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Towards more compassionate wildlife research through the 3Rs principles: moving from invasive to non-invasive methods

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Research in ecology and wildlife biology remains crucial for increasing our knowledge and improving species management and conservation in the midst of the current biodiversity crisis. However, obtaining information on population status often involves invasive sampling of a certain number of individual animals. Marking and sampling practices include taking blood and tissue samples, toe-clipping of amphibians and rodents, or using implants and radio-transmitters – techniques that can negatively affect the animal. Wildlife research may then result in a fundamental conflict between individual animal welfare and the welfare of the population or ecosystem, which could be significantly reduced if non-invasive research practices were more broadly implemented. Implementation of non-invasive methods could be guided by the so-called 3Rs principles for animal research (replace, reduce, refine), which were proposed by Russell and Burch 60 years ago and have become a part of many animal protection legislations worldwide. However, the process of incorporating the 3Rs principles into wildlife research has been unfortunately rather slow and their importance overlooked. In order to help alleviate this situation, here I provide an overview of the most common practices in wildlife research, discuss their potential impact on animal welfare, and present available non-invasive alternatives.

Keywords: 3Rs principles, animal welfare, ecology, reduction, refinement, replacement

Ecosystems worldwide are currently experiencing a dramatic species extinction process, which has been largely attributed to human activities (Harrop 2011, Ceballos et al. 2015). Recognizing the critical situation, several international conventions have been implemented with the aim to halt the biodiversity crisis and support conservation measures (e.g. Convention on Biological Diversity, Bonn Convention on the Conservation of Migratory Species of Wild Animals, Bern Convention on the Conservation of European Wildlife and Natural Habitats, Convention on International Trade in Endangered Species of Wild Fauna and Flora). These conservation efforts depend on accurate data on species distribution, population size and impact of global changes, and it is therefore necessary to continuously monitor populations of various plant and animal species.

In the noble pursuit of knowledge that is important for preserving wildlife populations, scientists can unfortunately inflict distress on animals, because wildlife biodiversity monitoring has traditionally employed some invasive or even destructive techniques (Vucetich and Nelson 2007, Minteer et al. 2014b, Field et al. 2019). Examples of research activities that might influence animal welfare are chasing, capturing, blood and tissue sampling, marking, attachment of data loggers and lethal sampling (Donnelly et al. 1994, Sutherland et al. 2004, Wilson and McMahon 2006, Walker et al. 2010). The impact on animal welfare is a problem not only for the affected animal but also for the reliability of study results (Powell and Proulx 2003, Cattet 2013, Jewell 2013). It has been shown that pain negatively affects data quality through behavioural, physiological and neurobiological changes (Jirkof 2017, Sneddon 2017). Because sound information about wildlife is of uttermost importance for sound management decisions, it is crucial that the research procedures affect animal welfare as little as possible.

An important milestone in thinking about animal welfare in research was achieved 60 years ago, when Russell and Burch proposed the 3Rs principles (replace, reduce, refine; Russell and Burch 1959). These principles encourage scientists to replace the use of animals with alternative methods whenever possible, to reduce the number of animals in experiments to the absolute minimum, and to refine or limit the pain and distress that animals are exposed to.

The 3Rs have since become an integral part of legislation and guidelines on animal experiments in many countries (Sneddon et al. 2017) and the research community itself has encouraged the development of guidelines to improve the use of animals for scientific purposes (Kilkenny et al. 2010, Buchanan et al. 2015, Mellor 2016). While the 3Rs principles were originally proposed for laboratory animals, they can be – and should be – applied also in wildlife research. One example is the use of non-invasive research methods, i.e. methods that do not affect the physical integrity of the animal (Lefort et al. 2019). Some non-invasive methods do not even require capturing and handling. Even though efforts have been made to support the process of incorporating the 3Rs into wildlife research (NORECOPA 2008, Lindsjö et al. 2016, Field et al. 2019, Sloman et al. 2019), there have been recently published several articles that indicate that wildlife biologists may be struggling with implementing these principles (Costello et al. 2016, Waugh and Monamy 2016, Russo et al. 2017, Lindsjö et al. 2019, Zemanova 2019).

In order to encourage the implementation of the 3Rs principles in wildlife research, I carried out a review of the literature on the potential impact of research methods on animal welfare, and provide here specific examples where the 3Rs principles have been successfully applied.

Methods

I derived my synthesis based on published journal articles and books. Specifically, I searched for relevant literature on the Web of Science and Google Scholar until March 2019 and also used references cited in the papers I found. For publications on impact of research methods on animal welfare, my search strings consisted of: Topic = (“welfare” OR “impact” OR “effect” OR “detrimental” OR “lethal” OR “survival”) AND “wildlife” OR “ecology” AND (“method” OR “technique”). To identify publications describing available non-invasive techniques and their implementation, I used the search terms: Topic = (“non-invasive” OR “non-lethal” OR “non-destructive” OR “alternative” OR “replacement” OR “reduction” OR “refinement” OR “improved”) AND “wildlife” OR “ecology” AND (“method” OR “technique”). I excluded publications in which content was not relevant to this synthesis.

Potential impact of commonly used methods in wildlife research on animal welfare

Capturing, trapping and experiments in captivity

In contrast with laboratory animals, wildlife animals are not used to interaction with humans, so any capture or handling can be very stressful (Wilson and McMahon 2006). Increased cortisol levels have been reported for example in captured Weddell seals *Leptonychotes weddellii* (Harcourt et al. 2010). Cattet et al. (2008) showed that grizzly bears *Ursus arctos* that have been repeatedly captured significantly differed in their body condition compared with bears that have been captured only once. Nest survival in captured seabirds, yellow-billed loon *Gavia adamsii* and pacific loon *G. pacifica*, was 30% lower than in non-captured adults (Uher-Koch et al. 2015). Stress of capture can even lead to capture myopathy, a metabolic muscle disease that often results in death (Nuvoli et al. 2014, Green-Barber et al. 2018).

