so that devices can be tracked and recovered once dropped from the individual. However, it appears that there are often some devices that are never recovered (Calambokidis et al., 2007), either because the VHF transmitters failed or because a device (without remote release) detached early. Remote release of devices is hugely beneficial as it eliminates the need to re-capture the animal, but Thompson et al. (2015) experienced a technical failure in the remote release systems which meant all individuals had to be re-captured to manually remove the collars. To diminish the likelihood of this occurring, some studies included more than one remote-release mechanism to guarantee that the device would detach when required (Nifong et al., 2014). Devices that were programmed on duty-cycles to conserve battery life were occasionally found to have malfunctioned and the cycle programming altered as a result, this leads to the loss of data during necessary periods and wastage of battery life on video footage that is unclear or unnecessary (Brockman et al., 2017). Moreover, Mattern et al. (2018) discovered that electromagnetic interference from the video camera caused the GPS to fail as soon as the devices were switched on. These technical faults are often costly, both in terms of the financial input to deploy the systems and the lack of subsequent data.

2.5.7. Robustness

The technical failures described above have also been attributed to the lack of robustness of some devices. Waterproofing is essential in all devices, not just for marine species, as water entering the casing of the device can cause data loss or complete malfunction (Watanabe and Takahashi, 2013). Weather-proofing the device is not challenging, as demonstrated by the numerous studies on marine species, and although it may increase the cost, it should be considered justifiable in order to ensure successful data acquisition. Depending on the species, some devices must be able to withstand harsh treatment such as biting from other animals, scratching with sharp claws, and, as in one case, damage by antlers during sparring (Brockman et al., 2017; Beringer et al., 2004). However, in order to achieve such bite-proof devices, the units will likely increase in weight and size so the utilisation of light-weight durable materials should be invested in.

2.5.8. Clarity

One major benefit of animal-borne video systems is the ability to observe from the perspective of the study species. However, a common limitation with this method is the lack of clarity in the video footage. This can be due to a number of variables such as lens fog, dense vegetation, murky water, or lack of light. Many studies have reported issues with the inability to classify behaviours or identify species due to low light (Brockman et al., 2017; Narazaki et al., 2013; Nakamura, Goto, and Sato, 2015). LED light emitters or infrared lenses have been used in conjunction with animal-borne video devices to aid nocturnal and low light video capture (Nifong et al., 2014), however, there are concerns regarding the use of light emitters on nocturnal foragers as this might reduce their foraging efficiency but it has been concluded that it is worth the risk in order to capture nocturnal behaviours (Kernaleguen et al., 2016). The ability to capture nocturnal behaviours is essential if researchers are aiming to study diel foraging activity and fortunately there are currently LED lights available which emit negligible light but are sufficient for increasing clarity of video footage (McGregor et al., 2015).

2.5.9. Ethics

As indicated previously, the weight and size of the animal-borne video system has potential negative impacts on the individuals bearing them. Additionally, the stress of capture can be high for some species and the presence of a foreign object might cause issues; such as behavioural changes. This raises ethical concerns about the necessity of subjecting wildlife to this potential damage. Arthur et al. (2007) stated that the stress of capture caused green turtles to swim continuously for a significant duration upon release and noted that foraging behaviour was altered as a result. As well as being ethically challenging, this reduces the validity of the data collected unless devices have a delayed start to allow for habituation. However, there are ways to mitigate these issues; such as only deploying the devices for short durations in order to reduce long-term effects (Handley et al., 2018) or habituating animals to the device by slowly introducing the device before the study begins [where possible](Grémillet et al., 2006). In extreme cases, the stress of capture can be fatal (Lavelle et al., 2012); in such cases a review into the capture protocol and necessity of the study should be conducted. Furthermore, there is also a risk that where no remote-release mechanisms are in place the individuals cannot be captured again (Handley et al., 2018), thus they will be left wearing the device indefinitely which could have detrimental effects on their fitness. For this reason, all devices should be fitted with fail-safe break-away mechanisms. When conducted with due care and caution, animal-borne video studies can be ethically sound as demonstrated by Mattern et al. (2018) who discovered that their tagged bird was one of only a few that successfully reared chicks during a poor breeding season.

3. Case study

3.1. Introduction

In Scandinavia, there has long been a history of large carnivore persecution which led to the functional extinction of brown bears as a result of bounty hunting in Sweden and Norway by the early 1900s (Swenson et al., 1995). Extensive farming of roaming livestock in areas populated by carnivores (most notably the Eurasian wolf *Canis lupus lupus* but including brown bears, wolverine *Gulo gulo*, Eurasian lynx *Lynx lynx*, and the golden eagle *Aquila chrysaetos*) has led to continual conflict as a result of livestock damage and depletion (Kaltenborn, Bjerke, and Vittersø, 1999). At present, brown bear populations are mainly concentrated in areas of Scandinavia which are not densely inhabited by human populations. This has created a divide between those who must co-exist with the bears whilst facing potential loss of livestock and those who live in bear-free areas who generally have a more positive attitude towards the presence of brown bears in Scandinavia (Kaltenborn, Bjerke, and Vittersø, 1999). Though sheep *Ovis aries* are the most frequently discussed livestock prey of brown bears, semi-domestic reindeer (*Rangifer tarandus f. domesticus*) are also highly preyed in the Northern areas of Scandinavia; with reindeer calf predation estimated at 0.4 calves per bear per day (Karlsson et al., 2012). Reindeer husbandry among the Sámi in Northern Scandinavia is an integral part of the culture and herders have the right to graze their reindeer on private and forested land and herds are seldom corralled (Zabel, Bostedt, and Engel, 2014). Owing to the economic loss by brown bear predation on livestock such as sheep and reindeer, compensation schemes are in place to mitigate the effects on farmers and herders, yet the conflict remains (Widman and Elofsson, 2018). Depredation of livestock may well be the major factor influencing brown bear-human conflicts in Scandinavia, but general fear of the species, as well as predation on game-hunting species are also key drivers of conflict (Johansson et al., 2011; Swenson and Andrén, 2005).