Capturing can also change the animal’s behaviour, which then significantly affects data collected in behavioural and recapture studies. For instance, polar bears *Ursus maritimus* in the study by Rode et al. (2014) displayed reduction in activity and movement rates 3.5 days post-capture. Linhart et al. (2012) showed that willow warblers *Phylloscopus trochilus* could recall the capture event by mist netting even a year later and learn to avoid mist nests.

Apart from stress and impact on behaviour, capturing can also result in physical damages. These damages can range from skin abrasions to broken limbs (Phillips et al. 1996, Fleming et al. 1998, Grisham et al. 2015). Trapped animals are also vulnerable to predation (Hilario et al. 2017).

Many experiments on behavior and cognition in animals take place in captive settings. While these conditions allow for logistical control, they often lead to harms for the captive animals (Marino and Frohoff 2011). The damaging effects of captivity have been well documented. Animals can exhibit stereotyped behavior (Wechsler 1991, Callard et al. 2000, Shyne 2006, Jett et al. 2017, Poirier and Bateson 2017, Williams et al. 2018a), and suffer from increased stress (Bordeleau et al. 2018, Ferreira et al. 2018), which can eventually result in higher incidence of diseases and mortality (Terio et al. 2004, Mitchell et al. 2018).

Marking

Research on wildlife often requires marking of animals to obtain data on behaviour, survival, reproduction or home range size. Virtually all marking methods require capture, which is stressful to wild animals, and many methods also involve tissue damage. Common marking techniques include for instance hot- or freeze-branding, mutilations, tags and bands, and the use of radio-transmitters.

Branding

Hot-branding and freeze-branding have been used for marking cattle *Bos taurus* and horses *Equus caballus* for centuries (Macpherson and Penner 1967), and have been modified for marking pinnipeds. Not surprisingly, hot-branding is a painful procedure, reflected in the behavioural changes of branded Stellar sea lions *Eumetopias jubatus* (Walker et al. 2010). Public concerns about animal welfare have resulted in lawsuits and withdrawal of research permits for sea lion research involving hot-branding (Dalton 2005). Moreover, the development of skin tumours following freeze- or hot-branding has been observed in cattle (Yeruham et al. 1996), raising caution for wildlife branding.

Mutilations

Toe clipping is a classic method for marking small vertebrates such as lizards, amphibians and rodents. Unique marking is achieved by clipping toes in different combinations on different limbs. Although considered harmless by some authors

(Grafe et al. 2011, Ginnan et al. 2014), toe-clipping can, in fact, result in reduced survival rate (McCarthy and Parris 2004, Olivera-Tlahuel et al. 2017). It also has negative effect on locomotor performance and endurance (Schmidt and Schwarzkopf 2010) as well as the clinging performance of pad-bearing lizards, which was documented in the Carolina anole *Anolis carolinensis* (Bloch and Irschick 2005).

Tags and bands

Another common method of marking animals is with tags or bands. Tags can be made from a variety of materials – most commonly metal or plastic – and are usually augmented by alphanumeric codes for individual or group recognition. Larger animals often require immobilization before marking and attaching tags, and the procedure of tag attachment can be painful (Cramer 2017, MacRae et al. 2018). In small animals, for instance, fish, tagging can affect the survival rate (Burdick 2011, Hoye et al. 2015).

Tags can be applied to many different parts of the body depending on the anatomy of the animal, most often to wings (Trefry et al. 2013), fins (Sonne et al. 2012) or flippers (Hazekamp et al. 2010). The study by Robinson and Jones (2014) revealed that tagged seabirds, crested auklets *Aethia cristatella*, showed reduced return rates and provisioning behaviour. Tags can increase the cost of swimming due to drag in grey seals *Halichoerus grypus* (Hazekamp et al. 2010), and tagged Magellanic penguins *Spheniscus magellanicus* have been observed to experience foraging difficulties during low food abundance periods (Wilson et al. 2015). Moreover, tags damaged flippers of Adélie penguins *Pygoscelis adeliae* (Jackson and Wilson 2002), and modified diving behaviour and decreased survival in the first year after banding in little penguins *Eudyptula minor* (Fallow et al. 2009).

Radio-transmitters

Radiotelemetry has been key to track the movement of animals. This method uses the transmission of radio signals to locate a radio-transmitter that has been attached to an animal. Radio-transmitters can be glued to the skin, designed as a GPS collar or a harness, or surgically implanted. To track mule deer *Odocoileus hemionus*, elk *Cervus elaphus nelsoni* and moose *Alces alces* females, even vaginal implant transmitters are being used (Bishop et al. 2007, Barbknecht et al. 2009, Thompson et al. 2018).

Several issues have been identified with radio-transmitters. For instance, Dixon et al. (2016) found evidence of decreased survival rate associated with harness-mounted satellite transmitters on falcons *Falco cherrug*. In passerine birds, both entanglement with vegetation or body parts and non-entanglement injuries have been observed (Hill and Elphick 2011).

Another issue is the method of attachment and weight of the instrument. If the radio-transmitter is attached by glue, this can lead to lesions and abrasions on the skin (Field et al. 2012). The study by Rasiulis et al. (2014) showed that heavy collars decreased survival rate in caribou *Rangifer tarandus*, and by Brooks et al. (2008) that grazing behavior of Burchell's zebras *Equus burchelli antiquorum* is affected by collar weight.

Particularly problematic is the use of implanted transmitters as this involves additional trauma to the animal. The recent study by Arnemo et al. (2018) showed that transmitters implanted into the abdominal cavities of brown bears *Ursus arctos* performed poorly and were not biocompatible, in several cases causing the animal's death. Several cases of mortality caused by implanted radio-transmitters have been reported also in European lynx *Lynx lynx* (Lechenne et al. 2012), Harlequin ducks *Histrionicus histrionicus* (Mulcahy and Esler 1999) and American badgers *Taxidea taxus* (Quinn et al. 2010).