These conflicts in Scandinavia led to the conception of large carnivore research projects, such as the Scandinavian Brown Bear Research Project, which aim to increase ecological knowledge about the species to ensure proper management and conservation. The research on brown bears in Scandinavia is already quite extensive, but coupled with advances in research methodologies there is a continual demand for new and updated knowledge to improve their conservation and management. One such area in which current information is needed is that of brown bear feeding ecology, as their choice of prey also has an impact on human populations such as reindeer herders and moose hunters.

GPS collars attached to brown bears and radio-transmitters attached to ungulate prey have both been used to estimate kill-rates among individual brown bears in Scandinavia (Swenson et al., 2007; Rauset, Kindberg, and Swenson, 2012). However, no research has yet been published on the use of visual data to estimate kill-rates. Using visual data, such as animal-borne video systems, to estimate kill-rates enables researchers to holistically examine the diel behaviour of species from the perspective of the subject. Thus researchers are able to study not only the kill-rates of brown bears but also their food preferences and daily behaviour. The case study below demonstrates the applications of animal-borne video systems to study the foraging ecology of brown bears in Scandinavia and aims to provide insight into the benefits and limitations of employing this technology with regard to other commonly used methods.

3.2. Methods

3.2.1. Study area

The study was conducted in the south-western part of Norrbotten County, Sweden (67°N, 18°E). This area is sparsely inhabited by humans but logging occurs, especially in the coniferous forests (Ordiz et al., 2014). The terrain is characterised by both rolling hills (below 300m) on the eastern side and mountainous landscape (with elevations of over 2000m) further to the west. The lower altitudes are dominated by Northern boreal coniferous forest of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) while the higher elevations are dominated by sub-alpine forests of birch (*Betula pubescens*) and willow (*Salix spp.*). From its lowest point in 1930 of around 130 individuals across 4 areas of Sweden (Swenson et al., 1995), the brown bear population in this area has increased markedly since and was estimated to be around 500 individuals in 2016. Due to efforts to maintain a healthy population, bear hunting was forbidden in this area in 2017 and only 16 were permitted to be hunted in the 2018 season (Länsstyrelsen Norrbotten, n.d.). The area is also heavily used for herding of semi-domestic reindeer by the indigenous Sámi population (Persson et al., 2003).

3.2.2. Bear capture and collar programming

As part of the Scandinavian Brown Bear Research Project, in June of 2017 one male brown bear was fitted with a video camera and GPS collar. A further 2 bears (2 females) were fitted in August 2017 and 1 (female) in May 2018. All collars were designed with remote-release and collars were located by very high frequency (VHF) transmitters 21 days after deployment. The bears were darted from a helicopter using a 'remote drug delivery system' (Dan-Inject®, Børkop, Denmark) and the capture

and collaring of bears followed the same protocols as stated in Arnemo and Evans (2017). Approval was granted from the relevant ethical committees and authorities.

For the June 2017 male, one of the August females, and the May female, videos were recorded for 10 seconds every 5 minutes. For the other August female, videos were recorded every 3.5 minutes for 5 seconds. All collars had GPS to receive fixes at the start of each video session. All video data were stored on board and GPS fixes were sent throughout the duration of the deployment via satellite or GSM.

Video collars were provided by VECTRONIC Aerospace GmbH, Berlin, Germany. For the June 2017 male and the May/June 2018 female, GPS PLUS X collars were used. For the two August 2017 females, VERTEX PLUS X collars were used. The June male's camera had the highest frame rate with 59.94 frames per second (fps), the 2 August females had 25 fps, and the May female had 29.97 fps. All videos were filmed with a resolution of 1080p. The May/June 2018 female's video collar also had the infrared-blocking filter removed so that it recorded in infrared which aided night-time filming but reduced the colour quality of images as they were tinted pink.

3.2.3. Video data analysis

Video clips for the June male were processed and analysed using Windows Live Movie Maker and Lightworks x64 (14.0.0.0) was used for the remaining 3 bears. Video files were first categorised as clear or unclear based upon whether or not the behaviour of the bear could be classified from the video. Files that were classified as clear were then further classified by primary behaviour; resting, travelling, feeding, hunting, etc. (see table 2). This list was generated from previous behavioural research studies (Brockman et al., 2017; Pagano et al., 2017) and behaviours were added if later observed on video clips.