Blood and tissue sampling

Genetic tools have become indispensable for biodiversity assessment and monitoring (Stetz et al. 2011). Genetics is important to assess abundance, occupancy, hybridization, genetic diversity, population structure and effective population size (Stetz et al. 2011, Carroll et al. 2018). Common methods used for DNA collection are blood and non-lethal tissue sampling, such as toe-clipping or fin-clipping. Blood is also commonly used for assessing levels of potential detrimental elements, such as heavy metals, and in physiology studies to assess hormonal levels (Bryan et al. 2007, Berglund 2018). Blood sampling could be however difficult in small animals, such as zebrafish *Danio rerio* (Zang et al. 2013), and has been even linked to lower survival rates during the first year after sampling in Amarican cliff swallows *Petrochelidon pyrrhonota* (Brown and Brown 2009). Fin-clipping has been shown to be painful for fish, common carp *Cyprinus carpio* and Atlantic salmon *Salmo salar*, and may affect their survival (Hansen 1988, Roques et al. 2010).

Lethal sampling

The use of lethal means for tissue sampling and collection of voucher specimens has a long tradition in wildlife research. Besides the obvious harm to the individual animal, removing a key member of the group in species with complex social formations can result in impaired well-being of the remaining individuals (Shannon et al. 2013). Moreover, lethal methods are unfortunately often used even in cases when this is not necessary, such as in gathering data on abundance, DNA sampling or dietary analysis (Vucetich and Nelson 2007, Hammerschlag and Sulikowski 2011, Costello et al. 2016, Russo et al. 2017, Zemanova 2019).

Application of the 3Rs into wildlife research

There is a significant difference between research on laboratory animals and on wildlife in that the former is used as models for humans, for example, in testing toxicity or effectiveness of new drugs. Wildlife research, on the other hand, focuses on the study animal itself, in order to understand its biology, behavior and health. Moreover, wildlife encompasses a very broad range of species with different ecological and physiological traits, which makes generalizations of guidelines challenging. Nevertheless, the 3Rs principles can be applied to wildlife research in several ways.

Replacement may not be always possible, because the animals are the objects of the study. However, individual identification with natural marking, use of camera traps, or non-invasive sampling can provide data without the necessity of handling an animal (Fig. 1, Table 1).

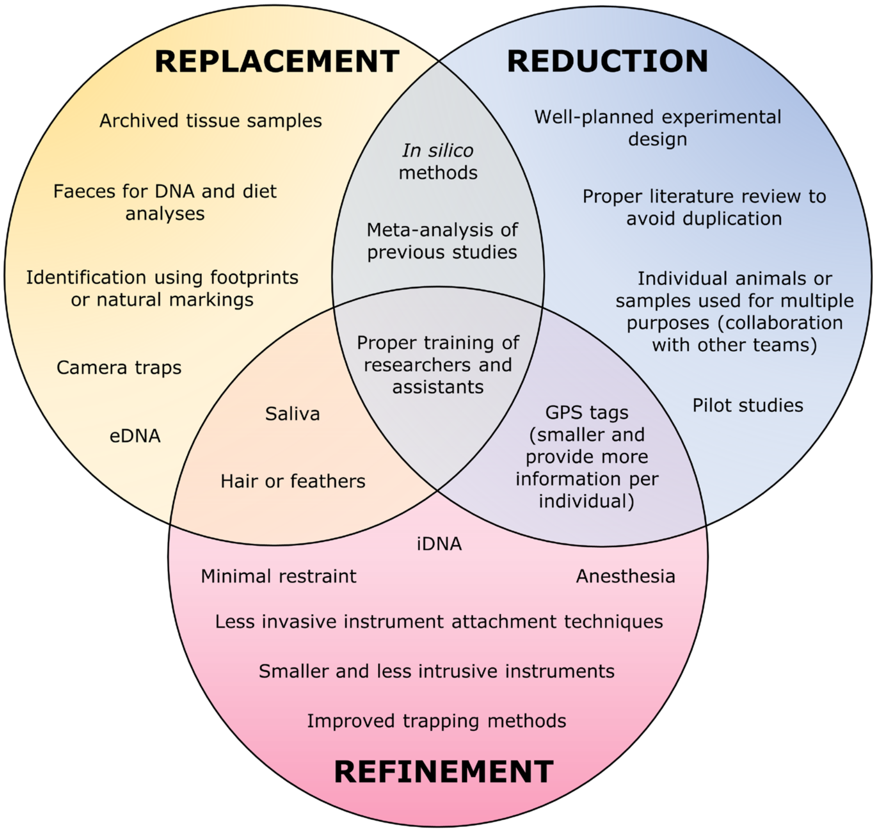

Figure 1. Implementation of the 3Rs principles (replacement, reduction, refinement) in wildlife research. Overlapping methods for replacement and refinement depend on whether the animal has to be captured or not. Please see Table 1–3 for more details.

Reduction (Fig. 1, Table 2) can be achieved, for example, through efficient experimental design and planning, calculating the minimum sample size, avoiding repetition through meta-analyses of previously published studies, sharing data and resources (NC3Rs 2018). Individual animals can also be used for multiple purposes – for instance by combining capture–mark–recapture and genotyping studies (Lampert et al. 2003). Another strategy for reduction is the implementation of in silico methods, which could be used for species distribution, population modelling in response to climate change or disease spread predictions (Smith and Cheeseman 2002, Zemanova et al. 2018).

Non-invasive methods can be considered as replacement, but also a part of reduction and refinement strategies (Lindsjo et al. 2016), depending on how the methods are used (Fig. 1, Table 1–3). Refinement (Table 3) includes, for example, the use anesthesia, tranquilization and light-weight radio-transmitters (Harcourt et al. 2010, McGuire et al. 2014). For minimum injuries and capture of non-target species, it has been recommended to use call playback and taxidermy decoys (Veltheim et al. 2015), and to use traps that have been shown to cause no or minimal injuries, for instance, replacing foothold traps with box traps (Kolbe et al. 2003, Bergvall et al. 2017).

Alternatives to capturing and trapping

Many data that used to require trapping can nowadays be achieved by different means. For instance, the presence/absence data can be collected using camera traps or drones, and DNA can be sourced from hair traps or faeces.

Camera traps

Camera traps can be applied to estimate species richness, habitat occupancy, population density or behavior, with little effort by the researcher (Di Cerbo and Biancardi 2013). The absence of a researcher is particularly beneficial in the study of wild primates, where habituation to human presence could be detrimental due to threat of hunting (Bezerra et al. 2014). Camera traps can be even a more efficient method of detection than other methods, such as hair traps, cage traps or scat count surveys (Monterroso et al. 2014, Welbourne et al. 2015, Day et al. 2016). This efficiency improves when using a lure or bait (Boulerice and Van Fleet 2016, McLean et al. 2017). Modern camera traps can record also videos that can be used in behavioural studies (Lobo et al. 2013, Flagel et al. 2016).

Camera traps have been used for detection of many species, including small terrestrial and arboreal mammals such as red and eastern grey squirrels, *Sciurus vulgaris* and *S. carolinensis* (Di Cerbo and Biancardi 2013), foxes *Vulpes velox* (Stratman and Apker 2014), feral cats and European wildcats, *Felis catus* and *F. silvestris* (Anile et al. 2014, Stokeld et al. 2015), dogs *Canis familiaris* (Rasambainarivo et al. 2017), Hermann's tortoises *Testudo hermanni* (Ballouard et al. 2016), northern flying squirrels *Glaucomys sabrinus* (Boulerice and Van Fleet 2016), North American river otters *Lontra canadensis* (Day et al. 2016) and grey wolves *Canis lupus* (Sver et al. 2016).

Table 1. Examples of studies implementing the 3Rs principle of Replacement. See Fig. 1 and the main text for more detail.

Replacement method	Instead of	Species	Animal class	Reference
Individual identification by footprints	Marking with invasive methods	white rhinocero *Ceratotherium simum*	mammals	Alibhai et al. 2008
	(e.g. tags, collars)	giant panda *Ailuropoda melanoleuca*	mammals	Li et al. 2018
		South American tapir *Tapirus terrestris*	mammals	Moreira et al. 2018
Individual identification by natural markings	Marking with invasive methods	pygmy blue-tongue skink *Tiliqua adelaidensis*	reptiles	Li et al. 2009
	(e.g. toe-clipping)	grey seal *Halichoerus grypus*	mammals	Vincent et al. 2001
		fire salamander *Salamandra salamandra*	amphibians	Sukalo et al. 2013
		alpine longhorn beetle *Rosalia alpina*	insects	Caci et al. 2013
		sperm whale *Physeter macrocephalus*	mammals	Alessi et al. 2014
		wunderpus octopus *Wunderpus photogenicus*	cephalopods	Huffard et al. 2008
		northern goshawk *Accipiter gentilis*	birds	Hoy et al. 2016
		Asian black bear *Ursus thibetanus*	mammals	Higashide et al. 2012
		common seadragon *Phyllopteryx taeniolatus*	fish	Martin-Smith 2011
Using faeces for DNA collection	Blood or tissue sampling	bumblebees *Bombus* spp.	insects	Scriven et al. 2013
		mountain gorilla *Gorilla beringei beringei*	mammals	Roy et al. 2014
		western capercaillie *Tetrao urogallus*	birds	Rosner et al. 2014
		Asian elephant *Elephas maximus*	mammals	Gray et al. 2014
		Cabrera's vole *Microtus cabrerae*	mammals	Proença-Ferreira et al. 2019
Using feaces for dietary analysis	(Lethal) intestinal content sampling or stomach flushing	Hawaiian tree snails *Achatinella* spp.	molluscs	Price et al. 2017
		wolf spiders *Pardosa* spp.	arachnids	Sint et al. 2015
		smooth snake *Coronella austriaca*	reptiles	Brown et al. 2014
Using faeces for ecotoxicology	Blood or tissue sampling	lesser horseshoe bat *Rhinolophus hipposideros*	mammals	Afonso et al. 2016
		European pied flycatcher *Ficedula hypoleuca*	birds	Berglund 2018
Using feaces for stress assessment	Blood sampling	red deer *Cervus elaphus*	mammals	Millspaugh et al. 2001
		African bush elephant *Loxodonta africana*	mammals	Ahlering et al. 2013
		mourning dove *Zenaida macroura*	birds	Washburn et al. 2003
		North Atlantic right whale *Eubalaena glacialis*	mammals	Hunt et al. 2006
		Columbian ground squirrel *Urocitellus columbianus*	mammals	Bosson et al. 2009
Camera traps	Capture	European wildcat *Felis silvestris*	mammals	Stokeld et al. 2015
		Hermann's tortoise *Testudo hermanni*	reptiles	Ballouard et al. 2016
		North American river otter *Lontra canadensis*	mammals	Day et al. 2016
		black rat *Rattus rattus*	mammals	Rendall et al. 2014
Environmental DNA (eDNA) from water	Blood or tissue sampling	freshwater mussels (Unionidae)	bivalves	Cho et al. 2016
		platypus *Ornithorhynchus anatinus*	mammals	Lugg et al. 2018
		wild boar *Sus scrofa*	mammals	Williams et al. 2018b
Using hair and feathers for DNA collection	Blood or tissue sampling	grey wolf *Canis lupus*	mammals	Ausband et al. 2011
		American black bear *Ursus americanus*	mammals	Gould et al. 2018
		cougar *Puma concolor*	mammals	Sawaya et al. 2011
		kiwis *Apteryx* spp.	birds	Ramon-Laca et al. 2018
Using hair and feathers for endocrinology	Blood or tissue sampling	American black bear *Ursus americanus*, brown bear *U. arctos*	mammals	Bryan et al. 2014
		Clark's nutcrackers *Nucifraga columbiana*	birds	Fairhurst et al. 2011
Using saliva for endocrinology	Blood or tissue sampling	Indian rhinoceros *Rhinoceros unicornis*	mammals	Gomez et al. 2004
		rhesus macaque *Macaca mulatta*	mammals	Higham et al. 2010

To estimate density, individuals are marked or identified by natural markings (Jordan et al. 2011, Thornton and Pekins 2015).