Table 2: List of behaviours , their codes, and definitions

Behaviour	Code	Definition
Drinking	Dr	Muzzle partially or fully submerged in water and stationary
Feeding	Fe	Clear movement of the mandible to indicate chewing or where the bear is engaged with visible food items in the frame
Grooming	Gro	Licking, scratching, shaking, tree rubbing often seen as continuous repetitive movement up or down or side to side.
Hunting	Hu	Indicated by fast pace, movement towards target prey visible in frame
Mating	Ma	Mounting of another bear, repetitive movements
Playing	Pl	Any solitary behaviour which does not seem to have a purpose other than to entertain the bear. Such as throwing and spinning a stick.
Resting	Res	No movement; bear is low to the ground and lying down
Socialising	Soc	Any interaction with another bear which is not fighting or mating. Such as playing and friendly chasing
Stationary	Sta	No movement but bear is standing
Swimming	Sw	Movement in bodies of water
Travelling	Tra	Movement on land; running or walking. Not running in chase of prey; see hunting
Unknown	Un	Behaviour unable to be classified

These primary feeding and hunting behaviours were then assigned prey items (table 3). In some instances it was possible to classify the species of the prey but not the age, in these cases prey was marked as unspecified moose or reindeer. As bears are able to forage on berries and maintain a normal walking pace (Bowersock et al., 2015), if bears were observed to be foraging on berries whilst travelling then the behaviour was classified as feeding: vegetation. As the objectives of this study were primarily to research predation, vegetation was not identified by species, nor was it possible to accurately assign species to vegetation as the video resolution was often too poor. As large quantities of insects (suspected to be predominantly ants) were consumed, the location of insect foraging was classified, such as anthill or deadwood, and the presence of pupae was noted. It was not possible to delineate insect species from the video data but instances of insect feeding were most often categorised as such due to visible movement from insect species which indicated foraging for insects instead of vegetation. Due to the bright white colour of the cocoon and abundance of pupae it was easy to classify from the video clips.

Table 3: List of hunted animals and food items

Item	Feeding/Hunting	Code	Comments
Unspecified moose	Feeding/Hunting	M	When age could not be determined
Adult moose	Feeding/Hunting	Am	Age >1 year
Moose calf	Feeding/Hunting	Mc	Age <1 year
Unspecified reindeer	Feeding/Hunting	R	When age could not be determined
Adult reindeer	Feeding/Hunting	Ar	Age >1 year
Reindeer calf	Feeding/Hunting	Rc	Age <1 year
Vegetation	Feeding	Veg	Forbs, graminoids, shrubs etc.
Insects	Feeding	Ant	Predominantly ants, but can also include ground insects and larvae
Unknown carcass	Feeding	UC	Not enough information or clarity to ascertain species or age
Suspected hunting	Hunting	S	No visible prey but speed of bear and urgency indicate hunting
Unknown	Feeding/Hunting	Un	Species cannot be identified

3.2.4. Field data

Field data were also collected from the May 2018 female based on the GPS fixes every 5 minutes which demonstrated a cluster of positions. Clusters were defined as 3 or more consecutive GPS fixes that were less than 30 meters apart. Clusters were visited by 1 or 2 researchers and examined for bear signs such as; day beds, scat, tracks, and food items. These data were noted in cluster protocols which collected information on the presence of a carcass, the carcass species, age, sex, and freshness.

3.2.5. Data analysis

Behaviour frequencies were calculated for each bear as the percentage of clear video data wherein a specific behaviour was classified. All analysed data were taken from 24 hours after collar deployment to avoid including behaviours during the post-sedation period where behaviours could be as a result of sedation.

The ungulate Kill-rate for each bear and for each prey item was calculated using the frequency of each prey item appearing in video clips. To assess the accuracy of this method compared to field data, information collected at cluster sites for the May 2018 bear were compared with the corresponding video data and the percentage of accurately identified prey species was calculated. Where more than one clip is classified as a specific prey item in succession or GPS positions are close

together, this is deemed one prey item and not multiple prey. Owing to the small sample size, no statistical analyses were able to be conducted, other than descriptive statistics.

Video clarity during potential predation events was assessed by calculating the percentage of video clips that were unclear during cluster positions from GPS fixes. Additionally, the clusters that were found to include carcasses were analysed to assess the impact the clarity of video clips had on the correct classification of carcasses in terms of; whether or not the carcass was seen on video, the species, the age, and the freshness.

3.3. Results

3.3.1. Video collar performance

The total number of video clips, both clear and unclear, for all four bears (from 24 hours after deployment) was 16,597 and the number of used clear video clips (from 24 hours after deployment) for all four bears was 10,101. This yielded 23 hours and 17 minutes of useable clear video footage. The June 2017 male generated the most amount of clear usable video footage with 8hrs 36mins of video clips and the May/June 2018 female generated the least with only 3hrs 30mins of usable video clips due to a collar malfunction that caused it to stop recording after approximately 1 week. For the June 2017 male, 70% of video clips were marked as clear, for the August 2017 females 53% and 57% of videos were clear, and for the May/June 2018 female 69% were clear. This brings the overall percentage of clear videos to 61%.

3.3.2. Behaviours

Table 4 presents an overview of the frequencies in which behaviours occurred for each bear. The June 2017 male and May/June 2018 female both spent the majority of the video footage travelling (59% and 41% respectively). The August female without cubs was filmed predominantly resting (41%) whilst the August female with cubs was classified as primarily feeding (40%). Both August females had considerably higher frequencies of feeding clips than the 2 May and June bears.

Drinking, hunting, mating, playing, and swimming were rarely seen in video clips and constituted less than 1% of behaviour for each of the 4 bears. Mating was only observed (n=29) in the June male which corresponds with time of year and sex of the bear. Playing was only observed (n=3) in the May/June 2018 female, whereby she lay on her back and tossed and spun a stick around using her paws. The June 2017 male often appeared to play with a mating partner but this was classified as socialising (n=70) as the purpose of interaction was unknown. The August 2017 female with cubs

seldom socialised with her offspring (n=12), nor were they often visible on the video footage. As a result of removal of unclear video footage, behaviours were rarely classified as unknown (<5% for each bear).

Table 4: Frequency (%) of behaviour as seen on video clips for each bear. Dominant behaviour for each bear in bold

Bear (month-sex)	June- male	August-female	August-female ^a	May/June-female
Year	2017	2017	2017	2018
Drinking	10 (<1)	0	1 (<1)	6 (<1)
Feeding	328 (11)	751 (33)	1381 (40)	218 (17)
Grooming	47 (2)	8 (<1)	4 (<1)	2 (<1)
Hunting	9 (<1)	0	4 (<1)	3 (<1)
Mating	29 (<1)	0	0	0
Playing	0	0	0	3 (<1)
Resting	576 (20)	948 (41)	914 (27)	481 (38)
Socialising	70 (2)	0	12 (<1)	3 (<1)
Stationary	125 (4)	26 (1)	125 (4)	29 (2)
Swimming	17 (<1)	0	1 (<1)	0
Travelling	1803 (59)	535 (23)	972 (28)	528 (41)
Unknown	85 (3)	18 (<1)	22 (<1)	7 (<1)
Total clear used	3,099	2,286	3,436	1280
Total unclear	1,326	2,008	2594	568
Total clips	4,425	4,294	6,030	1848

^a Accompanied by cubs

3.3.3. Food items

Vegetation was the dominant food choice for all bears except the June 2017 male, which consumed mainly moose calf (see table 5). The June 2017 male had a predominantly carnivorous diet during video collar deployment. Moose calf constituted 30%, unspecified moose 11%, adult moose 22%, unspecified reindeer 7%, and adult and calf reindeer 3% each. The two August 2017 females consumed less than 1% of any animal species each but were both recorded feeding on insects quite frequently (25% and 26%). Both the June 2017 male and May/June female were rarely seen feeding on insects with only 3% and 7% respectively. Interestingly, both the August females were classified as consuming the same percentage of vegetation (73%).

Table 5: Frequency (%) of food items as seen on video clips for each bear. Dominant behaviour for each bear in bold

Bear (month-sex)	June-male	August-female	August-female ^a	May/June-female
Year	2017	2017	2017	2018
Unspecified moose	37 (11)	10 (1)	4 (<1)	17 (8)
Adult moose	72 (22)	0	0	0
Moose calf	100 (30)	0	0	0
Unspecified reindeer	22 (7)	0	5 (<1)	0
Adult reindeer	11 (3)	0	0	0
Reindeer calf	10 (3)	0	0	33 (15)
Insects	11 (3)	191 (25)	354 (26)	15 (7)
Vegetation	33 (10)	545 (73)	1008 (73)	123 (56)
Unknown carcass	32 (10)	4 (1)	7 (1)	15 (7)
Unknown	0	1 (<1)	3 (<1)	15 (7)
Total	328	751	1381	218

^a Accompanied by cubs

The two August 2017 bears had 191 and 353 clips of insect feeding, the May/June 2018 female had 15 clips and the June 2017 male had only 11 clips (see table 6). For all bears except the August 2017 female with cubs, the dominant location of insect feeding was at anthills so it can be assumed that the species consumed were ant species (likely *Formica rufa*). For the two bears collared in May and June, anthills constituted almost the entirety of insect feeding. However, the two August 2017 females also were frequently seen feeding on insects buried in the earth and in deadwood or tree stumps. Additionally, the August 2017 female with cubs was the sole consumer of insects found by lifting and moving stones which occurred on 8 video clips. Finally, in clips where insect feeding occurred, pupae was marked as present in the majority for each bear (see table 7).

Table 6: Frequencies (%) of insect location for each bear. Dominant location in bold

Bear (month-sex)	June-male	August-female	August-female ^a	May/June-female
Year	2017	2017	2017	2018
Anthill	11 (100)	95 (50)	107 (30)	14 (93)
Earth	0	77 (40)	160 (45)	1 (7)
Deadwood/Tree-stump	0	15 (8)	78 (22)	0
Under stones	0	0	8 (2)	0
Unknown	0	4 (2)	0	0
Total	11	191	353	15

^a Accompanied by cubs

Table 7: Frequency (%) of clips where insect pupae is present and absent for each bear

Bear (month-sex)	June-male	August-female	August-female ^a	May/June-female
Year	2017	2017	2017	2018
Pupae present	6 (55)	59 (62)	85 (79)	12 (80)
Pupae absent	5 (45)	36 (38)	22 (21)	3 (20)

^a Accompanied by cubs

3.3.4. Comparison of video and field data

3.3.4.1. Video data

From 24 hours after collar deployment until the collar malfunctioned 154 hours later (6 days, 10 hours and 24 minutes) the May/June bear was observed consuming carcasses on 8 separate occasions (see table 8); which yields an estimated ungulate consumption rate of 1.2 ungulates per day for the May/June 2018 bear. Reindeer calves comprised the majority of carcasses, with 5 independent carcasses recorded. The remaining carcasses were 1 unspecified moose and 2 unknown carcasses. Four reindeer calf carcasses were classified as fresh and 1 as not fresh. The unspecified moose carcass was marked as not fresh and the freshness of the unknown carcasses could not be

classified. Under the assumption that all fresh carcasses were killed by the study bear, the 4 freshly killed reindeer calves translate to an estimated reindeer calf kill-rate of 0.6 per day for the May/June 2018 bear.