Drones

One recent technological advance applied in wildlife monitoring has been the unmanned aerial vehicles, also known as drones. Drones are particularly useful in approaching sensitive wildlife in inaccessible areas. Some studies revealed that drone-derived data are more accurate than data from ground-counting methods (Ezat et al. 2018, Hodgson et al. 2018). Moreover, drone technology can be cheaper than radio-collars (Mulero-Pazmany et al. 2015). Drones have been successfully implemented in monitoring populations of polar bears *Ursus maritimus* (Barnas et al. 2018b), saltwater crocodiles *Crocodylus porosus* (Bevan et al. 2018, Ezat et al. 2018), or snow geese *Anser caerulescens* (Barnas et al. 2018a). Drones can be also used for collecting exhaled breath condensate of humpback whales *Megaptera novaeangliae* for microbiome analysis (Apprill et al. 2017).

Alternatives to invasive marking

Dyes

For short-term studies, paint can be used to mark individual animals, as has been demonstrated in studies on lizards, *Anolis cristatellus*, *A. gundlachi*, *A. krugi* and *Sceloporus undulates* (Johnson 2005) or rainbow trout *Oncorhynchus mykiss* (Frenkel et al. 2002). Birds can be marked with dyes placed on eggs or nests (Cramer 2017).

Natural markings

For identification of individual animals, natural markings can be used, such as unique patterns and scars, fungal patches or pelage markings (Vincent et al. 2001, Maniscalco et al. 2006, Li et al. 2009). Identification based on natural markings has been successfully implemented in studies on e.g. fish (Arzoumanian et al. 2005, Meekan et al. 2006, Auger-Methe et al. 2011, Martin-Smith 2011, Correia et al. 2014, Monteiro et al. 2014, Gonzalez-Ramos et al. 2017), Indo-Pacific bottlenose dolphins *Tursiops aduncus* (Gomez-Salazar et al. 2011, Bichell et al. 2018), sperm whales *Physeter macrocephalus* (Alessi et al. 2014), Asian black bears *Ursus thibetanus* (Higashide et al. 2012), polar bears *Ursus maritimus* (Anderson et al. 2007), Australian sea lions *Neophoca cinerea* (Osterrieder et al. 2015), cougars *Puma concolor* (Alexander and Gese 2018), tigers *Panthera tigris* (Karanth et al. 2006), cheetahs *Acinonyx jubatus* (Kelly 2001), giant pandas *Ailuropoda melanoleuca* (Zheng et al. 2016), salamanders, *Eurycea tonkawae*, *Ambystoma opacum* and *Salamandrina perspicillata* (Gamble et al. 2008, Bendik et al. 2013, Romiti et al. 2017), crustaceans *Rhynchocinetes typus* and *Chionoecetes opilio* (Gallardo-Escarate et al. 2007, Gosselin et al. 2007), manatees *Trichechus manatus latirostris* (Langtimm et al. 2004), Majorcan midwife toads *Alytes muletensis* (Pinya and Perez-Mellado 2009), common European vipers *Vipera berus* (Bauwens et al. 2018), green sea turtles *Chelonia mydas* (Gatto et al. 2018), wunderpus octopuses *Wunderpus photogenicus* (Huffard et al. 2008), little brown bats *Myotis lucifugus* (Amelon et al. 2017), jewelled geckos *Naultinus gemmeus* (Knox et al. 2013), newts *Ichthyosaura alpestris* and *Lissotriton vulgaris* (Mettouris et al. 2016), and even beetles *Lucanus cervus*, *Rosalia alpina* and *Rhynchophorus ferrugineus* (Caci et al. 2013, Romiti et al. 2017, Diaz-Calafat et al. 2018).

Identification by footprints

Some mammal species can leave signs that are sufficiently distinctive for identification purposes. Footprints have been used as a tracking method for millennia (Pimm et al. 2015), and current specialized software allows for individual, sex and age group classification with more than 90% accuracy (Jewell et al. 2016). Shape and size of footprints was used to identify individual white rhinos *Ceratotherium simum* (Alibhai et al. 2008, Law et al. 2013), fishers *Martes pennanti* (Herzog et al. 2007), giant pandas *Ailuropoda melanoleuca* (Li et al. 2018), tigers *Panthera tigris* (Gu et al. 2014) or South American tapirs *Tapirus terrestris* (Moreira et al. 2018).

Table 2. Examples of studies implementing the 3Rs principle of Reduction. See Fig. 1 and the main text for more detail.

Reduction method	Instead of	Species	Animal class	Reference
Improved statistics methods and minimum sample size calculation	Using an excessive number of animals	moose *Alces alces*	mammals	Girard et al. 2002
		lesser black-backed gull *Larus fuscus*	birds	Thaxter et al. 2017
Computer modelling (in silico)	Using an excessive number of animals	black slug *Arion ater*, red slug *A. rufus*, Spanish slug *A. vulgaris*	molluscs	Zemanova et al. 2018
		eastern mosquitofish *Gambusia holbrooki*	fish	Panayotova and Horth 2018
		American badger *Taxidea taxus*	mammals	Smith and Cheeseman 2002
Using a single individual or sample for multiple purposes	Using multiple individuals for one purpose only	coyote *Canis latrans*	mammals	Prugh et al. 2008
		tungara frog *Physalaemus pustulosus*	amphibians	Lampert et al. 2003
Conducting meta-analysis of previous studies	Duplication of studies	African bush elephant *Loxodonta africana*	mammals	Guldemond and Van Aarde 2008
		passerine bird species	birds	Chamberlain et al. 2009
		bat species	mammals	Jung and Threlfall 2018

Table 3. Examples of studies implementing the 3Rs principle of Refinement. See Fig. 1 and the main text for more detail.