Table 8: Ungulate carcasses as seen on videos and found in the field for the May/June 2018 female for the period 18/05/2018 – 24/05/2018

Method	Food item	Fresh	Not fresh	Unknown freshness
Video	Unspecified moose	0	1	0
	Reindeer calf	4	1	0
	Unknown carcass	0	0	2
Field	Reindeer calf	9	0	0
	Adult reindeer	0	1	0
	Moose calf	1	1	0
Total video		4	2	2
Total field		10	2	0

3.3.4.2. Field data

The field data collected revealed the bear was located at 12 carcasses for the duration of the video collar deployment (see table 8). Nine individual reindeer calves, 2 moose calves, and 1 adult reindeer were recorded. All 9 reindeer calves were marked as fresh, 1 moose calf was marked as fresh and 1 as old, and the single adult reindeer was marked as old. Thus the estimated reindeer calf kill-rates based on field observations is 1.3 calves per day for the May/June 2018 bear. Parts of one moose carcass appeared in two cluster locations and it was apparent the moose was dragged. When compared with the video data, 67% of carcasses found in clusters were identified from video clips. Of those seen on video, 75% were correctly identified by species and 63% were correctly classified as the right age category. Furthermore, 63% of carcasses seen on video were also classified as the correct freshness.

3.3.4.3. Effect of unclear videos in clusters

Of clusters where carcasses were located, 92% contained over 50% clear video clips, 7 of which had clarity of 100% (see table 9). The percentage of clear video clips in each cluster did not appear to have an effect on the ability to correctly classify species, species age, or freshness; with the exception of the 1 cluster with 0 clear video clips that obviously meant it was not possible to classify behaviour. However, the clarity of video clips was based upon the ability to see what behaviour was occurring, therefore some video clips were classified as clear because it was evident the bear was feeding but the specific details of the food choice could not be determined due to poor clarity. In such cases, the video clips were marked as clear but would also have been marked as unknown feeding or unknown carcass.

Table 9: Comparison of field cluster data with video data for the May/June 2018 female. Columns ‘species’, ‘age’, and ‘freshness’ relate to data collected in the field at cluster sites

Cluster	Day/ Month	Species	Age	Freshness	On video?	Correct species?	Correct age?	Correct freshness	% clear on video	Comments
C-8	18/05	Reindeer	0-1	Fresh	No	No	No	No	0	
C-10	18/05	Reindeer	0-1	Fresh	Yes	No	No	No	100	Marked as unknown carcass
C-12	19/05	Reindeer	0-1	Fresh	Yes	Yes	Yes	Yes	78	
C-15	20/05	Moose	0-1	Old	Yes	Yes	No	Yes	100	Marked as unspecified moose
C-16	20/05	Moose	NA	NA	Yes	No	No	No	100	Same as C-18, listed as unknown feeding
C-18	20/05	Moose	0-1	Fresh	Yes	No	No	No	63	Same as C-16, listed as unknown carcass
C-26	22/05	Reindeer	0-1	Fresh	Yes	Yes	Yes	Yes	100	
C-28	22/05	Reindeer	0-1	Fresh	Yes	Yes	Yes	No	100	Marked as old
C-30	23/05	Reindeer	>1	Old	No	No	No	No	100	
C-31	23/05	Reindeer	0-1	Fresh	No	No	No	No	71	Marked as unknown feeding
C-33	23/05	Reindeer	0-1	Fresh	Yes	Yes	Yes	Yes	100	
C-34	23/05	Reindeer	0-1	Fresh	No	No	No	No	71	Marked as unknown feeding
C-35	24/05	Reindeer	0-1	Fresh	Yes	Yes	Yes	Yes	58	

3.4. Discussion

3.4.1. Behaviours

There was considerable individual variation in behaviour patterns. Resting and feeding were particularly frequent in the 2 August females, whereas travelling was dominant for the June 2017 male and May/June 2018 female. Though limited in the number of studies that have accurately been able to assess behaviour patterns of brown bears, the findings from this case study are more or less aligned with previous research with both Eurasian and North American brown bears (Pearson, 1975; Wabakken and Maartmann, 1994). However, previous studies of behaviour patterns were only able to gather data from remote observations or interpreting animal-borne sensor data and these are prone to bias and limitations. The two studies on video-collared North American brown bears indicated that the primary behaviour was resting, not travelling (Brockman et al., 2017; Bowersock et al., 2015). Nevertheless, the results from this case study and the 2 North American studies do not have a large enough sample to be able to generalise the results to the rest of the population. Therefore, the discrepancy here is likely due to individual difference which has been noted to be ubiquitous in this species (MacHutchon, 2001; Ordiz et al., 2017). To my knowledge, there has been no published research outlining the diel behaviour of Scandinavian brown bears by identifying behaviours in specific detail. Previous research in Scandinavia has only been able to deduce behaviour patterns through the use of accelerometers and GPS which allows the researcher to know if the bear is moving in a certain direction or speed (Gervasi, Brunberg, and Swenson, 2006; Moe et al., 2007). This method cannot differentiate between a number of passive behaviours such as standing still or resting, as well as active behaviours such as playing or foraging. Direct observations from the air have been used in North America to study diel behaviour patterns and though this enables specific classifications of behaviours, the method is limited by time and resources available to follow and observe for a full 24 hour period (MacHutchon, 2001). These findings might not be revolutionary for brown bear research, but the use of animal-borne video cameras to capture diel behaviour can allow researchers greater insight into the everyday lives of cryptic species.