Refinement method	Instead of	Species	Animal class	Reference
Using buccal swabs for DNA collection	Toe clipping, blood sampling	European tree frog *Hyla arborea*	amphibians	Angelone and Holderegger 2009
		red-cockaded woodpecker *Leuconotopicus borealis*	birds	Vilstrup et al. 2018
		rodent species (Muridae, Heteromyidae, Sciuridae)	mammals	Parmenter et al. 1998
		redside dace *Clinostomus elongates*, channel darter *Percina copelandi*	fish	Reid et al. 2012
Using buccal swabs for ecotoxicity	Blood or tissue sampling	rock dove *Columba livia*	birds	Shepherd and Somers 2012
		common wall lizard *Podarcis muralis*	reptiles	Mingo et al. 2017
Using skin swabs for DNA collection	Toe clipping, blood sampling	myotis bats *Myotis* spp.	mammals	Player et al. 2017
		Sierra Nevada yellow-legged frog *Rana sierrae*	amphibians	Poorten et al. 2017
Using hair samples for ecotoxicology	Tissue sampling	Neotropical fruit bats *Artibeus* spp.	mammals	Becker et al. 2018
		European hedgehog *Erinaceus europaeus*	mammals	Vermeulen et al. 2009
Anesthesia	Handling without anesthesia	gopher tortoise *Gopherus polyphemus*	reptiles	McGuire et al. 2014
		marbled newt *Triturus marmoratus*	amphibians	Le Chevalier et al. 2017
		timber rattlesnake *Crotalus horridus*	reptiles	Hale et al. 2017
Tranquilization	Not minimizing stress response	Weddell seal *Leptonychotes weddellii*	mammals	Harcourt et al. 2010
		zebrafish *Danio rerio*	fish	de Abreu et al. 2014
Improved trapping	Trapping methods that could lead to injuries	European lynx *Lynx lynx*	mammals	Kolbe et al. 2003
(e.g. box traps instead of foothold traps)		roe deer *Capreolus capreolus*	mammals	Bergvall et al. 2017
Smaller tracking instruments	Using heavy and robust instruments	California spotted owl *Strix occidentalis occidentalis*	birds	Atuo et al. 2019
		feral cat *Felis catus*	mammals	Recio et al. 2011
Suction cups for attaching devices on cetaceans	Skin penetrating instruments	Heaviside's dolphin *Cephalorhynchus heavisidii*	mammals	Sakai et al. 2011
Invertebrate-derived DNA (iDNA)	Blood or tissue sampling with instruments	meerkat *Suricata suricatta*	mammals	Habicher et al. 2013
		common swift *Apus apus*	birds	Bauch et al. 2013

Vocal individuality

Instead of marking, individual animals of certain species can be distinguished by their vocalization features (Terry et al. 2005). This method has been successfully applied not only in birds, such as the great grey owl *Strix nebulosa* (Rognan et al. 2009), but also in marmots *Marmota olympus* and Richardson's ground squirrels *Spermophilus richardsonii* (Pollard et al. 2010).

Alternatives to invasive blood and tissue sampling

Ecotoxicology

Improving our knowledge of the potential impacts of chemical pollutants on wildlife is an important aspect of biological conservation. Unfortunately, traditional methods of obtaining samples in ecotoxicology are invasive (Jasinska et al. 2015, Wilkie et al. 2018, Boisvert et al. 2019, Xing et al. 2019, da Costa Araujo et al. 2020), and research on non-destructive methods is severely lacking (Chaousis et al. 2018).

Nevertheless, non-invasive methods have already been applied in several ecotoxicology studies. For instance, heavy metals can be determined from hair samples, which was done in wood mice *Apodemus sylvaticus* (Tete et al. 2014), brown rats *Rattus norvegicus* (McLean et al. 2009), bats *Artibeus* spp., *Myotis bechsteinii*, *Myotis daubentonii*, *Myotis myotis* and *Pipistrellus pipistrellus* (Flache et al. 2015, Becker et al. 2018) or European hedgehogs *Erinaceus europaeus* (Vermeulen et al. 2009). Heavy metals can be also detected in faeces (Afonso et al. 2016, Berglund 2018). Mingo et al. (2017) were able to detect pesticide exposure in common wall lizards *Podarcis muralis* measured through buccal swabs. The in silico modelling of toxicity pathways has been recently applied to constructing adverse outcomes in wildlife (Madden et al. 2014).

Physiology

Chronic stress can have potentially deleterious effects (please see above for more details). Stress can be quantified by measuring the level of glucocorticoids, a class of steroid hormones (Millspaugh and Washburn 2004). Glucocorticoid levels used to be typically assessed from blood (Hood et al. 1998, Mathies et al. 2001), but this often requires the capture of the animal, which could influence the results. An additional drawback of blood samples is that they may not represent long-term hormone levels (Millspaugh and Washburn 2004).

A non-invasive alternative is the use of faecal samples. Studies in which faecal glucocorticoids were assessed were conducted in elks *Cervus elaphus* (Millspaugh et al. 2001), mourning doves *Zenaida macroura* (Washburn et al. 2003), greater sage grouse *Centrocercus urophasianus* (Jankowski et al. 2009), African bush elephants *Loxodonta africana* (Munshi-South et al. 2008, Ahlering et al. 2013), Columbian ground squirrels *Urocitellus columbianus* (Bosson et al. 2009), common degus *Octodon degus* (Soto-Gamboa et al. 2009), giant pandas *Ailuropoda melanoleuca* (Yu et al. 2011), aardwolves *Proteles cristata* (Ganswindt et al. 2012), eastern chipmunks *Tamias striatus* (Montiglio et al. 2012), coyotes *Canis latrans* (Schell et al. 2013), crab-eating foxes *Cerdocyoun thous* (Paz et al. 2015), marmots *Marmota flaviventris* (Wey et al. 2015), woylies *Bettongia penicillata* (Hing et al. 2017), pikas *Ochotona princeps* (Wilkening et al. 2016), North Atlantic right whales *Eubalaena glacialis* (Hunt et al. 2006) or primates (Behringer and Deschner 2017). In frogs, dermal swabs (Santymire et al. 2018) or urine samples (Narayan et al. 2010, Narayan 2013) collected by gentle massage of the lower abdomen can be used for the analysis.