3.4.2. Food items

Brown bears are resourceful omnivores that demonstrate 'ecological flexibility' as they have the capability to alter their diet in relation to food availability both spatially and temporally (Van Daele, Barnes, and Belant, 2012; Bojarska and Selva, 2012). The diets of the 4 bears show substantial seasonal variation yet the two bears from August have almost identical percentages in terms of frequency of food items consumed. Both bears primarily consumed vegetation which consisted of

73% of their food items consumed during filming, insects (thought to be predominantly ants) were the second most frequent food item consumed and comprised 25% and 26%. There is a limited amount of research available into the diets of brown bears from the study area but a handful of studies from surrounding areas such as central Sweden, north central Sweden, and north eastern Norway have classified brown bear diets using scat analyses (Dahle et al., 1998; Persson et al., 2001; Stenset et al., 2016).

From this research it appears that in spring (defined as March-May according to specific food availability), the predominant food consumed are ungulates for bears in Northern Scandinavia (Dahle et al., 1998; Persson et al., 2001) and ants for bears farther south in Scandinavia (Stenset et al., 2016). This discrepancy is corroborated by studies on Russian and Siberian brown bears which posit that meat is more important in the diet of northern bears than southern bears, though the reasons are unclear (Krechmar, as cited in Persson et al., 2001).

Though the data for the May 2018 female is limited, the food item with the most frequent occurrence was actually vegetation and then reindeer calf. Nevertheless, the clarity of the video clips due to the infra-red light meant that 14% of clips were classified as unknown carcass and unknown food item and 8% were classified as unspecified moose. Therefore, it is not an accurate representation of brown bear spring diet. For summer (May-July), however, the June male in this study predominantly consumed moose calf followed by adult moose and was seen consuming very little vegetation or insects. This is contradicted by Dahle et al. (1998) who propose forbs, specifically blue sow thistle (*Cicerbita alpina*), to be the primary source of faecal volume and ants the primary source of dietary energy. Yet, other studies found that ungulates provided the highest percentage of dietary energy content (Stenset et al., 2016; Persson et al., 2001). Unsurprisingly, for autumn (August- October) the unanimous dominant food was found to be berries (*Vaccinium spp.*) for all studies in Scandinavia. Second to berries, ungulates were the second most frequently consumed food item and then insects (Dahle et al., 1998; Stenset et al., 2016; Persson et al., 2001; Swenson et al., 1999). The two August females' predominantly berry diet is substantiated by this previous research as is the remaining high prevalence of insects in the diet.

Seasonal shifts in diet may coincide with resource availability, such as calving season or berry season, but these shifts also represent the changes in dietary needs. After den emergence, during the period of hypophagia and before hyperphagia, bears require protein-rich foods and this coincides with first the reindeer calving period and then moose calving in early summer. Prior to denning, bears need to fatten in order to survive the stress on the body of winter denning (Ordiz et al., 2013). Berries are high in carbohydrates which are more readily converted to fat than protein (Dahle et al., 1998). For

this reason, bears consume large quantities of berries once they ripen in late July/August which allows them to gain enough weight ready for denning around October.

Understanding the complexities of diet in brown bears allows greater knowledge surrounding the life-history of brown bears as well as highlights the importance of habitat maintenance. Though the brown bear exhibits ecological flexibility, it heavily relies on food availability during hyperphagia. Reduction in berry abundance has been shown to reduce fitness by reducing size and weight of yearlings and decreasing reproductive success (Dahle and Swenson, 2003; Zedrosser et al., 2007). Berry abundance is linked with patterns of climate fluctuation and in years of delayed winter thaw, berry patches ripen later into autumn which limits the amount bears can consume prior to denning (Bokhorst et al., 2011).

Using animal-borne video cameras to accurately measure diet in brown bears is likely not a reliable method. It is not possible to quantify the volumes of food items consumed, nor is it possible to quantify the frequency of occurrence when only 5-10 second clips are filmed. Furthermore, one cannot precisely identify food items easily, especially those that are small such as insects and berries. Analysing faecal remains to study diet allows researchers to quantify occurrence of food items, volume of food items consumed, and dietary energy. Nevertheless, a number of biases may be incurred such as; collecting a disproportionate number of samples compared with the population in the area, or by collecting samples in easier to access locations or those near carcasses, and collecting samples from the same bear (Dahle et al., 1998; Persson et al., 2001). In spite of these limitations, faecal analysis remains the popular choice for diet analysis and correction factors for digestibility and nutritional value have been able to improve the accuracy of the results (Hewitt and Robbins, 1996). Thus the use of animal-borne video cameras to analyse diet should be cautionary and are unlikely to replace existing methods.

3.4.3. Kill-rates

In northern Sweden there is great spatial overlap between the habitats of brown bears and semi-domestic reindeer. During the calving period for reindeer in May-June, brown bears have been found to prefer the same habitats as reindeer in parturition and select land-cover types likely to be inhabited by reindeer and calves during crepuscular predation hours (Sivertsen et al., 2016). It is during this calving season, in the first 4 weeks, that the majority of reindeer calves are killed, with a peak in mid to late May (Karlsson et al., 2012). The results from the May/June 2018 bear, during the peak reindeer calf predation season, suggest that according to video data 0.6 reindeer calves were killed by that individual per day during the study period. There were thought to be 8 independent

carcasses consumed and only 4 of these (all reindeer calves) were classified as fresh (an indicator that they were killed by the collared bear). This deployment was prior to moose calving season so, as expected, no moose calf consumption was observed, though there was one instance of an unspecified age moose being consumed and 2 cases of unknown carcasses being consumed. The field data collected for this bear revealed that the actual number of carcasses consumed during the study period was 12 and the estimated kill-rate according to the field data for the study period was 1.3 reindeer calves killed per day. This underestimation of kills for reindeer calves suggest animal-borne video cameras have limitations and biases which reduce the efficacy of assessing kill-rates in brown bears.

Brockman et al. (2017) estimated an ungulate calf kill-rate of 1.2 per day per bear, which resembles the rate of total estimated kills using the field data in this study. The data available for brown bear kill-rates on ungulates is varied and it is rare for 2 studies to report on the same population, same species, and same age-group. For North America, Boertje et al. (1988) reported that at least 5.4 moose calves were killed by individual Alaskan brown bears annually and stated that adult male bears had the highest overall kill-rates. Yet, Young and McCabe (1997) claimed that sows with cubs in Alaska had the highest kill-rate with a mean of 6.3 kills per day per bear. In Scandinavia on the other hand, estimates have been much lower with reindeer calf kill-rates estimated at 0.4 per day per bear (Karlsson et al., 2012) and moose calf kill-rates of 0.2 per day per bear (Swenson et al., 2007; Rauset, Kindberg, and Swenson., 2012). With these previous calf kill-rate estimates for both North America and Scandinavia in mind, it appears that they have been consistently underestimated when compared to the use of animal-borne video data which demonstrates higher estimates both in North America (Brockman et al., 2017) and in Scandinavia (this case-study).

Estimating calf kill-rates by brown bears allows researchers to provide data for management policies to reflect the impact bear predation may have on ungulate populations. The high individual variability in brown bear kill-rates was not reflected in this study owing to its sample of only 1 bear. However, this variability has been reported in other studies and accurately estimating kill-rates can aid management by allowing for selective removal of 'problem' bears which would lessen the effects on ungulate populations (Rauset, Kindberg, and Swenson, 2012). In spite of the lower kill-rate reported by Karlsson et al. (2012) it is expected that 63-100% of the reindeer calf mortality during one year was as a result of bear predation and similarly, 61-78% of moose calf mortality in central Sweden was attributed to brown bear predation (Swenson et al., 2007). Though moose populations in Scandinavia are important ecosystems drivers, semi-domestic reindeer also have financial value to herders so bear predation carries a social impact on human populations and this can influence

perceptions of predators and their place in human-dominated landscapes. Compensation is paid to reindeer herders who incur losses as a result of predation, but in Sweden, this sum does not appear to be proportionate to the overall financial loss (Karlsson et al., 2012). In addition to compensation, management agencies in Sweden annually cull bears in certain areas, often after receiving complaints of reindeer depredation (Swenson et al., 2017). This highlights the importance of up to date and accurate estimations of kill-rates in order to avoid escalating human-wildlife conflicts that have proven detrimental to predators in Scandinavia in the past. However, brown bears are not the only predator for reindeer in northern Sweden. Lynx and wolverine have been found to have a more considerable effect on reindeer harvest for Sámi pastoralists than brown bears (Hobbs et al., 2012) and in Norway only 2% of annual losses of reindeer were attributed to brown bears (Tveraa et al., 2014).

Despite the importance of knowing predator kill-rates, there still appears to be little consensus on agreed rates and this is most notably due to methodological differences. As with this case-study, visiting GPS cluster locations allows for knowledge on the species killed, its rough age, and how long ago it was killed. However, only using cluster sites means some kills could be missed if the bear was not in the same location for a long enough duration. Therefore, Rauset et al. (2012) suggest also visiting random GPS locations to check for carcass signs to reduce underestimation of kills. However, this is time consuming and kill-rates might be over-estimated regardless due to usurpation and opportunistic scavenging of carcasses which cannot be identified as the kill of the bear in question (Rauset, Kindberg, and Swenson, 2012). In order to be certain that the bear in question was the killer of the carcass discovered one must use direct observations of hunting behaviour. To do so for such a species would often require observation from aircraft but this is limited by the duration of flight, ability to see the subject and prey clearly, and the potential disturbance from the aircraft (Young and McCabe, 1997). Implementation of animal-borne video cameras, however, are able to capture events without disturbance to the subject or its surroundings and can continuously film as well as provide close-up views from the bear's perspective. There were minor discrepancies between the data collected from the field cluster sites and the video data. The video data were limited by the clarity of images and fragmented clips (10 seconds every 10 minutes). Consequently these discrepancies might have been lessened had the quality of video been improved and continuously filmed; thus demonstrating the similar capability of animal-borne video cameras to study kill-rates, as with other methods.

3.4.4. Clarity

The mean percentage of unclear video clips from all 4 bears was 38.75%; this is a large proportion of unusable footage and as such is a major limitation of this study. For one of the August females almost half (47%) of the data collected was marked as unclear. In addition to overall clarity, cluster clarity was also analysed for the May/June 2018 female as these are periods when feeding behaviours are most likely to occur and it was predicted that due to the body positioning and time of day during feeding behaviours it might reduce the clarity of clips. On the contrary, it was found that the majority of clips recorded during cluster periods were clear (92% of clusters with clips over 50% clear). Furthermore, of the clusters found to be carcass sites the vast majority of clips for each cluster were clear and carcasses were identified for over half the carcass clusters sites. In spite of this, there was a poor rate of correct prey species classification, age of prey, and freshness of prey. This was surprising given the high percentage of clear carcass clusters but perhaps a higher percentage of clear clips are necessary in order to identify the finer details of prey.