Due to their small molecular weight and lipid solubility, glucocorticoids pass quickly from blood serum to saliva, where it can be directly measured (Romano et al. 2010). Stress assessment from saliva has been implemented in Indian rhinoceros *Rhinoceros unicornis* (Gomez et al. 2004), and rhesus macaques *Macaca mulatta* (Higham et al. 2010).

One of the latest methods of non-invasive sampling is body odour collection. A wide range of volatile and semi-volatile organic compounds create chemical profiles, which can be used in studies on chemical signatures of health as well as kinship, diet and reproduction (Nair et al. 2018, Weiss et al. 2018a, b).

DNA sampling

Non-invasive genetic sampling has a great potential in wildlife biology, with a variety of applications (Waits and Paetkau 2005). Advancements in forensics, medical research and ancient DNA techniques generate new methods that can be relatively easily applied to improve data production and analysis of non-invasive genetic samples also in wildlife research (Beja-Pereira et al. 2009).

Faecal DNA-based sampling to identify individuals and estimate the population size was implemented in e.g. Asian elephants *Elephas maximus* (Gray et al. 2014), mountain gorillas *Gorilla beringei beringei* (Roy et al. 2014), Indian rhinoceros *Rhinoceros unicornis* (Das et al. 2015), Cabrera's voles *Microtus cabrerae* (Proença-Ferreira et al. 2019), African golden wolves *Canis anthus* (Karssene et al. 2018), kit foxes *Vulpes macrotis mutica* (Wilbert et al. 2015) or birds *Apteryx* spp., *Otis tarda*, *Tetrao urogallus* (Idaghdour et al. 2003, Perez et al. 2011, Rosner et al. 2014, Ramon-Laca et al. 2018, Vallant et al. 2018). Faecal DNA has been also used for identifying insects like *Bombus* spp. and *Ceutorhynchus assimilis* (Fumanal et al. 2005, Scriven et al. 2013) and spiders *Pardosa* spp. (Sint et al. 2015). To direct the survey efforts detection dogs may be used for locating faecal samples (Arandjelovic et al. 2015, Wilbert et al. 2015).

Another method of non-invasive genetic sampling is hair trapping. Hair can be collected either by catching an animal and plugging the hair, with baited methods, or passively through natural rubs or travel route snares. Baited methods of hair collection can be divided into four main types: 1) hair corrals with barbed wire encircling a bait, 2) rub stations, which are structures saturated with scent to induce rubbing, 3) trees wrapped with barbed wire or 4) boxes or tubes containing attractants and fitted with hair snaring devices (Kendall and McKelvey 2012). Baited hair collection has been often applied in large carnivores (*Canis latrans*, *C. lupus*, *Puma concolor*) (Ausband et al. 2011, Sawaya et al. 2011). Another method was introduced by Keeley and Keeley (2012), who developed a modified blowgun dart with sticky ends to collect hair from variegated squirrels *Sciurus variegatoides* without penetrating their skin.

An increasingly common non-invasive genetic sampling technique used primarily in frogs is buccal swabbing (Broquet et al. 2007, Angelone and Holderegger 2009, Gallardo et al. 2012). This method can be however applied also to other types of animals, for instance, birds (*Leuconotopicus borealis*) (Vilstrup et al. 2018), lizards (*Coronella austriaca*, *Lacerta agilis*, *Podarcis muralis*) (Beebee 2008, Schulte et al. 2011) and fish (*Clinostomus elongates*, *Percina copelandi*) (Reid et al. 2012). However, buccal swabbing may not be safe for certain reptiles, such as tortoises (due to their head retraction escape response) and snakes. In these species, cloacal swabbing can be used instead (Mucci et al. 2014, Ford et al. 2017).

Alternatively, skin and mucus swabbing can be implemented. Skin swabbing drastically limits handling in comparison to buccal swabbing, and it is particularly useful for vulnerable and small animals, which was shown in alpine newts *Ichthyosaura alpestris* (Prunier et al. 2012), fire salamanders *Salamandra salamandra* (Pichlmuller et al. 2013) and Sierra Nevada yellow-legged frogs *Rana sierrae* (Poorten et al. 2017). Wing swabbing has been successfully used for DNA collection in bats (*Myotis evotis*, *M. septentrionalis*, *M. yumanensis*, *M. lucifugus*) (Player et al. 2017). Mucus swabbing has been used to collect DNA in cephalopods (*Enteroctopus dofleini*, *Sepia officinalis*) (Hollenbeck et al. 2017, Sykes et al. 2017), land snails (*Arianta arbustorum*) (Armbruster et al. 2005) and slugs (*Arion spp.*, *Geomalacus maculosus*) (Morinha et al. 2014), intertidal snails (*Nucella* spp.) (Kawai et al. 2004), polyplacophoran molluscs (*Ischnochiton* spp.) (Palmer et al. 2008), freshwater pearl mussels *Margaritifera margaritifera* (Karlsson et al. 2013) and fish (*Manta birostris*, *Oreochromis niloticus*) (Kashiwagi et al. 2015, Taslima et al. 2016).

In birds, eggshells (Strausberger and Ashley 2001, Egloff et al. 2009, Kjelland and Kraemer 2012, Maia et al. 2017) or feathers (Rudnick et al. 2007, Kjelland and Kraemer 2012, Olah et al. 2016) can be used as a source of DNA. Feathers can be collected opportunistically or through a feather-trap (Maurer et al. 2010).