Other factors that may have reduced the ability to identify details about the carcass could be poor image resolution or camera positioning on the neck. Thompson et al. (2012) cited lack of resolution as a major limitation for the ability to classify the species of ground cover plants and Lavelle et al. (2012) stated that in order to study diet by animal-borne video cameras; the resolution had to be as high as possible. The image resolution for this case-study was sufficient to identify predation events but a higher resolution would facilitate the identification of fur colour (an indicator of species) and colour of flesh and blood (indicators of freshness). Camera obstruction by the chin or fur was noted in a number of other studies which used collars to attach the cameras to study species (Thompson et al., 2012; Brockman et al., 2017; Beringer et al., 2004). Without the obstruction, the field of view would be wider which would allow for more of the prey to be visible in one frame, thus aiding the identification of the size of the prey (an indicator of species and age).

Moreover, the clarity for each bear appears to be determined by the month in which the collar was deployed. The bear with the highest percentage of clear files was the June 2017 male. In June, northern Scandinavia experiences the midnight sun whereby there is a period of 24 hour daylight. This was beneficial as there was consistently enough light to capture events throughout the day. However, during the August deployments around 4-7 hours of footage was lost each day due to lack of daylight. The inability to study nocturnal behaviour has been a main critique of the technology as it reduces the accuracy of results when a large portion of diel behaviour cannot be accounted for (Thomson et al., 2018; Bombara et al., 2017).

Collecting video footage that is clear and can easily be identified is vital to the concept of animal-borne video camera technology. To research diel activity patterns, one must be able to obtain enough footage for the 24 hour period in order to report accurate and valid findings. To study diet and kill-rates, one must be able to identify prey in fine detail. The defining quality of animal-borne video cameras is also the limiting quality, the ability to observe behaviours from the animal's perspective is what sets it apart from other methods, yet when this ability is compromised it renders the technology useless.

In order to prevent loss of data due to clarity issues many solutions have been trialled such as in this study where an infra-red-blocking lens filter was removed from the camera for the May/June 2018 bear. However, this reduced clarity as it tinted the video clips pink which made it very difficult to identify species and freshness of carcasses. Nevertheless, the addition of an infra-red light next to the lens in a study on domestic cats allowed researchers to film at night and this was not reported to have affected the quality of the daytime footage (McGregor et al., 2015). Furthermore, the positioning of the camera around the neck is often the best placement for terrestrial mammals in spite of the potential for obstruction but this can be lessened by using a wide-angle lens so that the field of view is opened up (Bombara et al., 2017). Finally, ensuring that the footage is filmed with the highest possible resolution will significantly increase the clarity of images, even for those affected by lack of light.

4. Concluding remarks and future implications

The purpose of this thesis was to review the literature regarding animal-borne video systems in relation to foraging ecology and highlight their potential as a research methods, as well as demonstrate the novel insight they can provide, whilst underlining the limitations of this method and areas which need improvement. In addition, present a case study to demonstrate the use of animal-borne video systems on Scandinavian brown bears and the ability to study their foraging and diel behaviour.

The literature has revealed that animal-borne video systems can be an effective method to document kill-rates among elusive species and it benefits from the ability to log every kill when videos are continuously recorded over a period. Furthermore, the technology enables researchers to document food item consumption in certain species, such in caribou studies and this case study, but often the clarity of video makes detection and classification of food items difficult. Nevertheless, video data can be advantageous over stomach content or faecal analysis due to their biases from digestion rates. Animal-borne video can successfully capture the diel behaviour of many species.

With continuous video recording, researchers are able to get a clear understanding of what individuals do during periods of the day and can assess how much time is spent on individual behaviours. Not much research has been published on this aspect of their use but from the research published it has demonstrated its worth for species which are difficult to observe in the field. Yet perhaps the most useful advantage of animal-borne video cameras is their ability to capture the mechanics of foraging events, such as 360 degree rolls in blue whales and tool use in New Caledonian crows. In relation to the case study, when deployed on brown bears animal-borne video systems were able to capture the daily behaviour as well as give insight into food choices and predation on ungulates. A kill-rate of reindeer calves was estimated from the data but the accuracy of this estimate must be considered.

This method is, at present, primarily limited by device cost, size and weight, and battery life. In a number of studies, including the case study, the ability to analyse video data was also considerably limited by video quality and clarity. Additionally, when working with technical equipment, faults are always a possibility and often cannot be predicted or avoided. For species which require capture to attach the device, this could also raise concerns over the ethicality as there have been cases of mortality as a result of capture stress.

Animal-borne video cameras have been deployed on a range of species, both marine and terrestrial, with varying success and the use of animal-borne video on marine reptiles has been particularly phenomenal in documenting novel foraging behaviour and expanding the knowledge of marine trophic interactions. Based on the published literature and case study, it is reasonable to deduce that there is a future for animal-borne video studies, and its use is justified in ecological research. As the technology progresses and devices become more widely available, the effect of the limitations cited above will be minimised and the quality of research will improve. Though hypotheses driven research is often favoured, this technology is evidence that research conducted from pure curiosity can provide findings that are instrumental in broadening our understanding of the natural world.

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