Saliva is also a great source of DNA that can be collected non-invasively by using e.g. baits and porous material (Vargas et al. 2009, Lobo et al. 2015). Additionally, DNA samples can be obtained from mineral lick (Schoenecker et al. 2015), rests of prey (Harms et al. 2015, Wheat et al. 2016) or damaged crop (Saito et al. 2008).

Other potential sources of DNA include scent marks (Malherbe et al. 2009), snow footprints (Dalen et al. 2007), urine (Nagai et al. 2014, Nakamura et al. 2017), insect exuviae (Kranzfelder et al. 2016, Nguyen et al. 2017), spider webs (Xu et al. 2015, Blake et al. 2016), antlers (Hoffmann and Griebeler 2013, Kim et al. 2015) or shed skin (Swanson et al. 2006, Horreo et al. 2015).

As organisms move through the environment, they also leave some DNA traces behind. This environmental DNA (eDNA) can be used for detection of targeted organisms, and it is particularly useful for detection of invasive (Collins et al. 2013, Hunter et al. 2015) or rare species (Jerde et al. 2011). Most eDNA applications have targeted aquatic environments, for instance, in studies on harbor porpoises *Phocoena phocoena* (Foote et al. 2012), mussels (Unionidae) (Cho et al. 2016), hellbenders *Cryptobranchus alleganiensis* (Olson et al. 2012), fish (*Cyprinus carpio*, *Oncorhynchus mykiss*) (Eichmiller et al. 2016, Fernandez et al. 2018) or platypus *Ornithorhynchus anatinus* (Lugg et al. 2018). However, eDNA techniques have been used also in deer *Capreolus capreolus* (Nichols et al. 2012) or wild boar *Sus scrofa* studies (Williams et al. 2018b), using saliva from twigs or water from drinking reservoirs as the DNA source.

While not completely non-invasive method, blood-sucking insects have been used as a 'gentle' stress-free method of DNA collection in several mammalian species (Voigt et al. 2005, Calvignac-Spencer et al. 2013, Habicher et al. 2013, Lee et al. 2015, Rodgers et al. 2017), so-called invertebrate-derived DNA (iDNA). The potential of using terrestrial leeches (*Haemadipsa* spp.) for the same purpose has been also assessed (Schnell et al. 2015).

Alternatives to lethal sampling

Alternatives to collecting voucher specimen

One of the best methods as an alternative to voucher collection is a series of high-quality photographs, which can be even used to describe a new species (Athreya 2006, Minteer et al. 2014a), especially in combination with other lines of evidence (e.g. DNA from skin or buccal samples and recording a species' mating call).

Species abundance

Biodiversity assessment could be done through count surveys and visual sampling (Lecq et al. 2015, Ksiazkiewicz-Parulska and Goldyn 2017). Methodology on estimating species abundance from occurrence maps has been also recently published (Yin and He 2014).

Dietary composition

The recent application of next generation sequencing and enrichment methods to trophic ecology can enable rapid resolution to questions about diets of practically any animal from their faeces (O'Rorke et al. 2012, Pompanon et al. 2012). Faecal genotyping as a method to examine dietary composition was used in e.g. coyotes *Canis latrans* (Prugh et al. 2008), European pine martens *Martes martes* (O'Meara et al. 2014), seals (*Arctocephalus forsteri*, *Phoca vitulina*) (Emami-Khoyi et al. 2016, Hui et al. 2017), fish (*Barbus barbus*, *Chondrostoma toxostoma toxostoma*, *Chondrostoma nasus nasus*) (Corse et al. 2010), snakes (*Coronella austriaca*) (Brown et al. 2014), snails (*Achatinella* spp.) (O'Rorke et al. 2015, Price et al. 2017), fruit flies *Drosophila melanogaster* (Fink et al. 2013) or spiders (*Pardosa* spp.) (Sint et al. 2015).

Concluding remarks

Studies on wildlife are regularly conducted with the assumption that they have an insignificant impact on the studied animals (Jewell 2013) or that the impact is outweighed by any potential benefits to the population or species (Vucetich and Nelson 2007, Parris et al. 2010). Such assumptions however raise concerns for animal welfare, a topic that has been increasingly discussed among public, ethical committees, journal publishers and funding agencies (McMahon et al. 2012, Zemanova 2017).

In this review, I outlined the potential implications of commonly used invasive research methods for wildlife welfare. Some of the research practices can, however, have delayed consequences and monitoring of animals for any adverse impact should be required (Putman 1995). It is also important to note that in many cases, animal welfare implications of research methods are simply not known. In this case it is imperative to exercise the precautionary principle (Crozier and Schulte-Hostedde 2015).

In the past, a high level of invasiveness was necessary to obtain reliable data for understanding and designing management measures for wildlife. However, research methods have to be adjusted as our technical advancement and our understanding of species ability to feel pain grows (Costello et al. 2016, Waugh and Monamy 2016), and wildlife researchers need to limit the harm to the animals in order to ensure ethical acceptability of their work (Crettaz von Roten 2009, Lund et al. 2012). Even though non-invasive methods may not be yet suitable for all types of wildlife research, we should strive to implement them whenever possible. As I showed in this review, many researchers have already succeeded to do so.

Building upon the 3Rs principles (Fig. 1, Table 1–3), Curzer et al. (2013) proposed another R: refusal. Refused should be studies with badly conceived research plans, studies with no prospect of contributing significant knowledge, or studies in which the harm to the animal clearly exceeds any benefit of new knowledge. Some research practices might then have to be rejected simply on ethical grounds (Bekoff 2002).

In conclusion, the 3Rs principles are just as relevant to wildlife research as they are to laboratory animal studies. The current wildlife research needs to shift from using invasive and lethal methods to prioritizing non-invasive alternatives. Study and management of wildlife are necessary, but in doing so, we bear responsibility for ensuring that welfare of the studied animals is compromised as little as possible through our work.

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